# Benthic Macrofaunal and Megafaunal Distribution on the Canadian Beaufort Shelf and Slope

by

Jessica Nephin
B.Sc., University of British Columbia, 2009

A Thesis Submitted in Partial Fulfillment of the
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in the School of Earth and Ocean Sciences

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## ABSTRACT

The Arctic region has experienced the largest degree of anthropogenic warming, causing rapid, yet variable sea-ice loss. The effects of this warming on the Canadian Beaufort Shelf have led to a longer ice-free season which has assisted the expansion of northern development, mainly in the oil and gas sector. Both these direct and indirect effects of climate change will likely impact the marine ecosystem of this region, in which benthic fauna play a key ecological role. The aim of this thesis was to expand the current baseline knowledge of benthic fauna in the interest of developing the capacity to identify, predict and manage benthic change. The distribution of benthic macro- and megafauna was characterized utilizing community data from two recent benthic surveys on the Canadian Beaufort shelf and slope. Fauna were collected from 63 stations using box core and trawl sampling gear over the summers of 2009 through 2012 between depths of 30 and 1,000 m. Spatial patterns of abundance, biomass and $\alpha$ and $\beta$ diversity metrics were examined. Megafaunal abundance and $\alpha$ diversity were elevated on the shelf compared to the slope while the macrofauna did not vary significantly with depth. Multivariate analyses illustrated that both macro- and megafaunal community composition varied more across the depth gradient than from east to west along the shelf. However the change across the depth gradient was greater for the megafauna than for the macrofauna. I proposed that megafaunal slope taxa were differentiated from shelf taxa, as faunal replacement not nestedness appeared to be the main driver of megafaunal $\beta$ diversity across the depth gradient. The lack of correlation between macro- and megafauna in abundance, biomass and $\alpha$ and $\beta$ diversity suggests that these faunal components vary at different spatial scales. These results demonstrate how separately sampling the different benthic components can yield different spatial patterns, with implications for future benthic monitoring in the region. This work contributes to the current regional baselines by providing the first comprehensive description of megafaunal distribution on the Canadian Beaufort shelf and by extending our knowledge of benthic distribution patterns deeper on the slope.

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# Chapter 1

# Introduction

## 1.1 The Arctic and Canadian Beaufort Shelf in a warming climate

The Arctic Ocean is experiencing dramatic climate driven changes. The Arctic region has endured warming at a faster rate than the rest of the northern hemisphere [Bekryaev et al., 2010] causing a rapid [Comiso et al., 2008; Stroeve et al., 2007] yet variable [Liu and Key, 2014] decline of sea ice coverage and reduced ice thickness [Maslanik et al., 2007]. These physical changes are likely to affect primary producers, specifically altering the timing and relative contribution of ice versus pelagic algal blooms to the productivity of the region [Leu et al., 2011; Perrette et al., 2011]. Ice algal blooms are considered to be fundamental to the Arctic ecosystem, facilitating tight ***bentho–pelagic coupling*** [Renaud et al., 2007] leading to a diverse and abundant ***benthos*** even within largely oligotrophic regions [Piepenburg, 2005] like the Canadian Beaufort Shelf [Mundy et al., 2009].

It is believed that the greater transmission of solar radiation resulting from thinner sea-ice and a longer open-ocean season could stimulate larger ice algal blooms [Arrigo et al., 2012; Mundy et al., 2009] and increase overall primary productivity [Forest et al., 2007; Rysgaard and Glud, 2007] resulting in an increased benthic standing stock [Tremblay et al., 2011]. Alternatively, it is proposed that elevated river discharge [Peterson et al., 2002], responsible for early pack ice retreat prior to the major insolation driven melt [Carmack and Macdonald, 2002; Piepenburg, 2005], could move pack ice off the shelf too early for large ice algal blooms to occur and result in a later pelagic bloom [Hunt Jr et al., 2002]. Such a shift would likely have negative consequences for the benthos. The later pelagic bloom occurs when the zooplankton community is more established and therefore able to consume and recycle a higher degree of primary productivity in the water column [Coyle and Pinchuk, 2002; Olli et al., 2002] reducing the flux of organic matter to the benthos [Grebmeier et al., 2006b; Lalande et al., 2009]. Under this decreased bentho–pelagic coupling scenario, it is predicted that benthic communities will shift toward species that are adapted to low organic matter inputs [Conlan et al., 2008], potentially introduced from lower latitudes [Berge et al., 2005; Grebmeier et al., 2006b; Węsławski et al., 2010].

On the Canadian Beaufort Shelf these environmental changes have revived an interest in development, exposing the region to increased oil and gas exploration, shipping traffic and the possibility of commercial fishing. The discovery of large hydrocarbon deposits on the shelf in the 1970's [Dome Petroleum Limited et al., 1982] led to the initial benthic surveys [Chapman and Kostylev, 2008; Wacasey et al., 1977] performed to acquire a baseline from which to measure the potential impacts of the extractive industry on the benthos. However, the collapse of the original Mackenzie Valley pipeline project [Berger, 1977] halted hydrocarbon extraction and thus further benthic surveys on the Beaufort Shelf. Recent plans to resurrect the pipeline and the resurgence of oil and gas exploration on the shelf and farther down the slope, have revived benthic surveys in the region [Aitken et al., 2008; Conlan et al., 2008; Conlan et al., 2013; Kostylev and Chapman, 2005]. Presently, the collection of benthic samples from BREA (Beaufort Regional Environmental Assessment) and ArcticNet (Network of Centres of Excellence of Canada) expeditions are increasing our knowledge of the distribution of benthos on the shelf and slope and thus building greater capability to identify, manage and predict the looming anthropogenic impacts on the benthos and ultimately the entire marine ecosystem.

## 1.2 Benthic communities of soft-bottom continental margins

### 1.2.1 Distribution patterns

As the human footprint reaches further into the depths of the oceans, our understanding of faunal distribution patterns and their environmental drivers on ***continental margins***, like the Beaufort shelf and slope, has grown [Menot et al., 2010]. Variability in soft-bottom benthic communities, often referred to as patchiness, is characteristic of continental margins and occurs at multiple scales. Large scale patterns of faunal distribution are driven by environmental gradients [Barry and Dayton, 1991; Gaston, 2000], while smaller scale variability, which can be significant relative to larger scale variability [Kendall and Widdicombe, 1999], can depend on a combination of physical and biological (e.g. competition, predation, dispersal, mortality) factors [Chapman et al., 2010; Kraufvelin et al., 2011]. Therefore, the scale at which one investigates a pattern is important as it will govern the potential processes that may be underlying it [Levin et al., 2001; Morrisey et al., 1992].

In this work, I focus on large ($10 - 200$ km) scale patterns as these were the target of the sampling design used for benthic collection (see Section 1.4). Depth, a major environmental gradient on continental margins, is not likely a direct structuring factor of benthic distribution patterns [Gage and Tyler, 1991; Levin and Dayton, 2009]. However, depth is a good proxy for other variables such as organic matter input, temperature and dissolved oxygen that are likely to influence faunal distribution patterns [Barry and Dayton, 1991; Levin and Sibuet, 2012; McArthur et al., 2010; Smith et al., 2008]. As depth increases the sedimentation rate (including organic matter sedimentation) decreases, thus reducing the quantity and quality of food that reaches the benthos [Graf, 1992; Suess, 1980]. That gradient of food supply affects not only which species are likely to occur in a given area but also the number of individuals, number of species, biomass, and the distribution of individuals among species [Rex and Etter, 2010].

### 1.2.2 Diversity

The vast, largely nutrient poor and ostensibly ***homogeneous*** silty sediments of continental margins were historically viewed as devoid or at least lacking in diversity [Gage and Tyler, 1991]. We now know that these environments support a rich array of benthic fauna and can be as speciose as coastal environments with estimates of 50 species per 100 individuals sampled [Gage and Tyler, 1991; Grassle and Maciolek, 1992; Snelgrove and Smith, 2002]. However, local diversity is highly variable from place to place [Snelgrove and Smith, 2002] and as in most ***faunal assemblages***, individuals are not evenly distributed across species [Fisher et al., 1943; Gaston, 2000]. The shape of a characteristic ***species-abundance distribution*** is left-skewed such that a few dominant species are responsible for most of the abundance and the majority of species are represented by only a few individuals [Brown, 1984]. It is well known that the shape of the underlying species-abundance distribution, as well as the size of the sampled area of seafloor, will affect the number of species one collects in a sample [Gaston, 2000]. These patterns are useful in explaining the high degree of variability that is present between replicate samples but they do not explain the mechanism by which species richness is maintained in the seemingly non variable and homogeneous environment.

Although the processes which regulate the co-existence of many species in any one area remain poorly understood [Grant, 2000], several hypotheses have been brought forward to explain the high species richness of continental margins. Sanders [1968] developed the stability time hypothesis which posits that given sufficient time under stable environmental conditions species could have developed many specialized niches which would lead to a great diversity of species. Alternatively, Dayton and Hessler [1972] proposed that predation pressure from the action of cropping and scavenging benthic fauna could decrease prey competition allowing for more species to co-exist. However, the most likely and widely accepted theory [Rex and Etter, 2010] is Grassle and Sanders' [1973] disturbance theory that explains high species richness through small scale disturbances which effectively create a patchy or heterogeneous environment. Many patchy and ephemeral habitats are created in soft-bottom environments through temporally and spatially variable inputs of organic matter [Grassle and Morse-Porteous, 1987], the biogenic construction of burrows and mounds [Aller and Aller, 1986], the foraging of larger fauna [Dayton and Hessler, 1972] and occasional large food falls [Smith, 1985]. Grassle and Sanders' [1973] proposed that these disturbances could bring about ***ecological succession*** which would act to maintain high species diversity.

### 1.2.3 Faunal classes

The fauna which reside on continental margins have been delineated by size-class into four main groups: bacteria, ***meiofauna***, ***macrofauna*** and ***megafauna*** [Rex and Etter, 2010]. In this work, I focus on the two largest categories: macro- and megafauna. Macrofauna are defined as organisms that are retained on a 0.25 to 0.5 mm sieve [Snelgrove, 1998] typically sampled with grabs or box corers. The larger and mostly epifaunal megafauna are defined as organism that can be identified in bottom photographs [Snelgrove, 1999] typically sampled using trawls or video. For a summary of representative macro- and megafaunal taxa of the Beaufort Shelf see Table 1.1. The size-class categorization likely arose from the selective nature of the employed sampling gear used to collect benthic fauna. Macrofauna tend to reside within the sediment and thus require sampling gears that penetrate the sediments [Eleftheriou and McIntyre, 2005] while the larger megafauna can be widely dispersed or densely aggregated on the surface [Gage and Tyler, 1991] and thus require sampling over a larger area to obtain an accurate representation of their distribution [Lozach et al., 2011; Mclntyre, 1956]. In addition, benthic size classes tend to differ in relative mobility, bioturbation potential, life history and feeding strategies [Jørgensen et al., 2011; Ólafsson, 2003; Warwick, 1984]. Most of these differences are described between meio- and macrofauna classes. However, some differences are shown to occur between macro- and megafauna as well.

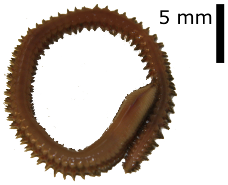
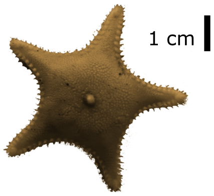
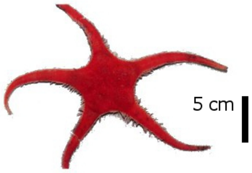
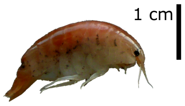
While some megafauna are sessile (e.g. Porifera), most are highly motile compared to the macrofauna which have relatively restricted mobility, only moving within a few meters perimeter in their lifetime [Gray and Elliott, 2009; Jørgensen et al., 2011]. The greater size and mobility of megafaunal scavengers permits them to take advantage of larger food particles and disperse them widely which may enhance the availability of food for the smaller macrofauna [Dayton and Hessler, 1972; Smith, 1985]. In addition, macro- and megafauna may also be functionally distinguishable [Lampitt et al., 1986] with a greater degree of suspension and predatory feeders in the megafauna and detritivores in the macrofauna [Jørgensen et al., 2011]. These observations have led to the hypothesis that macro- and megafauna may have divergent responses and sensitivity to environmental change [Grebmeier et al., 2006a; Jørgensen et al., 2011].

### 1.2.4 Arctic benthos

High seasonality, low productivity and tight bentho-pelagic coupling on Arctic margins [Piepenburg, 2005] cause Arctic benthos to differ from temperate benthos in several aspects of their biology. The comparatively short productive season and colder temperatures should favour against a pelagic larval stage [Curtis, 1975] and cause a greater degree of direct benthic development to persist on Arctic shelves [Kendall et al., 1997]. As this would likely reduce the dispersive ability of a species, it is not surprising that most of the dominant Arctic taxa (i.e. *Ophuira*, *Nephtys* and *Macoma* species) have retained a pelagic larvae stage [Curtis, 1975]. Arctic benthos may also differ in their distribution across a depth gradient. Many benthic taxa in the region have large depth ranges [Bluhm et al., 2011; Piepenburg et al., 2011] and therefore Arctic shelf and slope taxa appear less differentiated compared to shelf–slope benthos on non-polar continental margins [Carney, 2005].

In addition, Arctic benthos appear to accumulate greater biomass compared to

**Table 1.1. Examples of macro- and megafaunal taxa of the Beaufort Shelf**

| **Macrofauna** | | **Megafauna** | |
|---|---|---|---|
| Polychaete:<br>*Maldane sarsi* |  | Ophiuroid:<br>*Ophiocten sericeum* |  |
| Polychaete:<br>Nephtyidae |  | Asteroid:<br>*Ctenodiscus crispatus* |  |
| Bivalve:<br>*Thyasira* sp. |  | Asteroid:<br>*Pontaster tenuispinus* |  |
| Bivalve:<br>*Yoldia hyperborea* |  | Isopod:<br>*Saduria sabini* |  |
| Sipuncula |  | Amphipod:<br>Lysianassidae |  |

warmer regions of comparable environmental conditions [Petersen and Curtis, 1980]. The elevated benthic biomass can be explained by the high efficiency of energy transfer from the pelagic to benthic realm (bentho-pelagic coupling) as a result of reduced zooplankton grazing on early ice algal blooms [Petersen, 1984]. Furthermore, lower metabolic rates induced by colder temperatures allow benthos at both poles to accumulate more biomass compared to warmer regions of comparable productivity [Brey et al., 1993]. Thus, Arctic benthos play a substantial functional role within the larger marine ecosystem. They cycle organic matter from lower to higher trophic levels and recycle nutrients back into the water column utilized by primary producers [Piepenburg, 2005]. On Arctic shelves, benthos are an important food source for benthic and pelagic fish, marine mammals such as bearded seals (*Erignathus barbatus*) and gray whales (*Eschrichtius robustus*) and many seabirds [Grebmeier et al., 2006a].

## 1.3 Physical properties of the Canadian Beaufort Shelf

The Canadian Beaufort Shelf is a long and narrow (~450 km by ~130 km) Arctic shelf covering ~64,000 km$^2$ (Figure 1.1). Both the shelf and adjoining slope are bounded by the Mackenzie Trough to the west, the Mackenzie Delta to the south and Cape Bathurst to the east. The continental slope begins roughly at the 80 to 200 m isobaths [Carmack and Macdonald, 2002; O'Brien et al., 2006], between 100 and 150 km offshore. The slope gradually drops at an angle of 1° to 2° between the shelf break and 1,000 m. The region is characterized by extreme seasonality. Ice coverage in the Beaufort Shelf roughly begins in November and ends in June [Canadian Ice Service, 2013], lasting approximately 70% of the year [Forest et al., 2007].

The surface shelf water (Polar-Mixed Layer $< 50$ m) is subject to substantial, year round fresh water input from the Mackenzie River. Deeper in the water column lies nutrient-rich shelf water of Pacific origin (Pacific Halocline $50 - 200$ m) which confines the warmer, salty water of Atlantic origin to depth ($> 200$ m) [Carmack et al., 2004; Carmack and Macdonald, 2002; Forest et al., 2007; Macdonald et al., 1989]. Basic circulation of the Beaufort Sea is governed by the clockwise Beaufort Grye, and the anti-clockwise Beaufort Undercurrent which carries water of both Pacific and Atlantic origin eastward along the slope [Forest et al., 2007] and drives nutrient rich water onto the shelf [Carmack and Macdonald, 2002; Macdonald et al., 1987]. Upwelling can occur all along the shelf break, however several features on the shelf, the wide and deep Mackenzie Trough [Williams et al., 2006], the narrow Kugmallit Valley [Carmack et al., 2004; Walker et al., 2008] and the near shore steep slope east of Cape Bathurst [Conlan et al., 2013; Williams and Carmack, 2008] can enhance upwelling.

The main sediment source to the region, the Mackenzie River, carries predominately fine-grained sediments to the shelf [Jerosch, 2012]. Sediment composition varies across the shelf. Clay dominates on the western shelf, silt is concentrated in shallow coastal area of the Mackenzie Delta and sandier sediments dominate on the eastern shelf [Jerosch, 2012]. Larger grain size sandy sediments are found west of the Mackenzie Trough as a result of increased sorting driven by faster currents [Jerosch, 2012].

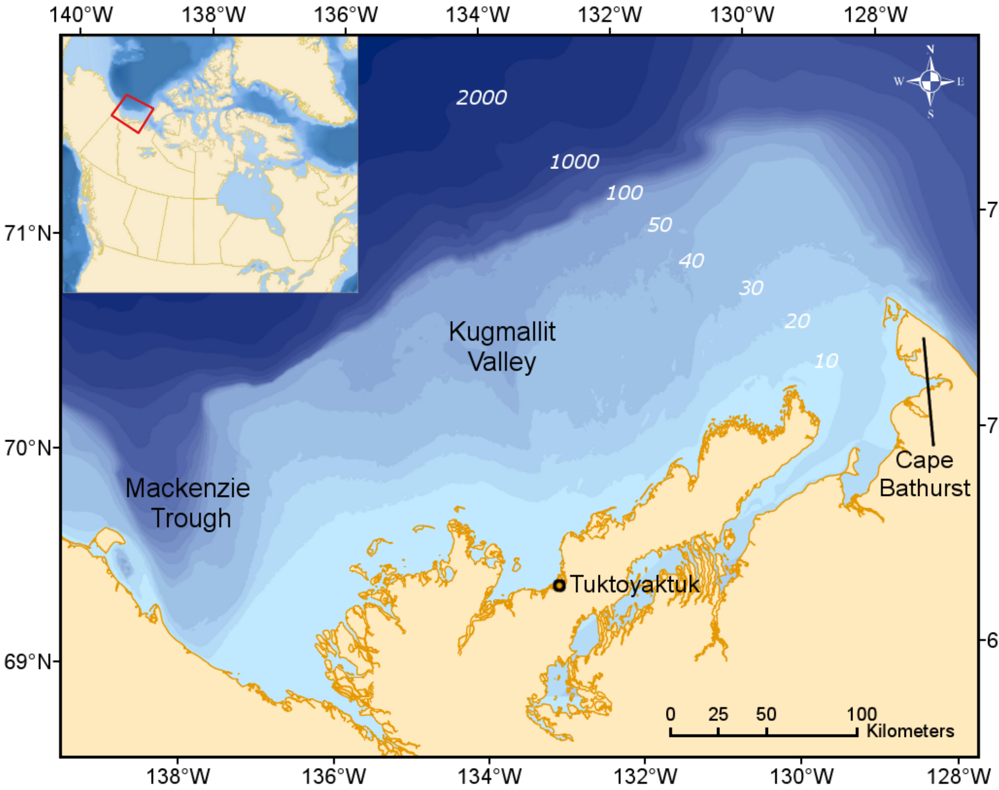


**Figure 1.1. Features of the Canadian Beaufort shelf and slope.** Bathymetry provided by the Geological Survey of Canada Atlantic.

## 1.4 Data collection

Data collected from two separate benthic field programs were utilized in this thesis. Chapter 2 data were from three summer expeditions on the CCGS Amundsen during the 2009, 2010 and 2011 ArcticNet field programs. Chapter 3 data were from the 2012 BREA Marine Fishing Program onboard the F/V Frosti. Each field program employed separate sampling gear to collect the macrofauna (box corers) and megafauna (trawls). For detailed sampling protocols on each field program see Section 2.2.1 and 3.2.1, respectively. I participated in benthic sampling onboard the CCGS Amundsen during the 2011 field program. Onboard I aided in collecting, sieving, sorting and identifying benthic fauna. Post-cruise, all benthic samples were processed and identified to the lowest taxonomic level possible using standardized protocols at the

Benthic Ecology Laboratory of the Institut des sciences de la mer (UQAR-ISMER) in Rimouski (Québec), Canada. The lab is specialized in benthic ecology and taxonomy with substantial experience in Arctic biodiversity. Taxonomic identifications were completed mainly by two trained technicians, with the aid of a few students, using a number of taxonomic keys compiled from approximately 1300 references.

For this work, I used a subset from each of the resulting datasets which included only stations where both sampling gear types where deployed (black circles in Figure 1.2), with the exception of two stations along the BREA transects (see Section 3.2.1 for details). Together, the BREA and ArcticNet sampling stations had a spatial extent along the shelf similar to previous benthic surveys on the Canadian Beaufort Shelf but extended much farther offshore (Figure 1.2). That allowed for a greater comparison of shelf–slope fauna than previously possible. In addition, the systematic use of both box core and trawl sampling gear was a novel approach in the region that allowed for a comparison of macro- and megafaunal spatial patterns. Past surveys used a combination of box corers and Veen grabs [Conlan et al., 2008], grabs, nets, trawls and dredges [Chapman and Kostylev, 2008], and drop-camera video [Kostylev and Chapman, 2005] for benthic sampling.

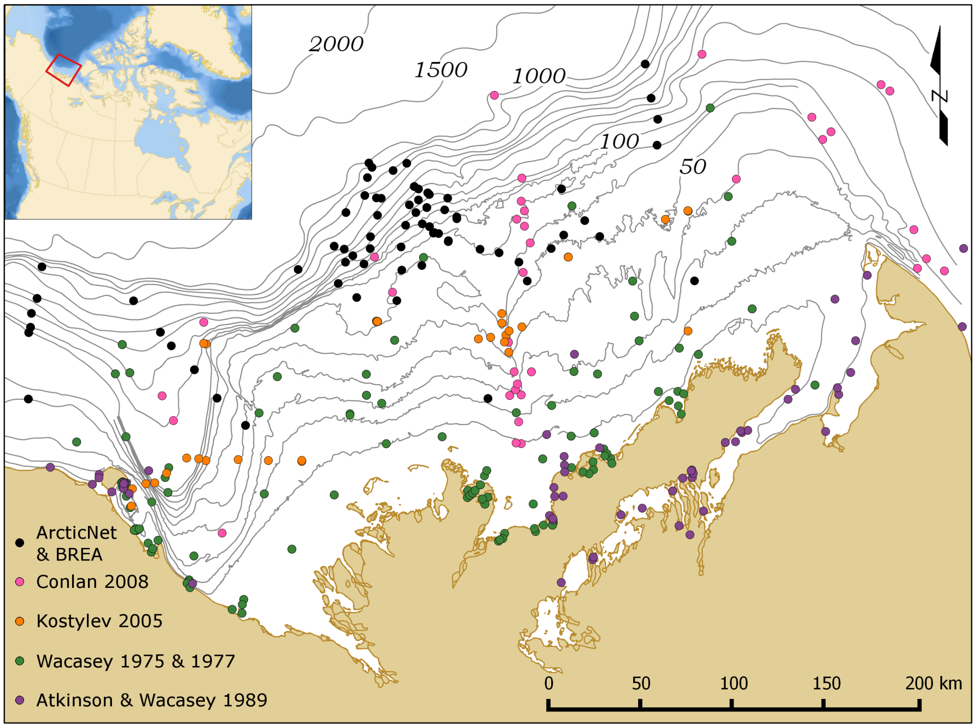


**Figure 1.2. Major benthic surveys on the Canadian Beaufort shelf and slope.** Bathymetry provided by the Geological Survey of Canada Atlantic. Sampling locations derived from Chapman and Kostylev [2008], Kostylev and Chapman [2005] and Conlan et al. [2008].

## 1.5 Thesis goals and chapter structure

The main goal of this thesis was to describe macro- and megafaunal distribution patterns on the Canadian Beaufort Shelf. A secondary goal was to determine the degree of congruence between macro- and megafaunal patterns. The structure of the thesis is as follows:

**Chapter 2** compares macro- and megafaunal distribution across the depth gradient, focusing on the distribution of rare taxa, and the similarity of macro- and megafaunal patterns of abundance, taxa richness ($\alpha$ ***diversity***) and $\beta$ ***diversity***.

**Chapter 3** contrasts along versus cross shelf variability in macro- and megafaunal abundance, biomass and $\alpha$ and $\beta$ diversity and compares macro- and megafaunal ***community structure*** to that described from past benthic surveys in the region.

**Chapter 4** summarizes the key conclusions and discusses their application to future benthic monitoring programs in the region.

**Appendix A** examines the co-occurrence of macro- and megafauna taxa and its consistency between benthic datasets.

**Appendix B** provides a qualitative look at the different faunal components that are identified from trawl versus video surveys on the Beaufort Shelf.

**Appendix C** compares the removed meiofaunal fraction to the macrofauna in box cores from the 2012 BREA sampling.

**Appendix D** lists all macro- and megafaunal taxa, represents the final datasets following data processing.

# Chapter 2

# Diversity, abundance and community structure of benthic macro- and megafauna on the Beaufort shelf and slope

This chapter is based on the contents of the paper:

J. Nephin et al. [2014]. “Diversity, abundance and community structure of benthic macro- and megafauna on the Beaufort shelf and slope”. *PLoS One* 9 [7], e101556

## 2.1 Introduction

In the Arctic, the pace of climate warming is accelerated, compared to other regions [Bekryaev et al., 2010], exposing areas like the Canadian Beaufort Shelf to new pressures such as shipping traffic, exotic species, oil and gas extraction and possibly commercial fishing. Arctic marine benthos, which provide key ecosystem functions such as nutrient cycling, organic matter transport, sediment mixing and metabolization of pollutants [Snelgrove, 1998] will likely be influenced by many of the direct and indirect effects of climatic driven changes [Wassmann et al., 2011].

The effect of a longer ice-free season on the benthos is currently under debate [Comiso et al., 2008; Stroeve et al., 2007]. Thinning and reduced ice conditions accompanied by upwelling favourable winds [Yang, 2009] may increase primary productivity and the benthic standing stock [Forest et al., 2007; Rysgaard and Glud, 2007; Tremblay et al., 2011]. Alternatively, the loss of sinking ice-algae and a shift toward open-water primary productivity may lead to a zooplankton-dominated ecosystem and a decrease of food supply for the benthos [Grebmeier et al., 2006b; Piepenburg, 2005]. In addition, warming Arctic seas may facilitate changes in benthic community structure through the introduction of lower latitude taxa [Berge et al., 2005; Grebmeier et al., 2006b; Węsławski et al., 2010]. Hence, the fate of Arctic shelf benthos and the tightly coupled pelagic environment [Renaud et al., 2007] in a continuing climate warming scenario remains unclear. Recently, a renewed interest in industrial exploration of the Canadian Beaufort Sea has prompted a resurgence of benthic surveys providing a baseline for which to monitor future change. Understanding regional spatial patterns and drivers of benthic abundance and diversity is needed to effectively monitor potential human induced shifts [Wassmann et al., 2011].

On continental margins benthic patterns principally vary across the depth gradient [Rex and Etter, 2010]. There is wide acceptance that continental shelf benthos decrease in abundance with increasing depth [Rex et al., 2006] as a result of decreases in the flux of particulate organic carbon on which they rely [Carney, 2005; Gage and Tyler, 1991]. Patterns of benthic taxa richness across depth gradients are less consistent [Stuart et al., 2003; Stuart and Rex, 2009], although theory predicts a unimodal distribution with peak diversity occurring at mid-slope where shallow and deep-sea species ranges overlap [Levin et al., 2001; Rex and Etter, 2010]. In the Arctic, macro- and megafaunal abundance and taxa richness are observed to decrease monotonically with depth from mid-shelf to slope [Bluhm et al., 2011; Conlan et al., 2008; Renaud et al., 2007] as does the flux of particulate organic matter [Link et al., 2011]. However, few marine studies have examined the contribution of rare species to local species richness [Ellingsen et al., 2007; Włodarska-Kowalczuk et al., 2012] and how the distribution of rare species may vary with depth. Factors that affect the distribution of rare species may be important for monitoring and conservation, as rare species are theorized to buffer against alterations in ecosystem function under environmental change, even those functionally similar to dominants [Ellingsen et al., 2007; Loreau et al., 2001; Lyons et al., 2005].

Benthic community composition also varies across the depth gradient. Previous work in the Canadian Beaufort has shown macrofauna composition to be similar at corresponding depths along the shelf [Conlan et al., 2008]. This observation is consistent with the expectation of faunal replacement ($\beta$ diversity [Whittaker, 1972]) across the bathymetric gradient, largely in response to decreased food availability [Carney, 2005]. However, Arctic benthos have been predicted to have larger depth ranges and thus display a slower rate of faunal replacement across depth gradients [Carney, 2005]. On the pan-Arctic scale, there is evidence of large overlap between shelf and slope taxa, suggesting that many taxa may be eurybathic [Bluhm et al., 2011; Piepenburg et al., 2011] and that the slope benthos is simply a nested sub-assemblage of shelf benthos rather than being a community that replaces the shelf fauna as depth increases or food supply diminishes. The distinction between spatial replacement and nested structure may be important to understanding how present day food availability is determining faunal distribution patterns and the response of benthos to predicted changes in future food availability. Furthermore, several studies have demonstrated that $\beta$ diversity (faunal replacement) can vary between faunal groups [Carney et al., 1983; Grassle et al., 1979; Haedrich et al., 1980; Rex, 1977], likely due to differences in metabolism, trophic structure, mobility and dispersal [Rex and Etter, 2010]. The degree to which the rate of faunal replacement differs between Arctic macro- and megafauna has yet to be quantified.

To inform future monitoring programs on the Canadian Beaufort Shelf I compared macro- and megafaunal patterns of rarity, abundance and community composition. Specifically my objectives were to determine: 1) what factors co-vary with the distribution of rare taxa, and the similarity of macro- and megafaunal patterns of 2) abundance and taxa richness ($\alpha$ diversity) and 3) $\beta$ diversity.

## 2.2 Methods

### 2.2.1 Study area and sampling

Within the spatial extent of this study area (shown by the dotted black line in Figure 2.2) the shelf break was located at 100 meters in depth. The shelf break was defined as the depth at which the rate of change of the average slope, modelled by the logistic function: $f(x) = a/(1 + b \cdot e^{-cx})$ where $x$ = depth, was the greatest (Figure 2.1). Within the study area, the depth range of the shelf is 50 m ($50 - 100$ m) and depth range of the slope is 900 m ($100 - 1,000$ m).

Benthic sampling was undertaken through a partnership between ArcticNet (`www.arcticnet.ulaval.ca`), British Petroleum, Imperial Oil and the Canadian Healthy Oceans Network [Snelgrove et al., 2012] to gather baseline benthic data in the oil and gas exploration lease areas of the Beaufort shelf and slope. Samples were collected within a 12,000 square kilometre spatial extent, northeast of the Mackenzie Trough

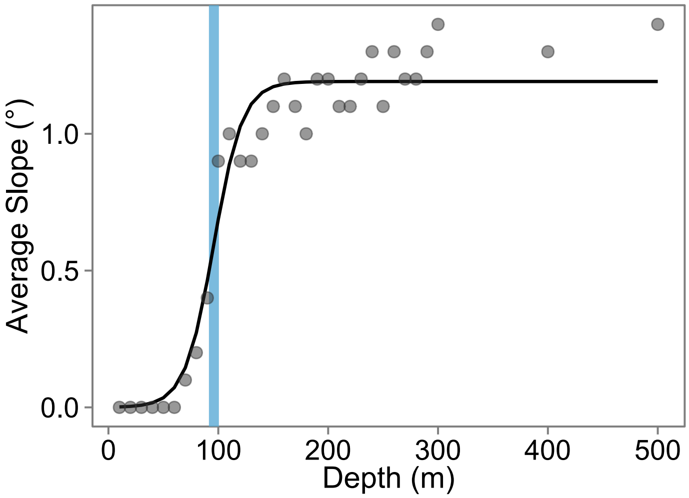


**Figure 2.1. Beaufort slope model.** Average slope of the Beaufort margin across the spatial extent of sampling stations. Blue bar shows the approximate location of the shelf edge where the greatest change in average slope occurs.

(Figure 2.2). Sampling occurred during three summer expeditions on the CCGS Amundsen during the 2009, 2010 and 2011 ArcticNet field programs. Data from 48 sampling stations within Imperial Oil's and British Petroleum's exploration license areas (Ajurak, Pokak, EL451 and EL453) were utilized in this study.

At each sampling station, macrofauna were sampled using a 0.25 $m^2$ USNEL box corer and megafauna were sampled with an Agassiz trawl (1.5 m in width, 0.7 m in height). On average the 48 paired box core and trawl samples were separated by 770 m (range 45−3460 m) in horizontal distance and 7 m (range 0−85 m) in depth. Sediment from half of the surface area of the box corer was utilized down to a maximum depth of 15 cm. The surface area sampled was 0.125 $m^2$ and the average volume sampled was 1200 $cm^3$. Macrofauna were collected on a 0.5 mm mesh sieve and fixed in 4% buffered formalin for later identification. Towing speed for trawls ranged from 1.5 to 2 knots and bottom time from 3 to 5 minutes, with the exception of the 2009 trawls where bottom time was 10 minutes. The trawl mesh was 5 mm and samples were sieved with a 2 mm mesh after collection, with the exception of 2009 sampling where a 0.5 mm sieve was used. Faunal densities were standardized to the average trawl area: 450 $m^2$ (trawl net width × ship speed × bottom time). Megafauna that could not be confidently identified onboard were preserved in 4% buffered formalin or frozen at −20° Celsius. Megafauna identified onboard were discarded or used for other analyses.

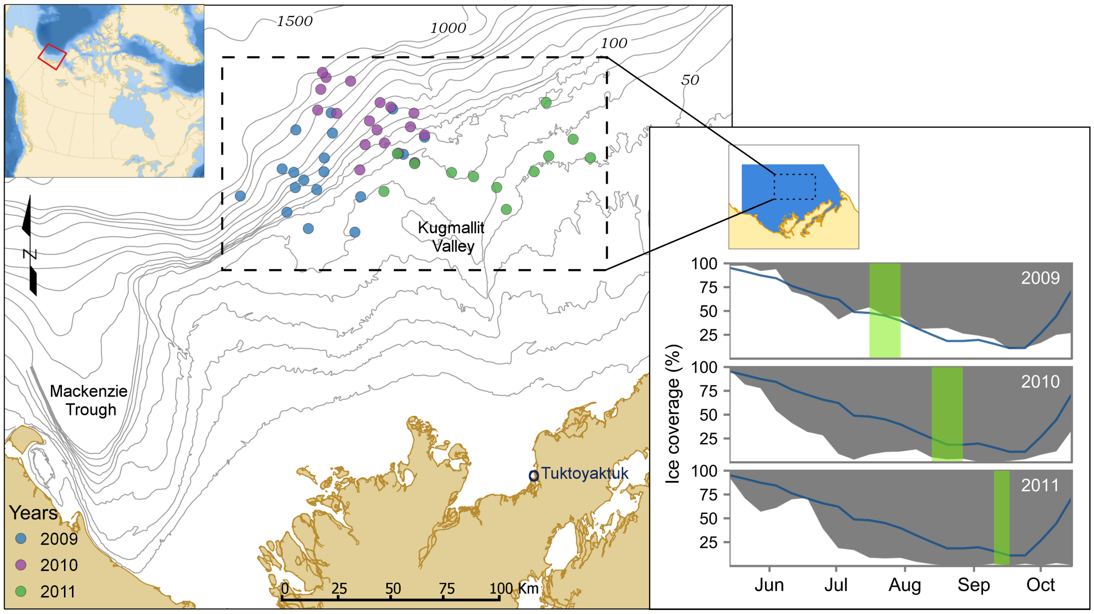


**Figure 2.2. Sampling stations and ice coverage on the Beaufort shelf and slope from 2009 to 2011.** One box core and trawl sample were collected from each station (left panel). Sample sizes were n=18 in 2009, n=18 in 2010 and n=12 in 2011. Black dotted line outlines the spatial extent of sampling used to calculate the average slope. Ice coverage (white area, right panel) for 2009, 2010 and 2011 benthic sampling periods. Blue coverage area outlines the area over which ice coverage was calculated. Blue lines in plots represent historic ice coverage (median from 1981 to 2010). Green bars indicate when benthic sampling occurred. Ice coverage data courtesy of Canadian Ice Service, Environment Canada.

Benthic sampling was not consistent between sampling years; samples were distributed asymmetrically between shelf and slope and with each subsequent year were taken later in the summer season and farther to the east (Figure 2.2). In addition, sea ice conditions in the Beaufort varied considerably during these years. The sea-ice breakup on the Beaufort shelf was earlier in the year and reached a lower minimum ice coverage in 2010 and 2011 (Figure 2.2).

## 2.2.2 Data preparation and quality control

All benthic samples were collected, processed and identified to the lowest ***taxonomic rank*** possible using the same protocol across all sampling years. The metadata can be accessed through the Polar Data Catalogue (`www.polardata.ca`) and datasets will be publicly accessible through Dryad (`datadryad.org`). The resulting faunal datasets needed some modifications prior to use in this study, primarily to ensure the consistent use of taxonomic names—in order to prevent the inflation of taxa richness. Both box core and trawl datasets were validated through the removal of synonyms and unaccepted names using the WoRMS (`www.marinespecies.org`) Taxon Match tool.

Only 46% of box core and 60% of trawl faunal groups (records in the dataset) were identified to the species level. The majority of these higher-order identifications were the result of broken or damaged specimens and the lack of taxonomic focus or expertise within certain phyla such as Sipuncula and Nemertea. Excluding all higher-order taxa to standardize the data to the species level would remove too large a portion of the total specimens. Alternatively, specimens consistently identified to higher-orders (e.g. Nemertea) remained in the database while specimens identified to several taxonomic ranks (e.g. Ophiuridae (Family), Ophiurinae (Subfamily), *Ophiocten* (Genus), *sericeum* (species)) were grouped to the family level. Records were removed from the database only if specimens that were identified to several taxonomic ranks were ranked higher than the family level (e.g. Ophiurida (Order)). This system was employed to balance the retention of detail and the loss of records from the dataset. The resulting datasets included 73% of box core records and 92% of trawl records. Grouping organisms identified to several taxonomic ranks acts as a quality control mechanism by minimizing any potential interannual variability in taxonomic identifications. Previous studies have validated a higher-taxa approach to data quality control by demonstrating that grouping taxa into higher taxonomic classes has little effect on the detection of diversity patterns [Cusson et al., 2007; Piepenburg et al., 2011; Włodarska-Kowalczuk and Kędra, 2007].

The box core and trawl tended to selectively sample macrofauna and megafauna, respectively. Seventy-nine taxa (32%) were sampled by both gear types. However, the shared taxa were not sampled in a quantitatively comparable way by the two gear types. The trawl, because of its limited penetration of the sediment and larger mesh size, would tend to undersample the macrofauna. On the other hand, the box corer would tend to inaccurately sample the more widely spaced megafaunal organisms, because of its relatively small surface area. Two distinct quantitative datasets were created by removing macrofauna from the trawl samples and megafauna from the box corer samples. Taxa were identified as macrofauna or megafauna based on the frequency at which they were sampled by each gear type, assuming that megafauna were collected more frequently and effectively by the trawl than by the box corer and vice versa (Tables 2.1 and 2.2). The removal of shared taxa resulted in a 40% reduction in box corer taxa and a 30% reduction in trawl taxa. In addition, meiofauna and colonial fauna were removed from the datasets; meiofauna are not consistently sampled with larger mesh sieves and colonial fauna are not suitable for individual count data.

**Table 2.1. Shared taxa that were classed as megafauna and removed from the macrofauna dataset.**

| **Phylum** | **Class** | **Taxon** | **Box Occurrence** | **Box (#/.125 m$^2$)** | **Trawl Occurrence** | **Trawl (#/450 m$^2$)** |
|---|---|---|---:|---:|---:|---:|
| Annelida | Polychaeta | Ampharetidae | 17 | 111 | 17 | 315 |
| | | *Cistenides* | 14 | 37 | 15 | 30814 |
| | | *N. zonata* | 6 | 7 | 9 | 152 |
| | | Polynoidae | 15 | 29 | 34 | 4662 |
| | | Sabellidae | 14 | 51 | 23 | 1174 |
| | | Terebellidae | 8 | 10 | 20 | 1131 |
| Arthropoda | Malacostraca | *A. cristatum* | 1 | 1 | 1 | 2 |
| | | *Ampelisca* | 3 | 298 | 13 | 40599 |
| | | *Anonyx* | 4 | 7 | 22 | 2309 |
| | | *Byblis* | 9 | 18 | 9 | 493 |
| | | *C. stygia* | 1 | 2 | 9 | 186 |
| | | *C. brachiata* | 6 | 10 | 8 | 27 |
| | | Calliopiidae | 1 | 1 | 5 | 75 |
| | | Diastylidae | 16 | 124 | 22 | 1076 |
| | | *Eualus* | 1 | 1 | 21 | 523 |
| | | *Gnathia* | 2 | 4 | 2 | 145 |
| | | *Haploops* | 13 | 35 | 15 | 264 |
| | | *Ilyarachna* | 1 | 1 | 1 | 1 |
| | | Lysianassidae | 12 | 58 | 12 | 3842 |
| | | Melitidae | 2 | 10 | 12 | 842 |
| | | *Metopa* | 1 | 1 | 2 | 6 |
| | | *Munnopsurus* | 1 | 1 | 3 | 9 |
| | | Oedicerotidae | 20 | 75 | 32 | 1665 |
| | | *P. femorata* | 14 | 75 | 14 | 446 |
| | | *Rhachotropis* | 1 | 1 | 15 | 3589 |
| | | *S. sabini* | 11 | 18 | 38 | 4953 |
| | | *S. bicuspida* | 4 | 9 | 10 | 792 |
| | | *Tmetonyx* | 3 | 5 | 5 | 36 |
| | | Gnathiidae | 4 | 7 | 11 | 331 |
| | | Ischyroceridae | 1 | 2 | 11 | 745 |
| | | Munnopsidae | 3 | 12 | 11 | 268 |
| | | Uristidae | 12 | 46 | 25 | 2378 |
| Brachiopoda | | Brachiopoda | 2 | 4 | 4 | 400 |
| Cephalorhyncha | Priapulida | Priapulidae | 1 | 1 | 7 | 22 |
| Chordata | Ascidiacea | Ascidiacea | 8 | 19 | 12 | 372 |
| Mollusca | Bivalvia | Astartidae | 7 | 54 | 25 | 7380 |

*Continued on next page*

Table 2.1 – *Continued from previous page*

| **Phylum** | **Class** | **Taxon** | **Box Occurrence** | **Box (#/.125 m$^2$)** | **Trawl Occurrence** | **Trawl (#/450 m$^2$)** |
|---|---|---|---|---|---|---|
| | | *Bathyarca* | 2 | 3 | 14 | 1263 |
| | | Cardiidae | 10 | 20 | 14 | 1397 |
| | | H. arctica | 3 | 3 | 6 | 100 |
| | | *Lyonsia* | 2 | 5 | 12 | 572 |
| | | *Mya* | 1 | 1 | 6 | 338 |
| | | Mytilidae | 15 | 49 | 16 | 5206 |
| | | *Nucula* | 2 | 2 | 8 | 9326 |
| | | *Nuculana* | 5 | 12 | 14 | 3267 |
| | | *P. glacialis* | 1 | 1 | 8 | 256 |
| | | *Yoldia* | 7 | 13 | 10 | 1533 |
| | Gastropoda | Cancellariidae | 3 | 4 | 7 | 382 |
| | | *Margarites* | 7 | 10 | 13 | 552 |
| | | Naticidae | 1 | 1 | 11 | 468 |
| | | *Philine* | 1 | 1 | 1 | 2 |
| | | Pyramidellidae | 2 | 2 | 2 | 62 |
| | | *Tachyrhynchus* | 7 | 37 | 14 | 10673 |
| | Scaphopoda | *Siphonodentalium* | 9 | 37 | 12 | 848 |
| Nemertea | | | 13 | 27 | 20 | 109 |
| Platyhelminthes | | | 1 | 1 | 5 | 205 |

**Table 2.2. Shared taxa that were classed as macrofauna and removed from the megafauna dataset.**

| Phylum | Class | Taxon | Box Occurrence | Box (#/.125 $m^2$) | Trawl Occurrence | Trawl (#/450 $m^2$) |
|---|---|---|---|---|---|---|
| Annelida | Clitellata | Clitellata | 4 | 66 | 2 | 2 |
| | Polychaeta | Cirratulidae | 33 | 239 | 13 | 205 |
| | | Flabelligeridae | 4 | 9 | 2 | 282 |
| | | Lumbrineridae | 27 | 121 | 4 | 12 |
| | | Maldanidae | 38 | 760 | 14 | 255 |
| | | Nephtyidae | 29 | 975 | 27 | 534 |
| | | Onuphidae | 11 | 58 | 10 | 3855 |
| | | Oweniidae | 11 | 178 | 7 | 2025 |
| | | Phyllodocidae | 7 | 12 | 3 | 24 |
| | | Scalibregmatidae | 5 | 10 | 2 | 3 |
| | | Sphaerodoridae | 7 | 11 | 1 | 15 |
| | | Spionidae | 24 | 123 | 9 | 27 |
| | | *Terebellides* | 11 | 78 | 9 | 133 |
| Arthropoda | Malacostraca | Gammaridea | 6 | 14 | 1 | 1 |
| | | Leuconidae | 25 | 442 | 12 | 842 |
| | | *P. fasciata* | 2 | 34 | 1 | 15 |
| Mollusca | Bivalvia | *Montacuta* | 2 | 25 | 1 | 3 |
| | | *Portlandia* | 6 | 8 | 3 | 43 |
| | | *S. greenlandicus* | 4 | 14 | 3 | 708 |
| | | Thyasiridae | 12 | 199 | 3 | 34 |
| | | *Yoldiella* | 11 | 96 | 3 | 271 |
| | Caudofoveata | | 10 | 15 | 3 | 10 |
| | Gastropoda | *Cylichna* | 22 | 105 | 18 | 2462 |
| Sipuncula | | | 27 | 154 | 21 | 5812 |

### 2.2.3 Analyses

All statistical analyses were completed in the R environment for statistical computing (`www.r-project.org`) with aid from community ecology and graphics packages: vegan, cluster, rich and ggplot. Maps and spatial analyses were completed using QGIS software (`http://qgis.osgeo.org`).

Total abundance (number of individuals) was calculated based on the standardized average sample (0.125 $m^2$ for macrofauna and 450 $m^2$ for megafauna). Spearman's rank correlation ($\rho$) was used to quantify the strength of abundance and occupancy trends. Occupancy is defined here as the number of sites at which a taxon was recorded. The $\chi^2$ test of independence was used to test for a relationship between depth (shelf vs. slope) or phylum and the ***relative abundance*** of rare taxa. Mean relative abundance was defined as the average contribution of a taxon to the total number of individuals in each sample where the taxa were present. The Wilcoxon rank sum test was used to assess the significance of shelf–slope differences in total abundance, taxa richness (number of taxa) and taxonomic distinctness [Clarke and Warwick, 1999]. A measure of evenness was not included in the analysis as evenness was constrained as a result of low counts and taxa richness at several stations (see [Robinson et al., 2014]). To differentiate between possible drivers of variation in abundance and taxa richness across depth and sampling years a two-way analysis of variance was used. Longitude and latitude were not included in this analysis as they were correlated with depth and year. Individual-based ***rarefaction*** curves were used to investigate the degree to which sample size and mesh size differences affected the abundance and taxa richness patterns across sample years.

Multivariate cluster and ordination techniques were utilized to explore the macro- and megafaunal assemblage patterns. A fourth-root transformation was applied to the matrices to reduce the influence of highly abundant taxa [Warwick and Clarke, 2001]. The Bray-Curtis (BC) dissimilarity measure was computed to obtain an ecologically meaningful distance measure based on the relative abundance and composition of taxa between stations. $\beta$ diversity was computed using BC similarity (BC dissimilarity$-1$). Ward's method of hierarchical clustering was used to define compact clusters of stations. The number of clusters was determined by selecting the maximum ***average silhouette width*** (ASW), a measure of average dissimilarity of stations between- versus within-clusters [Rousseeuw, 1987], for all combinations of cluster sizes. Station dissimilarities were also visualized through non-metric multidimensional scaling (nMDS) ordination. Average relative abundances of taxa, the contribution of each taxa to total abundance, by cluster were used to define dominant taxa representative of clusters.

## 2.3 Results and Discussion

### 2.3.1 Distribution of occurrence, abundance and rarity

Two hundred and forty-seven taxa were collected at the 48 stations sampled. A total of 4,752 individuals sampled from a 6 m$^2$ area were distributed among 80 macrofauna taxa and a total of 452,115 individuals sampled from a 21,600 m$^2$ area (approx.) were distributed among 167 megafauna taxa (see Table 2.3 for a summary of total abundance and richness by sample). Piepenburg et al. [2011] estimated the Beaufort Shelf holds around 1,100 species of major macro- and megafaunal taxa (annelids, arthropods, echinoderms and molluscs), which suggests we have only captured roughly one quarter of the taxa present. Most of the abundance was concentrated in polychaeta (66%), malacostraca (15%) and bivalvia (10%) classes in the macrofauna and ophiuroidea (28%), malacostraca (23%) and asteroidea (13%) classes in the megafauna. Many taxa had very low frequencies of occurrence. The macrofauna had 24 ***uniques*** (30%) (taxa present at only one station) and the megafauna had 32 uniques (19%), slightly lower compared to other continental shelves ($\approx 40\%$) [Ellingsen et al., 2007; Shin and Ellingsen, 2004] but similar to other Arctic regions ($20 - 30\%$) [Cochrane et al., 2012; Włodarska-Kowalczuk et al., 2012]. The true percent of uniques may be higher, considering that the number of uniques was likely deflated by the grouping of many taxa to the family taxonomic rank.

Beaufort macro- and megafauna displayed the typical right-skewed distribution of ***occurrence*** [Gaston, 1994], where most taxa are rare and few are widespread (Figure 2.3A). Rare taxa are defined here as taxa restricted in occurrence ($\leq$10% of stations), not necessarily in abundance. A property of this distribution is that rare taxa comprise a larger portion of total taxa richness at the regional scale (all samples) with a ratio of rare to common taxa of 1.3:1 for macrofauna and 1.2:1 for megafauna while at the sample scale common taxa comprise the largest portion of total taxa richness with a ratio of common to rare taxa of 6:1 for macrofauna and 8:1 for megafauna. At all scales, rare taxa comprise a greater proportion of total macrofaunal taxa. However, this may simply be an artifact of differences in sample area. The larger sample area of trawls makes them more likely to collect patchy and sparsely distributed taxa. Previous studies have demonstrated a positive correlation between the presence of rare taxa and depth [Cochrane et al., 2012]; however, I found no such relationship when taking into account proportion (data not shown). Rather, I found the number of rare taxa was a function of the total taxa richness (macrofauna: Spearman's $\rho = 0.9$, $p < 0.001$; megafauna: Spearman's $\rho = 0.8$, $p < 0.001$), similar to the findings of Etter and Mullineaux [Etter and Mullineaux, 2001]. Additionally, though rarity can be dependent of phyla in terrestrial systems [Grenyer et al., 2006; Pitman et al., 2001], I was not able to reject the null hypothesis that rare taxa were distributed with equal proportion among phyla (data not shown).

A positive relationship exists between occupancy and average relative abundance (Figure 2.3B) for both faunal groups (macrofauna: Spearman's $\rho = 0.6$, $p < 0.001$; megafauna: Spearman's $\rho = 0.5$, $p < 0.001$). As expected, common taxa tended to be higher in local relative abundance than rare taxa which on average contributed less

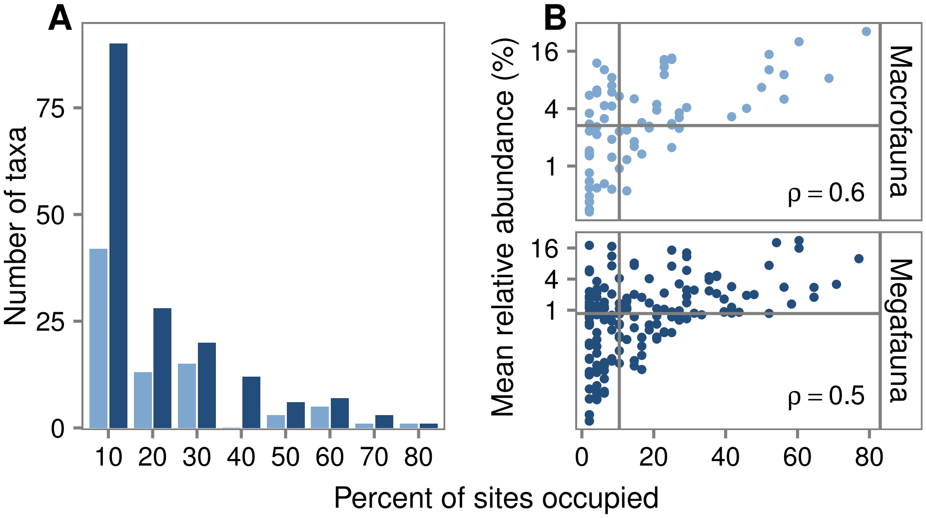


**Figure 2.3. Distribution of occurrence.** (A) Distribution of occurrence as percent of sites occupied (binned intervals starting with 1-10%) and (B) mean relative abundance (%) by percent of sites occupied. Relative abundance, a measure of local abundance, was averaged only across sites where taxa were present. Vertical grey line represents rarity cut-off at 10% and horizontal grey line denotes the median average relative abundance. Spearman's rank correlation coefficient denoted by $\rho$.

to total abundance per station. However, some rare taxa were relatively abundant at the few stations they were present (e.g. macrofauna: *Pseudosphyrapus serratus*, Thyasiridae, *Terebellides*; megafauna: *Apomatus similis*, Pectinidae, *Siphonodentalium*, *Ophiura*). These rare taxa, high in relative abundance, may be habitat specialists dominant in their niche but unable to persist in other habitats [Ellingsen et al., 2007; Verberk et al., 2010]. Or, their abundance may be the result of a localized disturbance or recruitment event. Alternatively, these taxa may be ***pseudo-rare***: taxa that appear rare because they are sampled on the fringe of their optimal depth range [Gaston et al., 1997; Rabinowitz, 1981] and thus were only present in larger numbers in samples from favourable depths (e.g. deep-sea taxa such as *Pseudosphyrapus serratus* and *Siphonodentalium*). Pseudo-rarity is the only testable hypothesis with the available data. To determine the likelihood that pseudo-rare taxa were present I examined whether highly abundant rare taxa (greater than the median) were more likely to be restricted to the shelf, slope or present on both than rare taxa that were low in abundance. Uniques were not considered in this analysis. I found a greater proportion of low in abundance rare taxa were restricted to the shelf and a greater proportion of highly abundant rare taxa were restricted to the slope (Figure 2.4), however the difference was only statistically significant for megafaunal taxa (macrofauna: $\chi^2 = 2.6, df = 2, p = 0.3$, megafauna: $\chi^2 = 17, df = 2, p = 0.0002$). This suggests that rare slope taxa are more likely to be pseudo-rare while rare shelf taxa may be restricted in occurrence due to ***sparsity*** (low population size).

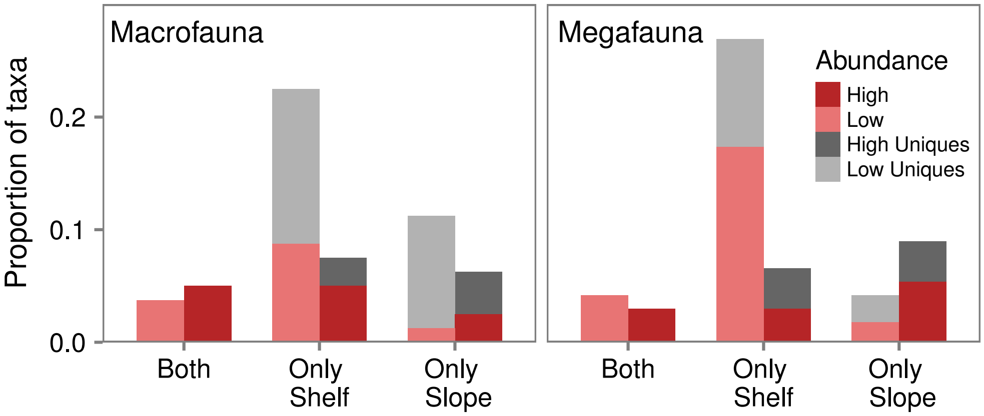


**Figure 2.4. Proportion of rare taxa unique to or shared between shelf and slope.** The proportion of low or highly abundant rare taxa sampled only on the shelf, slope or both localities. Rare taxa defined as taxa occurring at 10% of sites or less. Uniques (taxa that were sampled only at one site) are distinguished from other rare taxa. High and low relative abundance defined as greater or lower than the median.

**Table 2.3. Total abundance and richness by sample with corresponding year, depth and location of sampling.** Macrofaunal abundance (AB) and taxa richness (SN) per .125 $m^2$ and megafaunal abundance and taxa richness per 450 $m^2$.

| Site | Year | Depth (m) | Latitude | Longitude | Macro AB | Macro SN | Mega AB | Mega SN |
|---|---|---|---|---|---:|---:|---:|---:|
| 1 | 2009 | 60 | 70.48320 | -135.16805 | 15 | 5 | 116 | 28 |
| 2 | 2009 | 161 | 70.66263 | -135.61972 | 3 | 2 | 370 | 24 |
| 3 | 2009 | 397 | 70.70637 | -135.78607 | 23 | 7 | 59 | 13 |
| 4 | 2009 | 667 | 70.75538 | -136.03148 | 24 | 3 | 409 | 22 |
| 5 | 2009 | 795 | 70.91627 | -135.89958 | 4 | 2 | 132 | 20 |
| 6 | 2009 | 592 | 70.73975 | -135.90923 | 67 | 7 | 446 | 36 |
| 7 | 2009 | 420 | 70.79130 | -135.56227 | 120 | 6 | 531 | 20 |
| 8 | 2009 | 375 | 70.73538 | -135.56405 | 26 | 7 | 42 | 13 |
| 9 | 2009 | 63 | 70.63745 | -135.09220 | 15 | 5 | 482 | 32 |
| 10 | 2009 | 67 | 70.50420 | -135.67902 | 4 | 3 | 434 | 26 |
| 11 | 2009 | 93 | 70.57920 | -135.97723 | 4 | 4 | 564 | 15 |
| 12 | 2009 | 317 | 70.65033 | -135.94735 | 6 | 1 | 67 | 20 |
| 13 | 2009 | 788 | 70.61048 | -136.55805 | 127 | 11 | 141 | 21 |
| 14 | 2009 | 520 | 70.88410 | -135.39520 | 90 | 10 | 195 | 30 |
| 15 | 2009 | 648 | 71.00310 | -135.39415 | 9 | 4 | 1317 | 13 |
| 16 | 2009 | 320 | 71.00555 | -134.65338 | 16 | 4 | 111 | 33 |
| 17 | 2009 | 73 | 70.81595 | -134.52790 | 5 | 2 | 67 | 15 |
| 18 | 2009 | 80 | 70.89337 | -134.26478 | 16 | 9 | 3483 | 25 |
| 19 | 2010 | 74 | 70.73700 | -135.07650 | 60 | 17 | 553 | 28 |
| 20 | 2010 | 130 | 70.85870 | -135.00133 | 145 | 27 | 774 | 25 |
| 21 | 2010 | 379 | 70.95217 | -134.96133 | 206 | 19 | 88 | 16 |
| 22 | 2010 | 246 | 70.91833 | -134.85983 | 69 | 19 | 217 | 21 |
| 23 | 2010 | 442 | 71.02900 | -134.80017 | 207 | 17 | 310 | 19 |
| 24 | 2010 | 726 | 71.00000 | -135.61423 | 36 | 13 | 218 | 16 |
| 25 | 2010 | 846 | 71.08767 | -135.56733 | 32 | 8 | 302 | 16 |
| 26 | 2010 | 902 | 71.13467 | -135.50533 | 43 | 9 | 16 | 4 |
| 27 | 2010 | 932 | 71.15583 | -135.65133 | 26 | 6 | 18 | 5 |
| 28 | 2010 | 334 | 71.00900 | -134.66800 | 169 | 28 | 327 | 29 |
| 29 | 2010 | 89 | 70.86467 | -134.76567 | 78 | 20 | 140 | 18 |
| 30 | 2010 | 80 | 70.89498 | -134.25158 | 59 | 16 | 158 | 27 |
| 31 | 2010 | 72 | 70.82138 | -134.57720 | 151 | 11 | 312 | 16 |
| 32 | 2010 | 96 | 70.92433 | -134.43733 | 28 | 16 | 874 | 26 |
| 33 | 2010 | 260 | 70.98400 | -134.38333 | 88 | 16 | 240 | 16 |
| 34 | 2010 | 633 | 70.98633 | -135.37267 | 147 | 19 | 183 | 18 |
| 35 | 2010 | 731 | 71.11950 | -135.19533 | 43 | 12 | 207 | 13 |
| 36 | 2010 | 69 | 70.77917 | -134.38833 | 79 | 8 | 283 | 20 |
| 37 | 2011 | 74 | 70.82035 | -134.57960 | 174 | 8 | 892 | 42 |
| 38 | 2011 | 68 | 70.77883 | -134.39117 | 104 | 11 | 179 | 22 |
| 39 | 2011 | 72 | 70.73700 | -133.92000 | 183 | 16 | 1056 | 31 |
| 40 | 2011 | 68 | 70.72055 | -133.64408 | 238 | 29 | 6440 | 51 |
| 41 | 2011 | 52 | 70.67100 | -133.35433 | 303 | 32 | 74032 | 76 |
| 42 | 2011 | 49 | 70.73123 | -132.87798 | 290 | 29 | 50377 | 68 |
| 43 | 2011 | 59 | 70.79732 | -132.68438 | 277 | 18 | 1179 | 31 |
| 44 | 2011 | 53 | 70.66267 | -134.77533 | 118 | 26 | 47002 | 60 |
| 45 | 2011 | 60 | 70.85583 | -132.37800 | 163 | 21 | 27785 | 51 |
| 46 | 2011 | 54 | 70.78033 | -132.14750 | 283 | 16 | 49563 | 55 |
| 47 | 2011 | 54 | 70.57565 | -133.22817 | 302 | 16 | 11329 | 44 |
| 48 | 2011 | 67 | 71.01700 | -132.69000 | 77 | 20 | 168095 | 72 |

### 2.3.2 Patterns in abundance and taxa richness

Total abundance on the Beaufort shelf decreased with depth (Figure 2.5), confirming Conlan et al.'s [2008] result. Megafauna showed a stronger negative correlation between abundance and depth (megafauna: Spearman's $\rho = -0.6$, $p < 0.001$; macrofauna: Spearman's $\rho = -0.4$, $p < 0.05$) and had a larger range of abundance values on the shelf than slope (F-test: $p < 0.05$). Yet, no decrease in abundance with depth was observed when the depth range was restricted to the slope between 100 to 1,000 m (macrofauna: Spearman's $\rho = -0.1$, $p > 0.1$; megafauna: Spearman's $\rho = -0.2$, $p > 0.1$). Differences between macro- and megafauna in abundance and taxa richness ($\alpha$ diversity) across the depth gradient are illustrated by grouping shelf and slope stations (Figure 2.6). Macrofaunal shelf stations showed slightly greater mean abundance and mean richness compared to slope stations, but this difference was not statistically significant (Wilcoxon test: $p > 0.05$). Megafauna were on average significantly more abundant and taxa rich (Wilcoxon test: $p < 0.001$) at shelf stations than at slope stations. Renaud et al. [2007] showed similar declines in larger fauna with depth on the Beaufort Shelf. Declines in megafaunal abundance while macrofauna remain relatively constant across the depth range ($50 - 1,000$ m) supports the notion of increased prevalence of smaller body sizes with depth [Clough et al., 2005; Lampitt et al., 1986; Rex et al., 2006; Thiel, 1975; Thistle, 2001]. The most parsimonious explanation for the observed shift from larger to smaller size classes with depth is the diminishing supply of organic material [Forest et al., 2013] as larger fauna require more energy to survive and reproduce [Rex et al., 2006; Rex and Etter, 2010]. No difference in taxonomic distinctness was found between shelf and slope for macro- or megafauna (Wilcoxon test: $p > 0.05$, data not shown).

Shelf–slope differences are partially confounded by temporal and spatial variability introduced through the multiple year sampling scheme, 2009 to 2011. Over this time period, the spatial extent of sea-ice decreased, sampling was carried out further into the ice-free season and farther to the east (Figure 2.2). To illustrate the potential effects of this temporally associated variability in macro- and megafaunal abundance and taxa richness, shelf and slope stations were grouped by sampling year (Figure 2.6). Variation in macrofaunal abundance and richness was explained by both depth and year with year explaining more of the total variance (Table 2.4). Macrofaunal mean abundance and richness increased each year regardless of position on shelf or slope. Variation in megafaunal abundance and richness was also explained by both depth and year, however, depth explained more of the total variance (Table 2.4). I

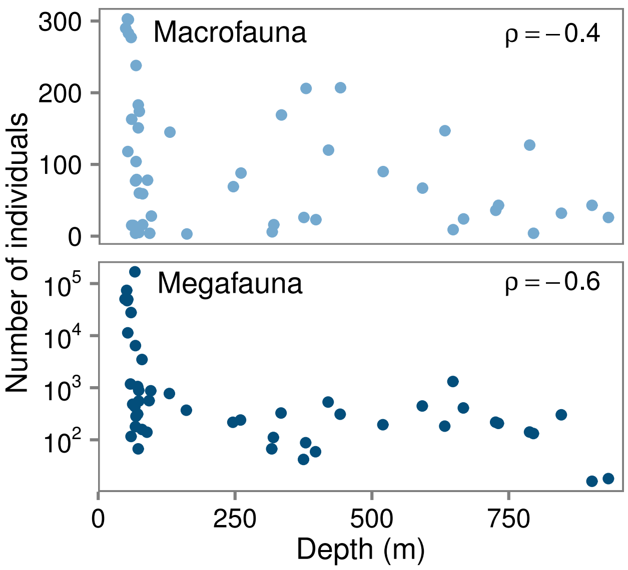


**Figure 2.5. Relationships of total macro- and megafaunal abundance with depth.** Abundance in number of individuals per sample. Sample area of macrofauna: $0.125\text{m}^2$ and megafauna: $450\text{m}^2$. Spearman's rank correlation coefficient denoted by $\rho$.

found a significant interaction between depth and year which indicates the effect of year on megafaunal abundance and richness was not consistent across shelf and slope stations. This interaction may be an artifact of inconsistencies in trawl sample areas (discussion below) in combination with the lack of slope stations in 2011.

Spatial location is likely to influence the distribution of abundance and taxa richness as a high degree of benthic spatial ***heterogeneity*** exists on Arctic shelves [Link et al., 2011; Tamelander et al., 2006]. In addition, seasonal and temporal variability of Arctic benthos across multi-year sampling programs have been found to be insignificant relative to spatial variability (V. Roy and P. Archambault, unpublished data). Therefore, the variance explained by sampling year in this analysis (Table 2.4) is more likely a result of location. As sampling occurred farther to the east with each subsequent year, greater macrofaunal abundance and richness may be a consequence of the proximity to nutrient rich upwelled water from Cape Bathurst [Conlan et al., 2013].

If the location of sampling was indeed affecting abundance and richness patterns, why were megafaunal abundance and richness similar in 2009 and 2010 (Figure 2.6)? Abundance and richness values from 2009 trawls may be inflated as a consequence of

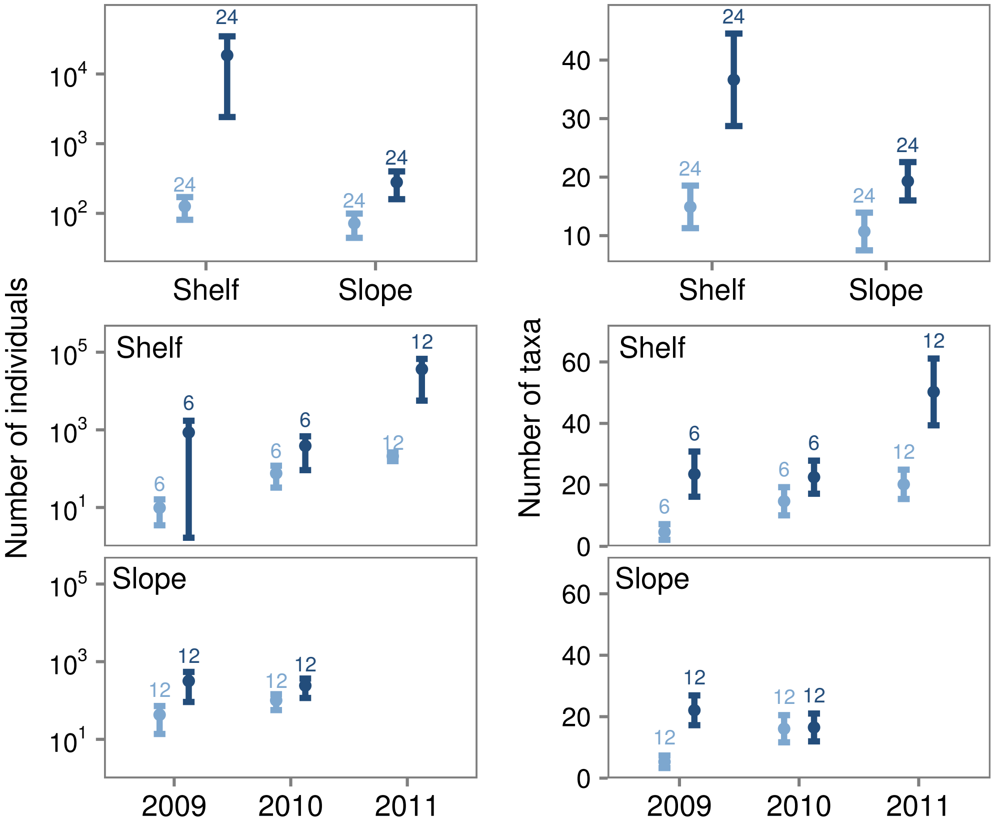


**Figure 2.6. Comparison of macrofaunal (light blue) and megafaunal (dark blue) abundance and taxa richness between shelf and slope stations and sampling years.** Mean total abundance (left panel) and mean taxa richness (right panel). Stations grouped by shelf and slope (top panel) and stations grouped by year on shelf or slope (bottom panels). Bars represent 95% confidence intervals. Sample size (N) is denoted by number on bar. Sample area of macrofauna: $0.125\text{m}^2$ and megafauna: $450\text{m}^2$.

the larger sample size and smaller mesh sieve utilized that year (described in Section 2.2.1). A larger sample size collects more individuals and a sieve with a smaller mesh retains more juveniles and small bodied species, thereby inflating the total number of individuals and taxa present in the sample [Hammerstrom et al., 2012]. Taxa richness can be further affected by sample size differences because it cannot be normalized to a standard sample size as richness does not vary linearly with sample area [Hammerstrom et al., 2012]. Normalizing total abundance by a standard sample size (utilized in this study) controls for the increase in individuals from the larger sample but not for the smaller mesh. In addition, normalizing counts to a standard sample size can

**Table 2.4. Analysis of variance of macro- and megafaunal abundance and taxa richness with year and depth.**

| | **Response** | **Source** | **MS** | **F** | ***p*** |
|---|---|---|---|---|---|
| **Macrofauna** | Abundance | Depth | 2.7 | 3.6 | $0.06^{*}$ |
| | | Year | 48 | 64 | $< 0.001^{***}$ |
| | | Depth x Year | 0.3 | 0.4 | 0.5 |
| | Richness | Depth | 210 | 6.6 | $0.01^{**}$ |
| | | Year | 1600 | 50 | $< 0.001^{***}$ |
| | | Depth x Year | 45 | 1.4 | 0.2 |
| **Megafauna** | Abundance | Depth | 65 | 27 | $< 0.001^{***}$ |
| | | Year | 35 | 15 | $< 0.001^{***}$ |
| | | Depth x Year | 17 | 7.2 | $0.01^{**}$ |
| | Richness | Depth | 3600 | 28 | $< 0.001^{***}$ |
| | | Year | 1900 | 15 | $< 0.001^{***}$ |
| | | Depth x Year | 1800 | 14 | $< 0.001^{***}$ |

Categorical variables: depth = shelf/slope and year = 2009/2010/2011. Abundance was log transformed to normalize residuals. Significance codes:
$< 0.001 =^{***}, 0.01 =^{**}, 0.1 =^{*}$.

be problematic when comparing taxa richness between samples. Normalization reduces the taxa-per-individual ratio for smaller sample sizes while increasing the ratio for larger sample sizes, in this case artificially bringing the 2009 and 2010 taxa-per-individual ratios and thus rarefaction curves closer together (Figure 2.7B). However, non-normalized individual-based rarefaction curves demonstrate that taxa richness in 2010 was actually higher than in 2009 when measured at comparable abundances (Figure 2.7), which agrees with my observation that richness increased with each sampling year as stations moved eastward along the shelf and slope.

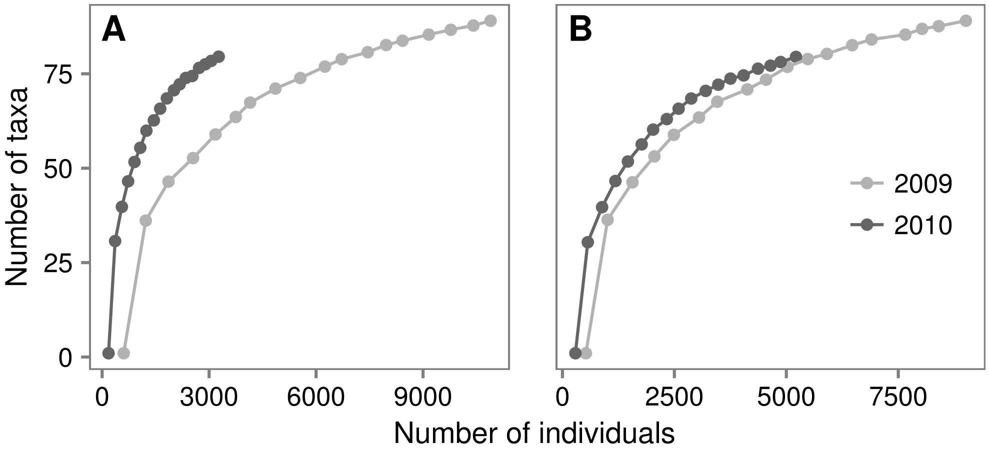


**Figure 2.7. Individual-based rarefaction curves for 2009 and 2010 megafaunal datasets.** (A) non-normalized counts and (B) counts normalized to the average trawl area. Curves represent the average of 900 resampling permutations.

### 2.3.3 Patterns in $\beta$ diversity

Macro- and megafauna differed in $\beta$ diversity patterns. Sixty-five percent of macrofaunal and only 46% of megafaunal taxa occurred on both the shelf and slope, not including uniques. Macrofauna shelf and slope taxa were similar in overlap to that previously observed at the pan-Arctic level (61%) [Bluhm et al., 2011; Piepenburg et al., 2011]. A significant negative correlation between community similarity and depth was only detected in the megafauna (macrofauna: Spearman's $\rho = -0.2$, $p_{adj} > 0.05$; megafauna: Spearman's $\rho = -0.7$, $p_{adj} < 0.001$, Figure 2.8), corroborating previous work that established megafauna had a faster rate of species replacement than macrofauna [Rex, 1977]. However, both species replacement and nestedness can drive $\beta$ diversity patterns [Baselga, 2010]. Nestedness, in contrast to species replacement, is caused by species loss without a gain of new species along a gradient [Gaston, 2000]. As described in the previous section, total abundance and taxa richness of the megafauna decreased more rapidly with depth. Considering that $\beta$ diversity is not independent of $\alpha$ diversity [Brault et al., 2013], megafaunal $\beta$ diversity could be purely driven by decreased $\alpha$ diversity with depth. Additionally, decreasing richness with depth could indicate that megafaunal $\beta$ diversity is more likely driven by faunal loss (nestedness) than faunal replacement.

To distinguish between replacement and nestedness drivers of $\beta$ diversity, sta-

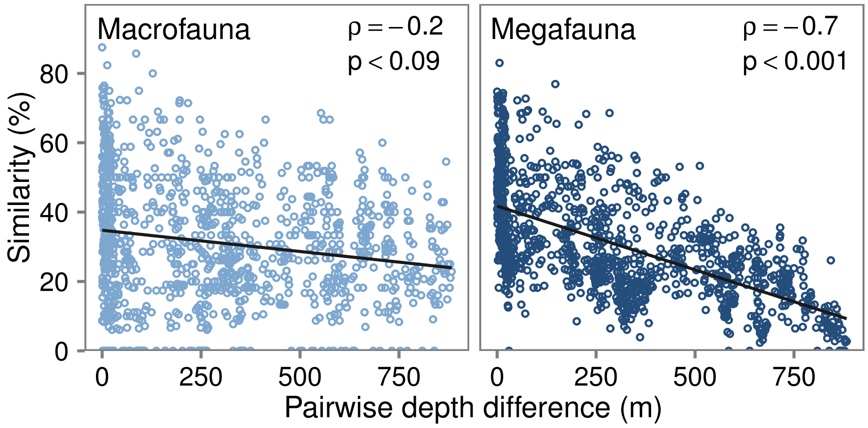


**Figure 2.8.** **$\beta$ diversity across the depth gradient.** $\beta$ diversity as a comparison of Bray-Curtis similarity between each pairwise depth difference. Spearman's rank correlation coefficient and significance (p-value) denoted by $\rho$ and p, respectively.

tions were clustered based on similarity in composition and relative abundance of taxa (Figure 2.9). Mean average silhouette widths (ASW), a measure of between versus within cluster variability at a scale from 0 to 1, were low for macrofauna (0.19) and megafauna (0.20) clusters. Low ASW is an indication that clusters represent loose groupings rather than distinct, structured assemblages [Kaufman and Rousseeuw, 2005], which fits the established view that faunal change is continuous across the depth gradient lacking distinct zones [Rex and Etter, 2010; Wei et al., 2010]. The spatial distribution of clusters (Figure 2.10) depicts the bathymetric gradient as the major structuring factor in station clustering. In agreement with the $\beta$ diversity results, megafaunal clusters were more clearly distributed according to depth. Megafaunal groupings on Arctic shelves have previously been noted to follow depth gradients [Piepenburg and Schmid, 1996b; Starmans et al., 1999], likely shaped by food availability [Graf, 1992; Soltwedel et al., 2009; Wei et al., 2010]. Sediment properties were not likely a major cause of the faunal clustering as sediment grain size on the Beaufort Shelf does not vary largely with depth [Renaud et al., 2007], but more so along the east-west axis [Jerosch, 2012]. Different water masses found on the shelf and slope are also unlikely to be shaping the bathymetric trends. Shelf water of mainly Pacific origin and slope water of mainly of Atlantic origin (>200m) have relatively little variation in salinity (32 to 34‰), temperature (-1.5 to 0.5°C)

[Carmack et al., 2004; Macdonald et al., 1989] and dissolved oxygen (6 to 7 ml $L^{-1}$) [Conlan et al., 2008; Link et al., 2013a].

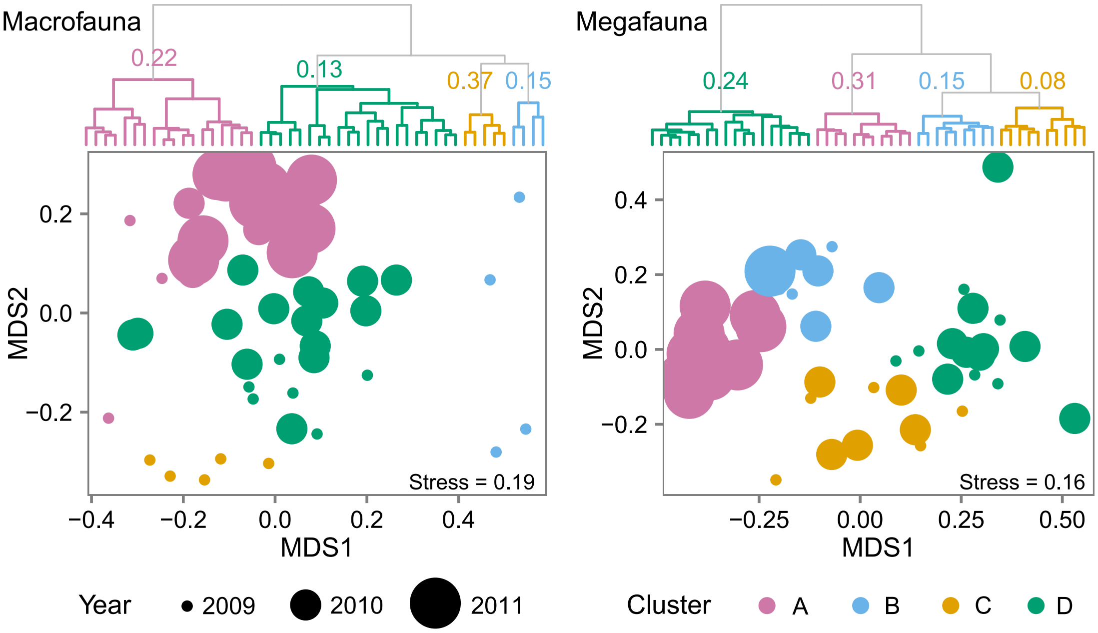


**Figure 2.9. Dendrogram and nMDS ordination of station similarities.** Hierarchical, Ward's method cluster dendrogram (top) and nMDS ordination highlighting clusters and sampling year (bottom) both derived from Bray-Curtis dissimilarity of macrofaunal and megafaunal abundance matrices. Average silhouette widths (scale $0-1$) noted atop each cluster. Coloured circles in ordination represent macro- and megafaunal clusters defined in dendrograms. Circle sizes correspond to sample years indicated on right.

The superposition of clusters and sampling year on macro- and megafaunal stations in ordination space illustrates the potential contribution of sampling year and location (as stations were farther to the east each year of sampling) to station similarities (Figure 2.9). Qualitatively, macrofaunal clusters were more likely shaped by sampling year and/or location than megafaunal clusters as stations that clustered together were more likely to be from the same year in the macrofauna than the megafauna. That observation is supported by my finding that macrofauna have a stronger negative correlation between community similarity and year ($\beta$ diversity across sampling years) than megafauna (macrofauna: Spearman's $\rho = -0.3$, $p_{adj} = 0.02$; megafauna: Spearman's $\rho = -0.2$, $p_{adj} = 0.05$).

Changes in the dominant macro- and megafaunal taxa between clusters reveal compositional differences (Figure 2.11A) that provide evidence of faunal replacement as a main driver of $\beta$ diversity. Dominant taxa were defined as the top four taxa in terms of average relative abundance for each cluster. The dominant taxa typically represented over 50% of the cumulative average relative abundance per cluster (macrofauna: A = 62%, B = 83%, C = 94%, D = 48%; megafauna: A = 63%, B = 52%, C = 52%, D = 57%). Across all clusters, the macrofauna were principally comprised of polychaetes. Macrofaunal cluster A (shelf cluster) was characterized by cirratulid and nephtyid polychaetes and leuconid cumaceans. Macrofaunal cluster D (slope cluster) was characterized by maldanid polychaetes, Sipuncula, thyasirid bivalves and tanaid *Pseudosphyrapus serratus*. Clusters B and C, also found on the slope but compositionally distinguishable from D cluster macrofauna, may be influenced by smaller scale processes and forces than depth gradients. Cluster B was distinct in having higher relative abundances of polychaetes Capitellidae, *Terebellides* sp. and Phyllodocidae compared to other slope clusters. Cluster C was distinguished by its extremely high relative abundance of maldanid polychaetes (60% of total abundance on average).

Across all clusters, the megafauna was principally comprised of echinoderms, typical of Arctic shelves [Piepenburg, 2005]. Megafauna shelf cluster A, containing only 2011 stations, was characterized by the ophiuroid *Ophiocten* sp. as well as polychaete *Cistenides* sp., amphipod *Ampelisca* sp. and bivalve *Nucula* sp.; shelf cluster B, located west of cluster A and Kugmallit Valley, was characterized by isopod *Saduria sabini*, gastropod *Tachyrhynchus* sp. and holothurian *Myriotrochus* sp. Megafauna shelf break cluster C was characterized by asteroid *Pontaster tenuispinus*, astartid bivalves, ophiuroid *Ophiocten* sp. and polynoid polychaetes. Megafauna slope cluster D was characterized by ophiurid *Ophiopleura* sp., asteroid *Pontaster tenuispinus* and scaphopod *Siphonodentalium* sp. Some megafauna taxa dominant in shelf clusters were not present on the slope and vice versa (Figure 2.11B) providing evidence that slope taxa are not just a nested subset of shelf taxa.

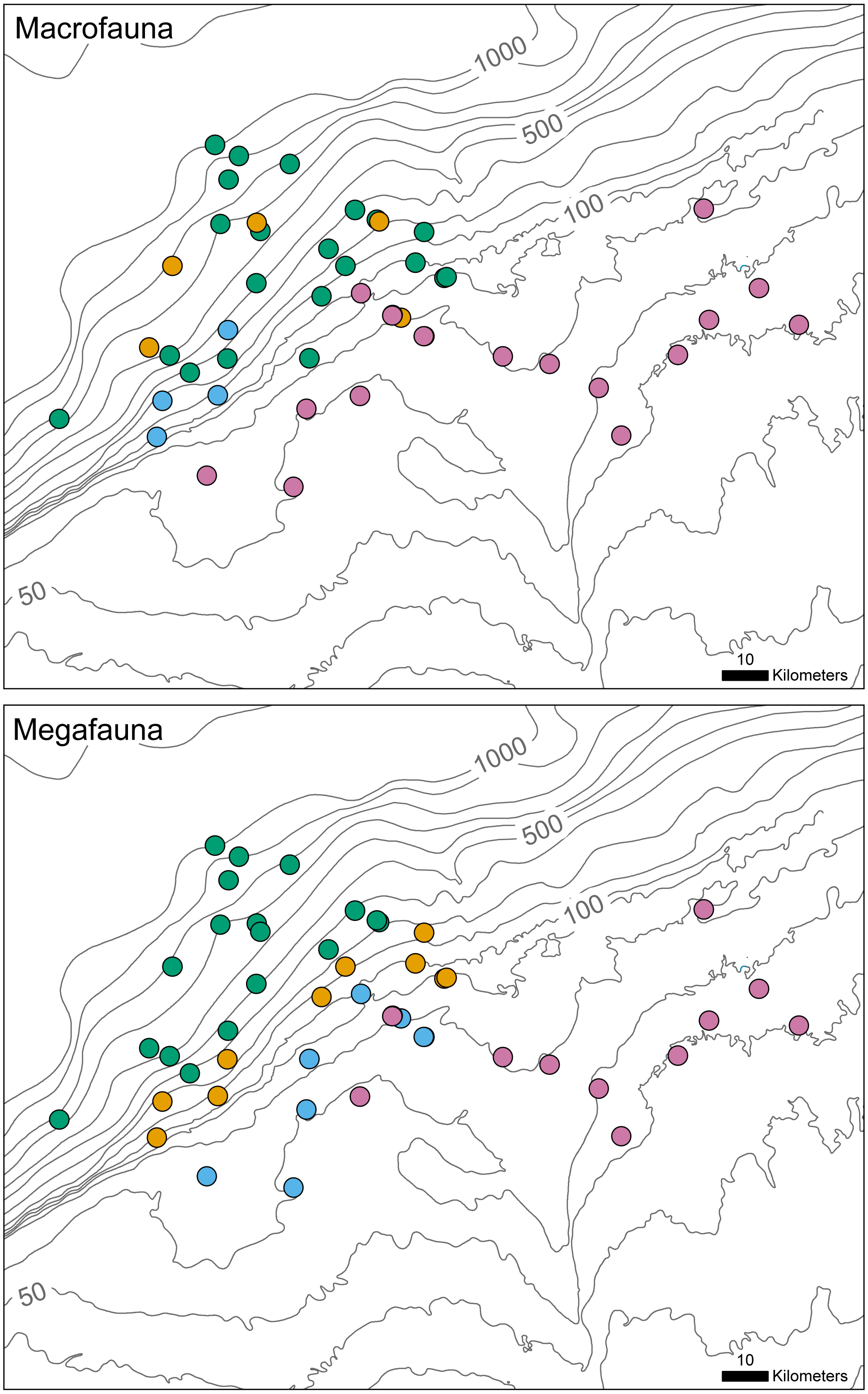


**Figure 2.10. Map of Beaufort sampling region with georeferenced clusters.** Colours represent macro- and megafaunal clusters defined in dendrograms (Figure 2.9).

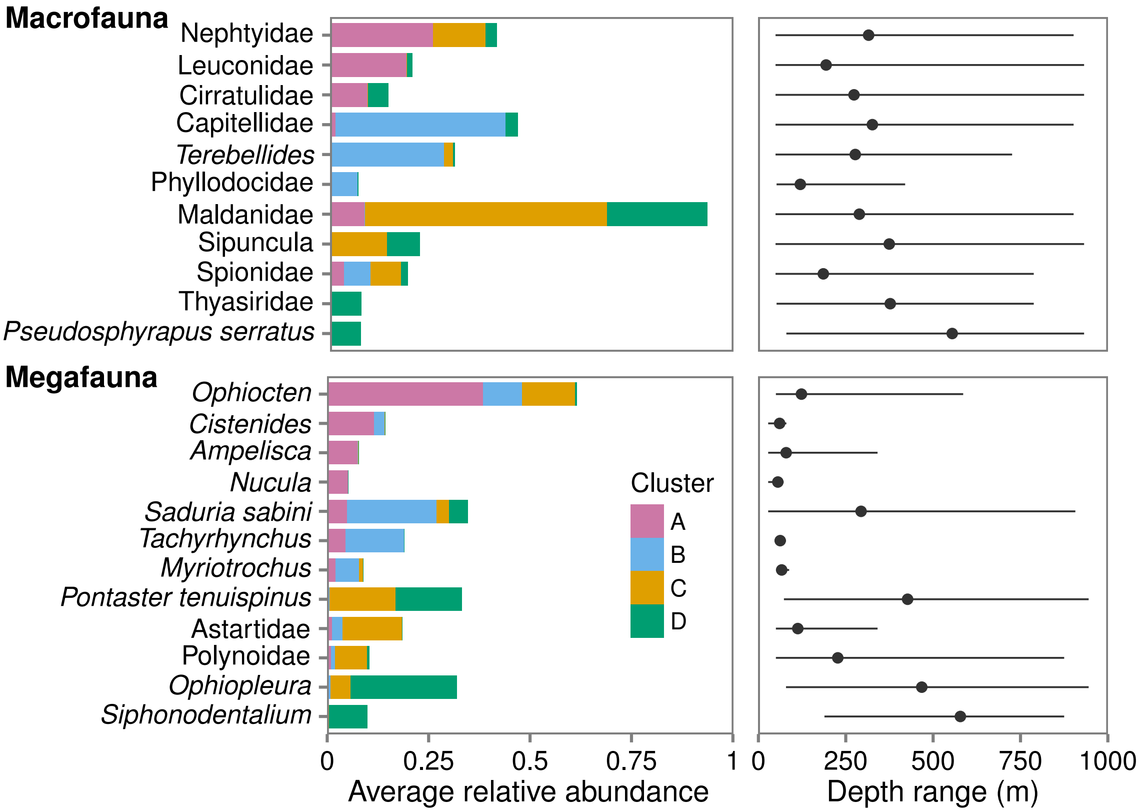


**Figure 2.11. Relative abundance and depth ranges of dominant taxa.** Average relative abundance of dominant taxa by cluster (left). Dominant taxa ordered by their contribution to average relative abundance in clusters A, B, C and D, are highlighted by cluster to illustrate the relative contribution of taxa to each cluster. Colours represent faunal clusters defined in dendrograms (Figure 2.9). Depth range of corresponding taxa (right); grey circles denote mean depth of samples where taxa were present.

## 2.4 Conclusions

The Canadian Beaufort shelf and slope host a diverse assemblage of macro- and megafauna, 247 taxa—many (30%) of which were classified at the family taxonomic rank or higher, indicating species richness may be much greater. At a regional scale, rare taxa constituted the majority of taxa represented while faunal numbers in individual samples were dominated by taxa common throughout the region. I found that the proportion of rare taxa was independent of depth and phylum, instead rarity was simply a function of the total taxa richness—the more taxa present in a sample the greater the number of rare taxa. I hypothesize that rare taxa are driven by different processes on the shelf (sparsity) and slope (pseudo-rarity), since rare taxa on the slope tended to contribute more to local faunal numbers compared to those on the shelf.

The results indicate that macro- and megafauna have divergent patterns of abundance and $\alpha$ and $\beta$ diversity on the Beaufort shelf and slope. Macrofauna showed greater change in $\beta$ diversity with year and/or location compared to the megafauna, although this relationship was weak for both faunal groups. Megafauna show greater change in abundance, taxa richness and $\beta$ diversity with depth compared to the macrofauna, conceivably owing to a greater cost of the declining food supply for larger bodied organisms. I infer that megafaunal $\beta$ diversity is not merely driven by $\alpha$ diversity, since shifts in dominant taxa are evident between shelf and slope clusters. Furthermore, I deduce that faunal replacement is a greater driver of megafaunal $\beta$ diversity than nestedness as some dominant megafauna in shelf clusters are not present on the slope and vice versa, suggesting that slope taxa are indeed differentiated from shelf taxa and not solely a nested subset of shelf taxa.

The effect of temporal variability on the benthos is less clear. Sampling year explained a portion of both macro- and megafaunal variability in abundance and richness, however, year effects were highly confounded by location on the shelf and the timing of sampling with respect to sea-ice conditions (with sampling occurring later into the summer season with each year). I speculate that the major source of this temporally associated variability was spatial heterogeneity; however, it may be a combination of several factors such as a longer growing season, temporally variable (spring vs. summer) recruitment events or faster growth with increased primary productivity input to the benthos under reduced ice conditions. The latter would support the notion that the benthic standing stock will increase as sea-ice retreats in the Arctic. Under the alternative scenario, the loss of sinking ice-algae and a shift toward open-water primary productivity leads to a decreased food supply for shelf benthos. If this scenario holds true on the Beaufort shelf, my observations suggest that shelf fauna could become more similar to the present day slope fauna. As slope megafauna are differentiated from shelf fauna and smaller body size organisms (macrofauna) contribute more to total abundance on the slope, this would likely have cascading effects on higher trophic levels [Grebmeier, 2012; Grebmeier et al., 2006a].

# Chapter 3

# Spatial patterns of macro- and megafauna on the Canadian Beaufort shelf and slope

## 3.1 Introduction

Global climate change has led to a longer Arctic ice-free season [Comiso et al., 2008; Stroeve et al., 2007], causing direct and indirect effects on the marine ecosystem [Wassmann et al., 2011]. In the Beaufort Sea, the current economic and political setting along with increased the accessibility of offshore hydrocarbon resources as a result of climate change have led to further northern development in the oil and gas sector [LTLC Consulting Inc and Salmo Consulting Inc, 2013]. In preparation for development, baseline data collection (Beaufort Regional Environmental Assessment, BREA) and a framework for management (Large Ocean Management Area [Cobb et al., 2008]) are in progress to ensure, as mandated under Canada's Oceans Act, that biodiversity and ecosystem functioning are maintained. Benthic studies are an important component in assessing impacts related to oil and gas development [Jørgensen et al., 2011] as benthic fauna are key indicators of ecosystem health [Bluhm et al., 2005; Gray and Elliott, 2009]. Shifts in benthic diversity and community structure can impact benthic ecosystem function [Danovaro et al., 2008; Piot et al., 2014; Solan et al., 2004], which on the Canadian Beaufort Shelf may have wide ecosystem impacts as benthos are tightly coupled to the pelagic environment [Renaud et al., 2007].

Currently, our knowledge of the distribution of benthic organisms on the Beaufort

Shelf is derived mainly from studies of macrofauna, organisms greater than 0.25 to 0.5 mm [Snelgrove, 1998] sampled using grabs or box corers. Beaufort Shelf macrofauna exhibit high $\beta$ diversity compared to other regions in the Canadian Arctic [Cusson et al., 2007] indicating a high degree of macrofaunal replacement occurs across the region. Baseline studies have demonstrated that macrofauna are similar in community composition along the shelf at similar depths [Conlan et al., 2008; Wacasey, 1975], which would suggest that the majority of faunal replacement occurs across the depth gradient. However, macrofauna do vary along the shelf; increased abundance and biomass are detectable near the Cape Bathurst (eastern shelf) and Mackenzie Trough (western shelf) upwelling regions [Conlan et al., 2008; Conlan et al., 2013]. Data utilized here came from a systematic box core and trawl sampling program designed to permit comparison of along and cross shelf variability in benthic faunal distribution. Quantifying the degree of along-shelf versus depth related variability will be important for siting future long-term monitoring stations.

In addition to macrofauna, a baseline understanding of the distribution of megafauna, the larger and mostly epifaunal benthic organisms sampled using trawls or video, will be important to future monitoring programs. The larger sample area covered by trawl and video surveys allows for a more accurate representation of the more widely dispersed megafaunal organisms [Eleftheriou and McIntyre, 2005]. Macrofauna and megafauna can also differ in relative mobility, bioturbation potential, life histories and feeding strategies [Jørgensen et al., 2011; Lampitt et al., 1986; Ólafsson, 2003]. These functional differences suggest that macro- and megafaunal taxa may vary in their relative sensitivity to environmental change [Jørgensen et al., 2011]. While several studies have noted similar spatial patterns of macro- and megafauna [Karakassis et al., 2006; Parry et al., 2003; Reiss et al., 2010], others have shown disparate spatial patterns across an environmental gradient [Duineveld et al., 2007; Macdonald et al., 2010]. The latter aligns with a major finding from Chapter 2, that megafaunal replacement was greater than macrofaunal replacement across the depth gradient leading to differentiated shelf and slope megafaunal assemblages, at least in the spatially limited area sampled on the central Beaufort shelf and slope. Identifying the nature of depth related faunal replacement helps us to understand how present day organic matter inputs may be structuring the different benthic components [Nephin et al., 2014]. Here, I extend the Chapter 2 comparison of these benthic size classes over a larger area to further examine their potentially divergent or incongruent responses across environmental gradients.

The congruence of macro- and megafauna on the Beaufort shelf could have important implications for the design of monitoring programs. If macro- and megafauna exhibit incongruent spatial patterns along the shelf from east to west, in addition to across the depth gradient (shown in Chapter 2), benthic surveys which sample only one of these benthic components could overlook a significant fraction of the total spatial variability present and related causes. For example, the more mobile epibenthic megafauna tend to be the first to exploit food sources [Premke et al., 2006; Smith, 1985] such that their distribution and abundance are more sensitive to changes in organic matter inputs. Trawl and video surveys, not the box corers or grabs typically used for assessing benthic impacts, would therefore be the preferred sampling gear to monitor future benthic responses to changes in food supply.

Here, I described cross and along shelf macro- and megafaunal distribution patterns to improve our understanding of how environmental forcing (e.g. organic matter inputs) is structuring the different components of the benthos. I examined 1) abundance, biomass and body size trends, 2) $\alpha$ and $\beta$ diversity, and 3) changes in community composition and function of macro- and megafaunal benthos, with the aim to inform future benthic monitoring programs in the region.

## 3.2 Methods

### 3.2.1 Study area and sampling

This study analysed faunal data from the western to central shelf, an area of approximately 25,000 km$^2$ (Figure 3.1). The shelf break is located approximately at the 100 m isobath (see Section 2.2.1). The Canadian Beaufort Shelf is characterized by extreme seasonality. Most of the Beaufort Shelf is covered by ice approximately 70% of the year [Forest et al., 2007], although the length of the relatively short ice free season is highly variable interannually [Galley et al., 2008; O'Brien et al., 2006] (see Figure 2.2). In 2012, when the benthic samples were collected, spring ice coverage on the shelf was approximately 30% lower than the historical median [Canadian Ice Service, 2013], indicating a relative long ice-free season occurred that year.

Benthic box cores and trawl samples were collected by the 2012 BREA (Beaufort Regional Environmental Assessment) Marine Fishing Program in August onboard the F/V Frosti. The main samples were collected along three transects (Transboundary (T), Gary (G) and Kugmallit (K)) with five box corer stations at 30, 75, 200, 500

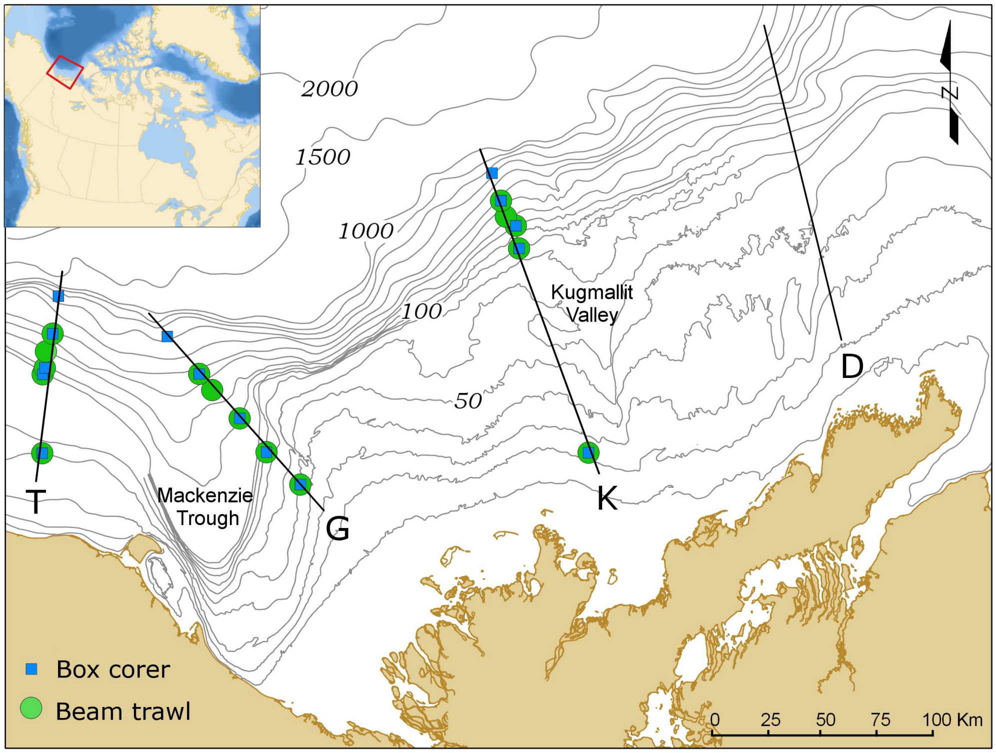


**Figure 3.1. Box corer and beam trawl sampling stations on the Beaufort shelf and slope.** Box corer and trawl samples from transect D are not shown here because they were not utilized in the main analyses. Isobath contours provided by the Geological Survey of Canada Atlantic.

and 750 m isobaths and five trawl stations at 30, 75, 200, 350 and 500 m isobaths (Figure 3.1). One box core and one trawl sample were taken from each station with the exception of the 350 m stations (only trawl samples) and 750 m stations (only box core samples). A fourth transect (Dalhousie (D)) on the eastern shelf, was only used qualitatively to compare mean abundances of taxa between transects. Transect D had box and trawl samples from corresponding depths, but many transect D trawl samples were collected using a larger trawl (Otter trawl) with a longer bottom time such that faunal counts were not quantitatively comparable to counts from the other transects.

Macrofauna were sampled using a 0.25 m$^2$ USNEL box corer from which half of the sediment surface (0.125 m$^2$) down to the clay layer was collected and sieved through a 0.5 mm mesh for faunal analysis. Collected fauna were preserved in buffered formalin for later taxonomic identification using standardized taxonomic protocols, at the Benthic Ecology Laboratory of the Institut des sciences de la mer (UQAR-ISMER) in Rimouski (Québec), Canada. Megafauna were sampled using a beam trawl, 3 m in width and 2-3 m in height with mesh size of 5 mm. Towing speed was held at 0.5 m/s with a bottom time of 20 minutes, making the average sample area 1,836 $m^2$. After collection, samples were sieved using a 2 mm mesh, and faunal abundance, biomass and taxonomy were recorded shipboard. Some taxa were preserved in buffered formalin or frozen for later analysis, using the same protocols as the macrofauna, if the identification was uncertain.

### 3.2.2 Data management

The benthic datasets needed some modifications prior to analyses. Taxonomic names were validated through the WoRMS (www.marinespecies.org) Taxon Match tool. Many specimens in both datasets were not identified to the species level; these comprised 65% of box core records and 40% of trawl records. The majority of these higher-order identifications were the result of broken or damaged specimens and the lack of taxonomic focus or expertise within certain phyla (e.g. Nemertea). To remove the affect of any variability in taxonomic identification between transects, taxa were grouped to the family taxonomic rank. Specimens that were consistently identified to higher than family taxonomic ranks also remained in the database. Grouping taxa sampled by box corers and trawls to the family rank facilitates comparison between these groups by removing any variability in the resolution of taxonomic identification. In addition, previous studies have clearly demonstrated that grouping taxa to higher-order ranks should not impact ability to detect benthic spatial patterns [Cusson et al., 2007; Piepenburg et al., 2011; Włodarska-Kowalczuk and Kędra, 2007].

In order to describe the potentially distinct spatial patterns of different benthic components, macro- and megafauna needed to be separated in the data. Seventy taxa were collected in both box core and trawl samples. Taxa were identified as macrofauna or megafauna based on the frequency at which they were sampled by each gear type, assuming that megafauna were collected more frequently and effectively by the trawl than by the box corer and vice versa. Thirty-five taxa (38%) were thus removed from box core dataset and 35 taxa (23%) were removed from trawl dataset (Tables 3.1 and 3.2). In addition, any meiofauna were removed from the datasets for most analyses as they would not be quantitatively sampled using the employed methodology.

**Table 3.1. Shared taxa which were classed as megafauna and removed from the macrofauna dataset.** Data from transects T, G & K only.

| **Phylum** | **Class** | **Family** | **Box Occurrence** | **Box (#/.125 m$^2$)** | **Trawl Occurrence** | **Trawl (#/1,836 m$^2$)** |
|---|---|---|---:|---:|---:|---:|
| Annelida | Polychaeta | Flabelligeridae | 3 | 3 | 5 | 142 |
| | | Nereididae | 1 | 1 | 5 | 55 |
| | | Onuphidae | 5 | 15 | 8 | 798 |
| | | Polynoidae | 6 | 16 | 15 | 941 |
| | | Sabellidae | 8 | 27 | 12 | 271 |
| | | Sphaerodoridae | 2 | 5 | 6 | 41 |
| | | Terebellidae | 6 | 13 | 8 | 93 |
| Arthropoda | Malacostraca | Ampeliscidae | 7 | 16 | 12 | 810 |
| | | Atylidae | 1 | 1 | 4 | 1400 |
| | | Caprellidae | 1 | 1 | 2 | 328 |
| | | Chaetiliidae | 3 | 3 | 8 | 187 |
| | | Crangonidae | 1 | 1 | 14 | 411 |
| | | Diastylidae | 10 | 109 | 13 | 4001 |
| | | Gnathiidae | 5 | 7 | 8 | 396 |
| | | Hyperiidae | 1 | 1 | 13 | 276 |
| | | Leptanthuridae | 4 | 8 | 8 | 121 |
| | | Lysianassidae | 6 | 11 | 14 | 163 |
| | | Munnopsidae | 3 | 7 | 12 | 823 |
| | | Oedicerotidae | 9 | 19 | 14 | 1221 |
| | | Uristidae | 4 | 5 | 15 | 1283 |
| Cephalorhyncha | Priapulida | Priapulidae | 2 | 3 | 5 | 27 |
| Mollusca | Bivalvia | Arcidae | 6 | 21 | 7 | 23316 |
| | | Astartidae | 4 | 20 | 7 | 47 |
| | | Cuspidariidae | 3 | 3 | 6 | 125 |
| | | Mytilidae | 7 | 27 | 10 | 173 |
| | | Nuculanidae | 3 | 5 | 6 | 390 |
| | | Nuculidae | 1 | 2 | 3 | 166 |
| | | Tellinidae | 4 | 21 | 5 | 179 |
| | | Thraciidae | 1 | 2 | 4 | 40 |
| | Gastropoda | Cylichnidae | 3 | 16 | 9 | 204 |
| | | Diaphanidae | 1 | 1 | 3 | 21 |
| | Gastropoda | Philinidae | 3 | 4 | 8 | 417 |
| | Solenogastres | Solenogastres | 1 | 2 | 5 | 150 |
| Nemertea | | | 8 | 37 | 10 | 186 |
| Sipuncula | Sipunculidea | Phascolionidae | 2 | 5 | 10 | 1299 |

**Table 3.2. Shared taxa which were classed as macrofauna and removed from the megafauna dataset.** Data from transects T, G & K only.

| **Phylum** | **Class** | **Family** | **Box Occurrence** | **Box (#/.125 $m^2$)** | **Trawl Occurrence** | **Trawl (#/1,836 $m^2$)** |
|---|---|---|---|---|---|---|
| Annelida | Polychaeta | Ampharetidae | 11 | 83 | 10 | 1937 |
| | | Capitellidae | 13 | 107 | 1 | 16 |
| | | Chaetopteridae | 3 | 14 | 2 | 20 |
| | | Cirratulidae | 13 | 254 | 2 | 52 |
| | | Dorvilleidae | 3 | 6 | 1 | 1 |
| | | Lumbrineridae | 12 | 125 | 7 | 94 |
| | | Maldanidae | 14 | 559 | 13 | 10221 |
| | | Nephtyidae | 15 | 179 | 12 | 178 |
| | | Opheliidae | 9 | 37 | 1 | 8 |
| | | Oweniidae | 5 | 29 | 2 | 20 |
| | | Pectinariidae | 2 | 2 | 2 | 4 |
| | | Pholoidae | 8 | 88 | 2 | 12 |
| | | Phyllodocidae | 4 | 7 | 4 | 41 |
| | | Serpulidae | 1 | 3 | 1 | 10 |
| | | Spionidae | 10 | 100 | 7 | 282 |
| | | Sternaspidae | 1 | 10 | 1 | 48 |
| | | Syllidae | 9 | 30 | 3 | 18 |
| | | Trichobranchidae | 8 | 34 | 6 | 59 |
| Arthropoda | Malacostraca | Ischyroceridae | 1 | 1 | 1 | 1 |
| | | Leuconidae | 10 | 58 | 4 | 520 |
| | | Nebaliidae | 1 | 1 | 1 | 4 |
| | | Pardaliscidae | 4 | 10 | 1 | 64 |
| | | Photidae | 3 | 17 | 1 | 8 |
| | | Pontoporeiidae | 5 | 17 | 3 | 237 |
| | | Sphyrapidae | 4 | 19 | 3 | 9 |
| Hemichordata | Enteropneusta | Enteropneusta | 2 | 2 | 1 | 2 |
| Mollusca | Bivalvia | Limidae | 2 | 2 | 1 | 2 |
| | | Thyasiridae | 8 | 210 | 8 | 1472 |
| | | Veneridae | 1 | 18 | 1 | 20 |
| | | Yoldiidae | 13 | 106 | 13 | 1089 |
| | Caudofoveata | Chaetodermatidae | 4 | 5 | 2 | 33 |
| | Gastropoda | Naticidae | 2 | 3 | 2 | 5 |
| | | Rissoidae | 4 | 14 | 1 | 16 |
| | | Gadilidae | 5 | 6 | 5 | 30 |
| Sipuncula | Sipunculidea | Sipunculidae | 9 | 82 | 2 | 534 |

### 3.2.3 Analyses

All data analyses were completed in the R environment for statistical computing (`www.r-project.org`) with aid from the community ecology and graphics packages vegan, cluster and ggplot. Maps were created using QGIS software (`http://qgis.osgeo.org`).

Total abundance (number of individuals), biomass (grams blotted wet weight) and diversity ($\boldsymbol{ES}_{50}$ the expected number of taxa in 50 individuals [Hurlbert, 1971]) were calculated per sample (0.125 $m^2$ for macrofauna and 1,836 $m^2$ for megafauna). An estimate of average body size was calculated from the ratio of biomass to abundance (ww g/ individual). Stations were grouped by depth (shelf ($< 100$ m) or slope) and transect to compare along versus cross shelf abundance, biomass and diversity trends using an analysis of variance. Spearman's rank correlation ($\rho$) was used to test for correlations between macro- and megafauna in abundance and biomass. Occurrence, the number of sites at which a taxon was recorded, and mean relative abundance, the average contribution of a taxon to the total number of individuals in each sample where the taxa were present, were calculated to explore differences in the spatial distribution of macro- and megafaunal taxa.

Multivariate analyses were completed using Bray-Curtis (BC) dissimilarity as a measure of station dissimilarity based on the relative abundance and composition of taxa among stations. Fourth-root transformation was applied to reduce the influence of highly abundant taxa [Warwick and Clarke, 2001]. Spearman's rank correlation ($\rho$) was used to measure $\beta$ diversity (BC similarity) across depth and longitude gradients and the relationship between macro- and megafaunal BC similarity. Spatial patterns in community composition were explored through Ward's method of hierarchical clustering and nonmetric multidimensional scaling (nMDS) ordination. Average silhouette width, a measure of average dissimilarity of stations within versus between clusters [Rousseeuw, 1987], was used to validate and select for clusters. Contingency table $\chi^2$ test was used to determine whether clusters were formed independent of depth and transect. Average relative abundance of taxa was used to define dominant taxa (top 6 taxa) representative of clusters.

## 3.3 Results

### 3.3.1 Total abundance, biomass and diversity

One hundred and seventy-one taxa (56 macrofauna and 115 megafauna), at the family taxonomic rank or higher, were collected from 15 sites within 3 transects along the shelf (see Table 3.3 for a summary of abundance, biomass and richness by sample). Few along or cross shelf trends were observed in total abundance, biomass and diversity (Figure 3.2). No significant differences were observed across depth and between transects in macrofaunal abundance and biomass and megafaunal biomass. Total megafaunal abundance showed marginally significant differences across depth and between transects (Table 3.4). Megafaunal abundance was higher on the shelf than slope and higher at western transects T and G compared to central transect K near the Kugmallit Valley. Although no significant differences were found in macrofaunal abundance and biomass between transects, they were both lowest at transect K similar to the megafauna. However, no correlation was detected between macro- and megafauna in local abundance (Spearman's $\rho = 0.2$, p = 0.5) or local biomass (Spearman's $\rho = 0.2$, p = 0.4) using only samples from matching depths. Macro- and megafauna also had contrasting diversity ($ES_{50}$) trends (Table 3.4). Macrofauna diversity was significantly different between transects with the lowest number of expected taxa at transect K where mean total abundance was also the lowest. Megafaunal diversity was significantly different between shelf and slope with the expected number of taxa greater on the slope where total abundance was the lowest.

**Table 3.3. Total abundance, biomass and richness by sample with depth and location of sampling.**

| | Transect | Site | Depth (m) | Latitude | Longitude | Abundance | Biomass (ww g) | Richness |
|---|---|---|---|---|---|---|---|---|
| Macrofauna | | | | | | | | |
| | G | 1 | 47 | 69.87448 | -137.26307 | 113 | 1.13 | 19 |
| | | 2 | 76 | 70.00031 | -137.67919 | 122 | 1.48 | 23 |
| | | 3 | 199 | 70.13233 | -138.01815 | 173 | 0.73 | 26 |
| | | 5 | 501 | 70.30433 | -138.53233 | 486 | 1.66 | 26 |
| | | 6 | 741 | 70.44800 | -138.94550 | 105 | 0.44 | 17 |
| | K | 1 | 20 | 70.01499 | -133.84718 | 3 | 0.03 | 2 |
| | | 2 | 75 | 70.84880 | -134.66050 | 93 | 0.60 | 13 |
| | | 3 | 200 | 70.94112 | -134.69930 | 73 | 0.25 | 18 |
| | | 5 | 500 | 71.04304 | -134.88396 | 213 | 2.08 | 15 |
| | | 6 | 758 | 71.15533 | -134.99573 | 28 | 0.35 | 10 |
| | T | 1 | 42 | 69.93617 | -140.33550 | 564 | 8.77 | 35 |
| | | 2 | 74 | 70.25583 | -140.41350 | 116 | 0.81 | 19 |
| | | 3 | 200 | 70.28233 | -140.39467 | 121 | 0.79 | 23 |
| | | 5 | 500 | 70.42383 | -140.33700 | 308 | 2.29 | 25 |
| | | 6 | 750 | 70.57800 | -140.30700 | 39 | 0.23 | 14 |
| Megafauna | | | | | | | | |
| | G | 1 | 47 | 69.87448 | -137.26307 | 1351 | 852.44 | 44 |
| | | 2 | 76 | 70.00031 | -137.67919 | 62592 | 24744.78 | 48 |
| | | 3 | 199 | 70.13233 | -138.01815 | 902 | 1067.27 | 45 |
| | | 4 | 348 | 70.24167 | -138.36517 | 5288 | 6147.91 | 38 |
| | | 5 | 501 | 70.30433 | -138.53233 | 369 | 370.47 | 27 |
| | K | 1 | 20 | 70.01499 | -133.84718 | 959 | 342.19 | 23 |
| | | 2 | 75 | 70.84880 | -134.66050 | 845 | 2222.08 | 37 |
| | | 3 | 200 | 70.94112 | -134.69930 | 739 | 797.46 | 41 |
| | | 4 | 350 | 70.97826 | -134.82275 | 463 | 460.29 | 32 |
| | | 5 | 500 | 71.04304 | -134.88396 | 1172 | 564.74 | 38 |
| | T | 1 | 42 | 69.93617 | -140.33550 | 7304 | 2953.38 | 57 |
| | | 2 | 74 | 70.25583 | -140.41350 | 21416 | 5683.87 | 47 |
| | | 3 | 200 | 70.28233 | -140.39467 | 4322 | 2045.38 | 47 |
| | | 4 | 350 | 70.34967 | -140.39917 | 960 | 3223.16 | 35 |
| | | 5 | 500 | 70.42383 | -140.33700 | 2006 | 1113.77 | 35 |

Macrofaunal abundance, biomass and taxa richness per 0.125 $m^2$ and megafaunal abundance, biomass and taxa richness per 1,836 $m^2$.

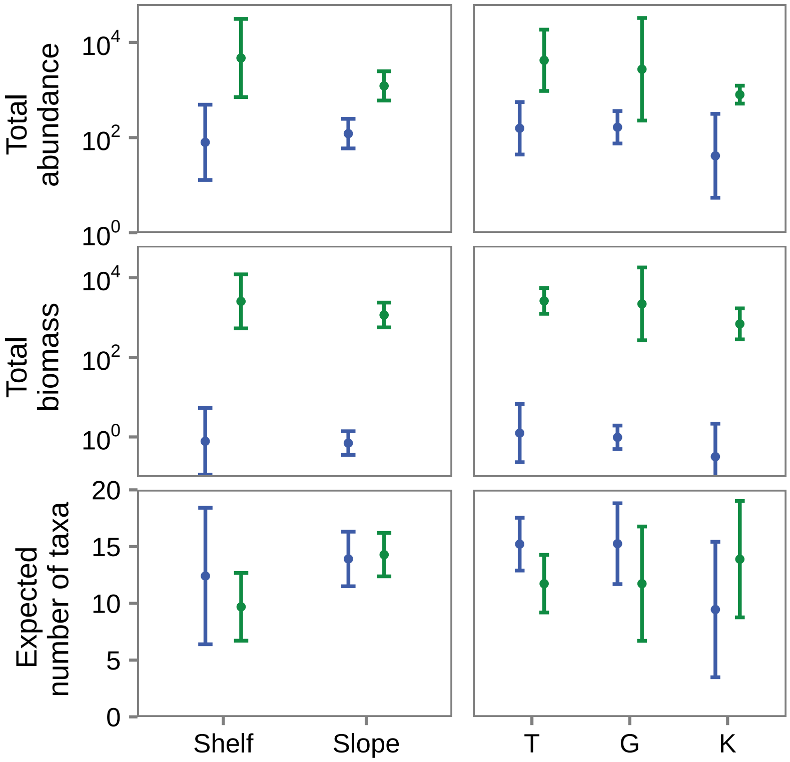


**Figure 3.2. Total abundance, biomass and diversity across depth and transects.** Macrofaunal (blue) and megafaunal (green) total abundance in number of individuals per sample, total biomass in grams per sample and expected number of taxa in 50 individuals. Bars represent 95% confidence intervals. Average sample area of macrofauna: 0.125 m$^2$ and megafauna: 1836 m$^2$. Transects are ordered west (T) to east (K).

**Table 3.4. Analysis of variance of macro- and megafaunal abundance, biomass and diversity ($ES_{50}$) with depth and transect.**

| | Response | Source | MS | F | *p* |
|---|---|---|---|---|---|
| **Macrofauna** | Abundance | Depth | 0.1 | 0.9 | 0.4 |
| | | Transect | 0.3 | 1.9 | 0.2 |
| | Biomass | Depth | 0.2 | 0.2 | 0.7 |
| | | Transect | 1.3 | 1.7 | 0.4 |
| | $ES_{50}$ | Depth | 8.1 | 0.7 | 0.4 |
| | | Transect | 56 | 4.6 | $0.03^{**}$ |
| **Megafauna** | Abundance | Depth | 0.1 | 4.6 | $0.06^{*}$ |
| | | Transect | 0.06 | 2.9 | $0.09^{*}$ |
| | Biomass | Depth | 0.03 | 1.7 | 0.2 |
| | | Transect | 0.05 | 2.5 | 0.1 |
| | $ES_{50}$ | Depth | 76 | 11.2 | $0.006^{***}$ |
| | | Transect | 7.7 | 1.1 | 0.4 |

Categorical variables: depth = shelf/slope and transect = T/G/K. Abundance and biomass were log transformed to normalize residuals. No interaction terms were significant in the model. Significance codes represent p-values $< 0.01 =^{***}$, $< 0.05 =^{**}$ and $< 0.1 =^{*}$.

### 3.3.2 Abundance, biomass and body size of faunal classes

For the macrofauna, 72% of all individuals sampled were from the class Polychaeta. Megafaunal individuals were more evenly spread among faunal classes with 49% from Ophiuroidea, 27% from Bivalvia and 17% from Malacostraca (crustaceans including amphipods, decapods, cumaceans, mysids, tanaids and isopods). Trends in macro- and megafaunal abundance, biomass and body size (biomass/individual) with depth varied between faunal classes. For the macrofauna, few depth trends were evident. However, malacostracans decreased in abundance and biomass at the deepest station (750 m) and sipunculids tended to increase in abundance and biomass with increasing depth (Figures 3.3 and 3.4). The megafauna had more pronounced depth related trends. Megafaunal bivalves, ophiuroids and holothurians had a strong peak in abundance and biomass at 75 m depth with particularly sharp declines in bivalve and holothurian abundance and biomass on the slope (Figures 3.3 and 3.4). Macrofaunal molluscs, bivalves and gastropods, showed a decrease in average body size with depth while the average body size of malacostracans, polychaetes and sipunculids remained relatively stable with depth (Figure 3.5). The average body size of megafaunal bivalves also decreased with depth as well as asteroidean body size. The average body size of asteroideans was 25±30 ww g/individual on the shelf and 5±6 ww g/individual on the slope. In contrast, the average body size of megafaunal malacostracans and ophiuroids tended to increase with depth peaking at 350 m (Figure 3.5). For both the macro- and megafaunal classes there was no indication of a shift in abundance, biomass or body size between transects (west to east) T, G and K (Figures 3.3, 3.4 and 3.5, right panel).

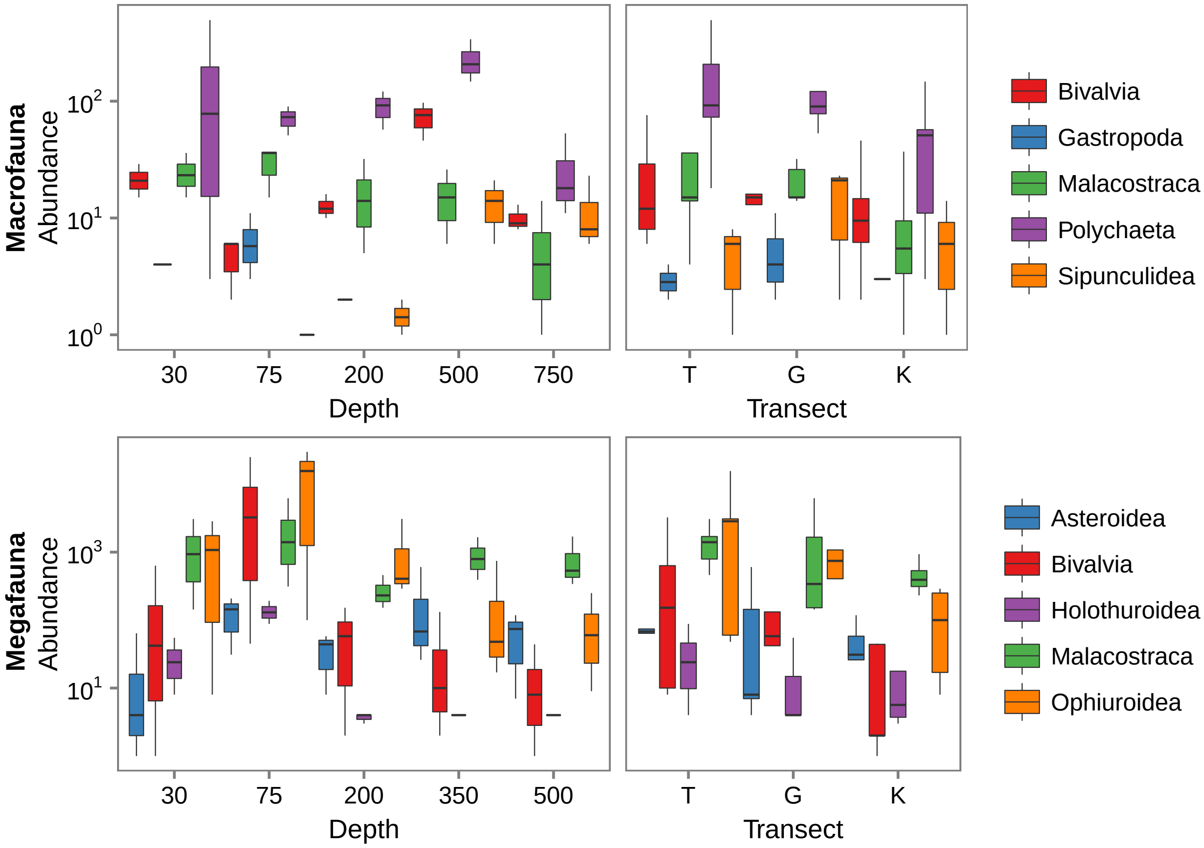


**Figure 3.3. Abundance of dominant classes across transects and depths.** Abundance (individuals/sample) is shown on a log scale. Macrofaunal sample area = 0.125 $m^2$, megafaunal sample area = 1,836 $m^2$. Displaying top 5 most abundant classes only.

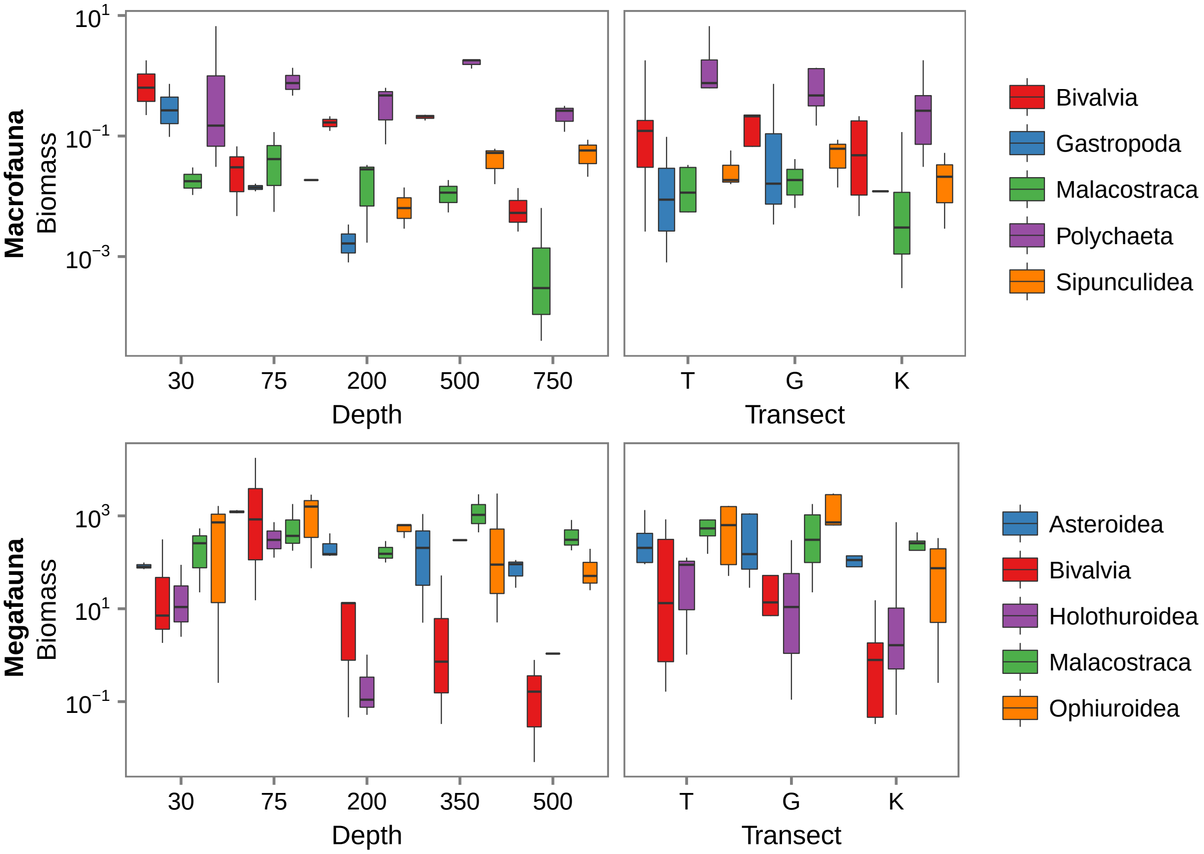


**Figure 3.4. Biomass of dominant classes across transects and depths.** Biomass (ww g/sample) is shown on a log scale. Macrofaunal sample area = 0.125 $m^2$, megafaunal sample area = 1,836 $m^2$. Displaying top 5 most abundant classes only.

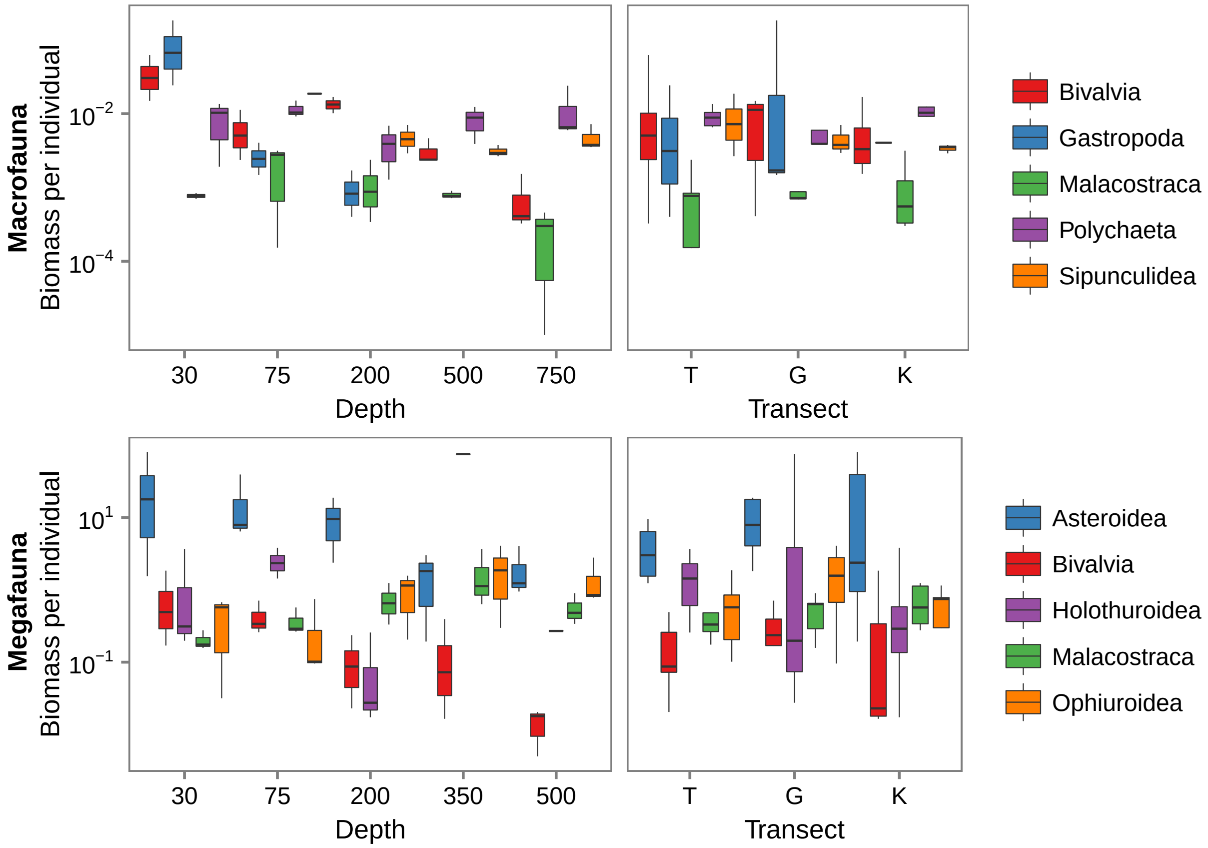


**Figure 3.5. Average body size of dominant classes across transects and depths.** Average body size (biomass (ww g) / individual) is shown on a log scale. Displaying top 5 most abundant classes only.

### 3.3.3 Spatial distribution of taxa

Macro- and megafauna taxa had similar patterns of spatial overlap. Fifty percent of macrofaunal and 57% of megafaunal taxa overlapped between shelf (30 – 75 m) and slope (macrofaunal range 200 – 750 m, megafaunal range 200 – 500 m). A similar degree of overlap also occurred between transects with 43% of macrofaunal and 48% of megafaunal taxa present in samples from all three transects (Figure 3.6). Conversely, the percent of taxa sampled on only a single transect was also relatively high, 30% of macrofaunal and 33% of megafaunal taxa, the majority of which were from transect T. As expected from their close proximity, transects T and G shared more taxa than either transect did with transect K. Interestingly, taxa present in samples from a single transect only were not likely to be present in multiple samples along that transect. Therefore, single transect taxa can be described as relatively rare taxa, restricted in occurrence and low in relative abundance compared to taxa present in samples from multiple transects.

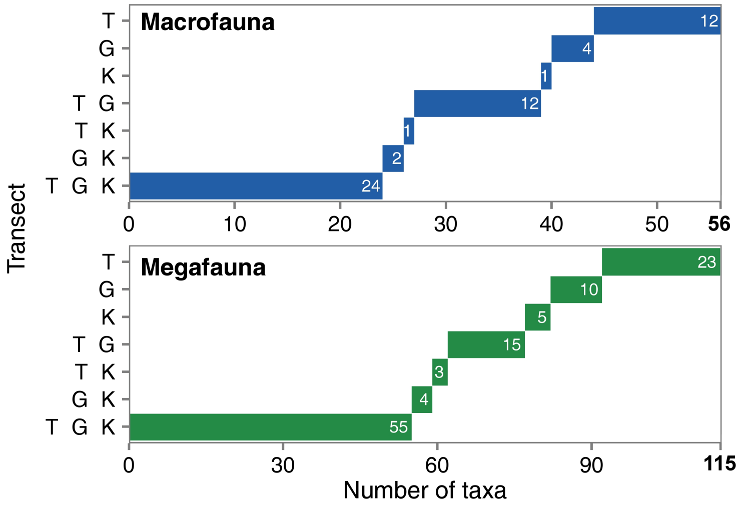


**Figure 3.6. Number of taxa unique to or shared between transects.** Numbers on bars represent the number of taxa unique to or shared between the corresponding transect(s) represented on the y-axis. The sum of all numbered bars represents the total number of macro- or megafauna taxa present.

### 3.3.4 $\beta$ diversity trends

Macro- and megafauna had similar $\beta$ diversity trends. A negative correlation between Bray-Curtis similarity and pairwise depth difference was observed for both macro-and megafauna (Figure 3.7). These correlations were marginally significant when corrected for multiple comparisons (macrofauna: $\rho$ = -0.4, $p_{adj}$ = 0.06, megafauna: $\rho$ = -0.4, $p_{adj}$ = 0.08). However, these correlation coefficients do not indicate that macro- and megafaunal $\beta$ diversity were identical across the depth gradient as box core and trawl samples were not collected across the same depth range, macrofaunal stations extended 250 m deeper on the slope than the megafaunal stations. In contrast, no along shelf (east to west) $\beta$ diversity trends were observed as neither faunal group had a significant correlation between Bray-Curtis similarity and pairwise difference in longitude (macrofauna: $\rho$ = -0.2, $p_{adj}$ = 0.2, megafauna: $\rho \approx 0$, $p_{adj}$ = 0.4). A direct comparison between macro- and megafaunal similarity, using only stations with corresponding box core and trawl samples, revealed a lack of congruence in their spatial structure (Figure 3.8). No significant correlation was observed between macro- and megafaunal Bray-Curtis similarity ($\rho$ = 0.4, $p_{adj}$ = 0.1) indicating they do not follow similar spatial patterns along the shelf and slope, or that the number of samples was too few to detect the significance of a rather weak relationship. In either case, at this scale and frequency of sampling, high similarity in megafaunal composition between two stations does not suggest that macrofaunal similarity will be high as well. Regionally, median macrofaunal $\beta$ diversity (49%) was marginally greater than median megafaunal $\beta$ diversity (45%) (Wilcoxon test: $p$ = 0.06, Figure 3.8). Therefore, across the same spatial extent and depth range megafauna had marginally greater degree of faunal replacement compared to the macrofauna.

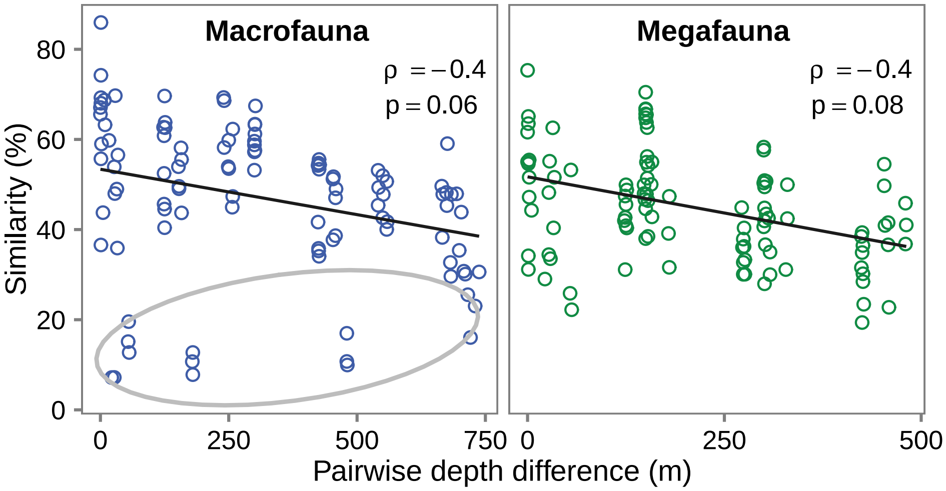


**Figure 3.7.** **$\beta$ diversity across the depth gradient.** $\beta$ diversity as a measure of Bray-Curtis similarity between each pairwise depth difference. Spearman's rank correlation coefficient and significance (p-value) denoted by $\rho$ and p, respectively. The 14 points within the grey ellipse are pairwise comparisons of the station at 30 m on transect K with all other stations.

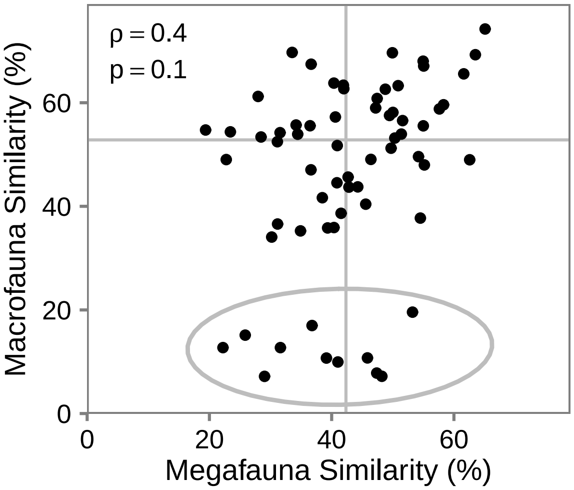


**Figure 3.8.** **Correlation between macro- and megafaunal Bray-Curtis similarities.** Pairwise comparison between all stations where both box core and trawl sampling occurred. Grey lines represent median similarities. Spearman's rank correlation coefficient and significance (p-value) denoted by $\rho$ and p, respectively. Points within the grey ellipse are macrofaunal pairwise comparisons of the station at 30 m on transect K with all other stations.

### 3.3.5 Spatial patterns in community composition

Macro- and megafaunal stations clustered into 3 main groupings (Figure 3.9). Average silhouette widths (ASW) which compare between- versus within-cluster variability, were low for macrofauna (0.19) and megafauna (0.23). This indicates clusters are loose groupings more likely representative of gradual faunal replacement than discrete assemblages. The sole macrofaunal station (transect K at 30 m, grey circle in Figure 3.9) which did not cluster with other stations had an extremely low number of macrofaunal individuals. The lack of macrofaunal individuals may be caused by a localized habitat disturbance such as an ice scour, pockmark, gas seep or mud volcano, all common features on the Beaufort Shelf.

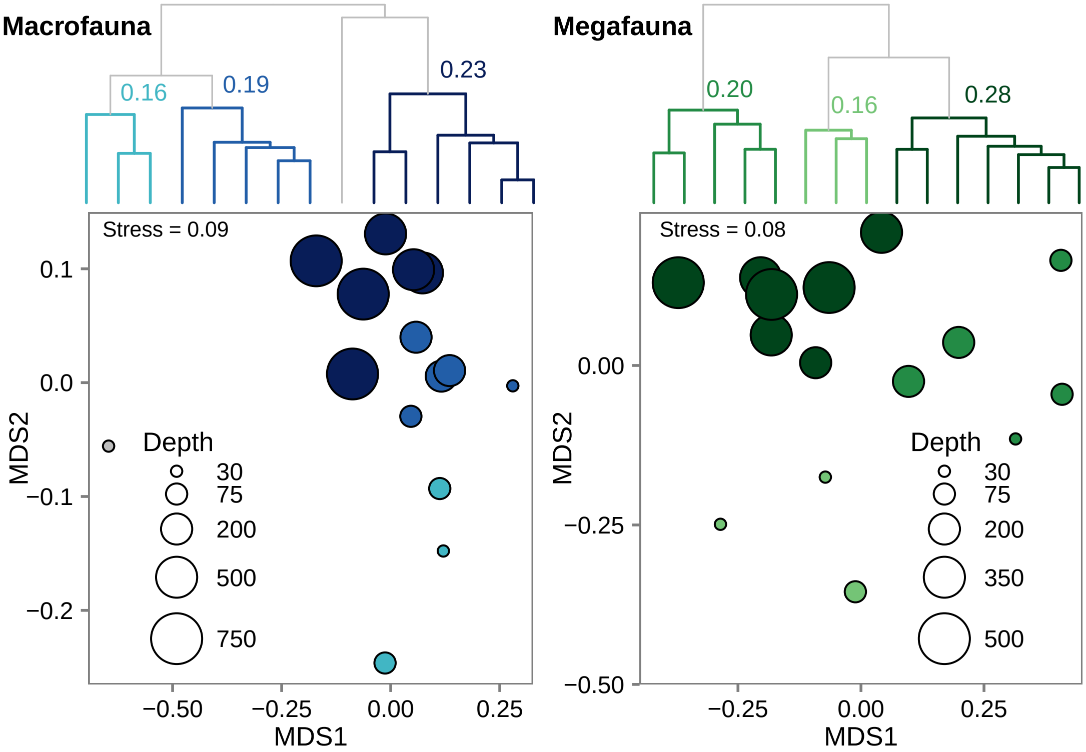


**Figure 3.9. Dendrogram and ordination depiction of station clusters.** Hierarchical, Ward's method, clustering of sstations derived from Bray-Curtis dissimilarity. Cluster dendrogram (top), nMDS ordination highlighted by cluster defined in dendrograms and depth (bottom).

Stations appear to cluster along the depth gradient in ordination space (Figure 3.9), which affirms the observed $\beta$ diversity trends. Thus, clusters can be described relative to the depth of their stations: shelf (light shade), shelf break (medium shade) and slope (dark shade) clusters (Figure 3.9). Contingency table analysis confirmed that stations clustered independently of transects (macrofauna: $\chi^2 = 5.6$, p = 0.5, megafauna: $\chi^2 = 5.1$, p = 0.3) and dependently of depth (macrofauna: $\chi^2 = 24$, p = 0.004, megafauna: $\chi^2 = 16$, p = 0.04). Interestingly, for both macro- and megafaunal clusters, ASW were higher for slope than shelf clusters which indicates that slope stations were more tightly clustered. Thus, average similarity in community composition was greater among slope than among shelf station.

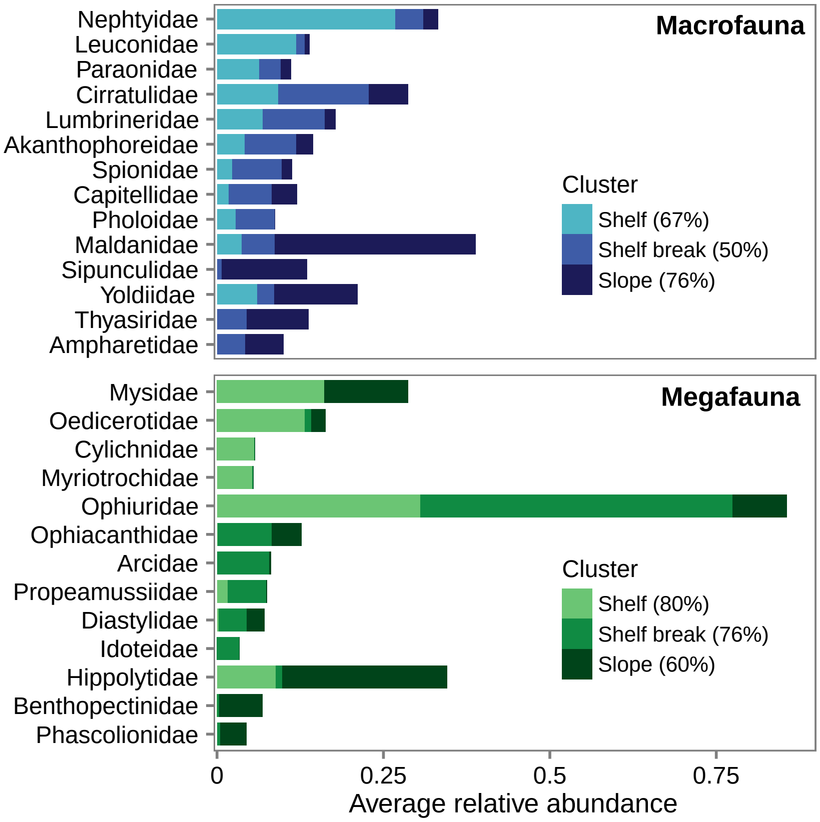


**Figure 3.10. Relative abundance of dominant taxa.** Average relative abundance of dominant taxa by cluster. Dominant taxa ordered by their contribution to average relative abundance in clusters. Percents denote the contribution of dominant taxa (6 most relatively abundant) to the total abundance/stations within clusters. Colours represent faunal clusters defined in dendrograms (Figure 3.9).

The macro- and megafaunal taxa which comprised the majority of individuals at a station varied between clusters and thus across the depth gradient (Figure 3.10). Although the macrofauna were sampled across a larger depth range than the megafauna, dominant megafauna taxa were not more likely to be present at stations in all 3 cluster than dominant macrofauna taxa. Macrofaunal clusters were characterized by nephtyid and paraonid polychaetes and leuconid cumaceans on the shelf; cirratulid, lumbrinerid, spionid, capitellid and pholoid polychaetes and akanthophoreid tanaids on the shelf break; and maldanid and ampharetid polychaetes, yoldiid and thyasirid bivalves and Sipunculidae on the slope. Megafaunal clusters were characterized by mysid crustaceans, oedicerotid amphipods, cylichnid gastropods and myriotrochid holothurians on the shelf; ophiurid and ophiacanthid echinoderms, arcid and propeamussiid bivalves, diastylid cumaceans, and idoteid isopods on the shelf break; and hippolytid decapods, benthopectinid asteroids, and phascolionid sipunculids on the slope.

### 3.3.6 Abundance of taxa by transect

As expected, higher-order and multivariate patterns reveal fauna varied largely across the depth gradient as the composition of macro- and megafauna were similar at corresponding depths along the shelf. Nevertheless, some dominant taxa did vary along the shelf in terms of mean abundance (Table 3.5). For the macrofauna, maldanid polychaetes were the most abundant fauna on the G and K transects, while the westernmost transect T was dominated by cirratulid polychaetes and the easternmost transect D by nephtyid polychaetes. Secondarily, relative to the other transects, lumbrinerid polychaete abundance was lowest at K, pholoid polychaete numbers were highest at T and thyasirid bivalves were more abundant in the west (G and T) than the east (D and K). For the megafauna, ophiurid echinoderms were the most abundant fauna in all transects but K where hippolytid decapods were marginally more abundant. In another secondary feature, arcid bivalves were highly abundant in G relative to all other transects, propeamussiid bivalves were higher in the west (G and T) than the east (D and K) and astartid bivalves, eusirid amphipods and phascolionid sipunculids and onuphid polychaetes were all highest in abundance at D where a different sampling procedure was used (see Section 3.2.1). Although mean abundances of taxa varied between transects, it is important to note that the comparison is qualitative, as standard deviations were typically (82% of the time) larger than their means.

**Table 3.5. Mean abundance of macro- and megafaunal taxa in all four transects.**

| | Class | Taxa | T | G | K | D |
|---|---|---|---|---|---|---|
| **Macrofauna** | Polychaeta | Cirratulidae | **264 ± 371** | 86 ± 46 | 56 ± 60 | 66 ± 112 |
| | | Maldanidae | 232 ± 369 | **448 ± 904** | **214 ± 413** | 139 ± 154 |
| | | Nephtyidae | 118 ± 225 | 104 ± 139 | 64 ± 116 | **222 ± 348** |
| | | Pholoidae | 109 ± 171 | 30 ± 31 | 2 ± 4 | 6 ± 10 |
| | | Spionidae | 83 ± 88 | 61 ± 60 | 16 ± 36 | 67 ± 110 |
| | | Lumbrineridae | 102 ± 89 | 93 ± 88 | 5 ± 4 | 24 ± 38 |
| | Bivalvia | Thyasiridae | 138 ± 238 | 142 ± 284 | 56 ± 92 | 10 ± 10 |
| | | Yoldiidae | 34 ± 23 | 90 ± 35 | 46 ± 61 | 86 ± 66 |
| | Sipunculidea | Sipunculidae | 24 ± 30 | 74 ± 94 | 34 ± 48 | 67 ± 107 |
| **Megafauna** | Polychaeta | Onuphidae | 2 ± 1 | 83 ± 185 | 2 ± 2 | 1300 ± 2908 |
| | Malacostraca | Atylidae | 18 ± 25 | 135 ± 300 | 0 ± 0 | 129 ± 289 |
| | | Diastylidae | 142 ± 237 | 288 ± 507 | 5 ± 7 | 136 ± 193 |
| | | Eusiridae | 20 ± 26 | 10 ± 17 | 4 ± 5 | 396 ± 837 |
| | | Hippolytidae | 126 ± 102 | 56 ± 46 | **70 ± 50** | 102 ± 104 |
| | | Idoteidae | 138 ± 284 | 11 ± 23 | 0 ± 0 | 89 ± 198 |
| | | Mysidae | 133 ± 270 | 6 ± 11 | 62 ± 103 | 120 ± 226 |
| | | Oedicerotidae | 24 ± 26 | 63 ± 121 | 45 ± 44 | 211 ± 360 |
| | Asteroidea | Benthopectinidae | 21 ± 17 | 64 ± 141 | 21 ± 26 | 5 ± 5 |
| | Ophiuroidea | Ophiuridae | **2260 ± 3362** | **3436 ± 7173** | 55 ± 56 | **9055 ± 20228** |
| | Bivalvia | Arcidae | 0 ± 1 | 2538 ± 5659 | 1 ± 2 | 0 ± 0 |
| | | Astartidae | 3 ± 2 | 2 ± 4 | 0 ± 0 | 1069 ± 2390 |
| | | Propeamussiidae | 423 ± 750 | 111 ± 231 | 3 ± 5 | 34 ± 76 |
| | Sipunculidea | Phascolionidae | 16 ± 20 | 120 ± 254 | 6 ± 12 | 1117 ± 2497 |

The top 5 taxa from each transect in terms of abundance are combined here. Macrofaunal abundance in individuals/m$^2$ and megafaunal abundance in individuals/1000m$^2$ ± standard deviation. Most abundant taxa at each transect emboldened. Megafaunal samples from transect D were collected using beam or otter trawls, which likely inflated abundances relative to other transects.

## 3.4 Discussion

### 3.4.1 Trends in abundance, biomass and body size

Total abundance and biomass was highly variable between stations, with estimates from 24 to 4,512 individuals/m$^2$ and 2.4 to 70 ww g/m$^2$ for the macrofauna and 20 to 3,409 individuals/100m$^2$ and 19 to 1,348 ww g/100m$^2$ for the megafauna. This large degree of natural variability combined with a lack of station replication made it difficult to detect significant differences between transects and depth classes in abundance, biomass and average body size. However, some trends did emerge. The eastern transect K, located just west of the Kugmallit Valley, tended to be lowest in total macro- and megafaunal abundance and biomass. This area may be too far west to benefit from the increased upwelling originating from the steep slopes of Cape Bathurst [Conlan et al., 2008; Conlan et al., 2013] and less productive compared to the area surrounding the Mackenzie Trough (where transects T and G were located) which enhances upwelling of deeper nutrient rich water [Williams et al., 2006].

Across the depth gradient (30 - 500 m), megafauna tended to decrease in total abundance and biomass. As predicted, the smaller macrofauna did not show a decrease in total abundance or biomass across a similar depth range (30 - 750 m). This discontinuity in macro- and megafaunal trends affirms Chapter 2 findings that megafaunal abundance decreased more rapidly with depth and supports the general theory that smaller bodied fauna become a larger component of the benthos at greater depths [Clough et al., 2005; Lampitt et al., 1986; Rex et al., 2006; Thiel, 1975; Thistle, 2001]. Depth, a proxy for organic matter input as the quantity and quality of organic matter decreases with depth [Graf, 1992; Levin and Sibuet, 2012; Suess, 1980], which could select against larger bodied individuals or species that have greater energy needs.

Further depth related trends emerge from an examination of average (estimated) body sizes of macro- and megafaunal classes. As predicted bivalves, gastropods and asteroideans tended to decrease in average body size with increasing depth. In opposition to the theory of decreasing body size with depth, megafaunal malacostracans and ophiuroids tended to increase in average body size to 350 m depth. This could be the result of a compositional change within malacostracan and ophiuroid classes. The dominant malacostracan taxa on the shelf, Mysidae (mysids) and Oedicerotidae (amphipod), are smaller on average than Hippolytidae (decapod) taxa which were highly abundant on the slope (Figure 3.10). Similarly, *Ophiocten sericeum*, the dominant ophiuroid species on the shelf, is much smaller than the dominant slope species: *Ophiopleura borealis* [Piepenburg and Schmid, 1996b].

### 3.4.2 Faunal replacement with depth

Patterns of $\beta$ diversity and community composition identified here generally parallel those described in previous benthic studies on the Beaufort Shelf [Aitken et al., 2008; Carey, 1984; Conlan et al., 2008; Conlan et al., 2013; Wacasey, 1975]. However, some differences emerge. Previous studies have described depth related trends in macrofauna composition on the Beaufort Shelf relative to the influence of estuarine and marine water masses [Wacasey, 1975] and ice zones [Conlan et al., 2008]. Contrary to an early baseline study on the distribution of benthic macrofauna which described distinct faunal zones across a depth gradient [Wacasey, 1975], my results indicate faunal change to be continuous within this depth range (30 - 750 m). Although my results identified three main clusters of stations (shelf, shelf break and slope), these clusters were not homogeneous. Rather, faunal change was continuous, as stations on the margin of one cluster were similar in composition to stations on the leading margin of a subsequent cluster. This fits the prevailing view that compositional changes across a gradient tend to be of a continuous nature [Rex, 1981], reflecting the gradual environmental change across a gradient that drives the replacement of species. Furthermore, if depth related faunal zonation were present, one would expect variability to be much greater on the margins of the zones [Carney, 2005] such as the shelf break. Instead, I observed more variability in community composition on the shelf than at the shelf break or on the slope where multivariate clusters had greater average silhouette widths and were therefore more homogeneous (Figure 3.9).

#### Macrofauna

The dominant macrofauna taxa on the shelf were nephtyid polychaetes of which the majority of individuals were *Micronephthys minuta*. The predatory *M. minuta* has previously been described as relatively abundant on the Beaufort shelf [Aitken et al., 2008; Conlan et al., 2008; Nephin et al., 2014; Wacasey, 1975]. Polychaetes also made up a large component of the shelf break macrofauna but here several groups (cirratulid, spionid and capitellid) of deposit feeders dominated. Deeper on the slope, between 500 to 750 m in depth, maldanid polychaetes (*Maldane arctica* and *Maldane sarsi*) dominate. The subsurface deposit feeding *Maldane* spp. are numerically abundant and widespread in the Arctic [Blanchard et al., 2013; Bluhm et al., 2011; Carroll et al., 2008; Rysgaard and Glud, 2007; Włodarska-Kowalczuk et al., 2012]. Additionally, they have previously been described as dominant on both the Beaufort shelf [Wacasey, 1975] and slope [Carey, 1984; Conlan et al., 2008]. Yet, here and in Chapter 2, *Maldane* spp. represented a much larger portion of the total number of individuals in slope samples. While most of the dominant macrofaunal taxa were classed as deposit feeders (Table 3.6) there was an observable shift from a predatory dominant (*M. minuta*) on the shelf to deposit feeding dominants (*Maldane* spp.) on the slope.

Some of the dominant taxa identified here were not described as relatively abundant in previously baseline studies on the Beaufort Shelf such as Aitken et al. [2008]; Carey [1984]; Conlan et al. [2008]; Conlan et al. [2013]; Wacasey [1975]. Leuconid cumaceans from *Eudorella* and *Leucon* genera are widely distributed across the Arctic [Piepenburg et al., 2011] yet had not prior to Chapter 2 been shown to contribute to a relatively large portion of the total number of individuals on the shelf. In addition, lumbrinerid (*Lumbrineris mixochaeta*) and ampharetid (*Pterolysippe vanelli*) polychaetes were not described as dominants in previous Beaufort Shelf studies, perhaps as a result of limited sampling on the slope.

### Megafauna

Regionally, the Canadian Beaufort Shelf is similar to other Arctic shelves where ophiuroids and bivalves tend to dominate the megafaunal biomass [Curtis, 1975]. Additionally, in this region, malacostracan taxa from amphipod, cumacean, isopod, mysid and decapod orders were important contributers to total abundance and biomass on the shelf and tended to increase in importance with depth. Current knowledge of the distribution of megafauna across the Canadian Beaufort Shelf is based on a single report [Kostylev and Chapman, 2005] of analysis of drop-cam video imagery at depths $< 150$ m. In addition to that report and Chapter 2, the distribution of a few dominant megafaunal taxa have been described from macrofaunal studies on the shelf (discussed above) as grab and box corers occasionally, though not effectively, collect megafauna.

Deposit feeding Ophiuridae (brittle stars) were by far the most relatively abundant megafaunal taxa. Within Ophiuridae, *Ophiocten sericeum*, which accounted for the vast majority of individuals, was relatively abundant on the shelf and *Ophiopleura borealis* was relatively abundant deeper on the slope near 500 m depth, which aligns with their distribution described in Chapter 2. Additionally, the distribution of *O. sericeum* affirms Conlan et al.'s [2008] observation that *O. sericeum* was more abundant on the Beaufort shelf than slope. As observed on other Arctic shelves [Piepenburg, 2005], *O. sericeum* formed dense beds on the shelf accounting for up to 80% of the total number of individuals in a single sample. *O. sericeum* is one of the most widely distributed species on Arctic shelves, [Piepenburg et al., 2011] abundant on the Alaskan Beaufort Shelf [Carey, 1984], the Laptev Sea Shelf [Piepenburg and Schmid, 1997], the northeast Greenland Shelf [Mayer and Piepenburg, 1996; Piepenburg and Schmid, 1996b; Starmans et al., 1999] and the Barents Sea Shelf [Piepenburg and Schmid, 1996a]. Yet, Kostylev and Chapman [2005] recorded very low abundances of *O. sericeum* on the Beaufort Shelf possibly because their small size (disc diameter = 7 mm) [Piepenburg and Schmid, 1996b] made detection difficult in video imagery.

Other dominant megafauna representative of the shelf cluster (samples from 30 to 75 m depth) were *Boreomysis arctica* mysid amphipods, *Acanthostepheia malmgreni* and *Arrhis phyllonyx* oedicerotid amphipods, *Cylichna alba* and *occulta* gastropods and myriotrochid holothurians. Myriotrochids, which have been observed in dense patches in the Chukchi Sea (around 50 m depth) [Bluhm et al., 2009], represented up to 14% of local abundance peaking at 75 m depth. Although I found many highly abundant amphipod taxa on the shelf, these were not described in previous surveys. The amphipod taxa may be difficult to collected by box corer or grabs, in which case trawls may be more appropriate for sampling, as shown by Connelly et al. [2014] who collected many amphipod taxa in relatively large abundance on the Beaufort Shelf and Amundsen Gulf using an epibenthic sled.

Several megafaunal taxa were representative of the shelf break cluster (samples from 75 to 200 m depth). Ophiacanthid brittle stars (*Ophiacantha bidentata*) and idoteid isopods (*Synidotea bicuspida*), *Bathyarca glacialis* and *Similipecten greenlandicus* bivalves and *Diastylis* spp. cumaceans. This is the first evidence showing that the bivalve *S. greenlandicus* can be relatively abundant on the Canadian Beaufort Shelf, although they were also present in considerable abundance in ArcticNet shelf samples (Chapter 2). *Synidotea bicuspida* has previously been collected in trawl and grab samples on the Beaufort Shelf ($< 200$ m) [Percy, 1983; Wacasey et al., 1977], however they typically occur alongside the more widespread *Saduria* spp. [Conlan et al., 2008; Nephin et al., 2014; Wacasey et al., 1977]. Here, *Saduria* spp. also occurred in a greater number of samples, however *S. bicuspida* was more abundant on average accounting for up to 16% of local abundance in one sample.

The dominant megafaunal taxa representative of the slope cluster (samples from 200 to 500 m depth) were hippolytid decapods, *Pontaster tenuispinus* asteroids, sipunculids and *Michthyops theeli* amphipods. The predatory hippolytid decapods were the most abundant megafaunal slope taxa. As the majority of dominant shelf taxa were deposit feeding, the increase of hippolytid decapods on the slope could signal a shift toward a greater relative abundance of predatory feeders (Table 3.7). The majority of hippolytid individuals were *Eualus gaimardii*, *Bythocaris* spp. and *Lebbeus polaris*. Hippolytid decapods may be an abundant and important food source for upper trophic levels [Birkely and Gulliksen, 2003], yet many previous studies of Beaufort benthos which focused on the macrofauna [Conlan et al., 2008; Wacasey, 1975] did not report this group. *Pontaster tenuispinus*, a highly abundant (also shown in Chapter 2) and widely distributed Arctic deep-sea species [Anisimova et al., 2010; Bluhm et al., 2011] and *Michthyops theeli* were also rarely collected in previous Beaufort benthic surveys likely a result of the small sample areas of grabs and box cores and the limited number of samples taken deeper than 200 m.

## Table 3.6. Feeding modes of dominant macrofaunal taxa.

| Class | Family | Dominant taxa | Location | Feeding mode | Source |
|---|---|---|---|---|---|
| Bivalvia | Thyasiridae | *Thyasira* | Slope | Deposit | [Conlan et al., 2008] |
| | Yoldiidae | *Portlandia* | Slope | Deposit | [Carey et al., 1984; Conlan et al., 2008] |
| Malacostraca | Akanthophoreidae | *Akanthophoreus* | Shelf break | Deposit | [Link et al., 2013b] |
| | Leuconidae | *Eudorella & Leucon* | Shelf | Suspension/Deposit | [Frid, 2011; Jones, 1976] |
| Polychaeta | Ampharetidae | *Pterolysippe vanelli* | Slope | Deposit | [Fauchald and Jumars, 1979] |
| | Capitellidae | *Heteromastus* | Shelf break | Deposit | [Fauchald and Jumars, 1979] |
| | Cirratulidae | *Aphelochaeta & Chaetozone* | Shelf break | Deposit | [Fauchald and Jumars, 1979] |
| | Lumbrineridae | *Lumbrineris mixochaeta* | Shelf break | Deposit/Scavenger | [Fauchald and Jumars, 1979] |
| | Maldanidae | *Maldane arctic & Maldane sarsi* | Slope | Deposit | [Fauchald and Jumars, 1979] |
| | Nephtyidae | *Micronephthys minuta* | Shelf | Predator/Carnivore | [Fauchald and Jumars, 1979] |
| | Paraonidae | *Aricidea & Paraonis* | Shelf | Deposit | [Fauchald and Jumars, 1979] |
| | Pholoidae | *Pholoe longa* | Shelf break | Predator/Carnivore | [Fauchald and Jumars, 1979; Link et al., 2013b] |
| | Spionidae | *Prionospio* | Shelf break | Deposit | [Fauchald and Jumars, 1979] |
| Sipunculidea | Sipunculidae | | Slope | Deposit | [Aitken and Fournier, 1993; Link et al., 2013b] |

Location where taxa were relatively abundant: shelf, shelf break or slope (shown in Figure 3.10).

**Table 3.7. Feeding modes of dominant megafaunal taxa.**

| Class | Family | Dominant taxa | Location | Feeding mode | Source |
|---|---|---|---|---|---|
| Asteroidea | Benthopectinidae | *Pontaster tenuispinus* | Slope | Deposit | [Hobson et al., 1995] |
| Bivalvia | Arcidae | *Bathyarca glacialis* | Shelf Break | Suspension | [Aitken and Fournier, 1993] |
| | Propeamussiidae | *Similipecten greenlandicus* | Shelf Break | Suspension | [Olabarria, 2005] |
| Gastropoda | Cylichnidae | *Cylichna alba & occulta* | Shelf | Predator/Scavenger | [Aitken and Fournier, 1993; Frid, 2011; Iken et al., 2010] |
| Holothuroidea | Myriotrochidae | *Myriotrochus* | Shelf | Deposit | [Aitken and Fournier, 1993; Connelly et al., 2014] |
| Malacostraca | Diastylidae | *Diastylis goodsiri, spinulosa & scorpioides* | Shelf Break | Suspension/Deposit | [Frid, 2011; Jones, 1976] |
| | Hippolytidae | *Eualus gaimardii* | Shelf & Slope | Predator/Scavenger | [Birkely and Gulliksen, 2003; Nygård et al., 2007] |
| | | *Lebbeus polaris & Bythocaris* | Slope | Predator/Scavenger | [Birkely and Gulliksen, 2003] |
| | Idoteidae | *Synidotea bicuspida* | Shelf Break | Deposit | [Link et al., 2013b] |
| | Mysidae | *Boreomysis arctica* | Shelf | Suspension/Deposit | [Connelly et al., 2014] |
| | | *Michthyops theeli* | Slope | Suspension/Deposit | [Connelly et al., 2014] |
| | Oedicerotidae | *Arrhis phyllonyx & Acanthostepheia malmgreni* | Shelf | Suspension/Deposit | [Connelly et al., 2014] |
| Ophiuroidea | Ophiacanthidae | *Ophiacantha bidentata* | Shelf Break | Deposit | [Aitken and Fournier, 1993; Hobson et al., 1995; Pearson and Gage, 1984] |
| | Ophiuridae | *Ophiocten sericeum* | Shelf/Shelf Break | Deposit | [Hobson et al., 1995] |
| | | *Ophiopleura borealis* | Slope | Deposit | [Aitken and Fournier, 1993; Hobson et al., 1995] |
| Sipunculidea | Phascolionidae | | Slope | Deposit | [Aitken and Fournier, 1993] |

Location where taxa were relatively abundant: shelf, shelf break or slope (shown in Figure 3.10).

### 3.4.3 Macro- and megafaunal congruence

For all metrics there was little congruence between the macro- and megafauna. There was no evidence of a relationship between macro- and megafauna in local abundance, biomass, diversity or community structure (Figure 3.2 and 3.8). This is perhaps a result of the low detecting power of the small number of samples (n=12) or the lack of replication at stations coupled with the high degree of small-scale variability or patchiness characteristic of soft-bottom benthic communities [Chapman et al., 2010]. Additionally, megafaunal variables were integrated over a much larger area (samples area $= 1,836\text{m}^2$) than those of the macrofauna (samples area $= 0.125\text{m}^2$). This could bias results if the trawl area encompassed heterogeneous environments (e.g. multiple patches of food of varying quality and quantity), while the corresponding box core sampled only part of this heterogeneity. If that were the case, divergent macro- and megafaunal patterns would not necessarily indicate that macro- and megafauna were not responding similarly to a changing environment. However, several previous studies, at varying scales, examining congruence of benthic size classes have also found no relationship between macro- and megafauna in local abundance [Grebmeier et al., 2006a; Reiss et al., 2010], biomass [Bluhm et al., 2009] and diversity [Karakassis et al., 2006; Reiss et al., 2010]. In addition, although Reiss et al. [2010] reported significant correlations between macro (infaunal)- and (epi-benthic) megafaunal similarity matrices, the correlation coefficients were rather low (.25 to .41) suggesting there is indeed a great deal of variability between macro- and megafaunal patterns of community structure.

Assuming that the scale of sampling here was appropriate for the comparison, several mechanisms could be responsible for the observed macro- and megafaunal dissimilarity. The greater mobility of the megafauna could permit a more rapid response to environmental change [Grebmeier et al., 2006a] on average compared to macrofauna. If megafauna are able to move comparatively quickly to regions with higher quality food, that could decouple megafaunal biomass from long-term food availability [Bluhm et al., 2009] which macrofaunal biomass is more likely to reflect. Alternatively, it has been proposed that since megafauna are more likely to be epibenthic or suprabenthic, they are likely the first to ingest recent inputs of organic matter [Jørgensen et al., 2011; Premke et al., 2006; Smith, 1985] and thus again may be responding to food inputs on different timescales than the macrofauna. These potential divergent responses of macro- and megafauna to food availability may also be responsible for the observed dissimilarity in community structure (Figure

3.8). In addition, macrofaunal community composition had greater similarity among stations than the megafauna which confirms Jørgensen et al.'s [2011] finding that box core replicates were more similar than trawl replicates and may be reflective of greater megafaunal replacement across the depth gradient as described in Chapter 2. Thus megafaunal diversity and abundance may be seen as indicators of benthic ecosystem responses to short-term environmental variability (such as variability in organic matter input) while these same characteristics in the macrofauna would better serve as indicators of long-term environmental change.

Yet, when examining patterns of taxa overlap, macro- and megafauna did share many similarities. Despite sample area differences, macro- and megafauna had similar proportions of taxa unique to or shared between transects (Figure 3.6). Rarely occurring taxa, which also tended to be low in local relative abundance, were unevenly distributed between transects with approximately 20% of macro- and megafaunal taxa found only at the westernmost transect (T). This may be evidence that there is a larger degree of macro- and megafaunal congruence at a larger scale (at the scale of transect as opposed to individual samples). These rare taxa, although constituting a rather large portion of the total species pool, were unlikely to have affected total abundance, biomass or community structure trends and thus are not represented in those metrics. Furthermore, increased numbers of rare taxa may not be merely a reflection of greater diversity in the area as mean $ES_{50}$ did not differ between the T and G transects (Figure 3.2), although the greatest number of rare taxa did occur where taxa richness was the greatest for the macro- and megafauna, at the 30 m station on transect T. The greater number of rare macro- and megafaunal taxa may be reflecting the uniqueness of the area around transect T as it is predicted to be where the majority of upwelled water from the Mackenzie Trough is focused [Conlan et al., 2013] and has a sandier sediment composition compared to other areas on the shelf [Jerosch, 2012]. In addition, the parallel occurrence of unique macro- and megafaunal taxa on transect T suggests that both of these benthic size-classes may have been responding similarly to environmental drivers that govern the presence or absence of taxa in a region. The number of unique taxa reported on the western shelf is an indication that the choice of location of a long-term benthic monitoring station(s) along the shelf is not inconsequential. This may be especially true as temporal variability in benthic functioning may be greater in areas of higher diversity [Link et al., 2013b] or higher number of rare taxa.

# Chapter 4

# Conclusion

In this thesis, I have described the distribution of benthos on the Beaufort shelf and slope and the relationship between macro- and megafaunal spatial patterns. Prior to this work, benthic surveys in the region focused mainly on the distribution of macrofauna on the shelf (Section 1.4). Thus, this work made three notable contributions to our understanding of benthic distribution patterns in the region by:

1) extending the baseline description of benthic distribution patters farther down the slope where oil and gas exploration is now expanding,
2) identifying along and cross shelf megafaunal distribution patterns and
3) providing the first examination of the similarity of macro- and megafaunal distribution patterns in the region.

In Chapter 2, I established the many taxa that were rarely occurring in benthic samples tended to contribute more to total abundance on the slope compared to the shelf. This difference could be explained by pseudo-rarity as deep-sea taxa present on the slope could appear rare if sampled on the fringe of their optimal depth range. I also demonstrated that macro- and megafauna had incongruent diversity patterns across the depth gradient. Only the megafauna had greater mean abundance and taxa richness ($\alpha$ diversity) on the shelf than the slope and although both dominant macro- and megafaunal taxa varied in their contribution to total abundance across the depth range, only the megafauna had significant faunal replacement ($\beta$ diversity). I deduced that the megafaunal $\beta$ diversity trend was not solely a product of the difference in $\alpha$ diversity as there was a shift in the dominant taxa between the shelf and slope. Thus, there are differentiated shelf and slope megafaunal assemblages. The most likely driver of these depth related trends is the decreasing flux of organic matter with depth [Carney, 2005; Gage and Tyler, 1991; Rex and Etter, 2010]. As the current warming trend is predicted to alter the amount of food available to the benthos [Forest et al., 2007; Grebmeier et al., 2006b; Piepenburg, 2005; Rysgaard and Glud, 2007; Tremblay et al., 2011], I hypothesized that the observed faunal differences between shelf and slope may help to predict future changes in the benthos. That is, if food availability decreases over the shelf, the benthos which reside there may become more similar to the slope fauna. That shift could lead to an increase in the ratio of macro- to megafaunal taxa on the shelf, which would likely have effects on higher trophic levels [Grebmeier, 2012; Grebmeier et al., 2006a].

In Chapter 3, I showed that macro- and megafauna varied more across the depth gradient than from east to west along the shelf. However, rarely occurring taxa were not evenly distributed along the shelf with a large number of uniques present on the far western shelf for both the macro- and megafauna. I propose that these locations with a higher number of rare taxa (or total taxa) may be important for future study, as these regions may be more likely to experience greater temporal variability in benthic function [Link et al., 2013b]. I also described the change in relative abundance of dominant taxa across the depth gradient then compared their distributions to that described from previous benthic surveys (including Chapter 2). Although there were many similarities, some dominant macrofaunal taxa and many dominant megafaunal taxa reported here had very rarely been collected or not at all documented on the Beaufort shelf or slope. Lastly, there was little congruence between macro- and megafauna, in terms of abundance, biomass and $\alpha$ and $\beta$ diversity. However, the power of detecting such a relationship was low as the sample size was small and as illustrated in Appendix A the underlying relationship was weak. I hypothesized that discontinuity between macro- and megafaunal abundance and biomass could arise if the faunal classes were responding to food inputs on different timescales. In addition, megafaunal composition varied more than macrofaunal composition within the same spatial extent (also shown in Chapter 2 and Appendix A) suggesting that these faunal classes vary at slightly different spatial scales.

These findings will likely have implications for future benthic monitoring on the Beaufort shelf and slope. Principally, separately sampling the different benthic components could yield different spatial patterns. Secondly, the location of sampling is important, not only relative to the position on the shelf versus slope between which major faunal change occurs but along the shelf where abundance, diversity and the number of rare species can vary between localities. When designing a benthic monitoring program, the need to sample both macro- and megafaunal benthic fractions will likely depend on the intended goal. If the goal is to conserve/manage benthic diversity and related ecosystem function it may be crucial to survey both the macro- and megafauna. A shift (e.g. the loss of diversity) in one component may not accurately predict a shift in the other as macro- and megafauna may be responding to environmental drivers of diversity (such as organic matter input) on different timescales. Conversely, if the sole purpose of benthic monitoring is to document anthropogenic impacts in a specific area (e.g. oil and gas platform or pipeline), it may only be necessary to sample one component. As benthic pollution is usually accompanied by a decrease in diversity [Boesch, 1972; Hiddink et al., 2006; Piola and Johnston, 2008], change in the degree of overlap of species between localities (impacted versus control areas) might signal a shift in the impacted area. For example, if species richness decreased in the impacted area relative to the surrounding control areas the number of species shared between them would likely decrease. Despite difference in the area sampled by the box core and trawl gear, this change in species overlap would likely be measurable in both the macro- and megafauna as they shared a similar degree of overlap between transects (Figure 3.6).

As the Beaufort shelf and slope are increasingly exposed to pressures from industry and climate warming, further benthic monitoring will be essential to the management and conservation of biodiversity and ecosystem services. However, several questions remain for future research to facilitate the establishment of effective long-term monitoring. How might the scale of sampling affect the detection of spatial patterns for the macro- and megafauna? How does the magnitude of spatial variability in faunal abundance and diversity compare to temporal variability, and at what scale? Answering these questions will be crucial to distinguishing long-term changes in the benthos from spatial and interannual variability. In addition, it may be important to consider whether the ecological differences between macro- and megafauna leave one faunal group more vulnerable than the other to climate driven forcing. Incongruent macro- and megafaunal patterns of abundance and biomass may reflect underlying functional differences (i.e. mobility, benthic position or response to food input) between the groups, in which case they may differ in their responses to environmental change. The hypothesis that the more mobile and epibenthic megafauna may response faster to environmental change, such as changes in food availability, merits further study and should be addressed before trawl or video surveys are used as the sole tool for benthic monitoring. Lastly, determining whether indicator taxa from one faunal group might describe faunal patterns in the other (see Appendix A) will be particularly important for developing rapid and cost-effective surveying and monitoring methods such as the use of video transects.

# Appendix A

# Co-occurrence of macro- and megafaunal taxa

In Chapters 2 and 3 I examined the congruence of macro- and megafaunal spatial patterns. The results suggested little to no congruence in their spatial structure such that similar macrofaunal community composition between two sites could not predict whether the megafaunal community composition would be similar as well. Here I utilize a larger dataset (Figure A.1), by combining both ArcticNet and BREA benthic datasets where box core and trawl samples were collected at the same station (see Sections 2.2 and 3.2 for details on sampling and data management procedures), to further examine macro- and megafaunal congruence. My goal was to first determine whether a relationship between macro- and megafaunal community structure can be detected with a greater number of samples and secondly whether certain macro- or megafaunal taxa tend to co-occur in samples from both benthic datasets.

The second goal is important when considering the use of ***biological surrogates*** in benthic monitoring. For example, if the abundance or presence of a few dominant megafaunal taxa correlates with a consistent cohort of macrofaunal taxa or macrofaunal diversity, megafaunal benthic surveys, perhaps using video imagery, may be sufficient for benthic monitoring. Video imagery, from cameras on remotely operated vehicles, stationary observatories and towed sleds, has been proposed as a preferred method to increase the frequency and spatial coverage of benthic monitoring while minimizing post-cruise processing and the destructive impact of traditional benthic sampling — boxcorers, grabs and trawls [Gradinger et al., 2010; Parry et al., 2003]. Video imagery can yield accurate faunal density estimates and capture the larger, highly mobile epifauna that are sometimes missed by traditional sampling methods

[Cuvelier et al., 2012]. Therefore, a description of an epibenthic megafaunal surrogate would be a beneficial tool for future benthic monitoring.

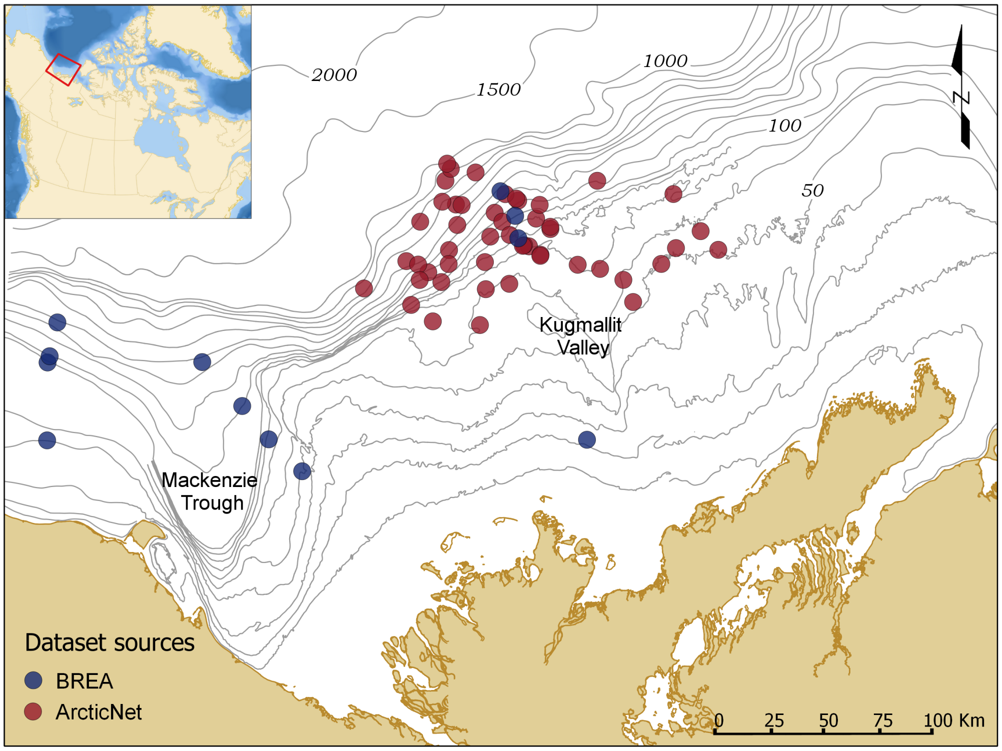


**Figure A.1. Subset of benthic stations on the Beaufort Shelf sourced from ArcticNet and BREA datasets.** At each station a box core and trawl sample were collected. Isobath contours provided by the Geological Survey of Canada Atlantic.

The analysis of macro- and megafaunal congruence in community structure with this larger dataset yielded slightly different results than reported in Chapter 3. Similar to Chapter 3, median Bray-Curtis similarities were slightly higher for the macrofauna (27%) than the megafauna (24%) indicating greater faunal replacement or differentiation occurs in the megafauna. However, the magnitude of faunal replacement was much lower compared to Chapter 3 (see Figure 3.8). This is expected as the greater number of samples included in this analysis would likely introduce greater variability in faunal composition. Contrary to Chapter 3, I did find a significant relationship between macro- and megafaunal similarity (Figure A.2, $\rho = 0.4$, $p_{adj} = 0.001$). However the correlation coefficient ($\rho = 0.4$) was the same in both analyses suggesting that the low number of samples in Chapter 3 was indeed preventing the detection of the rather weak relationship. The relatively weak correlation may be a result of the different scales at which these faunal groups vary across the depth gradient (Figure A.3) with the megafauna exhibiting stronger postive ***autocorrelation*** between stations of similar depth and stronger negative autocorrelation between stations with larger depth differences than the macrofauna. Thus, I can conclude while there is a some degree of continuity between macro- and megafaunal spatial structure there is a high degree of variability present.

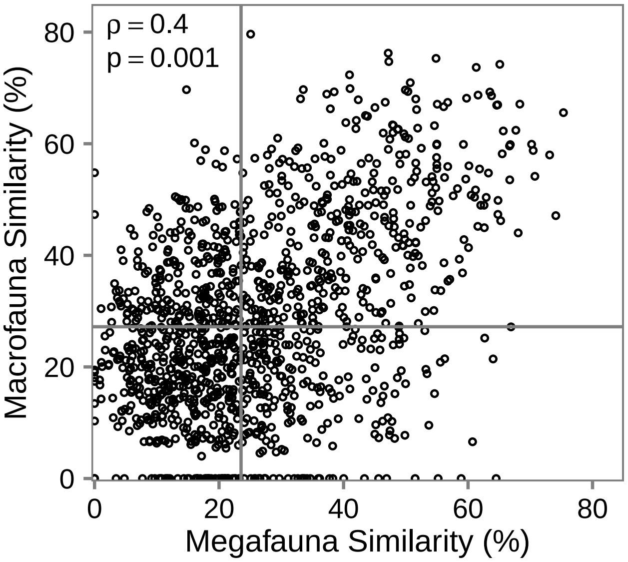


**Figure A.2. Correlation between macro- and megafaunal Bray-Curtis similarities.** Pairwise comparison between all stations. Grey lines represent median similarities. Spearman's rank correlation coefficient and significance (p-value) denoted by $\rho$ and p, respectively.

The congruence of macro- and megafaunal spatial structure indicates that the use of a megafaunal surrogate for benthic sampling may be feasible. To test for the presence of a megafaunal surrogate of macrofaunal diversity I looked for correlations between the abundance of megafaunal taxa and macrofaunal taxa richness. The highest correlation occurred with the abundance of ophiurid echinoderms — the most dominant megafaunal taxa in terms of total and relative abundance. Ophiuridae abundance was positively correlated with macro- and megafaunal richness (Figure A.4). Ophiuridae abundance explains almost 70% of the variability in megafaunal richness (linear model: $p < 0.0001$ , $R^2_{adj} = 0.67$). Conversely, using Ophiuridae abundance to predict macrofaunal richness would result in a high degree of uncertainty

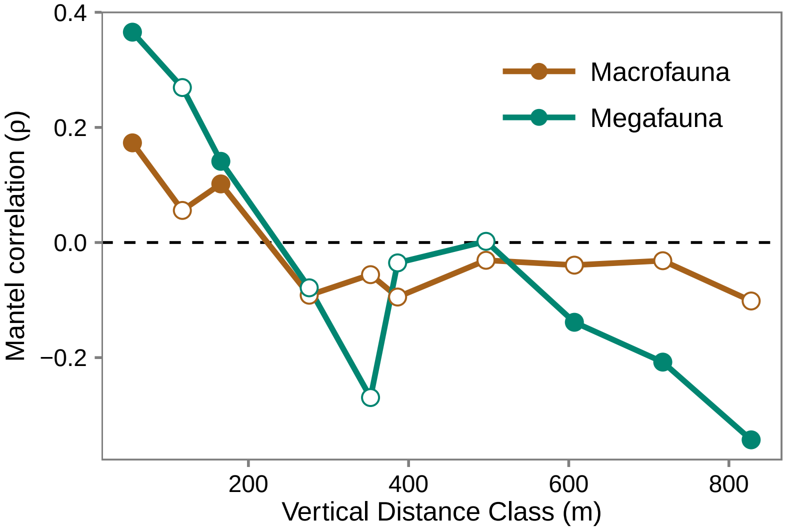


**Figure A.3. Mantel correlation of Bray-Curtis similarities between stations separated by vertical distance classes.** Mantel correlation is calculated with the Spearman's rank correlation coefficient ($\rho$). Circles: ○ denote values of $\rho$ with $p > 0.05$ and ● denote values of $\rho$ significantly different from zero, with $p < 0.05$. P-values are derived from permutations and the Holm correction method is used to account for multiple comparisons.

as Ophiuridae abundance only explains 28% of the variability in macrofaunal richness (linear model: $p < 0.0001$ , $R^2_{adj} = 0.28$). However, these results indicate that brittle stars from the family Ophiuridae can provide a reasonable estimate of total benthic taxa richness.

Lastly, I examined whether any macro- or megafaunal taxa tended to co-occur. The following ***R-mode*** analysis which looks for associations between species is distinct from the ***Q-mode*** analysis utilized in all other community analyses in this thesis which looks for associations between stations. Combining macro- and megafaunal datasets for R-mode analysis was problematic because raw abundance estimates from the widely different sample areas of box corers and trawls are not comparable. Therefore, abundance data were Hellinger transformed (the square root of numerical abundance divided by station totals (i.e. relative abundance)). After the abundance transformation, the macro- and megafaunal datasets were combined. Principal coordinate analysis was performed using Jaccard distance metric. Species scores, calculated from weighted sums of a Hellinger distance matrix, and environmental vectors were then overlain on the principal coordinate biplot (Figure A.5) to visualize correlations between macro- and megafaunal taxa and the environmental factors they vary with.

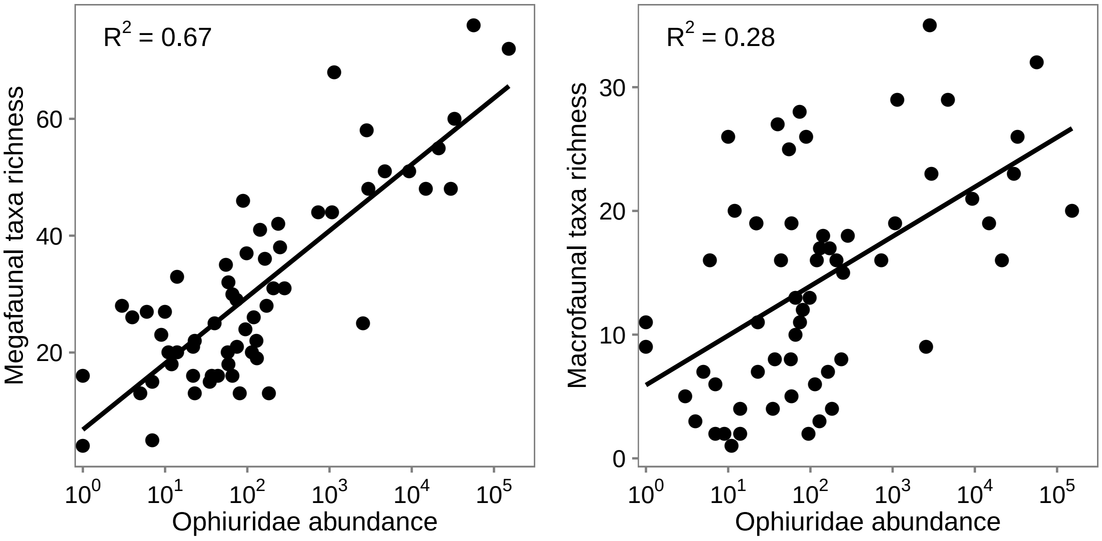


**Figure A.4. Ophiuridae abundance as a surrogate of macro- and megafaunal taxa richness.** $R^2$ output from a log-linear model.

Some dominant macro- and megafauna taxa that co-occurred in one dataset were likely to co-occur in the other (Figure A.5), however many were not. In both datasets, megafaunal Ophiuridae tended to occur in samples with macrofaunal Lumbrineridae, Oweniidae and Cirratulidae, and megafaunal Oedicerotidae tended to occur in samples with macrofaunal Nephtyidae and Leuconidae. However, many dominant taxa were highly correlated in samples from one dataset but not the other. The most apparent of these inconsistencies is the co-occurrence of megafaunal Benthopectinidae (*Pontaster tenuispinus*) with macrofaunal Maldanidae and Thyasiridae. These three taxa were more likely to be present and highly abundant on the slope than the shelf, yet were not likely to be found at similar stations on the slope in the ArcticNet samples. These conflicting results were likely a result of limited sampling (no replicates), the small sample area relative to the overall spatial extent of sampling and the patchy nature of the distribution of benthic fauna. Nevertheless, I can conclude that the most promising megafaunal surrogate appears to be brittle stars from the family Ophiuridae. This highly abundant and widespread family is a reasonable predictor of macrofaunal taxa richness and was consistently co-occurring with several macrofaunal taxa.

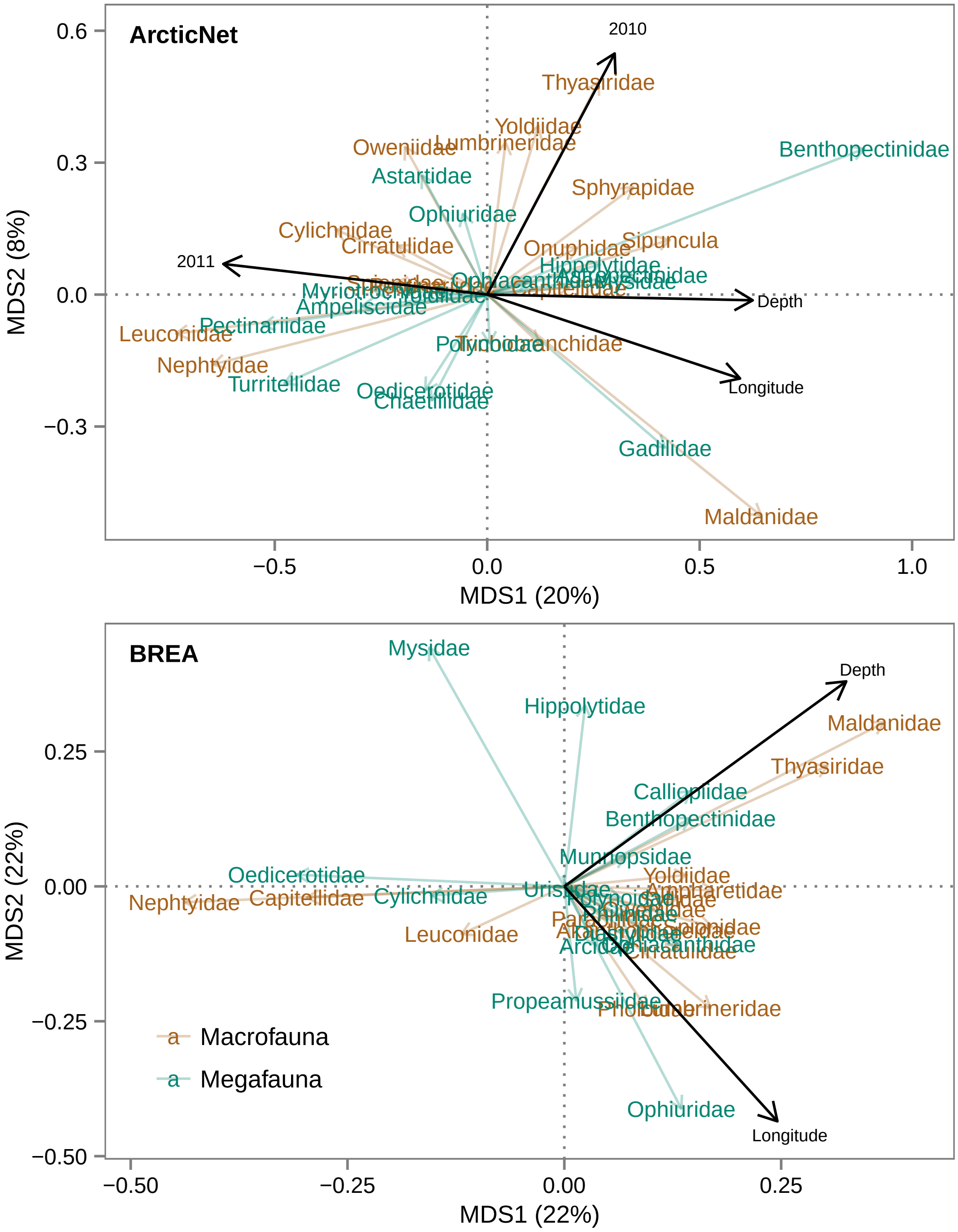


**Figure A.5. Principal coordinate analysis (MDS) biplot depicting correlations between taxa.** Black arrows display fitted vectors of environmental variables. Only top 25 taxa by relative abundance shown on plot. Distance from the centroid is reflecting Hellinger distance.

# Appendix B

# Variability in relative abundance of taxa from trawl and video data

Comparing data from multiple sampling gears is crucial to understanding connectivity between distinctive components of the benthos. In this thesis, I focus on the different faunal components sampled using box corers and trawls. Here, I examine how species surveyed by trawls and video on the Beaufort Shelf compare. This knowledge will be useful for the consideration of an epibenthic surrogate approach to benthic monitoring (discussed in Appendix A). The goal of this qualitative analysis was to determine which faunal groups were likely to be over or underrepresented in video imagery compared to trawl samples.

A third data source was used so that megafauna collected from trawls could be compared to the epibenthic megafauna visible in seafloor video imagery. Data from Kostylev and Chapman's [2005] report describing the distribution of epibenthic fauna from seafloor video on the Beaufort shelf in 2004 were used in conjunction with trawl data from both BREA and AricticNet datasets, for the comparison. Locations of video transects were overlain on a map of BREA and ArcticNet stations; the stations in closest proximity were determined to subset the data into comparable video–trawl stations (Figure B.1). The 8 resulting matched stations were located at similar depths, on average 23 kilometres apart. Modifications were made to the trawl and video datasets to facilitate comparison. Trawl taxa were grouped into higher-order taxonomic ranks to the level of corresponding video taxa as taxa from video data tended to be identified to higher taxonomic ranks.

My results show a large difference in the presence and relative abundance of common taxa exists between trawl and video data (Figure B.2). Annelid, sipunculid and

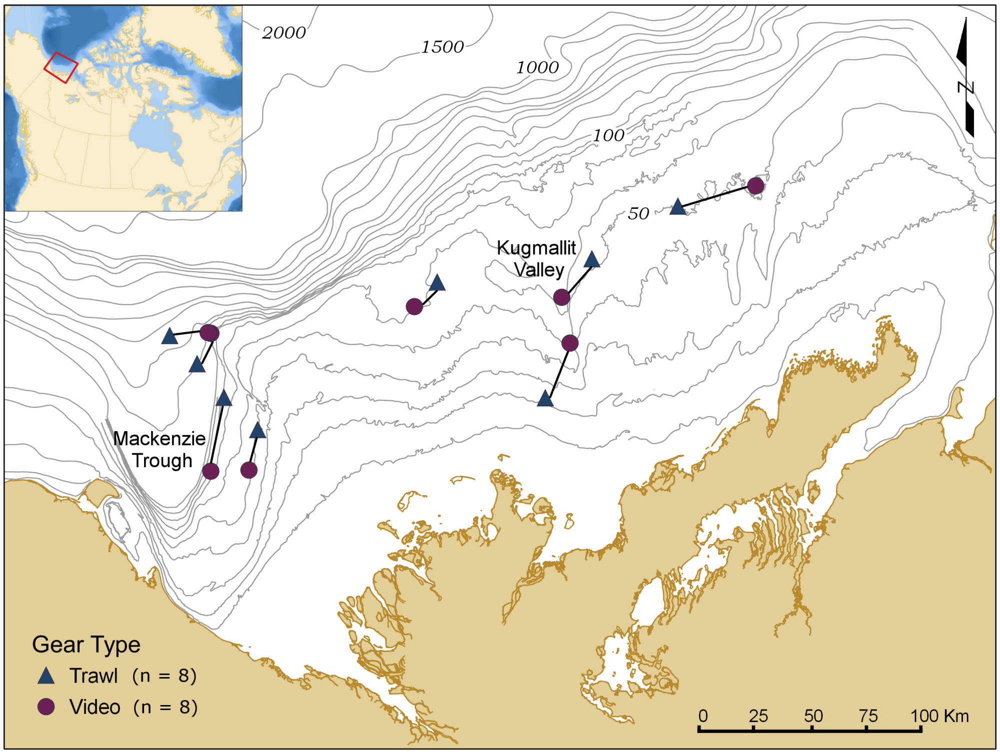


**Figure B.1.** Trawl and video transect stations across the Beaufort Shelf. Adjoining lines display post-hoc paired stations. Isobath contours provided by the Geological Survey of Canada Atlantic.

arthropod phyla were all underrepresented in video imagery, with the exception of *Saduria* spp. isopods. Species form the *Saduria* genera are a large and widespread Arctic taxa [Percy, 1983] that are likely easily identifiable in video imagery. In addition their mobility may make them less likely to be captured by trawls, thus they appear to represent a much larger component of the benthos when surveyed with video. Conversely, the large sessile Cnidaria (Actiniaria (anemones), Alcyonacea (soft corals) and Pennatulacea (sea pens)) were for the most part not collected by trawls while they represent roughly 5% of the relative abundance from the video surveys. Taxa from Echinodermata have similar estimates of relative abundance in trawl and video data, thus the most dominant megafaunal taxa on the Beaufort Shelf appear to be well represented in video surveys. The relative abundance of molluscan taxa were highly variable between trawl and videos. Bivalves did not appear in the video imagery as their mostly infaunal position makes them difficult to detect while the relative abundance of the more surficial Buccinidae (gastropod) taxa were potentially overestimated using video. In addition, the relative abundances of rare taxa (representing less than 1% of total relative abundance) were much more variable than common taxa with little to no overlap between trawl and video surveys. This is expected as these taxa are unlikely be sampled by either method.

Although, spatial and temporal faunal heterogeneity certainly play a role in the observed differences in the relative abundance of taxa between the trawl and video surveys, that variability is likely small compared to the major differences predicted to be observed between the sampling methods [McIntyre, 1956]. Therefore, the observed differences in the presence and relative abundance of phyla between trawl and video benthic surveys are likely representing true differences between these sampling methods.

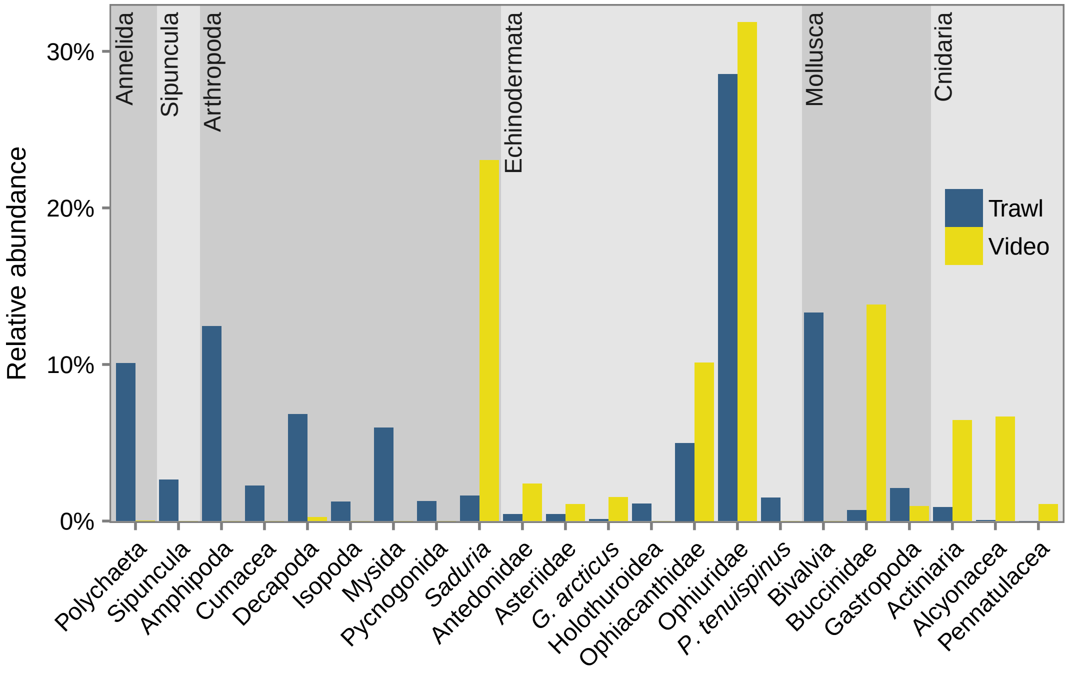


**Figure B.2.** Average relative abundance of common taxa in trawl and video samples.

In Appendix A I suggested that brittle stars from the family Ophiuridae were the most promising taxa for consideration as a megafaunal surrogate of macrofaunal diversity or composition. Here, Ophiuridae were again found to be the most relatively abundant taxa. Importantly, both trawl and video survey methods estimated Ophiuridae comprised roughly 30% of the total megafaunal abundance. This is an

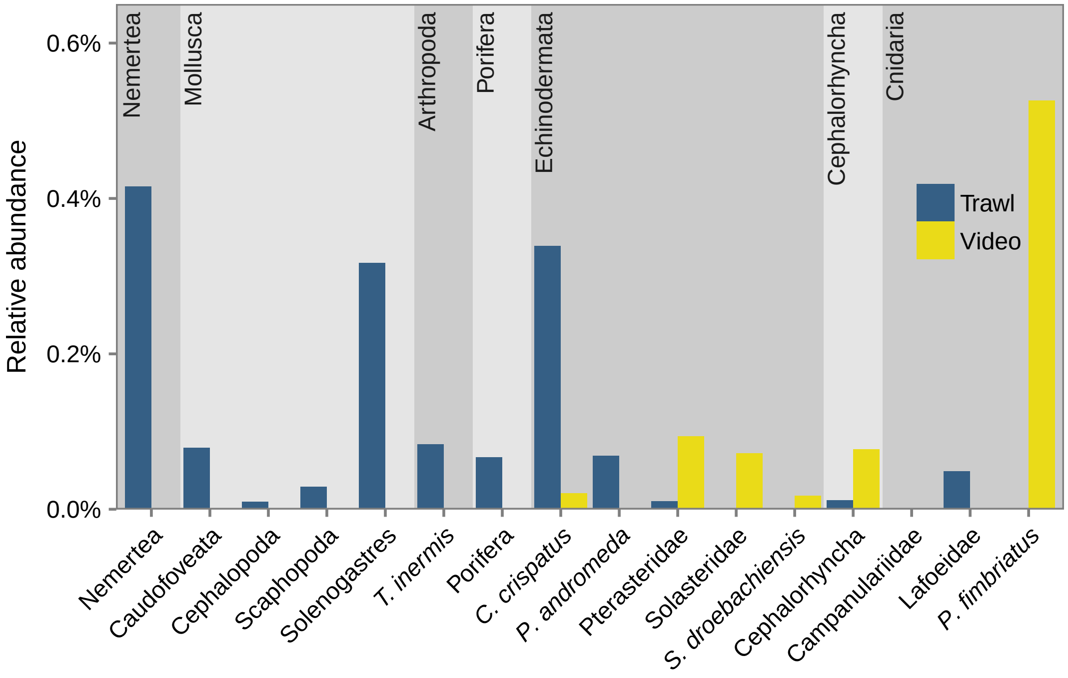


**Figure B.3.** Average relative abundance of rare taxa in trawl and video samples.

indication that benthic surveys using video imagery can produce reasonable estimates of relative abundance for the most dominant taxa. However, trawl estimates for total abundance of Ophiuridae were on average one order of magnitude larger than video estimates. Nevertheless, these results are promising such that the use of video imagery for benthic monitoring on the Beaufort Shelf warrants further investigation. I propose that video imagery may be a useful tool to identify locations of particular importance (for example where a change in the relative abundance of a dominant taxa is observed) for the collection of physical samples which could ultimately lead to the detection of shifts in community composition.

# Appendix C

# Meiofauna-macrofauna comparison

This thesis focussed on macro- and megafaunal benthic size classes. Meiofauna, a smaller benthic size class than the macrofauna, are defined as organisms that pass through a 1 mm sieve but are retained on a ~45 $\mu$m sieve [Higgins and Thiel, 1988]. Like the macrofauna, meiofauna are also collected within box core sediments, however the mesh size (500 $\mu$m) was too large to collect many meiofauna organisms. Some of meiofauna (Foraminifera, Nematoda and Ostracoda) were collected during sample processing but data were not included in the analyses in Chapters 2 and 3 because of the incomplete and non-quantitative nature of these collections. Nevertheless, since benthic meiofaunal data are rare for Arctic waters, these data merit some examination. Here, I compare that removed meiofaunal fraction to the macrofauna in box cores from the 2012 BREA sampling (Chapter 3).

Meiofauna taxa differed in total abundance and biomass (wet weight grams) between transects and depth classes (Table C.1). Totalling across all depths and transects meiofauna (of which 99% were foraminiferans) not only dominated box core abundance, as expected considering their smaller size, but also biomass. However, high meiofaunal biomass could be solely due to the weight of foraminiferan's large calcium carbonate tests. In contrast, macrofaunal weight is mostly comprised of organic material. The relative contribution of meiofaunal taxa to the total abundance and biomass of box core samples varied greatly with depth (Figure C.1). On average, macrofauna were responsible for a larger percent of total abundance and biomass on the shelf and conversely meiofauna became larger contributors on the slope. That affirms previous observations that the relative biomass of meiofauna tends to increase with depth as smaller bodied organisms make up a larger component of the benthos at depth [Rex et al., 2006]. However, this trend was not consistent among all transects; the shallowest (30 m) station of transect K was dominated by the meiofauna as a result of extremely low numbers of macrofaunal individuals at that one station.

It is important to note that the meiofauna considered here were collected using macrofaunal sampling protocols. Thus, these meiofaunal individuals constitute only the largest size fraction of organism typically categorized as meiofauna [Higgins and Thiel, 1988]. In addition, foraminiferans in these sampled could be planktic or benthic forms, both of which are abundant in this region [Scott et al., 2008b] and were not distinguished between here. However, the majority of foraminiferans in the surface sediments of the Beaufort Shelf are benthic forms while planktic forms increase in relative abundance on the slope around 1000 m in depth [Scott et al., 2008a]. Thus, the meiofaunal distribution described here is most likely driven by benthic foraminiferans. Lastly, meiofaunal abundance and biomass may be inflated relative to macrofaunal biomass due to the increased difficulty in distinguishing live from dead meiofaunal specimens.

**Table C.1. Total abundance and biomass of meio- and macrofauna by sample.** Meiofauna taxa include Foraminifera, Nematoda and Ostracoda. Sample area = 0.125 $m^2$.

| Transect | Depth (m) | Meiofaunal Abundance | Macrofaunal Abundance | Meiofaunal Biomass (ww g) | Macrofaunal Biomass (ww g) |
|---|---|---:|---:|---:|---:|
| D | 30 | 143 | 160 | 0.052 | 5.956 |
| | 75 | 3090 | 275 | 40.640 | 2.306 |
| | 200 | 809 | 81 | 2.859 | 0.375 |
| | 500 | 2498 | 150 | 13.602 | 1.115 |
| | 750 | 15095 | 30 | 12.453 | 0.077 |
| K | 30 | 255 | 3 | 0.112 | 0.031 |
| | 75 | 451 | 93 | 0.188 | 0.601 |
| | 200 | 596 | 73 | 2.551 | 0.245 |
| | 500 | 2178 | 213 | 3.043 | 2.079 |
| | 750 | 13692 | 28 | 9.515 | 0.351 |
| G | 30 | 732 | 113 | 0.355 | 1.133 |
| | 75 | 1415 | 122 | 1.534 | 1.479 |
| | 200 | 194 | 173 | 1.021 | 0.729 |
| | 500 | 4449 | 486 | 9.021 | 1.662 |
| | 750 | 4496 | 105 | 6.154 | 0.437 |
| T | 30 | 512 | 564 | 0.312 | 8.766 |
| | 75 | 88 | 116 | 0.328 | 0.810 |
| | 200 | 147 | 121 | 0.594 | 0.795 |
| | 500 | 3261 | 308 | 8.989 | 2.293 |
| | 750 | 1308 | 39 | 1.372 | 0.234 |

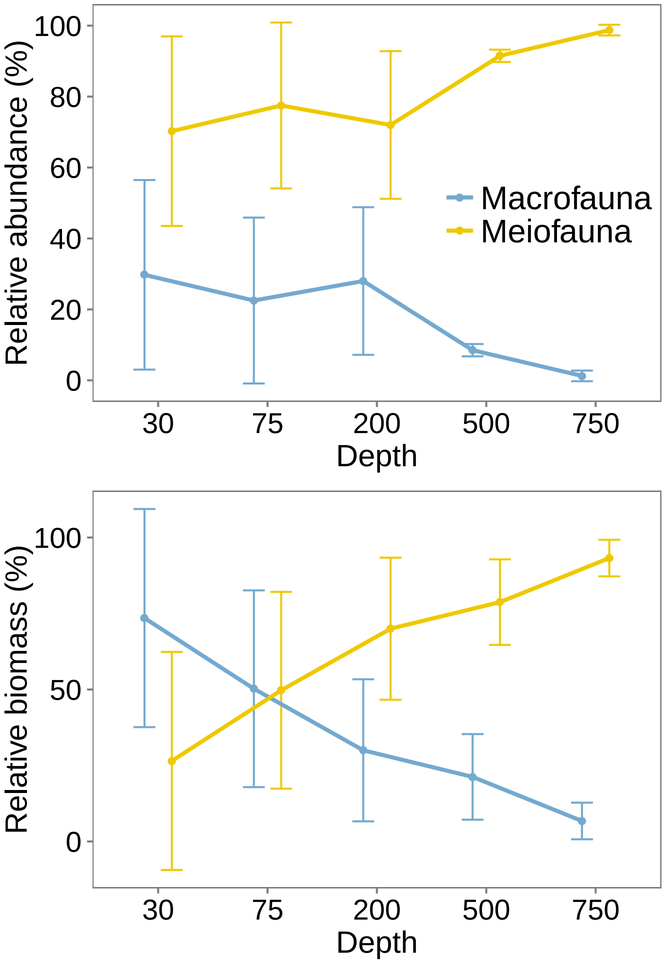


**Figure C.1. Relative abundance (top) and biomass (bottom) of meio- and macrofauna in box core samples.** Sample area = 0.125 $m^2$.

# Appendix D

# Macro- and megafaunal datasets

**Table D.1. Macrofaunal data from ArcticNet sampling (used in Chapter 2).** Total abundance from 48 samples. Represents the final dataset following data processing (see Section 2.2.2)

| **Phylum** | **Class** | **Family (or Order)** | **Species** | **Total abundance (#/6 m$^2$)** |
|---|---|---|---|---|
| Annelida | Clitellata | | | 66 |
| | Polychaeta | Apistobranchidae | | 1 |
| | | Capitellidae | | 134 |
| | | Chaetopteridae | *Spiochaetopterus typicus* | 5 |
| | | Cirratulidae | | 239 |
| | | Cossuridae | *Cossura* | 34 |
| | | Dorvilleidae | *Schistomeringos rudolphii* | 9 |
| | | Eunicidae | | 1 |
| | | Flabelligeridae | | 9 |
| | | Hesionidae | *Nereimyra* | 3 |
| | | Lumbrineridae | | 121 |
| | | Maldanidae | | 760 |
| | | Nephtyidae | | 975 |
| | | Onuphidae | | 58 |
| | | Opheliidae | *Ophelina* | 36 |
| | | Orbiniidae | | 43 |
| | | Oweniidae | | 178 |
| | | Paraonidae | *Aricidea* | 82 |
| | | | *Paraonis gracilis* | 23 |
| | | Pholoidae | *Pholoe* | 64 |
| | | Phyllodocidae | | 12 |
| | | Pilargidae | *Sigambra* | 4 |
| | | Scalibregmatidae | | 10 |
| | | Sphaerodoridae | | 11 |

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Table D.1 – *Continued from previous page*

| **Phylum** | **Class** | **Family (or Order)** | **Species** | **Total abundance (#/6 m$^2$)** |
|---|---|---|---|---:|
| | | Spionidae | | 123 |
| | | Syllidae | | 32 |
| | | Trichobranchidae | *Terebellides* | 78 |
| | | Trochochaetidae | *Trochochaeta multisetosa* | 1 |
| Arthropoda | Malacostraca | Aoridae | *Arctolembos arcticus* | 1 |
| | | | *Autonoe borealis* | 2 |
| | | Argissidae | | 1 |
| | | Nannastacidae | *Campylaspis* | 8 |
| | | Corophiidae | *Protomedeia fasciata* | 34 |
| | | Desmosomatidae | *Eugerda tenuimana* | 25 |
| | | | *Oecidiobranchus plebejum* | 1 |
| | | Gammaridea | | 14 |
| | | Isaeidae | | 11 |
| | | Leuconidae | | 442 |
| | | Macrostylidae | *Macrostylis* | 1 |
| | | Munnidae | *Munna* | 4 |
| | | Nannastacidae | *Campylaspis glabra* | 1 |
| | | | *Cumella carinata* | 2 |
| | | Paratanaoidea | *Akanthophoreus gracilis* | 94 |
| | | | *Chauliopleona* | 21 |
| | | | *Leptognathioides polita* | 4 |
| | | Pardaliscidae | | 19 |
| | | Photidae | *Photis pollex* | 14 |
| | | | *Photis reinhardi* | 1 |
| | | Phoxocephalidae | *Harpinia pectinata* | 1 |
| | | | *Harpinia salebrosa* | 7 |
| | | | *Harpinia serrata* | 10 |
| | | | *Paraphoxus oculatus* | 4 |
| | | Pleustidae | *Parapleustes gracilis* | 1 |
| | | | *Pleusymtes pulchella* | 1 |
| | | Pseudotanaidae | *Pseudotanais* | 8 |
| | | Sphyrapidae | *Pseudosphyrapus serratus* | 64 |
| | | Tanaellidae | *Araphura* | 1 |
| | | Typhlotanaidae | *Typhlotanais* | 7 |
| Mollusca | Bivalvia | Galeommatoidea | | 25 |
| | | Lasaeidae | *Veneroida* | 1 |
| | | Limidae | *Limatula hyperborea* | 1 |
| | | | *Limatula subauriculata* | 1 |
| | | Lucinidae | | 1 |
| | | Montacutidae | *Montacuta* | 25 |
| | | | *Mysella* | 18 |
| | | Nuculidae | *Ennucula tenuis* | 28 |

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Table D.1 – *Continued from previous page*

| **Phylum** | **Class** | **Family (or Order)** | **Species** | **Total abundance (#/6 m$^2$)** |
|---|---|---|---|---|
| | | Propeamussiidae | *Similipecten greenlandicus* | 14 |
| | | Tellinidae | | 40 |
| | | Thyasiridae | | 199 |
| | | Yoldiidae | *Portlandia* | 8 |
| | | | *Yoldiella* | 96 |
| | Caudofoveata | | | 15 |
| | Gastropoda | Cylichnidae | *Cylichna* | 105 |
| | | Retusidae | *Retusa* | 47 |
| | | Rissoidae | | 37 |
| | | Trichotropidae | | 1 |
| | | Turridae | | 1 |
| Sipuncula | | | | 154 |

**Table D.2. Megafaunal data from ArcticNet sampling (used in Chapter 2).** Total abundance from 48 samples. Represents the final dataset following data processing (see Section 2.2.2)

| **Phylum** | **Class** | **Family (or Order)** | **Species** | **Total abundance (#/21,600 m$^2$)** |
|---|---|---|---|---|
| Annelida | Polychaeta | Ampharetidae | | 315 |
| | | Nereididae | *Nereis pelagica* | 1 |
| | | | *Nereis zonata* | 152 |
| | | Pectinariidae | *Cistenides* | 30799 |
| | | Polynoidae | *Polynoidae* | 4662 |
| | | Sabellidae | *Sabellidae* | 1174 |
| | | Serpulidae | *Apomatus globifer* | 11 |
| | | | *Apomatus similis* | 237 |
| | | Terebellidae | | 1131 |
| Arthropoda | Malacostraca | Acanthonotozomatidae | *Acanthonotozoma cristatum* | 2 |
| | | | *Acanthonotozoma inflatum* | 38 |
| | | | *Acanthonotozoma serratum* | 31 |
| | | Acidostomatidae | *Acidostoma* | 1 |
| | | Amathillopsidae | *Amathillopsis spinigera* | 6 |
| | | Ampeliscidae | *Ampelisca* | 39484 |
| | | | *Byblis* | 493 |
| | | | *Haploops* | 264 |
| | | Aoridae | *Lembos* | 30 |
| | | Atylidae | *Atylus carinatus* | 59 |
| | | | *Atylus smittii* | 32 |
| | | | *Nototropis smitti* | 94 |

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Table D.2 – *Continued from previous page*

| **Phylum** | **Class** | **Family (or Order)** | **Species** | **Total abundance (#/6 m$^2$)** |
|---|---|---|---|---:|
| | | Bopyridae | *Hemiarthrus abdominalis* | 27 |
| | | Calliopiidae | *Calliopiidae* | 75 |
| | | Caprellidae | *Caprella linearis* | 22 |
| | | | *Tritella pilimana* | 9 |
| | | Chaetiliidae | *Saduria entomon* | 1 |
| | | | *Saduria sabini* | 4842 |
| | | | *Saduria sibirica* | 3004 |
| | | Crangonidae | *Argis* | 122 |
| | | | *Sabinea* | 233 |
| | | Cyclocaridae | *Cyclocaris guilelmi* | 1 |
| | | Diastylidae | *Diastylidae* | 1076 |
| | | Epimeriidae | *Epimeria loricata* | 7 |
| | | | *Paramphithoe hystrix* | 60 |
| | | | *Paramphithoe polyacantha* | 1 |
| | | Euphausiidae | *Euphausiidae* | 17 |
| | | Eusiridae | *Eusirus holmi* | 4 |
| | | | *Rhachotropis* | 3574 |
| | | | *Rozinante fragilis* | 147 |
| | | Gnathiidae | *Caecognathia stygia* | 186 |
| | | | *Gnathia* | 145 |
| | | Hippolytidae | *Bythocaris* | 93 |
| | | | *Eualus* | 508 |
| | | | *Lebbeus polaris* | 5 |
| | | | *Spirontocaris* | 90 |
| | | Hyperiidae | *Parathemisto* | 3 |
| | | | *Themisto* | 18 |
| | | Idoteidae | *Synidotea bicuspida* | 792 |
| | | | *Synidotea marmorata* | 39 |
| | | Ischyroceridae | *Ericthonius* | 113 |
| | | | *Ischyrocerus* | 445 |
| | | | *Jassa* | 9 |
| | | Leptanthuridae | *Calathura brachiata* | 27 |
| | | Lophogastridae | | 7 |
| | | Lysianassidae | | 3546 |
| | | Melitidae | | 768 |
| | | Munnopsidae | *Ilyarachna* | 1 |
| | | | *Munnopsis typica* | 258 |
| | | | *Munnopsurus* | 9 |
| | | Mysidacea | *Mysidacea* | 24 |
| | | Mysidae | *Mysidae* | 174 |
| | | Nebaliidae | *Nebalia* | 7 |
| | | Oedicerotidae | | 1591 |
| | | Oplophoridae | *Hymenodora* | 10 |
| | | Pardaliscidae | *Pardalisca cuspidata* | 97 |

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Table D.2 – *Continued from previous page*

| **Phylum** | **Class** | **Family (or Order)** | **Species** | **Total abundance (#/6 m$^2$)** |
|---|---|---|---|---|
| | | Pontoporeiidae | *Pontoporeia femorata* | 416 |
| | | Stegocephalidae | | 163 |
| | | Stenothoidae | *Metopa* | 6 |
| | | Uristidae | *Anonyx* | 2175 |
| | | | *Ichnopus spinicornis* | 33 |
| | | | *Tmetonyx* | 36 |
| | Pycnogonida | Nymphonidae | *Boreonymphon* | 48 |
| | | | *Nymphon* | 632 |
| Brachiopoda | | | | 400 |
| Cephalorhyncha | Priapulida | | | 22 |
| Chordata | Actinopterygii | Agonidae | *Aspidophoroides monopterygius* | 8 |
| | | | *Ulcina olrikii* | 180 |
| | | Cottidae | *Gymnocanthus tricuspis* | 14 |
| | | | *Icelus* | 296 |
| | | | *Myoxocephalus* | 51 |
| | | | *Triglops nybelini* | 9 |
| | | Cyclopteridae | *Careproctus* | 1 |
| | | | *Liparis fabricii* | 2 |
| | | | *Liparis gibbus* | 1 |
| | | Gadidae | *Boreogadus* | 19 |
| | | Liparidae | *Liparidae* | 151 |
| | | Psychrolutidae | *Cottunculus microps* | 2 |
| | | Stichaeidae | *Anisarchus medius* | 20 |
| | | Zoarcidae | *Lycodes* | 164 |
| | Ascidiacea | | | 372 |
| | Elasmobranchii | Rajidae | *Amblyraja hyperborea* | 1 |
| Cnidaria | Anthozoa | Actiniaria | | 332 |
| | | Cerianthidae | | 5 |
| | | Nephtheidae | *Gersemia* | 47 |
| | Hydrozoa | Campanulariidae | | 50 |
| | | Campanulinidae | | 48 |
| | | Eudendriidae | *Eudendrium* | 7 |
| | | Lafoeidae | | 24 |
| | | Sertulariidae | | 4 |
| | | Tiarannidae | *Stegopoma* | 12 |
| Echinodermata | Asteroidea | Asteriidae | *Icasterias panopla* | 514 |
| | | Astropectinidae | *Psilaster* | 122 |
| | | Benthopectinidae | *Pontaster tenuispinus* | 1306 |
| | | Ctenodiscidae | *Ctenodiscus crispatus* | 857 |
| | | Poraniidae | *Poraniomorpha* | 5 |

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Table D.2 – *Continued from previous page*

| **Phylum** | **Class** | **Family (or Order)** | **Species** | **Total abundance (#/6 m$^2$)** |
|---|---|---|---|---|
| | | Pterasteridae | *Hymenaster pellucidus* | 11 |
| | | | *Pteraster obscurus* | 15 |
| | | Solasteridae | *Crossaster papposus* | 55 |
| | | | *Solaster endeca* | 2 |
| | Crinoidea | Antedonidae | *Heliometra glacialis* | 11 |
| | | | *Poliometra* | 28 |
| | Echinoidea | Strongylocentrotidae | *Strongylocentrotus* | 10 |
| | Holothuroidea | Dendrochirotida | *Dendrochirotida* | 1473 |
| | | Molpadiidae | *Molpadiidae* | 15 |
| | | Myriotrochidae | *Myriotrochus* | 2653 |
| | Ophiuroidea | Amphiuridae | *Amphiura* | 1672 |
| | | Gorgonocephalidae | *Gorgonocephalus* | 148 |
| | | Ophiacanthidae | *Ophiacantha* | 1000 |
| | | Ophiactidae | *Ophiactidae* | 3 |
| | | Ophiuridae | *Ophiocten* | 261388 |
| | | | *Ophiopleura* | 1354 |
| | | | *Ophiura* | 21568 |
| Mollusca | Bivalvia | Arcidae | *Bathyarca* | 1263 |
| | | Astartidae | | 7380 |
| | | Cardiidae | | 1323 |
| | | Cuspidariidae | *Cuspidaria* | 166 |
| | | Hiatellidae | *Cyrtodaria siliqua* | 22 |
| | | | *Hiatella arctica* | 85 |
| | | Lyonsiidae | *Lyonsia* | 557 |
| | | Myidae | *Mya* | 294 |
| | | Mytilidae | | 5191 |
| | | Nuculanidae | *Nuculana* | 3267 |
| | | Nuculidae | *Nucula* | 9311 |
| | | Pandoridae | *Pandora glacialis* | 256 |
| | | Pectinidae | | 654 |
| | | Periplomatidae | *Periploma* | 42 |
| | | Tellinidae | *Tellininae* | 2240 |
| | | Veneridae | *Liocyma fluctuosa* | 1165 |
| | | Yoldiidae | *Yoldia* | 1533 |
| | Cephalopoda | Octopodidae | *Bathypolypus arcticus* | 12 |
| | | Sepiolidae | | 17 |
| | Gastropoda | Acmaeidae | *Acmaea* | 12 |
| | | Buccinidae | *Beringius behringi* | 5 |
| | | | *Buccinum* | 275 |
| | | | *Colus* | 409 |
| | | | *Neptunea* | 18 |
| | | | *Plicifusus kroeyeri* | 65 |
| | | | *Siphonorbis* | 62 |
| | | Cancellariidae | | 382 |

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Table D.2 – *Continued from previous page*

| **Phylum** | **Class** | **Family (or Order)** | **Species** | **Total abundance (#/6 m$^2$)** |
|---|---|---|---|---:|
| | | Capulidae | *Trichotropis borealis* | 678 |
| | | Conidae | *Oenopota* | 513 |
| | | Diaphanidae | *Diaphana globosa* | 78 |
| | | Mangeliidae | *Propebela* | 326 |
| | | Muricidae | *Boreotrophon* | 99 |
| | | | *Nodulotrophon* | 78 |
| | | Naticidae | *Naticidae* | 468 |
| | | Nudibranchia | | 17 |
| | | Philinidae | *Philine* | 2 |
| | | Pyramidellidae | | 62 |
| | | Solariellidae | *Solariella* | 223 |
| | | Turbinidae | *Margarites* | 537 |
| | | Turritellidae | *Tachyrhynchus* | 10673 |
| | | Velutinidae | *Velutina* | 10 |
| | Scaphopoda | Gadilidae | *Siphonodentalium* | 848 |
| Nemertea | | | | 109 |
| Platyhelminthes | | | | 205 |

**Table D.3. Macrofaunal data from BREA sampling (used in Chapter 3).** Total abundance and biomass from 15 samples along transects T, G, & K. Represents the final dataset following data processing (see Section 3.2.2)

| **Phylum** | **Class** | **Family (or Order)** | **Total abundance (#/1.875 m$^2$)** | **Total biomass (ww g/ 1.875 m$^2$)** |
|---|---|---|---:|---:|
| Annelida | Polychaeta | Acrocirridae | 1 | 0.000 |
| | | Ampharetidae | 4 | 0.052 |
| | | Apistobranchidae | 22 | 0.007 |
| | | Capitellidae | 107 | 0.475 |
| | | Chaetopteridae | 14 | 0.953 |
| | | Cirratulidae | 254 | 0.609 |
| | | Cossuridae | 27 | 0.004 |
| | | Dorvilleidae | 6 | 0.007 |
| | | Lumbrineridae | 125 | 0.545 |
| | | Maldanidae | 559 | 6.856 |
| | | Nephtyidae | 179 | 2.687 |
| | | Opheliidae | 37 | 0.058 |
| | | Orbiniidae | 16 | 0.022 |
| | | Oweniidae | 29 | 0.088 |
| | | Paraonidae | 100 | 0.096 |
| | | Pectinariidae | 2 | 0.034 |
| | | Pholoidae | 88 | 0.082 |
| | | Phyllodocidae | 6 | 0.020 |
| | | Pilargidae | 1 | 0.000 |
| | | Serpulidae | 3 | 0.189 |
| | | Spionidae | 100 | 1.474 |

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Table D.3 – *Continued from previous page*

| **Phylum** | **Class** | **Family (or Order)** | **Total abundance ($\#/1.875\ m^2$)** | **Total biomass (ww g/ $1.875\ m^2$)** |
|---|---|---|---|---|
| | | Sternaspidae | 10 | 1.284 |
| | | Syllidae | 1 | 0.000 |
| | | Trichobranchidae | 34 | 0.347 |
| Arthropoda | Malacostraca | Akanthophoreidae | 86 | 0.016 |
| | | Argissidae | 1 | 0.003 |
| | | Corophiidae | 4 | 0.003 |
| | | Desmosomatidae | 10 | 0.005 |
| | | Ischyroceridae | 1 | 0.001 |
| | | Leuconidae | 21 | 0.041 |
| | | Nannastacidae | 4 | 0.026 |
| | | Nebaliidae | 1 | 0.000 |
| | | Pardaliscidae | 10 | 0.015 |
| | | Photidae | 17 | 0.011 |
| | | Phoxocephalidae | 10 | 0.009 |
| | | Pontoporeiidae | 17 | 0.051 |
| | | Pseudotanaidae | 2 | 0.000 |
| | | Sphyrapidae | 19 | 0.016 |
| | | Stenothoidae | 1 | 0.000 |
| | | Typhlotanaidae | 2 | 0.000 |
| Brachiopoda | | | 1 | 0.174 |
| Hemichordata | Enteropneusta | | 2 | 0.010 |
| Mollusca | Bivalvia | Limidae | 2 | 0.041 |
| | | Montacutidae | 2 | 0.005 |
| | | Pectinidae | 6 | 0.020 |
| | | Periplomatidae | 1 | 0.491 |
| | | Thyasiridae | 210 | 0.934 |
| | | Veneridae | 18 | 1.165 |
| | | Yoldiidae | 106 | 0.618 |
| | Caudofoveata | Chaetodermatidae | 5 | 0.119 |
| | Gastropoda | Naticidae | 3 | 0.826 |
| | | Philinoidea | 2 | 0.001 |
| | | Retusidae | 7 | 0.013 |
| | | Rissoidae | 14 | 0.023 |
| | Scaphopoda | Gadilidae | 6 | 0.328 |
| Sipuncula | Sipunculidea | Sipunculidae | 82 | 0.331 |

**Table D.4. Megafaunal data from BREA sampling (used in Chapter 3).** Total abundance and biomass from 15 samples along transects T, G, & K. Represents the final dataset following data processing (see Section 3.2.2)

| **Phylum** | **Class** | **Family (or Order)** | **Total abundance ($\#/14{,}500\ m^2$)** | **Total biomass (ww g/ $14{,}500\ m^2$)** |
|---|---|---|---|---|
| Annelida | Clitellata | | 1 | 2.8 |
| | Polychaeta | Flabelligeridae | 4 | 1.8 |
| | | Hesionidae | 1 | 0.0 |
| | | Nereididae | 56 | 6.4 |

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Table D.4 – *Continued from previous page*

| **Phylum** | **Class** | **Family (or Order)** | **Total abundance (#/14,500 m$^2$)** | **Total biomass (ww g/ 14,500 m$^2$)** |
|---|---|---|---|---|
| | | Onuphidae | 798 | 22.3 |
| | | Polynoidae | 941 | 149.8 |
| | | Sabellidae | 3 | 1.8 |
| | | Scalibregmatidae | 24 | 2.7 |
| | | Sphaerodoridae | 41 | 1.0 |
| | | Terebellidae | 1 | 0.1 |
| Arthropoda | Malacostraca | Acanthephyridae | 1 | 1.7 |
| | | Acanthonotozomatidae | 1 | 0.0 |
| | | Acidostomatidae | 6 | 0.2 |
| | | Amathillopsidae | 16 | 13.1 |
| | | Ampeliscidae | 157 | 10.3 |
| | | Antarcturidae | 128 | 4.7 |
| | | Atylidae | 1400 | 157.0 |
| | | Bopyridae | 6 | 0.1 |
| | | Calliopiidae | 140 | 32.3 |
| | | Caprellidae | 292 | 1.2 |
| | | Chaetiliidae | 186 | 100.8 |
| | | Crangonidae | 154 | 1005.3 |
| | | Diastylidae | 1 | 0.0 |
| | | Epimeriidae | 90 | 16.7 |
| | | Euphausiidae | 9 | 1.1 |
| | | Eusiridae | 312 | 39.5 |
| | | Gammaridae | 1 | 0.7 |
| | | Gnathiidae | 396 | 10.0 |
| | | Hippolytidae | 320 | 416.8 |
| | | Hyperiidae | 14 | 0.2 |
| | | Idoteidae | 1362 | 269.2 |
| | | Lampropidae | 2 | 0.0 |
| | | Leptanthuridae | 121 | 6.0 |
| | | Lysianassidae | 163 | 14.7 |
| | | Melitidae | 8 | 0.9 |
| | | Melphidippidae | 12 | 0.1 |
| | | Munnopsidae | 124 | 2.9 |
| | | Mysidae | 604 | 222.9 |
| | | Ochlesidae | 8 | 0.0 |
| | | Oedicerotidae | 293 | 153.5 |
| | | Pleustidae | 32 | 1.6 |
| | | Podasconidae | 1 | 0.2 |
| | | Pontogeneiidae | 5 | 0.2 |
| | | Stegocephalidae | 61 | 0.7 |
| | | Stilipedidae | 2 | 0.0 |
| | | Synopiidae | 173 | 1.5 |
| | | Uristidae | 1 | 0.5 |
| | Pycnogonida | Callipallenidae | 4 | 1.9 |
| | | Colossendeidae | 18 | 70.0 |
| | | Nymphonidae | 7 | 4.1 |
| Bryozoa | Gymnolaemata | Alcyonidiidae | 124 | 6.7 |

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Table D.4 – *Continued from previous page*

| **Phylum** | **Class** | **Family (or Order)** | **Total abundance (#/14,500 m$^2$)** | **Total biomass (ww g/ 14,500 m$^2$)** |
|---|---|---|---:|---:|
| | | Bugulidae | 24 | 0.7 |
| | | Calloporidae | 16 | 17.4 |
| | | Celleporidae | 4 | 0.8 |
| | | Eucrateidae | 1 | 0.4 |
| | | Exochellidae | 5 | 0.2 |
| | | Flustridae | 6 | 0.8 |
| | | Myriaporidae | 40 | 24.4 |
| | | Romancheinidae | 4 | 1.2 |
| | | Smittinidae | 70 | 2.3 |
| | | Umbonulidae | 16 | 1.2 |
| | Stenolaemata | Lichenoporidae | 21 | 0.9 |
| | | Tubuliporidae | 18 | 0.3 |
| Cephalorhyncha | Priapulida | Priapulidae | 27 | 13.5 |
| Chordata | Ascidiacea | Ascidiidae | 4 | 46.8 |
| | | Molgulidae | 16 | 2.7 |
| Cnidaria | Anthozoa | Actiniaria | 134 | 878.1 |
| | | Nephtheidae | 27 | 699.8 |
| | Hydrozoa | Bougainvilliidae | 1 | 0.0 |
| | | Campanulariidae | 16 | 0.1 |
| | | Lafoeidae | 82 | 1.2 |
| Echinodermata | Asteroidea | Asteriidae | 254 | 2079.2 |
| | Asteroidea | Astropectinidae | 29 | 360.7 |
| | | Benthopectinidae | 977 | 2049.1 |
| | | Ctenodiscidae | 100 | 861.9 |
| | | Pterasteridae | 35 | 28.1 |
| | | Solasteridae | 48 | 489.7 |
| | Crinoidea | Antedonidae | 141 | 1233.2 |
| | Echinoidea | Strongylocentrotidae | 16 | 271.8 |
| | Holothuroidea | Dendrochirotida | 229 | 235.1 |
| | | Molpadiidae | 8 | 301.1 |
| | | Myriotrochidae | 149 | 725.3 |
| | Ophiuroidea | Amphiuridae | 16 | 0.7 |
| | | Gorgonocephalidae | 20 | 2557.0 |
| | | Ophiacanthidae | 1608 | 2083.2 |
| | | Ophiuridae | 51870 | 4294.6 |
| Mollusca | Bivalvia | Arcidae | 23316 | 16782.5 |
| | | Astartidae | 5 | 46.8 |
| | | Cardiidae | 12 | 5.4 |
| | | Cuspidariidae | 24 | 6.7 |
| | | Lyonsiidae | 2 | 1.9 |
| | | Mytilidae | 171 | 3.3 |
| | | Nuculanidae | 390 | 251.5 |
| | | Nuculidae | 166 | 72.5 |
| | | Pandoridae | 3 | 0.7 |
| | | Propeamussiidae | 4924 | 1488.2 |

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Table D.4 – *Continued from previous page*

| **Phylum** | **Class** | **Family (or Order)** | **Total abundance (#/14,500 m$^2$)** | **Total biomass (ww g/ 14,500 m$^2$)** |
|---|---|---|---:|---:|
| | | Tellinidae | 179 | 312.9 |
| | | Thraciidae | 40 | 1.5 |
| | Cephalopoda | Octopodidae | 8 | 305.9 |
| | Gastropoda | Buccinidae | 171 | 515.9 |
| | | Cancellariidae | 57 | 21.2 |
| | | Clionidae | 1 | 0.3 |
| | | Cylichnidae | 88 | 6.8 |
| | | Diaphanidae | 21 | 0.2 |
| | | Mangeliidae | 72 | 2.9 |
| | | Margaritidae | 144 | 14.9 |
| | | Nudibranchia | 12 | 15.2 |
| | | Philinidae | 417 | 19.1 |
| | | Velutinidae | 4 | 2.2 |
| | Solenogastres | | 150 | 1.1 |
| Nemertea | | | 186 | 119.8 |
| Platyhelminthes | | | 42 | 12.6 |
| Porifera | Demospongiae | | 32 | 42.1 |
| Sipuncula | Sipunculidea | Phascolionidae | 1299 | 49.5 |

# Glossary

$\alpha$ **diversity** Local diversity within a single habitat, in its simplest form: the number of species found at one locality [Whittaker, 1972]. 11

$\beta$ **diversity** The degree of differentiation occurring in communities along an environmental gradient (between habitats) [Whittaker, 1972]. 11

**Average silhouette width (ASW)** Measure of average dissimilarity of stations between- versus within-clusters [Rousseeuw, 1987]. For each station $i$, the silhouette width $s(i)$ is defined as:

$$s(i) = \frac{b(i) - a(i)}{max(a(i), b(i))}$$

where $a(i)$ is the average dissimilarity between $i$ and all other stations of the cluster to which $i$ belongs and $b(i)$ is the minimum dissimilarity between $i$ and all other stations belonging to its neighbouring cluster. 21

**Bentho–pelagic coupling** The relationship between pelagic primary productivity and the flux of organic matter to the underlying benthic realm [Hargrave, 1973]. 1

**Benthos** The organisms which live within, on or near the seafloor [Gage and Tyler, 1991]. 1

**Biological surrogate** Using one faunal component of a system to represent the whole. 74

**Community structure** The composition of species that occupy a given area and their relative abundance. 11

**Continental margins** A region of the seafloor past the coastal zone encompassing the shelf and slope down to the edge of the abyssal plane (roughly $100 - 4000$ m depth [Levin and Dayton, 2009]). 2

**Distribution of occurrence** A frequency distribution of the number of species found to occupy varying number of stations. Used as a proxy for the 'distribution of species range size' when the true range size of species are unknown. 22

**Ecological succession** The gradual process of faunal replacement over time where one community supplants another. 4

**ES$_{50}$** The expected number of taxa in 50 individuals,

$$ES_n = \sum_{i=1}^{S} 1 - \frac{\begin{matrix} N - N_i \\ n \end{matrix}}{\begin{matrix} N \\ n \end{matrix}}$$

with N individuals and S species [Hurlbert, 1971]. 45

**Faunal assemblage** A group of animals that occur together in a particular habitat or range. 3

**Heterogeneity** State of non-uniformity, any measured variable (e.g. sediment grain size, organic matter input, faunal density) varying from one location to the next [Kolasa and Rollo, 1991]. 27

**Homogeneity** The absence of variation, uniformity [Kolasa and Rollo, 1991]. 3

**Macrofauna** Benthic fauna that are retained on a 0.25 to 0.5 mm sieve [Snelgrove, 1998] typically sampled with grabs or box corers. 4

**Megafauna** The larger and mostly epifaunal (surficial) benthic fauna that can be identified in bottom photographs [Snelgrove, 1999] typically sampled using trawls or video. 4

**Meiofauna** Benthic fauna smaller than the macrofauna passing through a 1 mm sieve but retained on a ~45 $\mu$m sieve [Higgins and Thiel, 1988]. 4

**Pseudo-rarity** Taxa that appear rare because they are sampled on the fringe of their optimal geographic range [Gaston et al., 1997; Rabinowitz, 1981]. 23

**Q-mode analyses** Describes the association between objects (sampling stations) [Legendre and Legendre, 2012]. 77

**R-mode analyses** Describes the association between descriptors (species)[Legendre and Legendre, 2012]. 77

**Rarefaction** The number of species presented as a function of the number of individuals [Sanders, 1968] (i.e. the number of species that would likely be sampled for a certain number individuals collected). 21

**Relative abundance** The contribution of a species to the total number of individuals in an area. 20

**Sparsity** Widely spaced and low density individuals resulting in a low population size in a given area. 24

**Spatial autocorrelation** The tenancy for observations in close geographic proximity to lack independence [Diniz-Filho et al., 2003]. 76

**Species-abundance distribution** A description of the number of individuals (y-axis) of each species (x-axis) typically ranked from species with high to low abundance [McGill et al., 2007]. 3

**Taxonomic rank** The position in the hierarchy of biological classification (phylum–class–order–family–genus–species). 16

**Uniques** Species which are present in only one of many samples [Chao et al., 2004]. 22

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