ALASKAN ARCTIC EPIBENTHIC COMMUNITIES: DISTRIBUTION PATTERNS, LINKS TO THE ENVIRONMENT, AND BRITTLE STAR POPULATION DYNAMICS

BY

ALEXANDRA MARIELA RAVELO, B.A.

A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY
IN
MARINE BIOLOGY

UNIVERSITY OF ALASKA FAIRBANKS
AUGUST 2016

APPROVED:
Dr. Brenda Konar, Committee Chair
Dr. Bodil Bluhm, Committee Member
Dr. Andrew Mahoney, Committee Member
Dr. Peter Winsor, Committee Member
Dr. Christian Zimmerman, Committee Member
Dr. Sarah Hardy, Chair
Graduate Program in Marine Science and Limnology
Dr. S. Bradley Moran, Dean
School of Fisheries and Ocean Sciences
Dr. Michael Castellini
Interim Dean of the Graduate School

ABSTRACT

The Arctic marine shelves are characterized by areas of high and low invertebrate standing stock and communities that vary spatially in patches. Large-scale environmental characteristics, such as the distribution of water masses, the fenology of sea ice cover, and variability of water depth define changes in epibenthic community structure throughout the Arctic shelves. The longevity and relatively low mobility of epibenthic invertebrates make them especially relevant as indicators of long-term environmental patterns. In terms of standing stock and biomass, the most representative group among Arctic epibenthic taxa are brittle stars. Large areas of the Arctic shelves have dense assemblages of brittle stars; however, despite their ecological importance for Arctic shelf systems, little is known of their age, growth and turnover rates. The research developed through this dissertation examined how environmental drivers influence epibenthic invertebrate communities of the Alaska Arctic shelves and the population parameters of the dominant brittle star species. The first chapter of my dissertation focused on the northeastern Chukchi Sea and the second one focused on the Alaskan Beaufort Sea. The overarching questions addressed in chapters 1 and 2 focused on characterizing the epibenthic communities of the Alaskan Chukchi and Beaufort seas and defining environmental characteristics that influence the community structure. To answer this question, biological and environmental data were collected and analyzed in 2009 and 2010 in the Chukchi Sea, and in 2011 in the Beaufort Sea. For my third chapter, the overarching question was: what is the predictive power of the seasonality of sea ice for epibenthic community structure in the Alaskan Arctic, and how does it compare to more commonly used environmental descriptors. To test this relationship, six variables depicting the patterns of the seasonality of sea ice were computed from passive microwave sea ice concentration data. For the fourth chapter, the overarching question was, what are the population parameters of the two dominant brittle star species of the Alaskan Arctic. For this analysis, individuals of *Ophiura sarsii* and *Ophiocten sericeum* were collected in 2013 for age and organic mass determination.

Findings of this research indicate that epibenthic communities have a patchy distribution with one or a few taxa dominating the community over large spatial extents. In both the Chukchi and Beaufort seas, communities were dominated by either crustaceans or echinoderms. Only in the mid-depth stations of the Beaufort Sea were both groups equally abundant. The environmental measure that best correlated to epibenthic commuity structure in both regions was longitude. Biologically relevant variables, such as sediment grain size, sediment phaeopigments, bottom water temperature and salinity, though region specific, were also important drivers of commuity structure. As predictors of epibenthic community structure, sea ice variables resulted in moderate to high correlation values. In the Beaufort Sea, sea ice variables performed better than traditionally used environmental descriptors; however, this was not the case for the Chukchi Sea. This study is the first to report on the age, growth and turnover of Arctic brittle stars. The asymptotic age was higher for *O. sarsii* than for *O. sericeum*; however, both species had significantly higher maximum ages than temperate region congeners. The individual production of *O. sarsii* surpassed that of *O. sericeum* by an order of magnitude throughout the size spectra.

As a whole, this research highlights the complexity of the biological-environmental interactions that create the large spatial variability in community structure, benthic biomass and diversity throughout the Alaska Arctic. The variability in community structure throughout the Chukchi and Beaufort seas was linked qualitatively to large-scale environmental patterns. Quantitatively, these environmental forces were represented by the date of sea ice return and date of sea ice retreat in the Beaufort Sea. The predictive power of sea ice variables was reduced in the Chukchi Sea by the large inter-annual variability in wind direction and intensity that in turn affect the pattern of seasonality of sea ice. As integrators of large-scale environmental patterns, sea ice variables proved useful as additional predictors of epibenthic community structure.

The dominant shelf brittle star species do not experience short-term fluctuations in population size. Top-down and bottom-up controls on these populations, such as predation and food supply, may be governing their growth strategy and total annual growth. Considering the longevity and slow growth of many Arctic epibenthic species such as brittle stars, the recovery after disturbance could require decades to restore high biomass in some areas. Environmental changes associated with climate change and resource development in the Arctic shelves have the potential to create large changes in the benthic system, such as local changes epibenthic community composition, dominant taxa, community diversity and benthic biomass hotspots. Future research focusing on the biological interactions that influence epibenthic communities, the supply and success of new recruits to the benthos and the temporal stability of epibenthic communities would help complete our understanding of the spatial and temporal variability of Arctic epibenthic communities and make solid predictions of future scenarios.

TABLE OF CONTENTS

Page

LIST OF FIGURES

Page

LIST OF TABLES

Page

LIST OF APPENDICES

ACKNOWLEDGEMENTS

This dissertation would not have been possible without the intellectual and emotional support from many people. First and foremost, I would like to thank my mentor, Dr. Brenda Konar, her guidance and encouragement throughout my time at UAF have made possible the culmination of this journey. My relationship with Brenda was forged through many research expeditions in the Arctic, in Kachemak Bay and in the Aleutian Islands, and through invaluable time in her office, classrooms, and during lab meetings. Through working with Brenda, I not only learned about experimental design and theories, I also acquired many skills that will help me become a better scientist. Brenda has always encouraged me to push forward and dream big, I hope one day I will have the chance to follow Brenda's steps and pass on the knowledge and encouragement that she has shared with me.

I am deeply grateful for the hard work, time and dedication that my committee members, Bodil Bluhm, Andy Mahoney, Peter Winsor and Chris Zimmerman have given me. Throughout my graduate degree program, they have shown relentless efforts in trying to make me a better scientist. Their encouragement for critical thinking has greatly improved the founding of my scientific questions and hypothesis, as well as the relevance and quality of my research.

Through my years as a member of the Benthic Ecology lab at UAF, I had the privilege to work with outstanding people. By being a part of this team, I have benefited immensely from our lab meetings and interactions in the lab. Our lab meetings have not only offered an opportunity to share our research and learn about new topics through our peers' research, but they are a space where inquiring and expressing thoughts is highly encouraged. One of the driving forces behind these meetings is Katrin Iken. Her generosity in sharing her time and expertise to any student at UAF make her an irreplaceable asset of this institution. Katrin will always be for me a source of inspiration and an example of success.

One of the things that struck me when I started at UAF was the strong sense of cooperation and willingness to help of the researches, professors and staff. Among many, I would like to point out Tom Weingartner, Rolf Gradinger, Dave Verbyla, Seth Danielson, Sathy Naidu, Lara Hortsman, and Christina Newmann, who have played an important part in guiding me with always positive attitudes and kindness through this graduate degree. I am truly thankful for the Principal

Investigators, Ken Dunton, Lee Cooper, Jackie Grebmeier, Brenda Norcross and Katrin Iken that I had the opportunity to work with during many field expeditions and were a key part in making my research projects possible.

My time here in Fairbanks would have not been so full of joy, love and adventures if it wasn't for the wonderful people I met here. Among the many people, I would like to mention Marc Oggier, Lauren Bell, Lorena Edenfield, Raphaelle Descautox, Laura Oxtoby and Justin Kavanaugh. By offering me their friendship and trust, they have made Fairbanks feel like home and the dark winter nights not so dark and not so cold.

I am incredibly fortunate to count with the loving support of my family, whom I can always count on and are always with me. My family, Ana Maria Planchuelo, Andres Ravelo, Andrea Ravelo, Christopher Daily, Lucia Parra, Lucas Daily, Carina Ravelo, Cory Carson and Andrew Ravelo, have been with me celebrating the highs and helping me push through the lows of this journey with encouragement, love and the recurring question "how is that thesis coming along?" I am also very fortunate to have an extensive family of friends in many places in the world. They too have been with me throughout my time in Fairbanks and even from such far-away places in the world, their love and support have made those distances irrelevant.

GENERAL INTRODUCTION

The Arctic seas consist of a series of shelves with largely different bathymetries, geologic histories and overall oceanographic features. These shelves experienced dramatic changes throughout history, with vast regions left completely dry as recently as 13,000 years ago (Zenkevitch, 1963). Because of this, the recolonization of most Arctic shelves has occurred relatively recently and benthic fauna have many species in common with adjacent temperate regions. However, the permanent residents of Arctic shelves are well adapted to nearly constant cold waters and the extreme seasonality of food supply. This adaptation becomes especially important for regional resource management, which requires accurate estimates of species biomass, growth and turnover rate to create adequate ecosystem based resource management and conservation policies for the region (Federal Register, 2007; North Pacific Fisheries Management Council, 2009). The connectivity among Arctic shelves through currents allows for benthic species with planktonic dispersal to have circumpolar distributions. However, the differences in geographic features and histories across shelves make it improper to extend conclusions of the environmental and biological interactions taking place in one region to the entire Arctic.

The great cost of performing research in the Arctic and the historic intermittent interests for resource exploitation have added to the current state of limited knowledge, especially regarding benthic processes and species life histories across regions. The Alaskan Arctic is a clear example of this uneven state of knowledge, where certain topics or regions, such as oceanographic processes in the Chukchi Sea and western Beaufort Sea, benthic-pelagic coupling in the Chukchi Sea, benthic species descriptions in the Russian Chukchi Sea, etc., have been capturing the attention of research efforts for over three decades. (Aagaard, 1984; Grebmeier and McRoy, 1989; Piepenburg et al., 2011; Zenkevitch, 1963). Beyond these few and comparatively well understood topics, to date many research areas remain in the exploratory and descriptive stage. The knowledge gap that exists in the Alaskan Arctic today severely limits our understanding of the biological-environmental interactions that currently take place and our ability to make projections based on the most plausible climate scenarios. Through this dissertation, my goal was to increase our knowledge of the Alaskan Arctic shelf systems through three main topics: epibenthic community patterns across large spatial scales, the environmental influence on epibenthic communities, and population parameters of one of the most prominent groups on Arctic shelves: brittle stars.

Despite the relatively sparse coverage in benthic sampling throughout the Arctic, it is known that there is not one homogeneous Arctic benthic community, even within one region. Benthic communities on Arctic shelves vary spatially, with markedly distinct communities occurring in patches and often dominated by only a few taxa over large spatial scales (Bluhm et al., 2009; Mayer and Piepenburg, 1996; Piepenburg, 2005). This patchy distribution of communities and the great variability in dominant taxa can also be accompanied by striking changes in biomass and standing stock (Piepenbulrg, 2005). The high benthic biomass of many Arctic shelves is a reflection of a tight benthic-pelagic coupling, which is possible due to high seasonal primary production and low grazing pressure in the water column (Ambrose et al., 2001; Grebmeier et al., 2015).

Epibenthic organisms provide an important pathway for energy transfer from water column production to higher trophic levels, such as fish, diving ducks and marine mammals (Bluhm and Gradinger, 2008; Divine et al., 2015; Packer et al., 1994; Rand and Logerwell, 2011). Furthermore, their role as ecosystem engineers can be substantial, through bioturbation, reworking of sediments and by redistributing organic matter (Ambrose et al., 2001; Renaud et al., 2007). In the Alaskan Arctic, despite the large differences between shelf types, described below, certain commonalities exist across regions. One particular commonality across the Pacific Arctic is the disproportionately low biomass of demersal fish in comparison to epibenthic invertebrate biomass. On the western Alaskan Beaufort shelf, for example, fish biomass was negligible while epibenthic invertebrates made up to 94% of the total trawl catch weight (Rand and Logerwell, 2011). The importance of furthering our knowledge of epibenthic community variability in species composition and biomass stems from their high biomass and standing stock, but also from their many interactions with other ecosystem components and their involvement in many ecosystem processes.

The Alaskan Arctic is composed of two shelves, the Chukchi and Beaufort seas, which display widely different geographic settings. The northern Bering Sea also exhibits Arctic characteristics (e.g. Grebmeier et al., 2015), but is excluded here. The Chukchi Sea is a wide and relatively shallow inflowing shelf (c.f. Carmack and Wassmann, 2006); and as such, it is characterized by a relatively narrow coverage of landfast ice with a mean width of 13 km (Mahoney et al., 2014) and a dominance of first year ice over multiyear ice. The three distinct water masses that cross the region are defined by variations in salinity (Woodgate et al., 2005). Primary production is high in part of this region and grazing is comparatively low, allowing for a strong benthic-pelagic coupling, but at least as significant is the lateral advection of nutrients and suspended organic matter transported with the northward transiting water masses (Carmack and Wassmann, 2006). In contrast, the Alaskan Beaufort Sea has a narrow interior shelf, characterized by the large input of many rivers and extensive landfast ice (Carmack and Wassmann, 2006; Mahoney, 2012). In this region, landfast ice forms earlier than in the Chukchi Sea (October) and can extend as far as 50 km offshore by late winter (March) (Mahoney et al., 2014). Primary production is relatively low in this region, limited in part by the increased fresh water and terrigenous input from the Mackenzie, Colville and many other rivers (Goñi et al., 2013). The two Alaskan Arctic shelves connect primarily through the narrow and deep Barrow Canyon. Through this geographic feature, water masses that circulated through the Chukchi Sea enter the Beaufort Sea shelf and slope, with an estimated decay point of the shelf break jet around 149° W (von Appen and Pickart, 2012). The Chukchi Sea shelf is an ideal setting to test the influence of environmental drivers on epibenthic commuity structure, due to its large spatial extent with negligible changes in bathymetry. Conversely, the Beaufort Sea shelf provides a seascape to explore the influence of different dynamic environmental forces on epibenthic communities along a depth gradient.

Unlike pelagic or migratory Arctic fauna, epibenthic invertebrates remain in the region year round, have mostly little mobility and tend to be long-lived, on the order of years to decades (Bluhm et al., 1998; Carroll et al., 2011). In a nutshell, epibenthic invertebrates are an ideal study subject for a time-integrated view of the area they inhabit. Throughout the Arctic, changes in water depth, water mass properties, food availability and sediment composition are drivers of benthic community composition, standing stock and diversity (Bluhm et al., 2009; Carey and Ruff, 1977; Feder et al., 1994; Mayer and Piepenburg, 1996) in addition to biological interactions. However, the magnitude of influence of the environmental variables on epibenthic communities is highly conditioned by the local geography and atmospheric forcing in each region. Therefore, even if one environmental variable shows large explanatory power for an epibenthic community in one region (or area); this variable may not be as relevant for a community inhabiting a different region (or area).

In the pursuit of finding explanatory environmental variables for epibenthic communities, indirect measures influencing community change are often included in multivariate analysis, such as latitude, longitude and depth. While these indirect measures have proven useful in multivariate analysis, they are only proxies for biologically relevant environmental characteristics (Bluhm et al., 2009; Roy et al., 2014). In many cases, it is possible to qualitatively relate the indirect measures with spatial changes in biologically relevant environmental characteristics; however, this association does not have statistical or predictive power. Furthermore, indirect measures (latitude, longitude and depth) do not vary with changing environmental conditions, such as climate change, reducing their value for predicting future climate scenarios. Biologically relevant measures such as bottom water temperature, salinity and measures of food supply and quality are often collected *in situ* at the time the community data are collected. This paired biological-environmental data collection provides a great insight into the conditions the organisms are experiencing at the time of collection. However, those values only offer a snapshot in time of the range of conditions the epibenthic organisms experience throughout the seasons and their lifetime. As a whole, the environmental variables used currently are useful to match with epibenthic commuity structure; however, other measurable environmental characteristics should be considered to increase our statistical and predictive power.

From an environmental perspective, sea ice is the unifying feature that characterizes Arctic shelves. Throughout the Arctic shelves, sea ice responds to large-scale environmental forces, such as wind, water currents, warm water input, etc. (Barber et al., 2015; Mahoney, 2012; Woodgate et al., 2010). Therefore, sea ice reflects and integrates a set of environmental characteristics that vary seasonally. Furthermore, the seasonality of sea ice changes the physical and biological environment through cycles of freezing and melting, by providing habitat to sympagic flora and fauna, and controlling light and heat entering the ocean. In the winter, the formation of sea ice is accompanied by brine rejection and dense water formation, which can create not only changes in bottom water salinity, but also vertical mixing and resuspension of sediment particles (Winsor and Chapman, 2002). As sea ice retreats in the late spring, the addition of fresh water from ice melt induces stratification and stabilizes the photic zone, which has been replenished with nutrients throughout the winter months. Concurrently, ice algae are released into the water and an ice-edge phytoplankton bloom occurs. This bloom is especially relevant for benthic organisms because it represents a first pulse of fresh organic matter after the long ice-covered season. Additionally, this ice-edge bloom occurs early in the season when grazing by zooplankton is minimal (Leu et al., 2011). These characteristics thus make sea ice biologically relevant for epibenthic fauna, but also reflect large-scale temporal variation in environmental forces. The patterns of the seasonality of sea ice as a driver of epibenthic commuity structure could, therefore, provide another measure that reflects biologically relevant environmental conditions.

From an epibenthic community perspective, one of the most distinct taxa of the Arctic shelf biota is brittle stars (Piepenburg, 2005). Throughout the Arctic, brittle star assemblages can occur in high densities and account for a high fraction of the total epibenthic biomass (Piepenburg, 2000; 2005). In some regions, brittle stars are not only abundant, they are nearly the only epifaunal organism on the seafloor, with densities of up to 566 ind./m^2 (Piepenburg and Schmid, 1997). Off the northeast Greenland coast, for example, brittle stars accounted for more than 95% of the abundance of epibenthic fauna (Piepenburg and Schmid, 1996). High densities of brittle stars in the Arctic may be aided by the relatively low abundance and smaller size of their main predators, such snow crab and demersal fish (Aronson, 1989; Divine et al., 2015; Packer et al., 1994; Rand and Logerwell, 2011). From an ecosystem perspective, brittle star respiration can amount to a significant fraction of the total benthic respiration, ranging from 25 to 41% in the central Beaufort Sea and NE Chukchi Sea, respectively (Ambrose et al., 2001; Renaud et al., 2007).

On the Alaskan Arctic shelves, the two most abundant brittle star species are *Ophiura sarsii* and *Ophiocten sericeum* (Bluhm et al., 2009; Feder et al., 1994; Frost and Lowry, 1983). Both species are found throughout the Arctic shelves occupying, with some overlap, mostly different habitats (Frost and Lowry, 1983; Piepenburg and Schmid, 1997). The large bodied *O. sarsii*, with a maximum disc diameter of 40 mm, can be found as far south in the Pacific as 35° N (Piepenburg, 2000). The smaller-bodied *O. sericeum*, with a maximum disc diameter of 18 mm, is also found in various habitats north of 40° N and is especially abundant on interior shelves, such as the central Beaufort shelf and Laptev Sea (Piepenburg, 2000; Piepenburg and Schmid, 1997). Despite the prevalence of these two species throughout the Arctic, little is known of their age, growth and productivity. Furthermore, it is not clear if these dense and nearly monospecific brittle star assemblages are stable and persist through time.

The low temperatures and extreme seasonality of food supply characteristic of Arctic regions generally reduce growth rates and allow for increased longevity of marine invertebrates (Blicher et al., 2007; Bluhm et al., 1998; Brey and Clarke, 1993; Sejr et al., 2002). Brittle star species of the Southern Ocean revealed a trend of decreasing growth rate with increasing latitude, while maximum age showed an opposite trend (Dahm, 1999). Brittle stars from northern temperate regions were aged to be $\leq$10 years old and with slower growth rates than species from warmer regions (Dahm, 1996). To date, no Arctic brittle star species have been aged, but inferring from other aged polar echinoderms, they may be significantly older than a decade. Future Arctic climate scenarios predict increases in water temperature and local changes in water column primary production (Arrigo and van Dijken, 2015; Woodgate et al., 2010). These changes may affect the metabolic rate, growth and production of brittle stars, which will have repercussions for benthic production and energy transfer to higher trophic levels. The lack of knowledge of the population parameters of most Arctic species, and particularly brittle stars, limits our understanding of the Arctic marine environment and the marine systems energy flow. Furthermore, making solid predictions for future scenarios becomes impossible without first defining the rate of growth under current conditions.

This dissertation explores the Alaskan Arctic through four chapters with epibenthic invertebrates as the central focus. Chapter 1 describes the epibenthic communities of the Alaskan Chukchi Sea and the environmental variables influencing commuity structure. This first chapter explores the hypotheses 1) that epibenthic communities are distributed in patches dominated by distinct taxonomic groups, and 2) that the zonation patterns of the communities are determined by distinct environmental characteristics reflecting a combination of substrate, hydrographic and/or food web characteristics. Chapter 2 describes the epibenthic communities of the Alaskan Beaufort Sea and the environmental variables that influence commuity structure, with the objectives to: 1) analyze the spatial variability in abundance, biomass, taxonomic composition and diversity of epibenthic invertebrates on the Alaskan Beaufort Shelf, and 2) determine the set of environmental parameters that best correlate with the changes in the epibenthic community throughout the study region. Chapter 3 explores the quantitative link between epibenthic communities and environmental variables, and focuses on sea ice variables. The following hypotheses are tested in this third chapter: 1) the seasonality of sea ice is a significant predictor of total benthic (infauna and epifauna) biomass and number of taxa on the Chukchi and Beaufort Sea shelves, 2) sea ice explains a greater proportion of the variability in community structure ity when communities are classified by feeding guilds as opposed to species composition, and 3) the addition of sea ice variables to the commonly used variables explains a greater proportion of the variability in community structure. Lastly, chapter 4 focuses on the population dynamics of two dominant brittle star species, examining: 1) if the growth curves of *O. sarsii* and *O. sericeum* have similar shapes, with an initial period of fast growth that decreases gradually with increasing body size until achieving asymptotic size at similar maximum ages; 2) if their individual production values are similar; and 3) if *O. sarsii* has a higher turnover rate than *O. sericeum*. Altogether, this dissertation aims to increase our knowledge of the Arctic ecosystem from an epibenthic invertebrate perspective.

References

Aagaard, K., 1984. The Beaufort undercurrent, in: PW Barnes and E Reimnitz, D.M.S. (Ed.), The Alaskan Beaufort Sea: Ecosystems and Environments. Academic Press Inc., Orlando, pp. 47–71.

Ambrose, W.G.J., Clough, L., Tilney, P., Beer, L., 2001. Role of echinoderms in benthic remineralization in the Chukchi Sea. Mar Biol 139, 937–949.

Arrigo, K.R., van Dijken, G.L., 2015. Continued increases in Arctic Ocean primary production. Prog Oceanogr 136, 60–70. doi:10.1016/j.pocean.2015.05.002

Aronson, R.B., 1989. Brittle star beds: low-predation anachronisms in the British Isles. Ecology 70, 856–865.

Barber, D.G., Hop, H., Mundy, C.J., Else, B., Dmitrenko, I.A., Tremblay, J.E., Ehn, J.K., Assmy, P., Daase, M., Candlish, L.M., Rysgaard, S., 2015. Selected physical, biological and biogeochemical implications of a rapidly changing Arctic Marginal Ice Zone. Prog Oceanogr 139, 122–150. doi:10.1016/j.pocean.2015.09.003

Blicher, M.E., Rysgaard, S., Sejr, M.K., 2007. Growth and production of sea urchin *Strongylocentrotus droebachiensis* in a high-Arctic fjord, and growth along a climatic gradient (64 to 77° N). Mar Ecol Prog Ser 341, 89–102. doi:10.3354/meps341089

Bluhm, B.A., Gradinger, R., 2008. Regional variability in food availability for Arctic marine mammals. Ecol. Appl. 18, 77-96.

Bluhm, B.A., Iken, K., Hardy, S.M., Sirenko, B.I., Holladay, B.A., 2009. Community structure of epibenthic megafauna in the Chukchi Sea. Aquat. Biol. 7, 269-293.

Bluhm, B.A., Piepenburg, D., von Juterzenka, K., 1998. Distribution, standing stock, growth, mortality and production of *Strongylocentrotus pallidus* (Echinodermata: Echinoidea) in the northern Barents Sea. Polar Biol 20, 325–334.

Brey, T., Clarke, A., 1993. Population dynamics of marine benthic invertebrates in Antarctic and subantarctic environments: are there unique adaptations? Antarct Sci 5, 253–266.

Carey, J.A.G., Ruff, R.E., 1977. Ecological studies of the benthos in the western Beaufort Sea with special reference to bivalve molluscs, in: Dunbar, M.J. (Ed.), Polar Oceans. Arctic Institute of North America, Calgary, pp. 505–530.

Carmack, E.C., Wassmann, P., 2006. Food webs and physical–biological coupling on pan-Arctic shelves: Unifying concepts and comprehensive perspectives. Prog Oceanogr 71, 446–477. doi:10.1016/j.pocean.2006.10.004

Carroll, M.L., Ambrose, W.G., Levin, B.S., Locke V, W.L., Henkes, G.A., Hop, H., Renaud, P.E., 2011. Pan-Svalbard growth rate variability and environmental regulation in the Arctic bivalve *Serripes groenlandicus*. J Mar Syst 88, 239–251. doi:10.1016/j.jmarsys.2011.04.010

Dahm, C., 1999. Ophiuroids (Echinodermata) of southern Chile and the Antarctic: Taxonomy, biomass, diet and growth of dominant species. Sci Mar 63, 427–432. doi:10.3989/scimar.1999.63s1427

Dahm, C., 1996. Okologie und Populationsdynamik antarktischer Ophiuroiden (Echinodermata). Berichte zur Polarforsch 194, 1–289.

Divine, L.M., Bluhm, B.A., Mueter, F.J., Iken, K., 2015. Diet analysis of Alaska Arctic snow crabs (*Chionoecetes opilio*) using stomach contents and δ^{13}C and δ^{15}N stable isotopes. Deep Sea Res Part II Top Stud Oceanogr 1–13. doi:10.1016/j.dsr2.2015.11.009

Feder, H.M., Naidu, A.S., Jewett, S.C., Hameedi, J.M., Johnson, W.R., Whitledge, T.E., 1994. The northeastern Chukchi Sea: benthos-environmental interactions. Mar. Ecol. Prog. Ser. 111, 171-190.

Federal Register, 2007. Outer Continental Shelf (OCS), Alaska OCS Region, Beaufort Sea and Chukchi Sea, proposed oil and gas lease sales for years 2007 to 2012. Federal Register Vol 2, no. 179 (microfiche).

Frost, K.J., Lowry, L.F., 1983. Demersal fishes and invertebrates trawled in the northeastern Chukchi and western Beaufort Seas 1976-1977, NOAA Technical Report NMFS-SSRF-764.

Goñi, M.A., O'Connor, A.E., Kuzyk, Z.Z., Yunker, M.B., Gobeil, C., Macdonald, R.W., 2013. Distribution and sources of organic matter in surface sediments across the North American Arctic margin. J Geophys Res Ocean 118, 1–19. doi:10.1002/jgrc.20286

Grebmeier, J.M., Bluhm, B.A., Cooper, L.W., Danielson, S.L., Arrigo, K.R., Blanchard, A.L., Clarke, J.T., Day, R.H., Frey, K.E., Gradinger, R.R., Kędra, M., Konar, B., Kuletz, K.J., Lee, S.H., Lovvorn, J.R., Norcross, B.L., Okkonen, S.R., 2015. Ecosystem characteristics and processes facilitating persistent macrobenthic biomass hotspots and associated benthivory in the Pacific Arctic. Prog Oceanogr 136, 92–114. doi:10.1016/j.pocean.2015.05.006

Grebmeier, J.M., McRoy, C.P., 1989. Pelagic-benthic coupling on the shelf of the Northen Bering and Chukchi Seas. III. Benthic food supply and carbon cycling. Mar. Ecol. Prog. Ser. 53, 79-91.

Leu, E., Søreide, J.E., Hessen, D.O., Falk-Petersen, S., Berge, J., 2011. Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: Timing, quantity, and quality. Prog Oceanogr 90, 18–32. doi:10.1016/j.pocean.2011.02.004

Mahoney, A.R., 2012. Sea ice conditions in the Chukchi and Beaufort Seas, Pew Environment Group.

Mahoney, A.R., Eicken, H., Gaylord, A.G., Gens, R., 2014. Landfast sea ice extent in the Chukchi and Beaufort Seas: The annual cycle and decadal variability. Cold Reg Sci Technol 103, 41–56. doi:10.1016/j.coldregions.2014.03.003

Mayer, M., Piepenburg, D., 1996. Epibenthic community patterns on the continental slope off East Greenland at 75° N. Mar. Ecol. Prog. Ser. 143, 151-164.

North Pacific Fisheries Management Council, 2009. Public review draft—Fishery management plan for fish resources of the Arctic management area. Available at: www.fakr.noaa.gov/npfmc/current_issues/Arctic/Arctic EA109.pdf

Packer, D.B., Watling, L., Langton, R.W., 1994. The population structure of the brittle star *Ophiura sarsi* Lütken in the Gulf of Maine and its trophic relationship to American plaice (*Hippoglossoides platessoides* Fabricius). J Exp Mar Bio Ecol 179, 207–222.

Piepenburg, D., 2000. Arctic brittle stars (Echinoredmata: Ophiuroidea), in: Gibson, R.N., Barnes, M. (Eds.), Oceanography and Marine Biology: An Annual Review. New York, pp. 189–256.

Piepenburg, D., 2005. Recent research on Arctic benthos: common notions need to be revised. Polar Biol 28, 733–755.

Piepenburg, D., Archambault, P., Ambrose, W.G., Blanchard, A.L., Bluhm, B. a., Carroll, M.L., Conlan, K.E., Cusson, M., Feder, H.M., Grebmeier, J.M., Jewett, S.C., Lévesque, M., Petryashev, V.V., Sejr, M.K., Sirenko, B.I., Włodarska-Kowalczuk, M., 2011. Towards a pan-Arctic inventory of the species diversity of the macro- and megabenthic fauna of the Arctic shelf seas. Mar Biodivers 41, 51–70. doi:10.1007/s12526-010-0059-7

Piepenburg, D., Schmid, M.K., 1996. Distribution, abundance, biomass, and mineralization potential of the epibenthic megafauna of the Northeast Greenland shelf. Mar Biol 125, 321–332.

Piepenburg, D., Schmid, M.K., 1997. A photographic survey of the epibenthic megafauna of the Arctic Laptev Sea shelf: Distribution, abundance, and estimates of biomass and organic carbon demand. Mar Ecol Prog Ser 147, 63–75. doi:10.3354/meps147063

Rand, K.M., Logerwell, E.A., 2011. The first demersal trawl survey of benthic fish and invertebrates in the Beaufort Sea since the late 1970s. Polar Biol 34, 475–488.

Renaud, P.E., Morata, N., Ambrose, W.G., Bowie, J.J., Chiuchiolo, A., 2007. Carbon cycling by seafloor communities on the eastern Beaufort Sea shelf. J Exp Mar Bio Ecol 349, 248–260. doi:10.1016/j.jembe.2007.05.021

Roy, V., Iken, K., Archambault, P., 2014. Environmental Drivers of the Canadian Arctic Megabenthic Communities 9. doi:10.1371/journal.pone.0100900

Sejr, M.K., Sand, M.K., Jensen, K.T., Petersen, J.K., Christensen, P.B., Rysgaard, S., 2002. Growth and production of *Hiatella arctica* (Bivalvia) in a high-Arctic fjord (Young Sound, Northeast Greenland). Mar Ecol Prog Ser 244, 163–169. doi:10.3354/meps244163

von Appen, W-J., Pickart, R.S., 2012. Two configurations of the western Arctic Shelfbreak Current in summer. J Phys Oceanogr 42, 329–351. doi:10.1175/JPO-D-11-026.1

Winsor, P., Chapman, D.C., 2002. Distribution and interannual variability of dense water production from coastal polynyas on the Chukchi Shelf. J. Geophys. Res. 107, 10.1029.

Woodgate, R.A., Aagaard, K., Weingartner, T.J., 2005. A year in the physical oceanography of the Chukchi Sea: Moored measurements from autumn 1990-1991. Deep Sea Res. Part II Top. Stud. Oceanogr. 52, 3116-3149.

Woodgate, R.A., Weingartner, T., Lindsay, R., 2010. The 2007 Bering Strait oceanic heat flux and anomalous Arctic sea-ice retreat. Geophys Res Lett 37, L01602. doi:10.1029/2009GL041621

Zenkevitch, L., 1963. Biology of the Seas of the USSR. George Allen & Unwin Ltd., London

CHAPTER 1: Epibenthic community variability in the northeastern Chukchi Sea[1]

Abstract

Epibenthic organisms can occur in large numbers and high biomass on the continental shelf of the northeastern Chukchi Sea. From an ecosystem perspective, epibenthic organisms are important in recycling and redistributing organic matter deposited from the pelagic zone, and are also key members of the local food web. Data for biological (epibenthic species composition, abundance, and biomass) and environmental (bottom water temperature, salinity, dissolved oxygen and pH, sediment grain size, sediment organic matter and sediment chlorophyll content, latitude, longitude, and water depth) variables were collected at 53 stations in the northeastern Chukchi Sea during the summers of 2009-2010 to characterize the epibenthos and provide a benchmark for potential future changes due to possible anthropogenic disturbances. Community biomass, abundance, species composition and taxa richness varied in patches throughout the study area, but were generally dominated by crustaceans and echinoderms. These two groups had an inverse relationship in the distribution of their dominance. Communities dominated by crustaceans had significantly higher Simpson's dominance and Pielou's evenness values compared to echinoderm-dominated communities. Correlation coefficients for six environmental variables (longitude, bottom water temperature, water depth, bottom water dissolved oxygen, sediment grain size 2 phi and total organic carbon) with epifaunal abundance and biomass were moderate (0.42 for abundance and 0.51 for biomass at a significance level of 0.1%). However, assemblages within the study area followed a distinct spatial distribution pattern that matched the path of important water masses in the region.

1.1 Introduction

Epibenthic organisms on the continental shelf of the Chukchi Sea can be found in high abundance and biomass. Several members of the benthic community constitute key elements in the Arctic food web, as prey of marine mammals, birds and fish (Bluhm and Gradinger, 2008). Arctic epibenthic community structure is highly variable. Often there are peaks in abundance of specific groups, such as echinoderms and crustaceans, which create a mosaic or patchiness in species distribution (Ambrose et al., 2001; Bluhm et al., 2009; Piepenburg, 2005). Distinct communities are

---

[1] Ravelo, A.M., Konar, B., Trefry, J.H., Grebmeier, J.M., 2014. Epibenthic community variability in the northeastern Chukchi Sea. Deep Sea Res Part II Top Stud Oceanogr 102, 119–131. doi:10.1016/j.dsr2.2013.07.017

influenced by an array of environmental variables, including water depth, water current, seafloor composition and food availability (Bluhm et al., 2009; Piepenburg, 2005). However, which factors define the epibenthic commuity structure and to what extent is still uncertain for some areas and may vary by region (Bluhm et al., 2009). Echinoderms (particularly ophiuroids) typically dominate in abundance and/or biomass of Arctic epibenthic communities (Frost and Lowry, 1983;). Arctic ophiuroid assemblages are known to be less diverse than similar assemblages of Antarctica (Piepenburg, 2005). However, when comparing the diversity of all macrozoobenthos, the Arctic species richness is only marginally lower than comparable Antarctic communities (Piepenburg, 2005). The increasing resource exploitation in the Chukchi Sea has raised concern with regard to the negative effects that anthropogenic activities, such as offshore oil exploration, mineral extractions and fisheries (fish and shellfish) may have on the stability and growth of the epibenthic communities in this region (Bluhm et al., 2009; Grebmeier et al., 2006). In addition, global climate change and ocean acidification have the potential to create acute stressors for Arctic benthic organisms (Bluhm et al., 2009; Fabry et al., 2008; Grebmeier, 2012; Piepenburg, 2005). Thus to conserve and manage this significant ecosystem component, it is important to document the epibenthic community composition and its relationship with the environmental processes that define its natural variability.

The continental shelf of the Chukchi Sea is relatively shallow, with an average water depth of 50 m. The northeastern area is covered by ice seven to eight months of the year, causing light limitation and vertical stability of the water column (Woodgate et al., 2005). Compared to other Arctic regions, the Chukchi Sea is considered highly productive, with water column primary productivity values ranging from 80-90 g C m^{-2} y^{-1} in the northern shelf to 470 g C m^{-2} y^{-1} in the southern Chukchi Sea. Lower values of 20-70 g C m^{-2} y^{-1} have been recorded in coastal water (Sakshaug, 2004). Seasonal changes in salinity, solar irradiance and ice coverage in the Chukchi Sea directly affect primary production. In the spring, light increases and sea ice melt creates stratification in the water column, favoring phytoplankton blooms in the ice edge zone. These marginal ice zone blooms occur before phytoplankton growth in the open ocean, and add up to 50% of the total primary production in Arctic waters (Sakshaug, 2004). The distinct water masses found in the region are defined by variations in salinity. Low salinity levels (<31.8) characterize the low nutrient Alaska Coastal Water (ACW), which flow northward along the coast from Cape Lisburne up to Barrow Canyon (Figure 1.1) (Walsh et al., 1989). Bering Sea Water (BSW) also flows northward through the Bering Strait and heads westward in the Chukchi Sea and is characterized by high salinity and nutrient levels. South of Bering Strait this water mass is composed of Bering Shelf water and Anadyr water (AW) (Coachman et al., 1975; Pickart et al., 2005; Woodgate et al., 2005). In general, input of high nutrient water originates in the Bering Sea and is then transported northward through the Bering Strait. This water mass movement supports high seasonal primary production, which in conjunction with low grazing pressure, translates into high deposition of organic matter to the benthos (Grebmeier et al., 1988; Grebmeier et al., 2006). Once passed the Bering Strait, BSW flows northward in two branches. One branch moves eastward through Hope Valley and Herald Valley, and is characterized by high salinity and nutrient rich waters (Weingartner et al., 2005). The second branch travels east of Herald Shoal through the Central Channel (Figure 1.1) (Weingartner et al., 2005). On an annual average, this branch could be responsible for approximately 25% of the mean Bering Strait transport (Weingartner et al., 2005). The water moving through the Central Channel follows the bathymetry north and to the east of Herald Shoal, continuing in a slow flow up to Hanna Shoal, moving eastward and merging with the ACW close to Barrow Canyon (Coachman et al., 1975; Winsor and Chapman, 2004; Weingartner et al., 2005). This northeastward drift of nutrient and carbon rich waters could support high benthic standing stocks despite a relatively low annual primary production (Feder et al., 1994) (Figure 1.1).

Many characteristics of the epibenthic communities in the Arctic make them especially important to benthic systems. In the Chukchi Sea, echinoderms occur in dense assemblages (several hundred individuals per meter square) with high biomass up to 30% higher than the highest values reported for echinoderms in the Barents Sea (Ambrose et al., 2001). These assemblages also showed higher respiration values compared to the Barents Sea (up to 25% of the total benthic respiration). Many members of the epifaunal community have great mobility that allows them to access and redistribute organic carbon deposited from the pelagic zone. Epibenthic organisms are also significant bioturbators and contributors to the total benthic energy turnover (Grebmeier and McRoy, 1989; Piepenburg et al., 1995). The Chukchi Sea is populated by many species with slow growth rates and long life spans, such as echinoderms and molluscs (Gage, 1990; Piepenburg et al., 1995). These characteristics have added importance due to the high levels of trace metals these organism can bioaccumulate throughout their life and subsequently transfer to higher trophic levels (Clarke, 1983; Dehn et al., 2006; Mariani et al., 1980). Several epibenthic organisms constitute an important opportunistic dietary supplement for many Arctic marine mammals, such as bearded seals and walruses. With this in consideration, the potential for biomagnification of some potential pollutants to higher trophic levels becomes an issue of great concern, especially for species that are important to the subsistence harvests of local human communities (Bluhm and Gradinger, 2008; Dehn et al., 2006).

Epibenthic organisms that inhabit the Chukchi Sea, such as ophiuroids, endure a severe seasonal food limitation seven to eight months out of the year, which is reflected in the slow growth rates and long life spans of many of these Arctic benthic organisms (Clarke, 1983). As typical of any shelf benthos, the benthic community structure and biomass in the Chukchi Sea is strongly influenced by the carbon input from the water column and the quality of the organic carbon (Grebmeier and McRoy, 1989; Grebmeier et al., 1988; Grebmeier et al., 2006). Many studies have highlighted the importance of the pelagic-benthic coupling as a major factor altering the benthic communities in Arctic ecosystems (Grebmeier and McRoy, 1989; Grebmeier et al., 2006; Piepenburg, 2005). In addition, environmental variables such as sediment grain size, water depth, temperature, as well as sediment C/N ratios are of great importance in structuring benthic communities (Feder and Jewett, 1981; Feder et al., 2005; Piepenburg, 2005). A more recent study of the epibenthos in the Chukchi Sea suggests that benthic-pelagic coupling is less important in determining the epibenthic community composition with a more important role for macroinfauna (Bluhm et al., 2009). This study also highlights the need for further analysis with regard to using environmental variables when modeling the composition of epibenthic communities. Certain environmental variables used traditionally to explain epibenthic assemblages may also be acting as proxies for different environmental factors (Bluhm et al., 2009).

1.2 Materials and methods

The data used for these analyses were generated during the Chukchi Sea Offshore Monitoring In Drilling Area - Chemical And Benthos (COMIDA CAB) Project, in an area corresponding to Lease Sale 193. Stations extended from 69° to 72 °N and 168° to 157°W and ranged in water depth from 23 to 58 m. Site selection was determined via two methods: 1) a general randomized tessellation stratified design (GRTS) in the core COMIDA area, and 2) a spatially oriented, nearshore-to-offshore, south to north grid overlaying the GRTS design. Data were collected on two summer cruises (end of July to mid-August) of 2009 and 2010. Biological data were collected using one epibenthic trawl at each of the 53 stations (Figure 1.2). This analysis includes all 2009 stations and additional new stations in 2010.

The epibenthic trawl used in this study was a 3.05 meter plumb-staff beam trawl with a 7 mm mesh and a 4 mm codend liner, modified with a lead-filled line and 15 cm sections of chain seized to the footrope every 15 cm (Gunderson and Ellis, 1986). The trawl was towed for 2 to 5 minutes on the sea floor while the vessel was moving at 1 to 1.5 knots. The trawl time varied depending on the relative epibenthos density, determined by a drop video camera deployed before each trawl (Cooper personal communication). A rigid 3 m pipe forward of the net held the mouth open for an effective swath of 2.26 m. The vertical opening of the net was approximately 1.2 m. A typical beam trawl catch ranged from 40 to 100 kg in the codend. This trawl design is very effective at collecting epibenthic organisms >4 mm (Gunderson and Ellis, 1986). After the trawl was brought on board, catches were cleaned and organisms sorted to the lowest practical taxonomic level (in most cases to genus). Many genera within the infraorder Caridea, such as *Argis* spp., *Sclerocrangon* spp., *Sabinea* spp., *Spirontocaris* spp. and *Pandalus* spp., were present; however, due to time constraints in the field these genera were not sorted for abundance and biomass measurements and are reported in this analysis as Caridea. Within the class Ophiuroidea, the dominant species was Ophiura sarsii; however, other genera may have been present in our samples but not identified in the field, thus the category Ophiuroidea was used for our analysis. All groups were individually counted and their damp biomass determined. Voucher specimens were fixed in 10% buffered formalin for further taxonomic identification. All taxa encountered are shown in Figure 1.A, species and genus names updated to the latest accepted name according to World Registry of Marine Species (WoRMS) (Appeltans et al., 2012).

Environmental variables were collected by the COMIDA CAB team. Vertical profiles of water column salinity, temperature, dissolved oxygen, turbidity and pH were obtained at each trawled station using a YSI SONDE 6600. Sediments were collected using 0.1 m^2 van Veen grabs for total organic carbon, total nitrogen, grain size analyses and mean sediment chlorophyll a (details in Cooper et al., 2002).

1.2.1 Data analysis

Abundance and biomass data were standardized to the area trawled for spatial summary and diversity indices analysis. For statistical analysis, data were standardized to relative percentage per trawl and square root transformed. Standardizing to percent abundance or biomass per trawl allows smaller or less frequent taxa to be better represented in these types of community data. To determine the taxa that best represented the epifaunal community across all stations, a BVSTEP

(Biological variables stepwise procedure) in the PRIMER v.6 package (Clarke and Gorley, 2006) was used for abundance and biomass, using Bray-Curtis resemblance matrix and Spearman rank correlation. Cluster analysis for abundance was used to group stations by similarity (group average from Bray-Curtis resemblance matrix). An MDS (Multi-dimensional scaling) plot was used to visualize the grouping of stations by similarity. Simpson's diversity, Pielou's evenness and Margalef's richness indices were calculated from abundance for all stations standardized to area trawled and square root transformed, using the DIVERSE routine in PRIMER. For these indices, analysis of variance between cluster groups were calculated at a 95% confidence level and pairwise comparisons of means were calculated at 0.05 significance level using R and R-Commander (public access statistical software). Similarity Percentages Test (SIMPER) in PRIMER through the Bray-Curtis similarity matrix was used to determine the levels of similarity within clusters, the dissimilarity between clusters and the role of individual taxa in contributing to the separation between groups of stations. To identify the group of environmental variables that best correlated to the epibenthic community, the BIOENV (Biological-environmental interactions) routine in PRIMER selected a list of variables from a set of transformed and normalized environmental parameters (Euclidean distance resemblance matrix). The environmental variables that were included in these analyses were latitude, longitude and depth (as indirect determinants of community structure), bottom water salinity, temperature, dissolved oxygen, turbidity and pH (for bottom water characteristics) and sediment grain size. Also, mean sediment chlorophyll *a* concentration, total organic carbon (TOC) and nitrogen (TON) content, and carbon to nitrogen ratio (C/N) were analyzed as indicators of food supply and quality. When necessary, variables were log transformed and to avoid colinearity TON was excluded from the analysis.

1.3 Results

From the 53 stations, 44 taxa were found in six phyla, with an approximate average abundance of 33,445 ind./1000 m^2 (s.d. 87,792), ranging from 150 ind./1000 m^2 at Station 10 to 548,864 ind./ 1000 m^2 at Station 1010 (Figure 1.3.A). Taxon counts included four cnidarians, 11 echinoderms, 21 molluscs, five crustaceans, two pycnogonids, and two ascidians. The number of taxa present in each trawl varied from six at Station 109 to 25 at Stations 1014 and 5 (mean 16 ± 4 s.d.). Across all stations, Ophiuroidea represented 71% of the total abundance, the sea cucumber *Ocnus* spp. 19%, the shrimp Infraorder Caridea 3%, the snow crab *Chionoecetes opilio* 2%, and the hermit crab *Pagurus* spp. 1%. The average total biomass for all stations was 62.7 kg/1000 m^2 (s.d.

99.45), ranging from 0.57 kg/1000 m^2 at Station 3 to 644.1 kg/1000 m^2 at Station 1010 (Figure 1.3.B). Across all stations, Ophiuroidea accounted for 39% of the total biomass, *Chionoecetes opilio* for 17%, *Ocnus* spp. for 16%, *Pagurus* spp. for 5%, the sea star *Leptasterias* spp. 3%, the bryozoan *Alcyonidium* spp. 3%, and the cucumber *Psolus* spp. for 3%. For more information on the classification and common names of these organisms and the number of stations at which they were present, please refer to Figure 1.A.

Overall, the six taxa that best represented the epibenthic community in terms of abundance included *Chionoecetes opilio*, Ophiuroidea, *Pagurus* spp., Caridea, the sand dollar *Echinarachnius parma*, and the moon snail *Cryptonatica* spp. (BVSTEP Primer-e, Spearman correlation value of 0.958 with 0.1% significance level). For biomass there were nine taxa selected: *Chionoecetes opilio*, Ophiuroidea, *Pagurus* spp., the bryozoan *Alcyonidium* spp., Caridea, the sea cucumber *Psolus* spp., the whelk *Neptunea* spp., the sea star *Leptasterias* spp., and the basket star *Gorgonocephalus* spp. (BVSTEP Primer-e, Spearman correlation value of 0. 954 with 0.1% significance level; Figure 1.4A, B).

A cluster analysis based on abundance at a 55% similarity level resulted in four clusters and two independent stations (103 and 1010) (Figure 1.5). The same cluster analysis showed a greater number of smaller clusters of statistical significance (SIMPROF test in Primer) at higher similarity levels (average 76%) in addition to six independent stations. Despite the slightly higher average similarity within clusters (76% vs. 70%), the average dissimilarity between the smaller cluster groups was reduced significantly from an average of 68% to an average of 34%. The dominant taxa in the smaller clusters selected by the SIMPROF test were the same as the dominant taxa of the clusters at the 55% similarity that included the former, which means that the assemblages of the smaller clusters were explained by the same taxa as the larger clusters. Using this logic, we determined that the 55% similarity level cut off was an adequate level of segregation among cluster groups.

Ordination of stations in an MDS plot with a stress level of 0.12 showed no overlap of groups at the 55% similarity level (Figure 1.5). SIMPER analysis showed within group similarity to vary from 63% to 78% (70% average) (Table 1.2), dissimilarity between pairs of groups ranged from 50% to 90% (68% average) (Table 1.3). Margalef's richness index was not significantly different between groups of stations and was not included in further analysis. A pairwise comparison of means revealed significant differences between Group 4 and Groups 2 and 3 for Simpson's index. For Pielou's index statistically significant differences were found between Group 4 and Groups 2, 3 and independent stations 1010; also, between independent station 103 and Group 2 and independent station 1010.

Overall, stations in a cluster were geographically close together with the exception of a few stations in Group 2, located within the area of Group 4, and stations in Group 3 were divided in two separate areas (Figure 1.6). Group 1, which was formed by coastal stations, had a mean abundance of 197 ind./1000 m^2 and biomass of 2.19 kg/1000 m^2 (Table 1.1). This group was highly dominated by *Echinarachnius parma* in abundance (69% and 80% of total trawl abundance) and biomass (55% and 75% of the total trawl weight; Figure 1.4). Diversity indices (Simpson and Pielou's) were intermediate in relation to other groups and independent stations (Table 1.3). The 15 stations in Group 2 were located over a broad area south of Hanna Shoal, with the exception of stations 21 in the far west of the study area and station 44 located north of Hanna Shoal (Figure 1.6). The mean abundance and biomass in this group amounted to 1,678 ind./1000 m^2 and 2.21 kg/1000 m^2 (Table 1.1). High abundance and biomass of Ophiuroidea characterized stations in Group 2 (Figure 1.4). Simpson and Pielou's index values were low (Table 1.1). Group 3 included four stations, two on Hanna Shoal and the other two further south between Herald Shoal and the coast (Figure 1.6). These stations were characterized by high dominance of Caridea (Figure 1.4A). The mean abundance for this group amounted to 89 ind./1000 m^2 and the mean biomass was 0.3 kg/1000 m^2. Intermediate Pielou's evenness and Simpson's indices resulted from Group 3 (Table 1.1). Most of the station in the largest group, which was cluster 4, were located west of 165° longitude with eight stations following the western and southern limit of Hanna Shoal (Figure 1.6). Stations in this group were dominated by the crustaceans *Chionoecetes opilio*, *Pagurus* spp., and Caridea (Figure 1.4A). These stations had the highest average evenness and diversity index of all groups. The mean abundance and biomass of these stations were 82 ind./1000 m^2 and 0.66 kg/1000 m^2, respectively (Table 1.1). The independent Station 103 was the farthest south station with 3,447 ind./1000 m^2 and 44.49 kg/1000 m^2, with the gastropod *Cryptonatica* spp. accounting for 30% of the trawl abundance and 26% of the trawls biomass (Figure 1.4). This station had the highest diversity and evenness indices values compared to group averages. Station 1010 had the highest abundance of all stations at 548,864 ind./1000 m^2 and 644.1 kg/1000 m^2 (Figure 1.3.B, Table 1.1). This station was highly dominated by *Ocnus* spp., which had a biomass of 81% of the trawls total and abundance of 60% of the trawls abundance (Figure 1.4.A). This station had the lowest diversity and evenness values of all groups (Table 1.1).

Similarity analysis within groups of stations included Caridea within the top two contributors of the similarity for all groups, and alone contributing 68% of the similarity in Group 3. In Group 2, Ophiuroidea contributed 67% of the similarity among stations, *Echinarachnius parma* contributed to 50% in Group 1, and the similarity among stations in Group 4 was divided almost evenly among Caridea, *Chionoecetes opilio* and *Pagurus* spp. (approximately 20% each;Table 1.2). The presence of *Cryptonatica* spp. at Station 103 aided in the dissimilarity between this station and all other groups (including Station 1010) with an average contribution of 15%. In the case of Station 1010, *Ocnus* spp. added on average 26% of the dissimilarity among all other groups and Station 103 (Table 1.3).

The six environmental variables that best explained the community in terms of abundance were longitude, sediment grain size >5 φ, bottom water dissolved oxygen, sediment grain size 2 φ, bottom water temperature, water depth, and TOC. The correlation coefficient for this set of variables was moderate at 0.416; with the alternative of pH replacing temperature and a correlation coefficient of 0.415 (0.1% significance level) (Table 1.4). Similar variables were selected by the BIO-ENV analysis that matched with biomass. In this case seven variables were selected, also with a moderate correlation coefficient of 0.505, and included longitude, sediment grain size 4 φ, bottom water dissolved oxygen, sediment grain size 2 φ, water depth, bottom water temperature and TOC. The alternative of pH instead of bottom water temperature yielded a correlation coefficient of 0.503 (0.1% significance level) (Table 1.5). Mean values (and standard deviations) for all variables included in the BIOENV are presented in Table 1.6.

1.4 Discussion

1.4.1 Dominant taxa

Epibenthic communities in the northeastern Chukchi Sea were dominated in abundance and biomass by echinoderms or crustaceans. These two groups had an inverse relationship in the distribution of their dominance, as clearly shown in Figures 1. 3.4 A and B. Stations dominated by echinoderms (mainly Ophiuroidea, *Ocnus* spp. and *Echinarachnius parma*) had low crustacean abundance and biomass values, and at stations where crustaceans (mainly *Chionoecetes opilio*, Caridea and *Pagurus* spp.) were dominant, echinoderms were scarce or absent. Ophiuroidea were the most abundant of all taxa (average 23,893 ind./1000 m^2) and had the highest biomass (average 24.36 kg/1000 m^2) across stations. As noted above, their distribution was not homogeneous throughout the study area, although Ophiuroidea were present at 41 of the 53 stations sampled. The dominance of Ophiuroidea was concentrated south of Hanna Shoal with a couple of stations on the far west side of the study area (Figure 1.4). This extreme pattern of abundance did not correspond to any depth range or clear visual substrate characteristic. Many studies have previously described the overwhelming abundance of Ophiuroidea on the Arctic shelves including the Chukchi Sea (Ambrose et al., 2001; Bluhm et al., 2009; Piepenburg and Schmid, 1996a; Piepenburg and Schmid, 1996b; Piepenburg and Schmid, 1997). This study supports previous findings and confirms the extreme spatial variability in the distribution of these ophiuroid-dominated assemblages.

For the second most abundant echinoderm taxon in this study, *Ocnus* spp., an interesting pattern was found. Seven of the nine stations where *Ocnus* spp. was present were adjacent to one another. Perhaps this pattern is related to the reproductive mode of many holothurians. The Antarctic congener *Ocnus sacculus* is a brooding species with embryos of the same stage of development, which would infer one common breeding period (Pawson, 1983). This breeding synchronization, along with the restricted dispersal capacity of this taxon, could explain the close proximity of stations where *Ocnus* spp. was present in our study area. High abundance of the sand dollar *Echinarachnius parma* defined the cluster Group 1, with a biomass ranging from 55% to 75% of the total catch at those stations. Stations corresponding to Group 1 had a high proportion of sand (Table 1.6) and were located near shore in shallow water (depth <40 m) under the influence of the Alaskan Coastal Current (ACC). These data agree with those collected in the same area by Feder et al. (1994), who suggested that the strong effect of the ACC in particle entrainment and associated particulate organic matter favors the presence of suspension-feeder sand dollars (Feder et al., 1994).

1.4.2 Environmental analysis

We had hypothesized that a set of environmental variables would explain the different assemblages in our study area; however the environmental variables included in this analysis were only moderately correlated to the epibenthic community data (correlation coefficient ≤0.5 with 0.1% significance level). Two variables, longitude and sediment grain size 2 φ (0.25 to 0.5 mm, medium sand) contributed most to the correlation. Longitude is a reflection of the difference in stations located on the western side of the system with the ones on the ACC area. Only two of the six sediment grain-size categories were selected in the BIOENV analysis, and with a marginal contribution to the total correlation value. Other studies have shown the importance of sediment grain size and seafloor characteristics to taxonomic richness and taxon distribution (Bluhm et al., 2009; Feder et al., 1994; Mayer and Piepenburg, 1996). In our study we observed the significance of sediment grain size for certain taxa such as *Echinarachnius parma* and acknowledge the importance of including more environmental parameters, such as seafloor characteristics, to aid in a more comprehensive understanding of the distribution of assemblages in a particular area. Despite the variability in mean values of salinity, temperature, pH and dissolved oxygen among station groups (Table 1.6), the selected water mass characteristics (bottom water dissolved oxygen, bottom water temperature and bottom water pH) contributed little to structuring the epibenthic community. One possibility for the limited contribution of these variable values could be the narrow window in time these data were collected, which resulted in a failure in capturing the true temporal variability that the bottom water undergoes throughout the year (Weingartner personal communication). The only variable selected as a representative of food supply and quality was TOC; however, this variable showed a low contribution to the correlation coefficient for biomass and abundance, as observed in other similar studies in the area (Bluhm et al., 2009).

Water masses characterize the marine physical environment and they affect the distribution of food and dispersion of the planktonic larvae of benthic species. Therefore, different water masses may play an important role in the composition and abundance of benthic communities (Feder et al., 1994; Stewart et al., 1985). The two main water masses that occupy the northeastern Chukchi Sea shelf, the Bering Shelf Waters and Alaska Coastal Waters, have been well described (Coachman et al., 1975; Walsh et al., 1989) (Figure 1.2). Despite the low correlation of epibenthic assemblages and the environmental variables included in this analysis, the geographical distribution of the main cluster groups coincided with the trajectory of water masses in the region. The variable selected first in the BIOENV analysis for abundance and biomass was longitude. Most likely longitude is acting as a proxy for the effect of the different water currents and is reflected in the south-north trajectory over the sample stations. Stations in Group 4 are located off the coast of Cape Lisburne (at the 69° N parallel) and extend along the Central Channel following the east flank of Herald Shoal. Stations further north follow the western and southern flanks of Hanna Shoal. This distribution matches the location of the branch of Bering Sea Water that flows through the Central Channel and mixes with water that flows northward offshore of Cape Lisburne and around the southern limit of Hanna Shoal (Weingartner et al., 2005; Winsor and Chapman, 2004). Communities in Group 4 also had the highest diversity indices of all cluster groups and were dominated by crustaceans. Although not examined in detail in this analysis, the diversity in feeding habits could reflect an enhanced availability of food through the water column, the benthic boundary layer, and the substrate (Feder et al., 2005).

The stations with highest biomass coincided with the pathway of the central shelf water that carry nutrients and carbon flowing eastward in the northern Chukchi Sea (Central Channel flow and AW), following the south of Hanna Shoal and merging with the near coastal circulation (ACC) at the head of Barrow Canyon (Weingartner et al., 2005). However, variability in ice cover and the formation of winter polynyas (offshore between Icy Cape and Barrow), mainly caused by changes in wind direction and advection of heat and salt through the Bering Strait, create changes in the flow pattern of water masses off the coast of the northeastern shelf and dense water formation_(Spall, 2007; Weingartner et al., 1998; Winsor and Chapman, 2002). With reduced seasonal ice cover and smaller winter polynyas, the flow of Bering Shelf water through this area becomes more passive and reduces the ventilation of water towards Barrow Canyon (Weingartner et al., 2005). This reduced flushing time of dense hyper-saline water creates a "dome" of dense water and reduced mixing over the sea floor (Winsor personal communication). The stations corresponding to Group 2, dominated by Ophiuroidea, could be affected by the persistence of dense water in the area (Weingartner personal communication). These localized periodic hyper-saline conditions may prove too stressful for many benthic organisms such as crustaceans and fish, favoring the development of dense assemblage of more tolerant groups, such as ophiuroids. Our observation is supported by evidence from the Paleozoic era that shows dense beds of brittle stars covering the seafloor around the British Isles. This extremely high abundance is explained by the scarcity of predators such as teleost fish and decapod crustaceans that did not radiate until the Cenozoic era (Aronson, 1989; Piepenburg et al., 2001).

1.5 Summary

To better understand the effect that anthropogenic disturbances have on the epibenthic communities of the productive Chukchi Sea, it is necessary to comprehend the different aspects that might cause variability in the epibenthic community in this region. In the area included in this study, there were marked differences in the total biomass and abundance recorded for each station, with the highest biomass values corresponding to the area close to the mouth of Barrow Canyon. Community assemblages also varied in diversity values. Stations in the center of the study area had the lowest diversity and stations following the trajectory of the Central Channel had the highest diversity index values. Moreover, there was a marked variability in the dominant taxa across stations.

Ophiuroidea, crustaceans (*Chionoecetes opilio*, Caridea and *Pagurus* spp.), sand dollars, and sea cucumbers were dominant groups. The variability in the communities was influenced by the flow and trajectory of water masses, sediment characteristics, and possibly variability in food quality and quantity. The taxa that form a community have specific requirements for their success. To determine the factors that are affecting the community, it is necessary to both measure environmental variables in the correct scale (i.e. seabed categories and sediment grain size) and account for the variability and fluctuations that many of the influencing factors may have (i.e. temporal changes in water current direction and dense water formation). Considering the complexity of the variability in the epibenthic assemblages in the Chukchi Sea, the effect of disturbances could be fundamentally different from one area to the next within a specific, defined region.

Acknowledgements

We would like to acknowledge the Bureau of Ocean Energy Management (BOEM), U.S. Department of Interior for funding to support this study, with special thanks to Dick Prentki, for his support, experience and love for birds. We thank Ken Dunton for his role as lead scientist of the COMIDA Project, and the entire COMIDA crew, for it was a pleasure working with them. We thank Captain John Seville and his crews on the *Alpha Helix* and *Moana Wave* for making this project possible and their great seamanship. Very special thanks to Martin Schuster for his most valuable help on deck, cheerful attitude and great music selection, Eric Hersh for his technical support and extreme patience in creating most of the maps presented here, and Susan Schonberg and Nora Foster for help in identifying many of the organisms collected. From the University of Alaska Fairbanks, we are very grateful to Tom Weingartner for his map demonstrating the circulation patterns of the main Chukchi Sea water masses and personal communications, to Katrin Iken for sharing her time and extensive knowledge, and to Peter Windsor, Bodil Bluhm, for their most valuable comments on this paper, enthusiasm and long hours discussing this analysis. Also Alexandra Ravelo would like to thank Ana Planchuelo, Andres Ravelo and Justin Kavanaugh for their support.

References

Ambrose, W., Clough, L., Tilney, P., Beer, L., 2001. Role of echinoderms in benthic remineralization in the Chukchi Sea. Mar. Biol. 139, 937-949.

Appeltans W, Bouchet P, Boxshall GA, De Broyer C, de Voogd NJ, Gordon DP, Hoeksema BW, Horton T, Kennedy M, Mees J, Poore GCB, Read G, Stöhr S, Walter TC, Costello MJ. (Eds.), 2012. World Register of Marine Species. Accessed at http://www.marinespecies.org on 2013-05-21.

Aronson, R.B., 1989. Brittlestar beds: low-predation anachronisms in the British Isles. Ecology, 856-865.

Bluhm, B., Gradinger, R., 2008. Regional variability in food availability for Arctic marine mammals. Ecol. Appl. 18, 77-96.

Bluhm, B.A., Iken, K., Hardy, S.M., Sirenko, B.I., Holladay, B.A., 2009. Community structure of epibenthic megafauna in the Chukchi Sea. Aquat. Biol. 7, 269-293.

Clarke, A. 1983. Life in cold water: the physiological ecology of polar marine ectotherms. Oceanogr. Mar. Biol. 21, 341-453.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User manual/tutorial, in: PRIMER-E, Plymouth.

Coachman, L.K., Aagaard, K., Tripp, R.B., 1975. Bering Strait: the regional physical oceanography. Univ of Washington Pr.

Cooper, L.W., Grebmeier, J.M., Larsen, I.L., Egorov, V.G., Theodorakis, C., Kelly, H.P., Lovvorn, J.R., 2002. Seasonal variation insedimentation of organic materials in the St. Lawrence Island polynya region, Bering Sea. Mar Ecol Prog Ser 226, 13–26.

Dehn, L.A., Follmann, E.H., Thomas, D.L., Sheffield, G.G., Rosa, C., Duffy, L.K., O'Hara, T.M., 2006. Trophic relationships in an Arctic food web and implications for trace metal transfer. Sci. of the Total Environment. 362, 103-123.

Fabry, V.J., Seibel, B.A., Feely, R.A., Orr, J.C., 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. ICES J. Mar. Sci. 65, 414-432.

Feder, H.M., Jewett, S.C., 1981. Feeding interactions in the eastern Bering Sea with emphasis on the benthos. The eastern Bering Sea shelf: oceanography and resources 2, 1229-1261.

Feder, H.M., Jewett, S.C., Blanchard, A., 2005. Southeastern chukchi sea (Alaska) epibenthos. Polar Biol. 28, 402-421.

Feder, H.M., Naidu, A.S., Jewett, S.C., Hameedi, J.M., Johnson, W.R., Whitledge, T.E., 1994. The northeastern Chukchi Sea: benthos-environmental interactions. Mar. Ecol. Prog. Ser. 111, 171-190.

Frost, K.J. and Lowry, L.F., 1983. Demersal fishes and invertebrates trawled in the northeastern Chukchi and western Beaufort Seas 1976-1977 NOAA Technical Report NMFS SFR-764.

Gage, J., 1990. Skeletal growth bands in brittle stars: microstructure and significance as age markers. J. Mar. Biolog. Assoc. U.K. 70, 209-224.

Grebmeier, J.M., 2012. Shifting Patterns of Life in the Pacific Arctic and Sub-Arctic Seas. Ann. Rev. Mar. Sci. 4, 63-78.

Grebmeier, J.M., McRoy, C.P., 1989. Pelagic-benthic coupling on the shelf of the Northen Bering and Chukchi Seas. III. Benthic food supply and carbon cycling. Mar. Ecol. Prog. Ser. 53, 79-91.

Grebmeier, J.M., McRoy, C.P., Feder, H.M., 1988. Pelagic-benthic coupling on the shelf of the Northern Bering and Chukchi Seas. I. Food supply source and benthic biomass. Mar. Ecol. Prog. Ser. 48, 57-67.

Grebmeier, J.M., Overland, J.E., Moore, S.E., Farley, E.V., Carmack, E.C., Cooper, L.W., Frey, K.E., Helle, J.H., McLaughlin, F.A., McNutt, S.L., 2006. A major ecosystem shift in the northern Bering Sea. Science 311, 1461-1464.

Gunderson, D.R., Ellis, I.E., 1986. Development of a Plumb Staff Beam Trawl for Sampling Demersal Fauna. Fish. Res. 4, 35-41.

Mariani, G., Sick, L., and Johnson, C., 1980. An environmental monitoring study to assess the impact of drilling discharges in the mid-Atlantic. III. Chemical and physical alterations in the benthic environment. Symposium on Research on Environmental Fate and Effects of Drilling Fluids and Cuttings. Lake Buena Vista, Florida.

Mayer, M., Piepenburg, D., 1996. Epibenthic community patterns on the continental slope off East Greenland at 75° N. Mar. Ecol. Prog. Ser. 143, 151-164.

Pawson, D.L., 1983. *Ocnus sacculus* new species (Echinodermata: Holothuroidea), a brood-protecting holothurian from southeastern New Zealand. N. Z. J. Mar. Freshwater Res. 17, 227-230.

Pickart, R.S., Weingartner, T.J., Pratt, L.J., Zimmermann, S., Torres, D.J., 2005. Flow of winter-transformed Pacific water into the Western Arctic. Deep Sea Res. Part II Top. Stud. Oceanogr. 52, 3175-3198.

Piepenburg, D., 2005. Recent research on Arctic benthos: common notions need to be revised. Polar Biol. 28, 733-755.

Piepenburg, D., Blackburn, T.H., Vondorrien, C.F., Gutt, J., Hall, P.O.J., Hulth, S., Kendall, M.A., Opalinski, K.W., Rachor, E., Schmid, M.K., 1995. Partitioning of benthic community respiration in the Arctic (Northwestern Barents Sea). Mar. Ecol. Prog. Ser. 118, 199-213.

Piepenburg, D., Brandt, A., von Juterzenka, K., Mayer, M., Schnack, K., Seiler, D., Witte, U., Spindler, M., 2001. Patterns and determinants of the distribution and structure of benthic faunal assemblages in the Northern North Atlantic in: Schafer, P., Ritzrau, W., Schluter, M., Thiede, J. (Eds.) The Northern North Atlantic: A Changing Environment. Springer, Berlin, pp. 179-198.

Piepenburg, D., Schmid, M., 1996a. Distribution, abundance, biomass, and mineralization potential of the epibenthic megafauna of the Northeast Greenland shelf. Mar. Biol. 125, 321-332.

Piepenburg, D., Schmid, M.K., 1996b. Brittle star fauna (Echinodermata: Ophiuroidea) of the Arctic northwestern Barents Sea: composition, abundance, biomass and spatial distribution. Polar Biol. 16, 383-392.

Piepenburg, D., Schmid, M.K., 1997. A photographic survey of the epibenthic megafauna of the Arctic Laptev Sea shelf: Distribution, abundance, and estimates of biomass and organic carbon demand. Mar. Ecol. Prog. Ser. 147, 63-75.

Sakshaug, E., 2004. Primary and secondary production in the Arctic seas, in: Stein, R., et al. (Eds.), The organic carbon cycle in the Arctic Ocean. Springer, Berlin, pp. 57–82.

Spall, M. A. 2007. Circulation and water mass transformation in a model of the Chukchi Sea. J. Geophys. Res. 112, 1-18.

Stewart, P.L., Pocklington, P., Cunjak, R.A., 1985. Distribution, abundance and diversity of benthic macroinvertebrates on the Canadian continental shelf and slope of Southern Davis Strait and Ungava Bay. Arctic 38, 281-291.

Walsh, J., McRoy, C., Coachman, L., Goering, J., Nihoul, J., Whitledge, T., Blackburn, T., Parker, P., Wirick, C., Shuert, P., 1989. Carbon and nitrogen cycling within the Bering/Chukchi Seas: source regions for organic matter affecting AOU demands of the Arctic Ocean. Prog. Oceanogr. 22, 277-359.

Weingartner, T., Aagaard, K., Woodgate, R., Danielson, S., Sasaki, Y., Cavalieri, D., 2005. Circulation on the north central Chukchi Sea shelf. Deep Sea Res. Part II Top. Stud. Oceanogr. 52, 3150-3174.

Weingartner, T.J., Cavalieri, D.J., Aagaard, K., Sasaki, Y., 1998. Circulation, dense water formation, and outflow on the northeast Chukchi shelf. J. Geophys. Res. 103, 7647-7661.

Winsor, P., Chapman, D.C., 2002. Distribution and interannual variability of dense water production from coastal polynyas on the Chukchi Shelf. J. Geophys. Res. 107, 10.1029.

Winsor, P., Chapman, D.C., 2004. Pathways of Pacific water across the Chukchi Sea: A numerical model study. J. Geophys. Res. 109, 1-16.

Woodgate, R.A., Aagaard, K., Weingartner, T.J., 2005. A year in the physical oceanography of the Chukchi Sea: Moored measurements from autumn 1990-1991. Deep Sea Res. Part II Top. Stud. Oceanogr. 52, 3116-3149.

Table 1.1. Number of taxa present by group, mean abundance (ind./1000 m^2) and biomass (kg/1000 m^2) of station groups and totals for independent Stations 103 and 1010. In parenthesis s.d. refers to standard deviation. Diversity indices: 1-λ (Simpson's dominance index) and J' (Pielou's evenness index).

Group/ Station	Number of taxa	Abundance ind./1000 m^2 (s.d.)	Biomass kg/1000 m^2 (s.d.)	1-λ (s.d.)	J' (s.d.)
1	17	197 (1,307)	2.19 (12.0)	0.78 (0.1)	0.75 (0.1)
2	36	1,678 (15,503)	2.21 (14.1)	0.68 (0.1)	0.63 (0.1)
3	29	89 (584)	0.30 (1.0)	0.72 (0.1)	0.74 (0.1)
4	42	82 (334)	0.66 (3.4)	0.87 (0.1)	0.86 (0.1)
103	14	3,447	44.48	0.89	0.90
1010	16	548,864	644.05	0.64	0.51

Table 1.2. Percent similarity among samples within cluster groups, with percent contribution of each taxon up to approximately 80%. In parenthesis s.d. refers to standard deviation. Av.: Average. Contrib.: Percent Contribution. Cum.: Percent Cumulative.

	Av. Abundance (% in trawl)	Av. % similarity (s.d.)	Contrib. (%)	Cum. (%)
Group 1 - Av. similarity: 78 %				
Echinarachnius parma	8.61	39.20	50.06	50.06
Caridea	3.56	15.98	20.40	70.46
Hyas spp.	1.53	6.70	8.56	79.02
Chionoecetes opilio	0.99	4.61	5.89	84.91
Group 2 - Av. similarity: 72 %				
Ophiuroidea	9.28	48.49 (5.2)	67.19	67.19
Caridea	2.08	6.78 (2.5)	9.40	76.59
Chionoecetes opilio	0.95	3.26 (1.8)	4.51	81.10
Group 3 - Av. similarity: 63 %				
Caridea	9.11	42.86 (5.2)	68.02	68.02
Pagurus spp.	1.45	4.97 (3.8)	7.89	75.92
Chionoecetes opilio	1.48	4.76 (3.6)	7.55	83.47
Group 4 - Av. similarity: 65 %				
Caridea	4.68	13.76 (3.3)	21.17	21.17
Chionoecetes opilio	4.74	13.62 (2.4)	20.95	42.12
Pagurus spp.	4.24	12.85 (4.6)	19.77	61.89
Leptasterias spp.	1.35	3.73 (2.1)	5.73	67.63
Ophiuroidea	2.62	3.54 (0.5)	5.45	73.08
Neptunea spp.	1.26	3.45 (2.6)	5.31	78.39
Colus spp.	1.07	2.56 (1.6)	3.93	82.32

Table 1.3. Dissimilarity between station groups and independent Stations 103 and 1010, determined by taxa with approximately 50% contribution. In parenthesis s.d. refers to standard deviation. Contrib.: Percent Contribution. Cum.: Percent Cumulative.

	Av. Abundance (% in trawl)		Av. % Dissimilarity (s.d.)	Contrib. (%)	Cum. (%)
Groups 1 & 2 - Av. dissimilarity = 67 %	Group 1	Group 2			
Echinarachnius parma	8.61	0.07	21.61 (8.1)	32.05	32.05
Ophiuroidea	2.04	9.28	18.51 (3.4)	27.46	59.51
Groups 1 & 3 - Av. dissimilarity = 63 %	Group 1	Group 3			
Echinarachnius parma	8.61	0	20.78 (6.1)	33.15	33.15
Caridea	3.56	9.11	13.51 (4.4)	21.55	54.7
Groups 1 & 4 - Av. dissimilarity = 65 %	Group 1	Group 4			
Echinarachnius parma	8.61	0.03	17.57 (10.7)	26.82	26.82
Chionoecetes opilio	0.99	4.74	7.73 (2.1)	11.8	38.62
Pagurus spp.	0.96	4.24	6.68 (2.8)	10.20	48.83
Ophiuroidea	2.04	2.62	5.42 (1.3)	8.28	57.10
Groups 1 & Station 103 - Av. dissimilarity = 72 %	Group 1	Station 103			
Echinarachnius parma	8.61	0	16.95 (11.2)	23.58	23.58
Cryptonatica spp.	0	5.44	10.71 (26.3)	14.89	38.47
Stomphia spp.	0.12	3.32	6.28 (70.3)	8.74	47.20
Actiniaria	0	3.13	6.15 (26.3)	8.56	55.76
Groups 1 & Station 1010 - Av. dissimilarity = 81 %	Group 1	Station 1010			
Echinarachnius parma	8.61	0	22.78 (9.8)	28.06	28.06
Ocnus spp.	0	7.71	20.37 (19.6)	25.10	53.16
Groups 2 & 3 - Av. dissimilarity = 67 %	Group 2	Group 3			
Ophiuroidea	9.28	1.08	21.50 (3.4)	32.09	32.09
Caridea	2.08	9.11	18.51 (2.9)	27.62	59.72

	Av. Abundance (% in trawl)		Av. % Dissimilarity (s.d.)	Contrib. (%)	Cum. (%)
Groups 2 & 4 - Av. dissimilarity = 61 %	Group 2	Group 4			
Ophiuroidea	9.28	2.62	14.49 (2.1)	23.60	23.60
Chionoecetes opilio	0.95	4.74	8.31 (2.1)	13.54	37.14
Pagurus spp.	0.86	4.24	7.34 (2.4)	11.95	49.10
Caridea	2.08	4.68	6.44 (1.7)	10.49	59.58
Groups 2 & Station 103 - Av. dissimilarity = 75 %	Group 2	Station 103			
Ophiuroidea	9.28	0	19.30 (7.3)	25.61	25.61
Cryptonatica spp.	0.36	5.44	10.55 (8.6)	14	39.61
Stomphia spp.	0.03	3.32	6.80 (12.1)	9.03	48.64
Actiniaria	0.06	3.13	6.37 (11.2)	8.45	57.09
Groups 2 & Station 1010 - Av. dissimilarity = 50 %	Group 2	Station 1010			
Ocnus spp.	0.45	7.71	20.67 (5.5)	40.98	40.98
Ophiuroidea	9.28	6.30	8.60 (3.3)	17.04	58.02
Groups 3 & 4 - Av. dissimilarity = 54 %	Group 3	Group 4			
Caridea	9.11	4.68	9.24 (2.5)	17.18	17.18
Chionoecetes opilio	1.48	4.74	6.92 (1.8)	12.87	30.05
Pagurus spp.	1.45	4.24	5.86 (2.1)	10.90	40.95
Ophiuroidea	1.08	2.62	5.28 (1.1)	9.82	50.77
Groups Station 3 & 103 - Av. dissimilarity = 60 %	Group 3	Station 103			
Cryptonatica spp.	0.34	5.44	10.15 (8.1)	16.87	16.87
Caridea	9.11	4.64	8.99 (4.2)	14.94	31.81
Stomphia spp.	0.26	3.32	6.13 (4.4)	10.20	42.01
Actiniaria	0.09	3.13	6.08 (6.0)	10.11	52.12
Groups 3 & Station 1010 - Av. dissimilarity = 85 %	Group 3	Station 1010			
Caridea	9.11	0.67	22.98 (4.3)	27.07	27.07
Ocnus spp.	0	7.71	20.83 (5.8)	24.54	51.61

	Av. Abundance (% in trawl)		Av.% Dissimilarity (s.d.)	Contrib. (%)	Cum. (%)
Groups 4 & Station 103 - Av. dissimilarity = 47 %	Group 4	Station 103			
Cryptonatica spp.	0.79	5.44	8.06 (6.5)	16.98	16.98
Stomphia spp.	0.22	3.32	5.39 (7.5)	11.36	28.35
Actiniaria	0.04	3.13	5.38 (13.1)	11.33	39.68
Ophiuroidea	2.62	0	4.53 (0.9)	9.55	49.23
Chionoecetes opilio	4.74	3.03	3.69 (1.8)	7.77	57
Groups 4 & Station 1010 - Av. dissimilarity = 80 %	Group 4	Station 1010			
Ocnus spp.	0.04	7.71	17.22 (13.5)	21.63	21.63
Chionoecetes opilio	4.74	0.22	10.23 (2.5)	12.84	34.47
Pagurus spp.	4.24	0.17	9.11 (3.7)	11.44	45.91
Ophiuroidea	2.62	6.30	9.11 (1.6)	11.43	57.34
Groups Station 103 & Station 1010 - Av. dissimilarity = 90 %	Station 103	Station 1010			
Ocnus spp.	0	7.71	16.60	18.37	18.37
Ophiuroidea	0	6.30	13.56	15.01	33.38
Cryptonatica spp.	5.44	0.20	11.28	12.48	45.86
Caridea	4.64	0.67	8.56	9.47	55.33

Table 1.4. Combination of variables that best explain the community abundance (similarity matrix based on relative abundance per trawl). Correlation coefficients appear in parenthesis. The significance level for this analysis was 0.1%. TOC: total organic carbon.

Number of variables	Best variable combination	Second best variable combination
1	longitude (0.330)	TOC (0.232)
2	longitude, TOC (0.375)	longitude, sediment grain size 2 φ (0.365)
3	longitude, sediment grain size 2 φ, water depth (0.396)	longitude, TOC, water depth (0.388)
4	longitude, bottom water temperature, water depth, sediment grain size 2 φ (0.406)	longitude, water depth, sediment grain size 2 φ, TOC (0.401)
5	longitude, water depth, sediment grain size 2 φ, bottom water temperature, TOC (0.413)	longitude, water depth, oxygen, sediment grain size 2 φ, TOC (0.409)
6	longitude, bottom water temperature, water depth, bottom water dissolved oxygen, sediment grain size 2 φ, TOC (0.416)	longitude, water depth, pH, bottom water dissolved oxygen, sediment grain size 2 φ, TOC (0.415)

Table 1.5. Combination of variables that best explain the community biomass (similarity matrix based on relative biomass per trawl). Correlation coefficients appear in parenthesis. The significance level for this analysis was 0.1%. TOC: total organic carbon.

Number of variables	Best variable combination	Second best variable combination
1	longitude (0.319)	sediment grain size 2 φ (0.283)
2	longitude, sediment grain size 2 φ (0.421)	longitude, sediment grain size >5 φ (0.396)
3	longitude, sediment grain size 2 φ, bottom water dissolved oxygen (0.458)	longitude, sediment grain size 2 φ, water depth (0.439)
4	longitude, sediment grain size 2 φ, bottom water dissolved oxygen, sediment grain size 4 φ (0.476)	longitude, sediment grain size 2 φ, bottom water dissolved oxygen, TOC (0.474)
5	longitude, sediment grain size 2 φ, bottom water dissolved oxygen, sediment grain size 4 φ, water depth (0.488)	longitude, sediment grain size 2 φ, bottom water dissolved oxygen, TOC, sediment grain size 4 φ (0.486)
6	longitude, sediment grain size 2 φ, bottom water dissolved oxygen, sediment grain size 4 φ, water depth, pH (0.496)	longitude, sediment grain size 2 φ, bottom water dissolved oxygen, TOC, sediment grain size 4 φ, water depth (0.496)
7	longitude, sediment grain size 2 φ, bottom water dissolved oxygen, sediment grain size 4 φ, water depth, bottom water temperature, TOC (0.505)	longitude, sediment grain size 2 φ, bottom water dissolved oxygen, TOC, sediment grain size 4 φ, pH (0.503)

Table 1.6.Mean values for selected environmental variables, bottom water characteristics, depth, sediment grain size, sediment total organic carbon, sediment Chlorophyll *a* and sediment C/N for each cluster group and the two independent stations. SD: stands for standard deviation. The following abbreviations were used, BW for bottom water, Temp. for temperature, Sal. for salinity, diss. O_2 for dissolved oxygen, Sed. for sediment, TOC for total organic carbon, Chl *a* for Chlorophyll *a*.

		BW Temp (°C)	BW Sal (ppt)	BW pH	BW Diss O_2 (%)	Depth (m)	Sed grain size <0 φ (%)	Sed grain size 1 φ (%)	Sed grain size 2 φ (%)	Sed grain size 3 φ (%)	Sed grain size 4 φ (%)	Sed grain size >5 φ (%)	TOC (%)	C/N (%)	Sed Chl*a* (mg/m^2)
Group	Mean	0.14	32.25	7.95	90.55	31.63	0.57	2.47	25.38	49.55	8.20	13.85	0.20	7.84	5.41
1	SD	0.3	0.0	0.0	5.5	7.7	0.6	2.0	7.8	8.2	4.7	2.5	0.0	0.2	3.3
Group	Mean	-1.01	32.62	7.68	95.06	38.42	4.30	0.70	1.74	11.12	14.18	67.96	0.97	7.44	10.86
2	SD	0.9	0.2	0.2	6.0	3.1	10.4	1.5	2.4	14.4	10.7	23.3	0.4	0.4	3.0
Group	Mean	-0.61	32.47	7.78	100.20	33.93	7.99	2.19	8.15	36.90	18.48	26.30	0.34	6.13	16.79
3	SD	1.0	0.4	0.3	2.8	6.6	8.4	2.4	5.5	13.9	8.8	15.8	0.3	1.9	10.1
Group	Mean	-0.05	32.45	7.78	92.02	40.28	2.03	0.29	1.39	9.10	16.18	71.01	0.95	7.48	13.12
4	SD	1.7	0.4	0.2	6.9	3.9	5.3	0.4	2.1	11.3	11.2	22.1	0.3	1.3	10.6
Station 1010		-1.37	32.97	7.35	69.60	47.99	0.00	0.00	0.21	0.63	3.62	95.54	1.57	7.14	10.78
Station 103		3.08	32.53	7.85	86.40	46.73	0.00	0.05	0.10	0.55	19.35	79.95	1.32	6.29	18.90

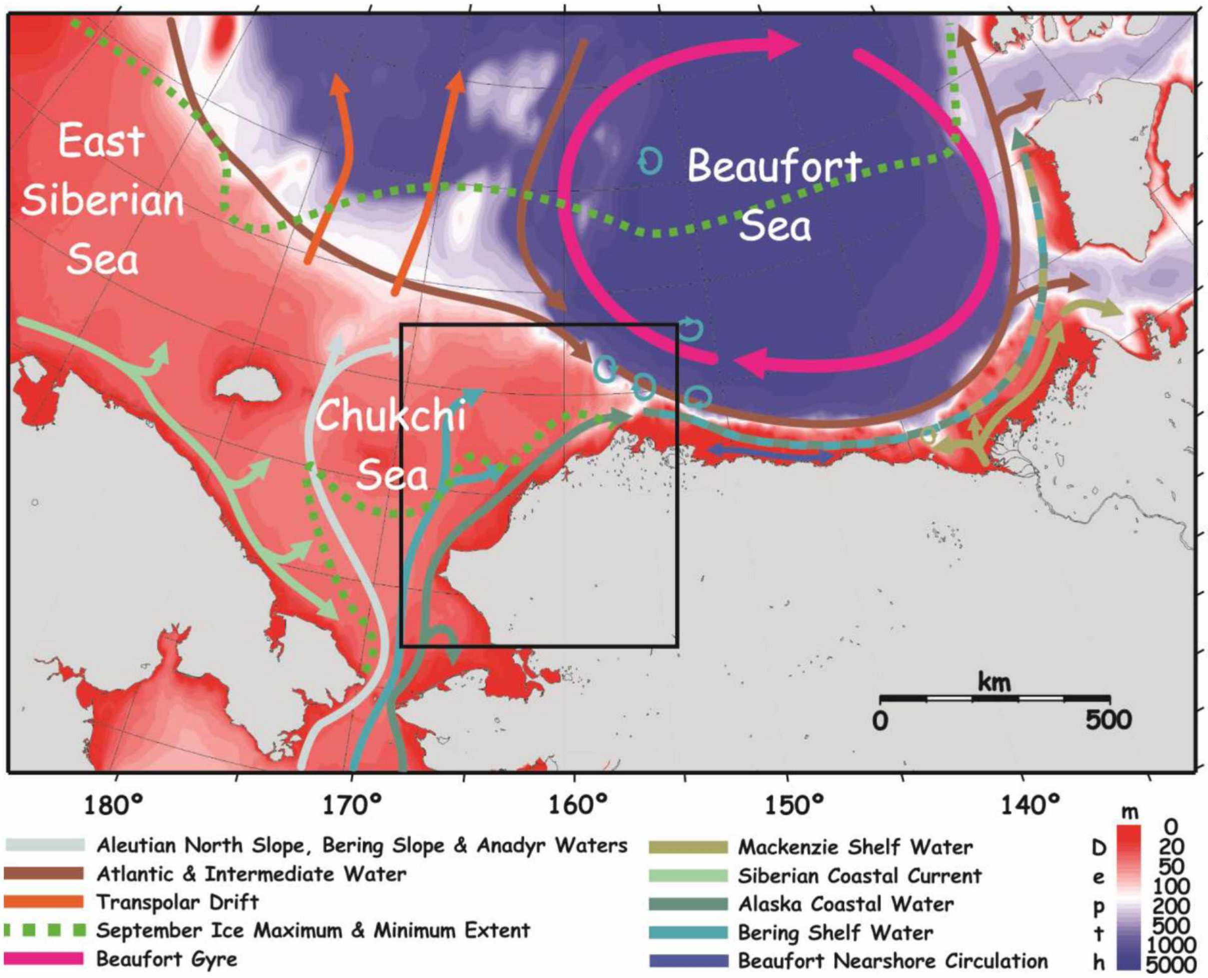

Figure 1.1. A schematic of the circulation over the Chukchi Sea and Beaufort/Chukchi slope, showing the three branches along which Pacific waters cross the Chukchi shelf. These are color-coded with navy blue being the most nutrient-rich waters (Bering Sea water) and light blue being the least nutrient-rich (ACC water). Courtesy of Tom Weingartner, modified from http://www.ims.uaf.edu/chukchi/#chan. The dark rectangle is enclosing the area of interest for this study

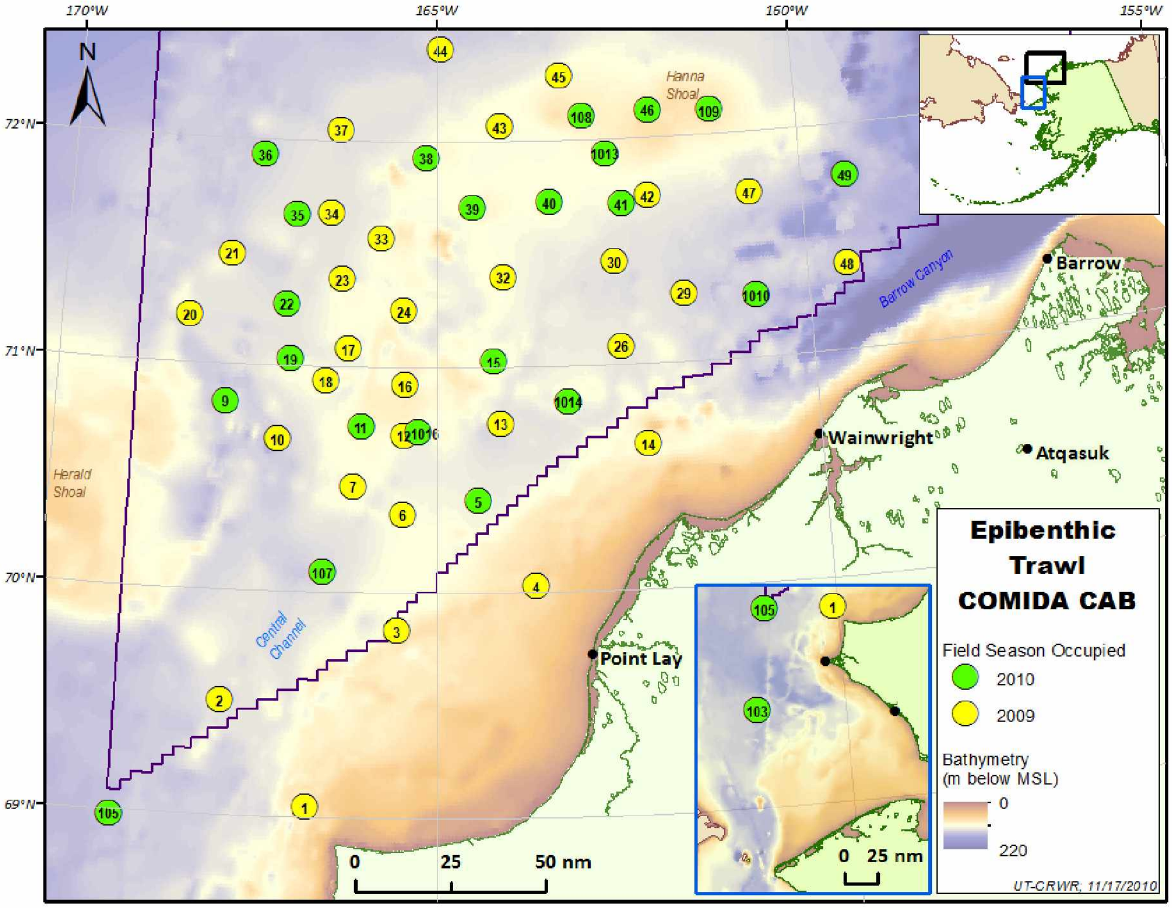

Figure 1.2. Epibenthic stations sampled in 2009 and 2010 in the Chukchi Sea. In the top right corner insert, the main study area is outlined by a black box and the blue box includes stations sampled in the upstream Bering Strait/SE Chukchi region, seen in detail in the insert at the bottom right.

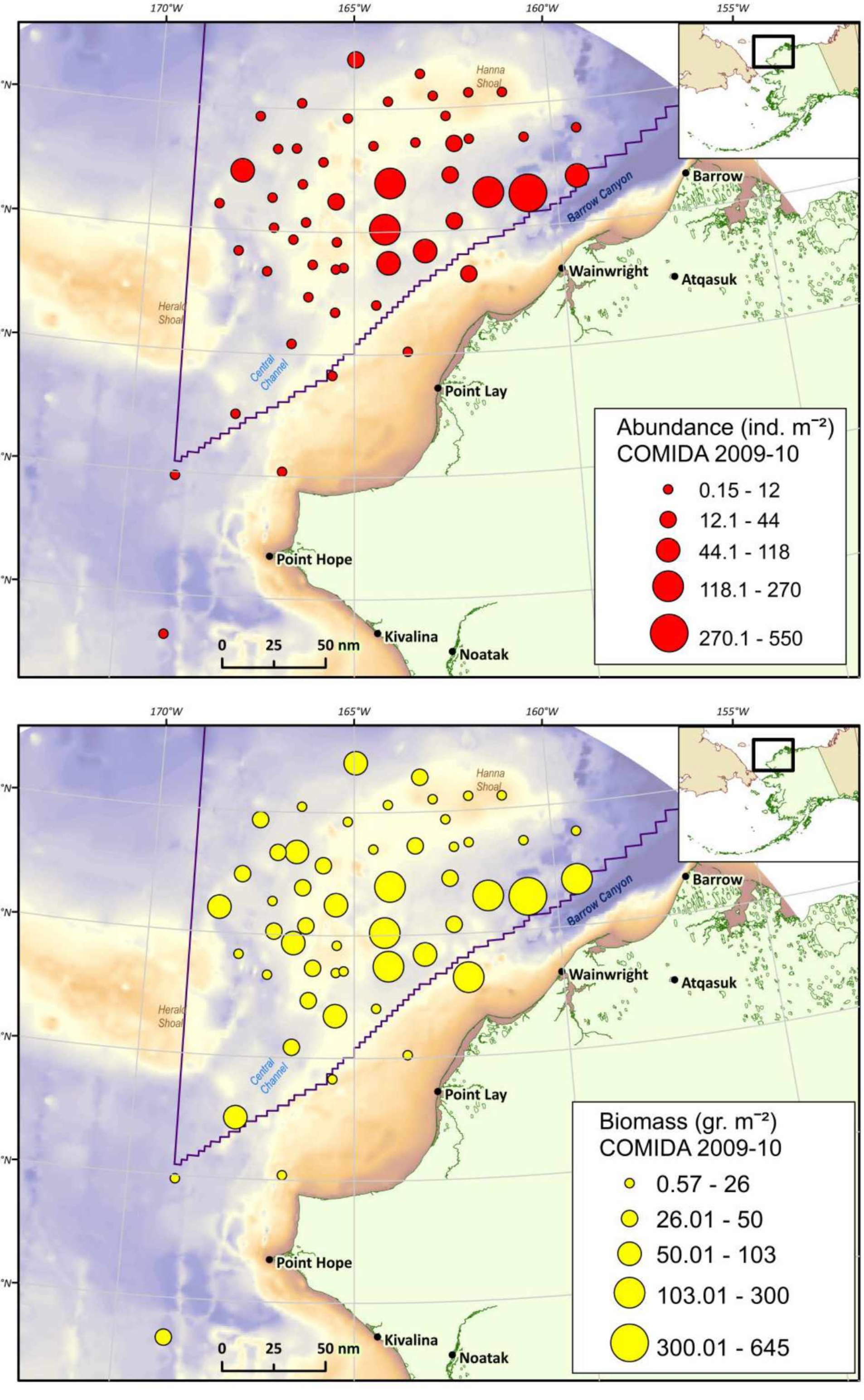

Figure 1.3. Map of stations total abundance and biomass, showing (A) the total abundance (number of individuals/m^2) and (B) biomass (g/m^2) for each station. Circle size intervals were determined by natural breaks by ArcMap 10.

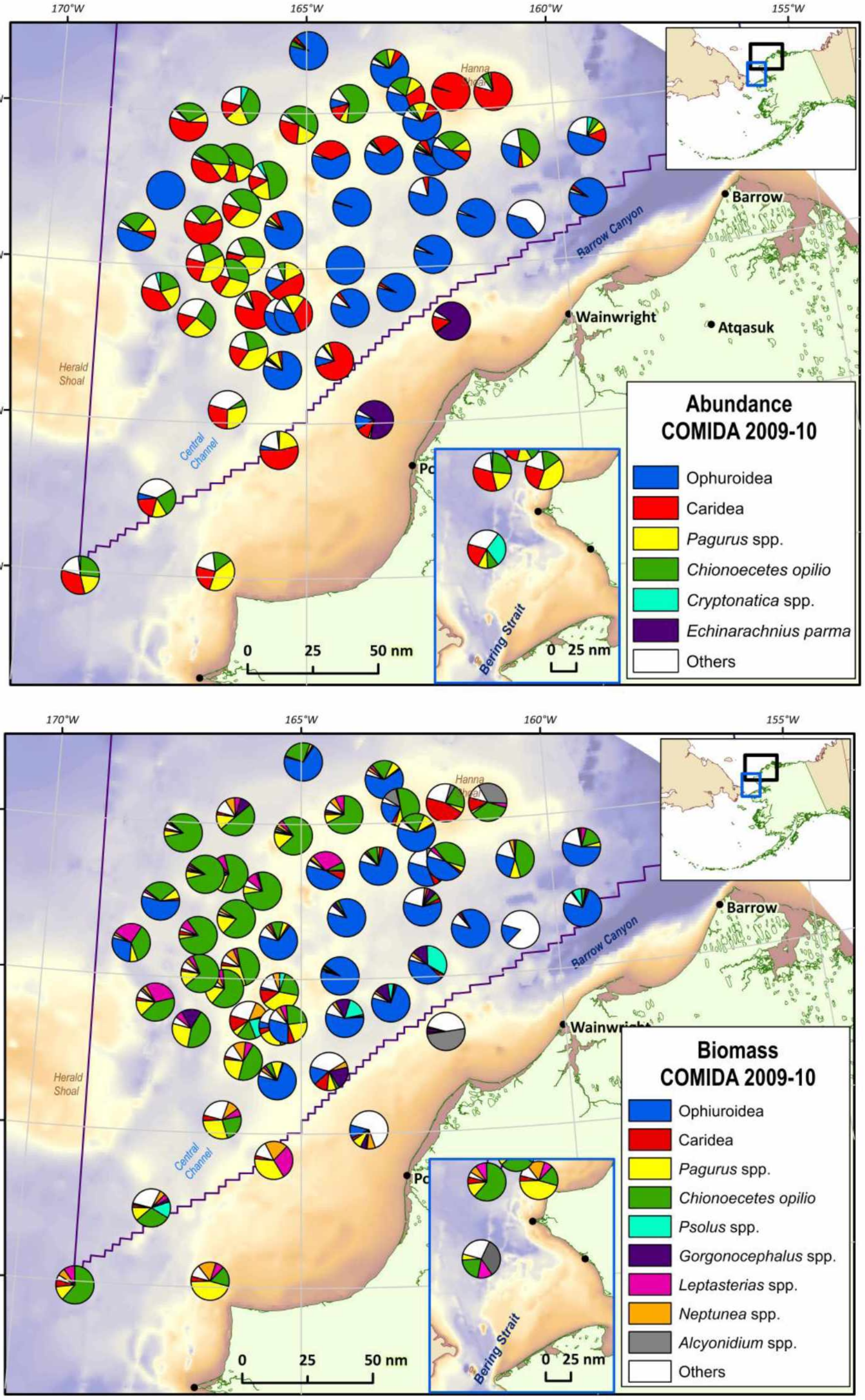

Figure 1.4. Maps of stations relative abundance and biomass (A and B, respectively) for taxa selected by the BVSTEP (Biological variables stepwise procedure in the PRIMER v.6 package) analysis as important representatives in the community.

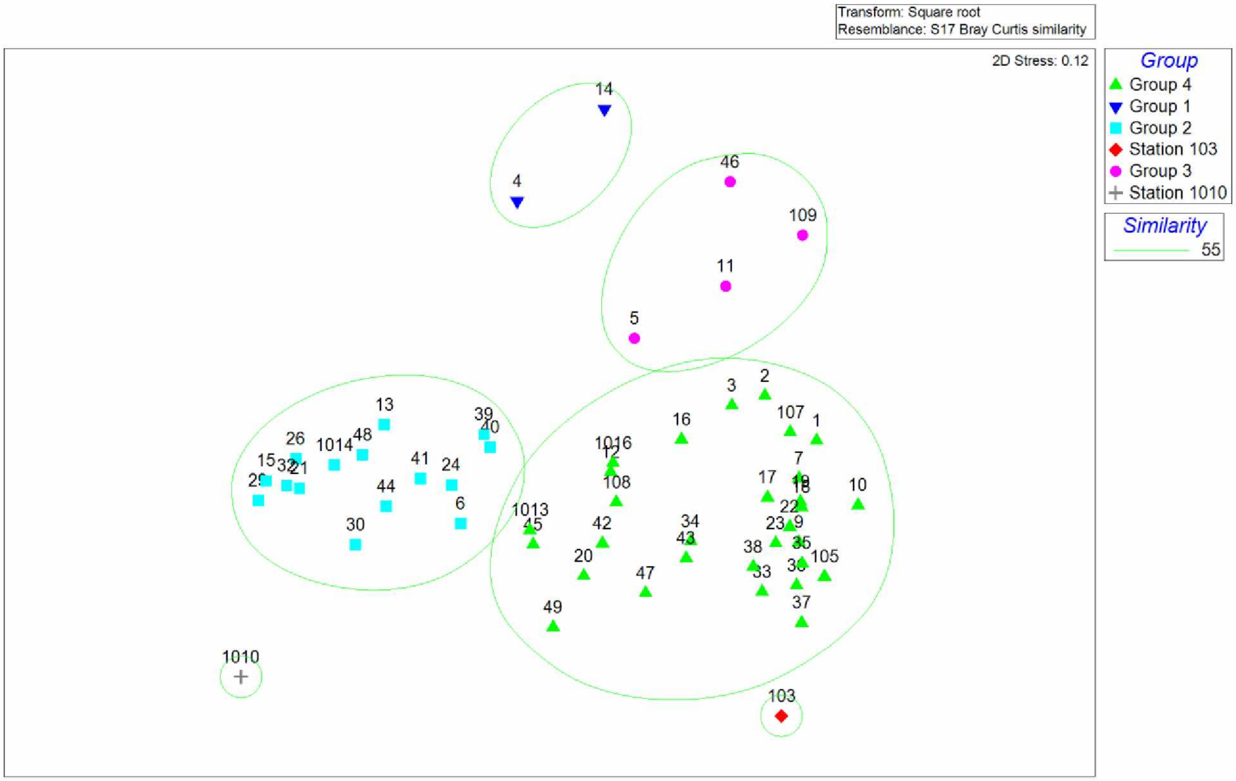

Figure 1.5. Multi-Dimensional Scaling plot of relative abundance, the different station groups outlined by the 55 % similarity level and using a 0.12 stress level. Station clusters from the relative percentage per trawl of abundance (square-root-transformed, Bray-Curtis similarity).

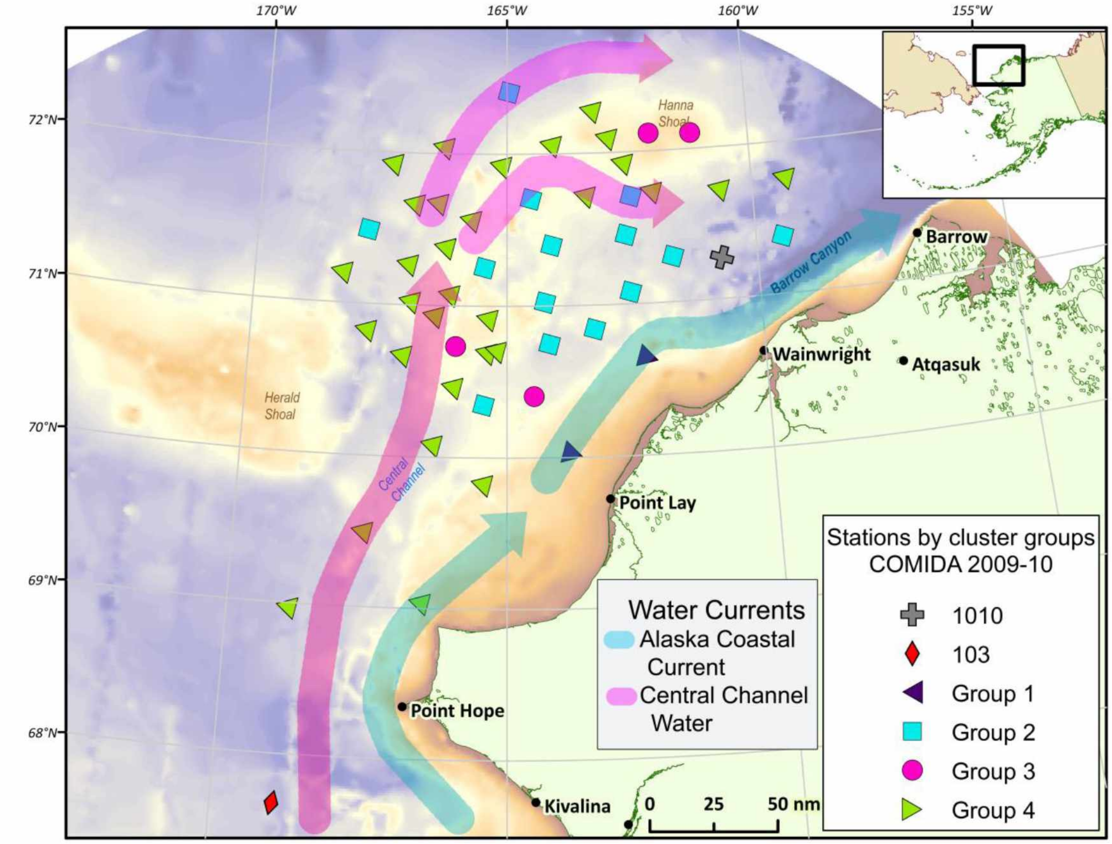

Figure 1.6. Map shows the spatial distribution of cluster groups and independent stations with a schematic of the general trajectory of water currents over the study area.

1.6 Appendix

Table 1.A. Taxa identified across the study area, the Class, Phyla and number of stations they were present.

Phylum	Class	Taxa	Common name	Presence
Mollusca	Gastropoda	*Admete solida*	Nutmeg shell snail	24
		Boreoscala greenlandica	Greenland Wentletrap snail	1
		Boreotrophon spp.	Trophon snail	38
		Buccinum spp./*Beringius* spp.	Whelk	42
		Calycidoris guentheri	Nudibranch	4
		Colus spp.	Colus snail	45
		Cryptonatica spp.	Moon snail	37
		Euspira spp.	Moon snail	40
		Iphione spp.	Hairy snail	14
		Margarites spp.	Margarite snail	26
		Neptunea spp.	Neptune whelk	47
		Obesotoma simplex	snail	10
		Onchidiopsis spp.	Blob snail	1
		Plicifusus spp.	Colus	29
		Tachyrhynchus spp.	Turrit shell snail	41
		Trichotropis spp.	Hairy snail	4
	Bivalvia	*Musculus niger*	Black Mussel	4
		Chlamys spp.	Scallop	1
		Nudibranch UnID	Nudibranch	3
	Polyplacophora	*Amicula vestita*	Concealed chiton	3
	Cephalopoda	*Muusoctopus sibiricus*	Octopus	4
Echinodermata	Asteroidea	*Crossaster papposus*	Common rose star	11
		Ctenodiscus crispatus	Mud star	8
		Henricia spp.	Henricia star	7
		Leptasterias spp.	Sea star	47
		Pteraster spp.	Cushion star	7
	Ophiuroidea	*Gorgonocephalus* spp.	Basket star	19
		Ophiuroidea	brittle star	41
	Holothuroidea	*Ocnus* spp.	Sea cucumber	9
		Psolus fabricii	Arctic Armored Cucumber	8
	Echinoidea	*Echinarachnius parma*	Northern Sand dollar	5
		Strongylocentrotus spp.	Sea urchin	2
Arthropoda	Malacostraca	Caridea	shrimp	53

		Chionoecetes opilio	Snow crab	53
		Hyas coarctatus	Arctic Lyre crab	39
		Pagurus spp.	Hermit crab	52
		Saduria spp.	Isopod	2
	Pycnogonida	Pycnogonidae	Sea spider	5
Chordata	Ascidiacea	*Boltenia* spp.	Tunicate	4
		Halocynthia spp.	Tunicate	1
Cnidaria	Anthozoa	Actiniaria	Anemone	7
		Gersemia spp.	Raspberry Soft Coral	28
		Metridium spp.	Anemone	1
		Stomphia spp.	Anemone	19
Bryozoa	Gymnolaemata	*Alcyonidium* spp.	Bryozoan	19

CHAPTER 2: Spatial variability of epibenthic communities on the Alaska Beaufort Shelf[1]

Abstract

Arctic marine epibenthos contribute significantly to the regional biomass, remineralization and redistribution of organic carbon, and are key elements of local food webs. The main purpose of this study was to describe the epibenthic invertebrate community on the Alaska Beaufort Shelf and identify links between community patterns and environmental drivers. Using a plumb-staff beam trawl, 71 stations were sampled between 13-220 m and from 145.09° W to 155.25°W along the shelf, in Aug/Sept of 2011. At each station, epibenthic taxonomic composition, abundance and biomass data were collected together with environmental data. Significant spatial variability in community composition and standing stock of the dominant taxa were observed along changes in depth and along-shelf position. The significant interaction between along-shelf position and depth helped define six geographic domains (two regions with three depth groups each). Shallow stations (<25 m) were dominated by mobile crustaceans and had the lowest values in diversity indices and total number of taxa. Mid-depth stations (26-100 m) had the highest values in diversity indices and were dominated by molluscs, crustaceans and echinoderms. Deep stations (101-220 m) were mostly represented by echinoderms and crustaceans with intermediate diversity values but high abundance and biomass values. However, at constant depth ranges, there were very few similar representative taxa in the eastern and western regions. Also, a clear reduction in abundance and biomass along the shelf break was observed from west to east. The six most influential environmental drivers (sediment phaeopigments, bottom water salinity, bottom water temperature, sediment organic matter, bottom water pH and percent sand) explained up to 50% of the variance in epibenthic community structure. Through this study we learned that the epibenthic community on the Alaska Beaufort Shelf is diverse, spatially heterogeneous and can have high biomass and density. Also we show how these community assemblages and total epibenthic biomass are linked to spatial changes in the environment through changes in bottom water temperature, salinity, sediment grain size and proxies for food quantity and quality.

---

[1] Ravelo, A.M., Konar, B., Bluhm, B.A., 2015. Spatial variability of epibenthic communities on the Alaska Beaufort Shelf. Polar Biol 38, 1783–1804. doi:10.1007/s00300-015-1741-9

2.1 Introduction

Throughout the Arctic shelves, benthic communities can differ greatly in standing stock, diversity and taxonomic composition due to differences in hydrography, food supply and substrate (Piepenburg 2005). Pacific Arctic shelves comprise areas of both high and low standing stock of benthic invertebrates, but comparatively small densities and biomass of pelagic and demersal fishes (Rand and Logerwell 2011; Day et al. 2013). On the western Alaska Beaufort shelf, epibenthic invertebrates made up to 94% of the total trawl catch weight while fish biomass was negligible (Rand and Logerwell 2011). Within the benthos, mega-epibenthic communities contribute up to 41% of the carbon demand and are dominated by echinoderms with peaks in abundance and biomass in the 60–90 m depth range in the Canadian Beaufort Sea (Renaud et al. 2007). Although epibenthic communities are patchy with variable biomass and taxonomic diversity, communities dominated by echinoderms are a common feature in many Arctic regions, such as the Chukchi, Greenland and Barents Seas (Starmans et al. 1999; Piepenburg 2005; Bluhm et al. 2009; Ravelo et al. 2014). Despite the great variability observed throughout the Arctic shelves, benthic species richness is intermediate on a global scale and comparable to values from the Antarctic region (Piepenburg et al. 2011).

Benthic community patterns reflect and integrate the environmental forces that take place in the region they inhabit; therefore differences in the ecologically relevant environmental drivers among shelves can help explain the great variety in community patterns throughout the Arctic shelves. At a local scale, the main forces that shape benthic communities are biological interactions, while environmental drivers may act at a local and regional scale (Connell 1961). Predation can have a profound effect on benthic community composition, as many epibenthic organisms in the Arctic are important prey items to marine mammals, fishes and birds (Packer et al. 1994; Coyle et al. 2007; Bluhm and Gradinger 2008; Cooper et al. 2013). Competition for resources (food from vertical flux advected to the benthos from the pelagic zone, and infaunal organisms) can also have an important effect on epibenthic community composition (Feder et al. 2011). Through tight benthic-pelagic coupling, benthic organism distribution and standing stock can to some degree be determined by the level of productivity in the water column above (Grebmeier 2012). In the Chukchi and Beaufort Seas, seasonal primary production is large and its phenology such that large quantities fall to the seafloor ungrazed, supporting high benthic biomass (Carmack et al. 2004; Grebmeier et al. 2006a; Campbell et al. 2009). As in most Arctic shelves, changes in current speed, water mass properties, and water depth are accompanied by changes in seafloor characteristics, sea ice cover, water column productivity, etc., all of which can have a large effect on benthic community standing stock, diversity and taxonomic composition (Mayer and Piepenburg 1996). For example, patterns in epibenthic community composition have been linked to a combination of environmental drivers such as changes in water mass, food supply and sediment grain size throughout the Chukchi Sea (Bluhm et al. 2009; Ravelo et al. 2014). However, this link between environmental drivers and epibenthic communities is largely undescribed for the Alaska Beaufort Shelf.

Of particular importance to epibenthic communities in the Alaska Beaufort Shelf is its narrow (50-100 km wide) and shallow interior nature (Carmack and Wassmann 2006). Sediments are poorly sorted muds or sandy-muds on the shelf, with distinct differences in the overall mean grain size on the shelf, slope and basin (Naidu 1974). Carbon sources on the Beaufort Sea shelf include both advected and *in situ* components of marine production and riverine and coastal erosion-related inflow of terrestrial carbon (Goñi et al. 2013). As an Arctic interior shelf, water originated both in the Atlantic and the Pacific flow over this region. The eastward-flowing Atlantic Water, that is part of the Arctic-wide cyclonic boundary current system, is found below the 200 m isobath along the Alaska Beaufort slope (McLaughlin et al. 2006). Pacific originated water enters the Arctic through Bering Strait and follows a northward trajectory through the Chukchi Sea, entering the Beaufort shelf through Barrow Canyon, where it forms the “Beaufort shelf-break jet” (Pickart 2004; Nikolopoulos et al. 2009). This shelf-break jet has an eastward trajectory and distinct seasonal configurations. During the spring it is bottom intensified, transporting dense winter transformed water from the Chukchi Sea, while in the summer it becomes surface intensified transporting warm Alaska Coastal Current waters (Pickart 2004; Nikolopoulos et al. 2009). Wind has a strong effect on the direction, extent and intensity of this jet (Pickart et al. 2011). During the fall and winter, easterly winds prevail or increase and can reverse the direction of the shelf-break jet, thus promoting upwelling along the Alaska north slope, making nutrients available for primary productivity (Aagaard 1984; Weingartner et al. 1998; Pickart et al. 2013). The high benthic biomass on the Chukchi Sea shelf and western Beaufort Sea has been linked to the highly productive waters of Pacific and Bering Sea origin (Logerwell et al. 2011; Ravelo et al. 2014). Further along the eastern Alaska Beaufort shelf (east of 150°W), the fate of the shelf-break jet is still unclear (Nikolopoulos et al. 2009). On the Canadian Beaufort Shelf, low sediment organic carbon content has been attributed to low water column primary production mostly limited by nutrients and light availability, resulting in a total annual estimate ranging from 12 to 16 g C m^{-2} for this region (Naidu 1974; Carmack et al. 2004). Another allochthonous source of carbon in the region comes from the seasonal discharge of many rivers, particularly the Colville and the Mackenzie rivers, which can affect large areas of the shelf with terrigenous organic matter, inorganic sediments and reduced salinity (Macdonald et al. 1998; Carmack and Macdonald 2002; Carmack and Wassmann 2006). Changes in food web structure with increased terrestrially derived carbon from rivers have been determined for the Alaska Beaufort Sea shelf and slope (L. Bell, unpublished data); however, the changes in community structure associated with the proximity of river inflow are largely unknown for the outer shelf in this region.

Currently, pack ice advances over the region in November and starts to retreat by July (Maslanik et al. 2007). Landfast ice forms gradually in the fall (October) and by late winter (March), its extent can reach up to 50 km offshore (Mahoney et al. 2014). In the winter, the offshore movement of the Beaufort Gyre pushes the pack ice westward, which breaks against the fixed landfast ice, forming a large pressure-ridge system that can run aground along nearshore areas (Barnes et al. 1984). In this area, known as the Stamukhi zone, the seafloor is scoured by dragging ice keels. Some ice gouges are more than 4 m deep (Barnes et al. 1984), with the highest density found between water depths of 20 to 40 m (Reimnitz and Kempema 1984). This seasonal gouging disturbs the benthic communities, which may take more than a decade to recover to the original state (Conlan and Kvitek 2005).

Most of our knowledge on the benthic communities of the Alaska Beaufort Shelf date from the 1970's, sparked by interests in off-shore oil exploration (Carey and Ruff 1977; Frost and Lowry 1983; Carey et al. 1984; Dunton 1984). Benthic offshore studies focused on fish and infauna while nearshore studies for the past three decades have focused on kelp communities associated with boulders (Dunton 1984; Dunton and Schonberg 2000; Konar and Iken 2005; Konar 2007). The overall purpose for this study stems from our lack of knowledge of epibenthic communities in this area, the biological importance of the epibenthos to Arctic shelf systems, the rapid environmental changes occurring in the Arctic and the increase in economic interest in this region (Loeng et al. 2005; Dunton et al. 2009; Dunton et al. 2012; Grebmeier 2012). Our general objective was to describe the epibenthic community on the Alaska Beaufort Sea shelf. We specifically wanted to 1) analyze the spatial variability in abundance, biomass, taxonomic composition and diversity of epibenthic invertebrates on the Alaska Beaufort Shelf; and 2) determine the set of environmental parameters that best correlate with the changes in the epibenthic community throughout the study region.

2.2 Methods

In August-September of 2011, 71 stations were sampled from 70.45°N and 145.09°W to 71.66°N and 155.25°W, in water depths from 13 to 220 m (Figure 2.1). The stations sampled by this project were in part chosen to repeat previously sampled locations by other research projects. The station spacing was chosen at approximately 0.5° latitude and 0.25° longitude with the goal to cover the majority of the along-shelf extent of the Alaska Beaufort Shelf and include replicate sampling locations in the shallow nearshore, mid-shelf and at the upper slope. Two gear types were used, a plumb-staff beam trawl (PSBT) designed after Gunderson and Ellis (1986) and a modified version of this beam trawl (PSBT-A). Both gear types were 3.05 m plumb-staff beam trawls with a 7 mm mesh and a 4 mm codend liner. A rigid 3 m pipe forward of the net held the mouth open for an effective swath of 2.26 m; the vertical opening of the net was approximately 1.2 m. The modification of the PSBT-A gear consisted of the addition of rubber rollers on the bottom of the net following the design of Abookire and Rose (2005). The PSBT-A was used at stations with very soft bottom, where the rubber rollers allowed a more surficial swath of the gear over the seafloor. At five opportunistically chosen stations (WB13, WB14, WB18, WB21 and CB33) both trawl types were used to allow a comparison of the catch of both trawls and to ensure that comparisons of epibenthic communities among stations sampled using different trawls were valid. The trawl time for either gear ranged from 1 to 5 minutes on the seafloor at a vessel speed of 2 to 5 knots. Trawl bottom time was estimated based on vessel wire scope and vessel GPS position at the beginning and end of the trawl. The distance covered ranged from 63 m to 383 m. Information for each station (georeferenced position, depth, gear type, date sampled and *a posteriori* defined region and depth group) is provided in Figure 2.A.

After a trawl was brought on board, catches were rinsed of sediments and organisms sorted to varying taxonomic levels, in some cases species level, in most cases to genus. All community analyses were made using the taxonomic resolution achieved in the field. Bryozoa and Hydrozoa were grouped at the phylum and class level, respectively. Voucher specimens were fixed in 10% buffered formalin for later taxonomic verification and finer taxonomic resolution for a taxa list (Figure 2.B). Taxon names were verified using WoRMS (WoRMS Editorial Board 2015). All individuals were counted by taxon and their damp biomass determined by digital scales with 1 gram accuracy. Single trawl hauls were collected at each station due to the considerable time commitment they involve. At six opportunistically chosen stations(WB07, WB31, WB32, CB33, CB34 and CB35) a second haul was collected with no more than five days apart from the first haul and using the same gear type (PSBT-A in all cases). These trawls were performed to determine the representativeness of the area sampled by one trawl.

At each station, sediment samples collected from a van Veen grab were immediately frozen at -20°C for later determination of chlorophyll *a* concentration, organic matter content, total organic carbon (TOC) and nitrogen content (TN), carbon to nitrogen ratios (C/N), and sediment grain size. All sediment samples were processed at the University of Alaska Fairbanks. Sediment chlorophyll *a* ($\mu g/cm^3$) and phaeopigments ($\mu g/cm^3$) were determined from a 4.16 cm^3 sub-core (2.77 cm diameter x 1.5 cm deep) taken from each van Veen grab. Sediment samples were processed within three months of collection. Samples were thawed and pigments extracted with 25 ml of 90% acetone for 24 h in the dark at -20°C. Pigment concentration was determined using a fluorometer following the procedure described by Arar and Collins (1997). Sediment organic matter (% dry weight) was determined from surface subsamples from van Veen grabs, which were dried at 105°C for 24 h. Organic matter content was determined by the difference in weight of the sample before and after ignition in a muffle furnace at 440°C for 1 h (Schumacher 2002). Two types of substrate descriptors were included as variables in the environmental analysis, quantitative values of sediment grain size and qualitative categories of seafloor characteristics. Sediment grain size samples were collected from the sediment surface with a scoop from each van Veen grab and classified into fractions of gravel, sand, mud and sediment water content, following the protocol described by Strobel et al. (1995). Seafloor characteristics were noted from the van Veen grab (i.e. presence of soft sediments only) and the trawl (i.e. cobbles and boulders present) at each station. These observed seafloor characteristics were included as dummy variables in the environmental analysis; where the categorization was based on the presence/absence of cobbles, boulders or a combination of the two (0: only soft sediments, 1: cobble, 2: boulders, 3: cobble and boulders). Sediment TOC (%), TN (%) and molar C/N values were obtained from measurements of sediments processed following the same protocol as in Iken et al. (2010). In addition, bottom water characteristics (temperature (°C), salinity (‰), pH) and water samples for bottom water chlorophyll *a* (μg/l) and phaeopigments (μg/l) were collected using a SeaBird 25 CTD equipped with Niskin bottles (average distance from the seafloor was 8 m, s.d. 7 m). The CTD data were processed using SeaBird software and averaged vertically into 1-m bins. Water samples were filtered and processed for chlorophyll *a* content following Parsons (1984).

2.2.1 Data analysis

To analyze spatial variability in epibenthic abundance, biomass, taxonomic composition and diversity on the Alaska Beaufort Shelf, community structure was investigated with non-parametric multivariate statistical analysis using the software package PRIMER v. 6 (Clarke and Gorley 2006). For this purpose, all taxa abundance and biomass values were standardized to their relative contribution per trawl (in percent) and a square root transformation was applied. Proportional data are commonly used in multivariate analysis when the size of the samples is not fixed, such as the area trawled (Clarke and Warwick 2001). For each statistical test used, all assumptions were verified. To confirm that there was no significant difference in the performance of the two types of trawl gear used in this study, relative abundance and biomass data from five stations were sampled using both gear types (n = 10) were analyzed using a one-way design with "gear type" as the factor level using PERMANOVA+ (Clarke and Gorley 2006). The PERMANOVA+ analysis tests the simultaneous response of the variables to the factor in an analysis of variance type experimental design on the basis of the resemblance measure, using a permutation method (Anderson et al. 2008). In this analysis, the null hypothesis of no difference between the factor levels is determined by a pseudo-F ratio and permutation p-value (P(perm)) (Clarke and Gorley 2006). The same statistical procedure was used to test the difference between samples collected at the same station using the same gear type (six stations, n = 12). This was done to assess the overall representativeness of the area sampled by only one trawl collected at each station, using the factor levels "sample 1 or 2".

To respond to the general objective and determine the taxa that best explain the pattern of the epifaunal community across all stations, BVSTEP (Biological Variables Stepwise Procedure) was used separately on the abundance and biomass data, using a Bray-Curtis resemblance matrix and Spearman rank correlation. The BVSTEP procedure carries a step wise approach, searching for high rank correlations between a faunal data matrix and a Bray-Curtis similarity matrix. Community cluster analysis calculated with abundance data provided station grouping by similarity, using group averaging based on Bray-Curtis resemblance matrix. The SIMPROF test (Similarity Profile) detected the statistical significance of the internal structure at each node of the dendrogram. Based on the results of the community cluster analysis, stations were grouped into six "geographic domains", consisting of three depth categories (shallow, mid-depth and deep) for each two regions (east and west) (Figure 2.5). Depth categories were determined by environmental features characteristic of the shelf. For the shallow stations ($\leq$ 25 m), the limit was determined by the extent of the ice scouring that occurs on the sea floor up to 20-25 m in depth (Mahoney et al. 2014). The deeper limit for the mid-depth stations was determined by the shelf break (100 m). The deep station category corresponded to the shelf break and the upper slope (101-220 m). To better understand the changes along the shelf from the western to the eastern extent of the study area, stations within the three depth categories were also divided into two regional categories (east and west), loosely determined again by the cluster analysis and a spatial gap in the station distribution. We stress that we do not consider longitude in itself as a factor for these two groups, but consider the group 'west' as having strong influence from Chukchi Sea inflows, and 'east' as having weaker Chukchi influence. A two-way crossed PERMANOVA+ design was used to determine the statistical significance of the *a posteriori* defined geographic domains within the study area. For this analysis, the fixed factors used were "region" with two levels, east (32 stations) and west (39 stations) and "depth" with three levels, shallow (17 stations), mid-depth (33 stations) and deep (21 stations). To determine the taxa representing each of these assemblages, a BVSTEP analysis was performed separately with the relative abundance and biomass data. Epibenthic abundance and biomass data were standardized to 100 m^2 for community standing stock description (i.e. Figures 2.2a and 2.2b) and estimation of diversity indices. Shannon-Wiener's diversity ($H' = -\Sigma\ Pi\ \log_e(Pi)$), Pielou's evenness ($J' = H'/\log_e S$) and Margalef's richness ($d = (S-1)/\log_e N$) indices were calculated from biomass (g wet wt/100 m^2) for all stations using the DIVERSE routine in PRIMER. S denotes species, which in our case also included taxa identified to coarser resolution. Biomass over abundance was chosen because biomass data include colonial taxa not captured by the abundance data. For these diversity indices, two-way crossed ANOVAs using "region" and "depth" as factors were conducted at a 95% confidence level and Tukey tests were applied at 0.05 significance level using R (www.r-project.org, V2.15.0). All assumptions for ANOVA tests were met. All maps presented were generated using ArcMap from ESRI software. Total abundance and biomass data were projected onto maps by scaled circles, with breaks determined by Jenks' natural breaks.

To determine the set of environmental parameters that best correlate with the changes in the epibenthic community throughout the study region, the BIOENV (Biological-Environmental Interactions) routine using normalized variables was applied (Clarke and Gorley 2006). The stations that had one of the below-mentioned variables missing were excluded from the analysis, reducing the number of stations included to 55. No variables were excluded from the BIOENV analysis due to high colinearity (< 90%). The full set of environmental variables included in this analysis were: (1) indicators of food supply and quality, including sediment chlorophyll *a* (µg/cm^3) and phaeopigment (µg/cm^3) concentration, organic matter content in surface sediments (% dry weight), surface sediment total carbon (TOC) and nitrogen (TN) content, molar carbon to nitrogen ratio (C/N), bottom water chlorophyll *a* (µg/l) and bottom water phaeopigment content (µg/l), (2) habitat descriptors, such as sediment grain size including gravel, sand, and mud (silt and clay) fractions and sediment water content; as well as qualitative substrate descriptors "seafloor characteristics", and (3) hydrographic descriptors including bottom water salinity (‰), temperature (°C) and pH. To explore the environmental patterns in the study region, a principal component analysis (PCA) was performed using the most relevant variables as identified by the BIOENV analysis.

2.3 Results

There was no significant difference between the five stations sampled with PSBT and PSBT-A trawl gears for relative abundance (PERMANOVA+, Pseudo-F: 0.163, P(perm): 0.992) or relative biomass (PERMANOVA, Pseudo-F: 0.246, P(perm): 0.991). Therefore, we included all stations in the community analysis regardless of the gear type used. Similarly, there was no significant difference in relative epifaunal abundance (PERMANOVA, Pseudo-F: 0.211, P(perm): 0.868) or biomass (PERMANOVA+, Pseudo-F: 0.239, P(perm): 0.986) between the repeated samples collected at the six stations that were revisited. These results increase our confidence that the single sample collected at each station is sufficient to represent the epibenthic community at that station at a given time.

The mean total abundance per station was 2,531 ind/100 m^2 (sd 5,349), ranging from a total abundance of 4 ind/100 m^2 at station WB30 to 27,559 ind/100 m^2 at station WB04 (Figure 2.2). The mean total biomass amounted to 3,656.9 g wet wt/100 m^2 (sd 7,854), ranging from 5.8 g wet wt/100 m^2 at station CB07 to 50,103.1 g wet wt/100 m^2 at station WB04 (Figure 2.3). Across all stations, a total of 133 taxa in nine phyla were identified from voucher specimens and in the field; including 54 Mollusca, 27 Echinodermata, 24 Arthropoda, eight Cnidaria, seven Chordata, six Porifera, five Bryozoa, one Platyhelminthes, and one Brachiopoda (Figure 2.B). The average number of taxa across all stations was 22 (sd 9), with the total number of taxa ranging from three at stations CB10, CB31 and WB30 to 42 at station EB21 (Figure 2.4). Of the total abundance across all stations, the brittle star *Ophiura sarsii* represented 74.5% of all individuals, followed by the brittle star *Ophiocten sericeum* with 6.3%, the brittle star *Ophiacantha bidentata* with 4.1%, the sea cucumber *Ocnus glacialis* with 3.4%, and the shrimp family Pandalidae with 1.1%. All other taxa contributed ≤1% each to the total abundance across the study region. Of the total biomass across all stations, *Ophiura sarsii* represented 41.3%, the basket stars *Gorgonocephalus* spp. 13.3%, the sea star *Ctenodiscus crispatus* 11.3%, the sea cucumber *Psolus peronii* 4.5%, *Ophiacantha bidentata* 3.3%, the sea urchin *Strongylocentrotus pallidus* 2.4%, and the anemone order Actiniaria 2.3%. The biomass of the following taxa was each ≤2% of the total biomass; the soft corals *Gersemia* spp., the whelks *Neptunea* spp., the snail *Buccinum polare*, the sea anemones *Stomphia* spp. and *Ocnus glacialis*. The individual biomass of all other taxa each amounted to ≤1% of the total biomass.

Nine taxa best represented epibenthic abundance across all stations, including (in order of importance) *Ophiura sarsii,* Pandalidae, *Ophiocten sericeum,* the order Amphipoda, the shrimp *Sabinea septemcarinata*, *Ophiacantha bidentata*, the hermit crabs *Pagurus* spp., the isopods *Saduria* spp., and the snails *Boreotrophon* spp. (BVSTEP, Spearman correlation coefficient: 0.956 with 0.1% significance level; Figure 2.5). Using biomass data, 16 taxa best represented the epibenthos in the study area. These taxa included (in order of importance) *Ophiura sarsii, Sabinea septemcarinata*, *Saduria* spp., *Pagurus* spp., *Ophiocten sericeum* and *Ophiacantha bidentata,* Amphipoda, Pandalidae, *Ctenodiscus crispatus*, the snail *Buccinum elatior, Strongylocentrotus pallidus*, the sea stars *Leptasterias* spp., the crab *Hyas coarctatus*, the order Actiniaria, the phylum Bryozoa, and the sea star *Urasterias lincki* (BVSTEP, Spearman correlation coefficient: 0. 955 with 0.1% significance level; Figure 2.6).

From the cluster analysis of abundance data, 11 statistically significant clusters and one independent station were determined with an average similarity within clusters of 42.5% (sd 11.4) (Figure 2.7). Stations grouped in clusters had similar water depths and/or were located in close proximity of each other. Guided by the cluster analysis results, we defined six "geographical domains" delineated by depth and along-shelf position. This simplified grouping increased the sample size in each group and allowed for a more detailed description of each community assemblage. Stations were grouped in three depth categories (shallow, mid-depth and deep) and two regions (east and west), loosely determined again by the cluster analysis and a spatial gap in the station distribution (Figure 2.8). A two-way crossed PERMANOVA+, using region and depth category as fixed factors, revealed a significant difference between regions and among depth categories, as well as a significant interaction between factors for abundance and biomass (Table 2.2). The pairwise comparisons of means for regions at the same depth category and depth categories within the same region were all significant, with the exception of the east and west shallow stations for biomass (Table 2.2).

Diversity indices were calculated for all stations and then grouped by region or depth as factors for analysis of variance. Mean values for each geographic domain show higher number of taxa for mid-depth stations and lowest number of taxa for the shallow stations across regions (Table 2.2). Overall, mean values for Margalef index were highest for mid-depth stations and lowest for deep stations (Table 2.2). Two-way ANOVA for Margalef was significant across depths ($p<0.001$), with significant differences between mid-depth and deep stations, as well as between mid-depth and shallow stations (Table 2.3). For Shannon index, results from the two-way ANOVA showed a significant difference among depths as well as a marginally significant interaction between depth and region ($p=0.0006$ and $p=0.0549$, respectively); western shallow stations were significantly different from eastern mid-depth stations and western mid-depth stations respectively (Table 2.3). Pielou's index was relatively high for all geographic domains, reflecting comparable dominance levels of one or a few taxa in each community across the region. For this index, the two-way ANOVA was significant only in the interaction between depth and region (p-value: 0.0215) and from the comparison of means test, the only significant difference among groups was between east and west shallow stations (Table 2.3).

Different characteristic taxa were selected for each geographic domain, with high correlation coefficients in the BVSTEP analysis (0.771 to 0.961) (Tables 2.4 and 2.5). The eastern deep group had only 6 stations resulting in a comparatively weak significance level, which reduces the meaningfulness of the correlation value and the list of taxa selected. Out of the total 34 most representative taxa of the six geographic domains, only seven were selected for the same depth category across regions (taxa in bold in Tables 2.4 and 2.5). The gradual transition in taxonomic composition with increasing water depth is well reflected in the high number of characteristic taxa that are shared between mid-depth and shallow stations, and mid-depth and deep stations for both regions. Also the mid-depth stations had the highest number of representative taxa selected, which also belonged to a greater number of phyla (six) compared to the two other depth groups. Shallow stations were represented by crustaceans and echinoderms, while deep stations were represented by different echinoderms, crustaceans, and anemones (Tables 2.4 and 2.5). Most characteristic taxa showed obvious changes in their relative biomass from west to east (Figure 2.9); however the vast majority of these taxa were present at least in some small proportion in both regions. Only four representative taxa of the community in the western region were absent east of 149.5°W. These taxa are the brittle stars *Stegophiura nodosa*, *Amphiodia craterodmeta*, and *Ophiopholis aculeata* and the hermit crab *Labidochirus splendescens* (Figure 2.9, Tables 2.4 and 2.5).

Variability across geographic domains was also evident in the measured environmental variables (Table 2.6). The eastern stations had overall higher mean bottom water salinity, gravel and sand fractions across depth categories. The western stations had overall higher mean sediment organic matter content, sediment phaeopigment concentration, mud and sediment water content, TN, and TOC across depth categories. In both the eastern and western regions, shallow stations had the highest mean bottom water temperature, pH, sand fraction, and C/N ratios. Also, shallow stations had the lowest mean gravel fraction and sediment chl *a* values. Across regions there was an increase with depth in mean bottom water salinity, sediment organic matter content, sediment phaeopigment concentration, sediment water content, TN, and TOC content. Mean pH, percent sand, and C/N values decreased with depth in both regions (Table 2.6).

The environmental and biological resemblance matrices were moderately correlated. For abundance, a combination of five variables had the highest correlation coefficient of 0.48 at a significance level of 0.1%. These variables were (in order of importance), sediment phaeopigments, bottom water salinity, bottom water temperature, organic matter content, and bottom water pH. For biomass, at a correlation value of 0.38 and 0.1% significance level, the five variables selected were (in order of importance) sediment phaeopigments, bottom water salinity, bottom water temperature, percent sand, and bottom water pH.

To explore the spatial variability in environmental drivers throughout the study region, a principal component analysis (PCA) was performed using the variables identified by the BIOENV analysis as most relevant in determining epibenthic community structure (Figure 2.10). Combined, PC1 and PC2 explained 74.7% of the variability among stations (Table 2.7). Overall, stations clustered in depth categories along PC1 (49.4% explained variation). The tight clustering of all deep stations was determined by a strong negative correlation with bottom water pH, as well as a high positive correlation with bottom water salinity and sediment phaeopigments. The opposite trend was observed for shallow stations along the PC1 axis. Most stations in the mid-depth group were mostly neutral along the PC1 axis, but eastern and western mid-depth stations dispersed on opposite ends of the PC2 axis (25.2% explained variation). This was driven by a positive correlation with percent sand and a negative correlation with bottom water temperature and sediment organic matter for most eastern mid-depth stations, while the opposite trend occurred for the western stations of the mid-depth group. Shallow stations also dispersed along the PC2 axis with no eastern or western distinction along this axis (Figure 2.10). The bottom water salinity-temperature plot revealed shallow and mid-depth stations dispersing along a strong temperature gradient spanning ~6°C. The warmest bottom waters were found in the western shallow and mid-depth stations. Deep stations had higher salinities than shallow and mid-depths stations with the largest range in salinity found among the western deep stations (Figure 2.11).

2.4 Discussion

In general, the epibenthic community varied with depth and along the shelf throughout the Alaska Beaufort Shelf and upper slope with interactions between these two factors. This change in community pattern was reflected in significant differences in abundance, biomass, taxonomic composition and diversity with both changes in along-shelf position and water depth.

The number of taxa identified from voucher specimens in this study was 133, which is substantially less than the 238 epifaunal invertebrates reported for the same region in 1977 (Frost and Lowry 1983). The combination of a coarser taxonomic resolution and the exclusion of certain groups (i.e. polychaetes) in this study is most likely the reason for the fewer taxa. The range of epifaunal taxa per trawl was three to 42, which is similar to the adjacent Chukchi Sea, where the number of taxa surveyed with the same gear type ranged from 13 to 47 (Bluhm et al. 2009; Ravelo et al. 2014). In part, a higher taxonomic resolution in Bluhm et al. (2009) may be responsible for the smaller range in number of taxa identified across stations. For example, in the present study only four taxa in the order Amphipoda were identified to lower taxonomic levels, as opposed to 12 in Bluhm et al. (2009), thus underrepresenting to some extent the taxonomic diversity at stations with the least of number of taxa (mostly the shallow stations, dominated by amphipods). In addition, the lower number of taxa encountered at some stations in the present study compared to the Chukchi Sea survey, could be a consequence of the difference in water depths sampled. This study caught the lowest number of taxa inshore of 20 m depth (mean 7, sd 3), a depth range not sampled by the Chukchi Sea studies. The environmental stressors are intense in these shallow waters and forcing factors change rapidly with depth over this range; in particular low salinity and sediment re-working by waves and ice keels, see discussion on changes in water depth.

The highest biomass and abundance were located close to Barrow Canyon on the western side of the study region and continued along the shelf slope diminishing east of 149°W. Overall, the shelf (<100 m) showed homogeneously lower abundance and biomass than the shelf break and upper slope, with the exception of a few stations with higher abundance and biomass in the far east of the study area (145° - 146°W). Maximum epibenthic biomass reported in the Chukchi Sea sampled using the same gear ranged from 21,702 to 64,500 g wet wt/100 m^2 (Bluhm et al. 2009; Ravelo et al. 2014). The maximum biomass presented here (50,103 g wet wt/100 m^2) falls in the range of values reported for the adjacent Chukchi Sea, documenting that at least the Pacific water-influenced western Beaufort Sea is capable of sustaining comparable standing stocks to the much more productive Chukchi Sea. Past benthic sampling efforts on the Alaska Beaufort Shelf were performed using different sampling gear and only few report values for total epibenthic abundance or biomass (Carey and Ruff 1977; Frost and Lowry 1983; Rand and Logerwell 2011). Perhaps because of the discrepancy in collection methods, in particular the larger mesh size of the trawl gear used in past surveys, total biomass reported in these previous studies is lower than the biomass presented here. A 2008 trawl survey reported biomass for the Alaska Beaufort Shelf from 638.8 g wet wt/100 m^2 to 8,695 g wet wt/100 m^2 (depth range from 40 to 500 m, Rand and Logerwell 2011), while a survey in the 1970s reported 12,000 g wet wt/100 m^2 to 22,700 g wet wt/100 m^2 (depth range from for 21-2,600 m; Carey and Ruff 1977).

This study supplies further evidence for the dominance of *Ophiura sarsii* as well as several other ophiuroid species in Arctic epibenthic communities. In concordance with past surveys, epibenthic communities in the western Beaufort Sea were dominated in abundance by *Ophiura sarsii* (Frost and Lowry 1983; Rand and Logerwell 2011). In the present study, this species also dominated the total epibenthic biomass west of 148°W. In the Chukchi Sea, many studies reported *Ophiura sarsii* as the single-most abundant brittle star species throughout the region and in many areas, the dominant epibenthic species over all other taxa (Ambrose et al. 2001; Feder et al. 2005; Bluhm et al. 2009; Ravelo et al. 2014). In this study, *Ophiocten sericeum* dominated stations east of 149°W, with a maximum density of 21 ind/m^2. Photographic surveys of the Canadian Beaufort shelf communities showed highest ophiuroid abundance at 60 ind/m^2 (Renaud et al. 2007). The brittle star *Ophiocten sericeum* was also reported as an important representative of the epibenthic community in the Atlantic Arctic, with densities ranging from 32 to 524 ind/m^2 in the Barents Sea (Piepenburg and Schmid 1996). Brittle stars that inhabit cold regions are thought to be long lived with Antarctic species aged to be at least a decade old (Dahm 1993). These characteristics, longevity and high standing stock, along with their limited mobility make brittle stars ideal indicators of the environmental conditions year round. Also, the distinct distribution pattern described here and the large difference in maximum size of the two most common brittle star species *Ophiura sarsii* (maximum disc diameter 40 mm) and *Ophiocten sericeum* (maximum disc diameter 18 mm) can be useful for Arctic wide comparisons of population productivity and growth, which in turn may reflect differences among shelf productivity and environmental characteristics.

Along with the significant changes in community with depth and along-shelf position, the PERMANOVA+ analyses showed a significant interaction between these two factors. Except for the biomass of the eastern and western shallow stations, all geographic domains were significantly different from one another, as shown in the comparison of means analyses (Table 2.1). These significant differences validate the separation of the shelf into these six domains and highlight the importance of considering them as distinct units. However, although, these geographic domains (determined both by along-shelf position and depth) were a strong determinant of community patterns, the next two sections will discuss depth and along-shelf position separately with the interaction implied. Also, because ultimately depth and along-shelf position are proxies for environmental drivers acting seasonally or year-round, the description of community changes by depth and along-shelf position cannot be separated from the changes of the environmental drivers examined in this study. In addition, while the correlation values of environmental parameters with the community matrix for abundance and biomass were moderate (correlation coefficients ≤0.5 with 0.1% significance level), they were meaningful in a biological community context (Bluhm et al. 2009; Ravelo et al. 2014) and demonstrate clear links between community structure and environmental forcing as it changes with depth and along-shelf position in the study area.

2.4.1 Changes with depth

Depth can act as an easily measurable proxy for a combination of environmental drivers that influence epibenthic organisms (Piepenburg 2005). This relationship also holds true for this and for other Arctic shelf epifauna studies (Bluhm et al. 2009; Blanchard et al. 2013; Jørgensen et al. 2015; Ravelo et al. 2014; Roy et al. 2014). A previous trawl survey performed on the Alaska Beaufort shelf also described a distinct depth zonation in the epibenthic community composition; however, no inferences were made specifying the possible environmental variables or biological interactions driving these depth patterns (Carey and Ruff 1977). In the PCA analysis, using only the selected environmental variables, station clusters segregated by depth groups along the PC1 axis. This pattern reinforces the concept that the effect of depth on benthic communities is mostly reflecting the changes with depth of one or a combination of environmental drivers. Even though most of the environmental data used in our analysis are point in time measurements, the clear separation by depth of the community cluster groups and select environmental drivers indicate that changes in water depth are acting as a proxy for persistent environmental forces in the region.

Organisms that inhabit the shallow region of the Alaska Beaufort Shelf (<~25 m) are affected by multiple seasonally distinct physical forces. This creates a year round high stress environment that could explain the low taxon richness in this area. The formation of ice keels from grounded ice ridges in the Stamukhi zone can occur quite rapidly and the seafloor from 15 to 45 m depth is scarred by deep draft-ice keels, with the largest density of gouging reported at 17 m water depth (Mahoney et al. 2014). In addition to gouging, the ice keels create a barrier for water movement near the seafloor, modifying currents and in turn affecting the distribution of sediments (Barnes et al. 1982; Reimnitz and Kempema 1984). An increase in salinity occurs in the near shore environment from October through mid-May, the main factors are the reduction of riverine input and brine injection from the formation of sea ice (Dunton et al. 2006). On the Alaska Beaufort Shelf, after breakup and until late fall, there are 14 major rivers discharging freshwater and terrigenous sediments that mix rapidly off the coast (Hearon et al. 2009). As rivers start to flow in the spring and early summer, prior to break-up, the nearshore environment is flooded with fresh inflow water forming the Riverine Coastal Domain (Carmack et al. in press) and, if trapped behind ice ridges, may pool as a brackish water lake of high turbidity (Carmack and Macdonald 2002). In summary, the nearshore environment of the Alaska Beaufort Shelf is a highly dynamic environment, with extreme changes in salinity, temperature, water movement and physical disturbance (Barnes 1999; Mahoney et al. 2014). For these reasons the Alaska Beaufort Sea nearshore has been characterized as a biological "desert", with attached or burrowing organisms almost absent, a concept that our study confirms (Reimnitz and Kempema 1984).

The shallow stations along the inner shelf were characterized by overall low epifaunal abundance and biomass, along with a distinct group of taxa with several common characteristics. The representative taxa of the shallow shelf were pandalid shrimp, Amphipoda and the isopods *Saduria* spp., all characteristically mobile groups. Mobility can be of great importance for survival in a region regularly disturbed by ice scouring (Conlan et al. 1998). Amphipods and pandalid shrimp were rather homogeneous in abundance and biomass at different depths and dominated the nearshore community mostly due to the absence of other taxa, as previously found in this region (Frost and Lowry 1983). These taxa provide a food source for diving ducks, stressing the importance of their presence in the shallow nearshore environment (Dunton et al. 2012). Shrimps and amphipods are highly mobile with a wide range of feeding habits, from predators of small benthic organisms to herbivores (Graeve et al. 1997; Macdonald et al. 2010). In the southeastern Chukchi Sea, shrimp species revealed diluted regional signals in δ^{13}C values and a wide range of δ^{15}N, which was interpreted as the ability to feed over large horizontal spatial areas on multiple food sources, from the overlaying water column to the seafloor (Feder et al. 2011). Inferring from the high bottom water chl *a* and phaeophytin concentrations, in conjunction with the low sediment organic matter, sediment chl *a* and phaeopigment concentrations found in the nearshore, it is possible that some dominant taxa may be grazing on near bottom particles while others may scavenge on the sparse disturbed benthos available in fresh ice scoured sediments.

Other characteristic taxa of the shallow stations were the isopods *Saduria* spp. This genus was encountered exclusively shallower than 40 m, representing more than 30% of the total biomass at ten of the 18 stations where they were present. *Saduria* spp. are characterized by a wide range of feeding modes from scavenger to non-selective predators. In addition, *Saduria entomon* (one of the species in this study) has a very large salinity tolerance and has been found inhabiting salinity ranges from 0.2 to 30, possibly allowing this species to remain in the nearshore year round (Haahtela 1990; Sandberg and Bonsdorff 1990). The combination of representative taxa and the overall low epibenthic standing stock of the nearshore Alaska Beaufort Shelf clearly reflect the many environmental disturbances that take place year round in this region.

Many studies in the Arctic have highlighted the importance of food quantity and quality for benthic systems (Ambrose and Renaud 1995; Grebmeier et al. 2006a, 2006b; Bluhm et al. 2009). In the present study, we found changes in community patterns with changes in indicators of food supply. Surface sediment chl *a*, phaeopigment concentrations and sediment C/N ratio were included as proxies of the quality of organic matter advected to the benthos (Iken et al. 2010; Dunton et al. 2012). The sediment C/N ratio mean values in this study (Table 1.6) were within the range of values published for the Beaufort Sea region and show the expected trend of lower values at deeper stations with increasing values at shallower stations (Naidu et al. 1975; Naidu et al. 2000). This pattern across the shelf reflects the higher carbon input originated from riverine sources close to shore, and the higher oceanic nitrogen export to the benthos offshore. The measured proxies for food supply increased with depth, indicating higher food availability for epibenthic organisms on the shelf break and upper slope, especially in the western region. This increase in quantity and quality of food at the shelf break and upper slope were coupled with increases in total epibenthic biomass and abundance at most deep stations. Benthic-pelagic coupling has been well documented in many other polar regions (Ambrose and Renaud 1995; Grebmeier et al. 2006b; Link et al. 2013) and the results of this study again show a strong relationship between benthic biomass and abundance and proxies for food supply from the overlaying water column. One specific example of this coupling is the occurrence of snow crab, *Chionoecetes opilio*, which was encountered almost exclusively at deep stations along the shelf (12 out of 15 stations encountered were deeper than 150 m). In the 2008 western Beaufort survey, snow crab had the second largest biomass values after ophiuroids at the 100 to 500 m depth range (Rand and Logerwell 2011). On the Chukchi Sea shelf, snow crab are an important representative of epibenthic communities, but in that region their presence/abundance has not been correlated to water depth, probably owing to the relatively homogeneous depth profile of the Chukchi Sea shelf (Bluhm et al. 2009). Instead, Chukchi Sea snow crab are particularly dominant following the trajectory of the nutrient rich Central Channel water mass (Ravelo et al. 2014). Two results shown here concur that the deep stations, most of which had snow crab present, were among the coldest bottom water temperature stations and were characterized by a positive correlation with bottom water salinity and sediment phaeopigments (Figures 2.7 and 2.8). Considering the time of year of this study, snow crab were found exclusively at the boundary between the Chukchi Sea winter water and Atlantic Water layers (Nikolopoulos et al. 2009; Carmack and McLaughlin 2011). This winter water has the potential to support high secondary production due to the higher levels of organic carbon associated with this water mass (Mathis et al. 2007). The presence of snow crab and particularly high biomass of brittle stars in these productive waters could imply that their distribution in the Alaska Beaufort Sea may reflect the trajectory of the nutrient rich waters that flow through Barrow Canyon heading east along the Alaska Beaufort shelf break and upper slope. This relationship has previously been observed for snow crab and a number of fish species in the region, where the highest CPUE was positively correlated to the portions of the shelf slope occupied by Chukchi Sea winter water (Logerwell et al. 2011).

Besides food supply and disturbance nearshore, seafloor characteristics and sediment grain size are important determinants of Arctic benthic community composition (Feder et al. 1994; Mayer and Piepenburg 1996; Bluhm et al. 2009). Of the substrate variables included in this analysis, sand was most important in determining the epibenthic community. The sand fractions were higher at the shallow nearshore locations, where rivers and wave action have a direct influence over the region, depositing medium-size entrained particles while finer particles tend to get moved offshore (Naidu et al. 1975). In this study, the nearshore areas with sandy sediments and – as discussed above – variable salinities and high mechanical disturbance were also the most impoverished in terms of taxonomic diversity, abundance and biomass. The combination of large seasonal changes in salinity (large riverine input) and physical disturbance (wave action and ice gauging) may restrict the diversity of this area to more seasonally transient or mobile epibenthic fauna. The relatively higher percent gravel found at the deeper stations could be a result of ice-rafting and the reworking of sediments over a very long time scale (Naidu et al. 1975; Reimnitz et al. 1993; Carmack et al. in press).The mid-depth stations had intermediate sediment values for mud, sand, and gravel fractions. These soft sediments are important habitat for infaunal organisms, many of which are prey for the epibenthos (Dale et al. 1989; Feder et al. 1994). Interspersed within the soft sediment, some mid-depth stations contained hard surfaces, such as gravel, boulders, and shell hash, which provide substrates for attachment for sessile and colonial organisms that in turn provide refuge to larval stages and smaller organisms (Dale et al. 1989; Bluhm et al. 2009). Therefore, the increased sediment heterogeneity at mid-depth (and deeper) stations may promote the wide range of taxa inhabiting the outer Alaska Beaufort Shelf and upper slope. The mid-depth stations in the eastern and western regions had the highest diversity values and the highest number of taxa selected in the BVSTEP analysis. The increase in diversity at the 25-100 m depth range was consistent along the shelf and had no particular regional difference, though the taxa selected as representatives of the community in the eastern and western regions differed significantly. In other Arctic regions, higher substrate heterogeneity has also been linked to higher epibenthic diversity values (Dale et al. 1989; Mayer and Piepenburg 1996; Bluhm et al. 2009). As discussed above, the mid-depth stations did not have the highest biomass despite having the highest diversity; a pattern that was also observed on the adjacent Chukchi Sea shelf, where the highest biomass and abundance stations were dominated by ophiuroids and had the lowest mean diversity values (Ravelo et al. 2014).

2.4.2 Changes along the shelf

While spatial and latitudinal patterns in community structure have been described in the Chukchi Sea (Bluhm et al. 2009), descriptions of changes in communities with longitude within the

Pacific Arctic region are rare (Ravelo et al. 2014; Roy et al. 2014). In the present study, we found that at constant depth ranges, there were very few similar representative taxa west of 150°W longitude compared to east of that longitude. Although most taxa had a wide along-shelf distribution throughout the study area, their relative abundance and dominance changed greatly from east to west. This distribution pattern was also observed for infaunal polychaetes in a 1970's survey in the same region (Bilyard and Carey 1979). In the present study, all eight ophiuroid species identified were encountered west of longitude 148°W, with only *Ophiocten sericeum* and *Ophiacantha bidentata* found east of this line.

The dominance of *O. sarsii* over all other ophiuroids, and in many stations over all other taxa, was observed only at the western slope of the Alaska Beaufort Sea (western-deep and some western-mid-depth stations). The prevalence of the two most abundant ophiuroid species changed along the shelf, from eastern stations dominated by *O. sericeum* and *O. sarsii* being absent, to the western stations dominated by *O. sarsii* while *O. sericeum* was only present at very high total standing stocks stations. As with the above discussed abundance pattern of snow crab, the dominance of *O. sarsii* throughout the Chukchi Sea and the observed distribution limit at ~148°W in the Alaska Beaufort Sea seem to be linked to the distribution of water masses in the two regions. Much of the Pacific-origin water flowing through the Chukchi Sea flows eastward rounding Point Barrow and entering the Beaufort shelf as the Beaufort shelf-break jet (Pickart 2004; Nikolopoulos et al. 2009). This shelf-break jet advances over the western Beaufort shelf break with a complete decay point at approximately 147°W (von Appen and Pickart 2012). The transport of *O. sarsii* larvae from the Chukchi Sea population could, therefore, be limited to the western Beaufort Sea shelf break by the diminishing shelfbreak jet over the Beaufort Sea shelf.

The change in dominant taxa along the shelf was also evident for other taxa such as the scallop *Similipecten greenlandicus*, which dominated in abundance at eastern stations but was rare west of 150°W in the present study as well as in the 1976-77 survey (Frost and Lowry 1983). The brittle stars *Stegophiura nodosa*, *Amphiodia craterodmeta* and the hermit crabs *Labidochirus* spp. were the only other representative taxa that did not occur east of 148°W. However, there were several other, less abundant taxa that occurred only either west or east of ~148-150°W, such as the chiton *Amicula vestita* and the brittle star *Ophiopholis aculeata*. Along with the clear along-shelf change in epibenthic taxon composition, there is a decrease from west to east in total epibenthic abundance and biomass along the shelf break. This pattern can also be linked to the transit and decay of the shelfbreak current over the region. Changes in the direction of the prevailing winds over the Beaufort shelf have a strong effect on the intensity and direction of the water entering the region through Barrow Canyon, affecting the distribution of benthic productivity and taxonomic composition on the Alaska Beaufort Shelf, especially for the mid-depth and deep stations of this study region (Dunton et al. 2005; Pickart et al. 2011). Evidence from long-term atmospheric data collected from Point Barrow indicates that an increase in prevalence and intensity of easterly winds in the Alaska Beaufort shelf region has occurred over the past 40 years, causing more persistent and prolonged reversals of the Beaufort shelf-break jet (Hufford 1973; von Appen and Pickart 2012; Pickart et al. 2013). Considering the strong link between water masses and community composition shown in our results, the epibenthic community we find today on the Alaska Beaufort shelf may be experiencing a very different environment from the community sampled by Frost and Lowry in 1976-77. The best evidence of these long term changes in environmental and community patterns for this region can be seen in the large shift in distribution we observed of most brittle star species from 1977 to 2011 (Frost and Lowry 1983). The species *O. sarsii*, *Ophiopholis aculeata*, *Ophiura robusta* and *Amphiodia craterodmeta* were encountered in past studies, from two to seven degrees further east from the eastward most point each species was encountered in the present study (Carey 1977; Frost and Lowry 1983). Considering that this shift in distribution from the 1970's survey was only observed for certain taxa and no quantitative comparison could be made (due to different survey methods used), we can only speculate towards the implications of these environmental changes on the benthic community as a whole. In this regard, it remains for future research to define the implications of these species distribution shifts for the benthic realm, as well as to determine the ecological winners and losers in this increasingly changing Arctic system (Carmack et al. 2010).

2.5 Summary

In summary, this paper is the first to detail the depth-related and along-shelf changes in the epibenthic community along the Alaska Beaufort Shelf. We found that the western deep portion of the Beaufort shelf has many elements in common with the adjacent Chukchi Sea shelf. This was evident from the high biomass values found in the western deeper part of the Beaufort Sea study region that is connected to the Chukchi Sea through the path of the shelf-break jet. Also, many dominant taxa of the western deep stations of the Alaska Beaufort Shelf are found throughout the Chukchi Sea. In combination with the reduction in total epibenthic biomass from west to east along the shelf break, changes in dominant taxa and overall community composition were observed along the shelf and upper slope. The change in epibenthic community with depth was most obvious in the nearshore environment (<20 m), which was characterized by low epibenthic abundance, biomass and taxonomic diversity. We suggest this was probably mostly due to the seasonal scouring of the sediments by ice keels, and highly variable bottom water salinity throughout the seasons due to the influence of the many rivers and landfast ice in the region. The higher mean diversity values in the mid-depth stations can be linked to overall higher sediment heterogeneity (soft and hard substrates). Through this analysis we show how epibenthic communities change spatially and we mark the relevant environmental drivers that model these communities. Even though the most relevant drivers were point-in-time measurements of the environment, depth and along-shelf helped define assemblages and can be seen as proxies for a combination of environmental drivers acting at different time scales.

Acknowledgements

This study was made possible in part by samples collected under a Bureau of Ocean Energy Management (BOEM) Cooperative Agreement M10AC 2004 "Beaufort Sea Marine Fish Monitoring in the Central Beaufort Sea" U.S. Department of the Interior, BOEM. We thank Kathleen Wedemeyer for her role as project officer. Financial support also was provided by The Prince William Sound Oil Spill Recovery Institute (with very special thanks to Scott Pegau) and the Coastal Marine Institute. Many thanks go to Brenda Norcross from the University of Alaska Fairbanks for her role as lead scientist. Lorena Edenfield, Brenda Holladay and the rest of the team of the University of Alaska Fairbanks (UAF) Fisheries Oceanography Laboratory are acknowledged for providing outstanding deck support and logistics during the research cruise, as did the captain and crew of the R/V *Norseman II*. Special thanks are due to Martin Schuster and Katrin Iken from UAF for sampling assistance. We are grateful to Katrin Iken, Lee Cooper, Ken Dunton, Rolf Gradinger, Andy Mahoney, Sathy Naidu, Tom Weingartner, Peter Winsor from UAF and Christian Zimmerman from the US Geological Survey for their intellectual input in this research and comments on this manuscript. Mette Kaufman from UAF helped process the sediment chlorophyll samples. Cheryl Hopcroft from UAF processed the bottom water chlorophyll samples. Katrin Iken and Lauren Divine shared the sediment C/N data. The Fisheries Oceanography laboratory at UAF processed the sediment grain size samples. Seth Danielson from UAF proofed the CTD data. Lara Horstmann-Dehn from UAF loaned a muffle furnace to process the sediment organic matter samples, Dave Verbyla from UAF gave technical support with ArcMap, and Bob Clarke from the

Plymouth Marine Laboratory gave technical support for PRIMER analysis. Comments by Philippe Archambault, an anonymous reviewer and Heike Link improved an earlier version of the manuscript.

References

Aagaard K (1984) The Beaufort undercurrent. In: Barnes P, Schell D, Reimnitz E (eds) The Alaskan Beaufort Sea: ecosystems and environments. Academic Press Inc., Orlando, pp 47-71

Ambrose JWG, Renaud PE (1995) Benthic response to water column productivity patterns: evidence for benthic-pelagic coupling in the Northeast Water Polynya. J Geophys Res 100:4411-4421

Ambrose JWG, Clough L, Tilney P, Beer L (2001) Role of echinoderms in benthic remineralization in the Chukchi Sea. Mar Biol 139:937-949

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: Guide to software and statistical methods. First edn., Plymouth, UK

Arar EJ, Collins GB (1997) Method 445.0: In vitro determination of chlorophyll a and pheophytin a in marine and freshwater algae by fluorescence. United States Environmental Protection Agency, Office of Research and Development, National Exposure Research Laboratory, Cincinnati, Ohio

Barnes DK (1999) The influence of ice on polar nearshore benthos. J Mar Biol Assoc UK 79:401-407

Barnes PW, Reimnitz E, Fox D (1982) Ice rafting of fine-grained sediment, a sorting and transport mechanism, Beaufort Sea, Alaska. J Sediment Petrol 52:493-502

Barnes PW, Rearic DM, Reimnitz E (1984) Ice gouging characteristics and processes. In: Barnes P, Schell D, Reimnitz E (eds) The Alaskan Beaufort Sea: Ecosystems and Environments. Academic Press Inc., San Diego, pp 185-212

Bilyard GR, Carey JAG (1979) Distribution of western Beaufort Sea polychaetous annelids. Mar Biol 54:329-339

Blanchard AL, Parris CL, Knowlton AL, Wade NR (2013) Benthic ecology of the northeastern Chukchi Sea. Part II. Spatial variation of megafaunal community structure, 2009–2010. Cont Shelf Res 67:67-76

Bluhm BA, Gradinger R (2008) Regional variability in food availability for Arctic marine mammals. Ecol Appl 18:77-96

Bluhm BA, Iken K, Mincks Hardy S, Sirenko BI, Holladay BA (2009) Community structure of epibenthic megafauna in the Chukchi Sea. Aquatic Biol 7: 269-293. doi:10.3354/ab00198

Campbell RG, Sherr EB, Ashjian CJ, Plourde S, Sherr BF, Hill V, Stockwell DA (2009) Mesozooplankton prey preference and grazing impact in the western Arctic Ocean. Deep Sea Res Part II 56:1274-1289

Carey JAG (1977) Summarization of existing literature and unpublished data on the distribution, abundance, and life histories of benthic organisms vol I - IV. National Oceanographic and Atmospheric Administration and Bureau of Land Management, Oregon

Carey JAG, Ruff RE (1977) Ecological studies of the benthos in the western Beaufort Sea with special reference to bivalve molluscs Polar Oceans. Arctic Institute of North America, Calgary

Carey JAG, Scott PH, Walter KR (1984) Distributional ecology of shallow southwestern Beaufort Sea (Arctic Ocean) bivalve Mollusca. Mar Ecol Prog Ser 17:125-134

Carmack EC, Macdonald RW (2002) Oceanography of the Canadian Shelf of the Beaufort Sea: a setting for marine life. Arctic 55:29-45

Carmack EC, Macdonald RW, Jasper S (2004) Phytoplankton productivity on the Canadian Shelf of the Beaufort Sea. Mar Ecol Prog Ser 277:37-50

Carmack EC, Wassmann P (2006) Food webs and physical–biological coupling on pan-Arctic shelves: unifying concepts and comprehensive perspectives. Prog Oceanogr 71:446-477

Carmack EC, McLaughlin FA, Vagle S, Melling H, Williams WJ (2010) Structures and property distributions in the three oceans surrounding Canada in 2007: A basis for a long-term ocean climate monitoring strategy. Atmos Ocean 48:211-224

Carmack EC, McLaughlin F (2011) Towards recognition of physical and geochemical change in Subarctic and Arctic Seas. Prog Oceanogr. 90:90-104

Carmack EC, Winsor P, Williams W (in press) The contiguous panarctic riverine coastal domain: a unifying concept. Prog Oceanogr

Clarke KR, Gorley RN (2006) PRIMER v6: User manual/tutorial, Plymouth

Clarke KR, Warwick RM (2001) Changes in Marine Communities: an approach to statistical analysis and interpretation. 2nd edn. PRIMER-E Ltd., Plymouth

Conlan K, Lenihan H, Kvitek R, Oliver J (1998) Ice scour disturbance to benthic communities in the Canadian High Arctic. Mar Ecol Prog Ser 166:1-16

Conlan KE, Kvitek RG (2005) Recolonization of soft-sediment ice scours on an exposed Arctic coast. Mar Ecol Prog Ser 286:21-42

Connell JH (1961) The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus. Ecology 42:710-723

Cooper L, Sexson M, Grebmeier J, Gradinger R, Mordy C, Lovvorn J (2013) Linkages between sea-ice coverage, pelagic–benthic coupling, and the distribution of spectacled eiders: Observations in March 2008, 2009 and 2010, northern Bering Sea. Deep Sea Res Part II 94:31-43

Coyle KO, Bluhm B, Konar B, Blanchard A, Highsmith RC (2007) Amphipod prey of gray whales in the northern Bering Sea: Comparison of biomass and distribution between the 1980s and 2002-2003. Deep Sea Res Part II 54:2906-2918

Dahm C (1993) Growth, production and ecological significance of *Ophiura albida* and *O. ophiura* (Echinodermata: Ophiuroidea) in the German Bight. Mar Biol 116:431-437

Dale JE, Aitken AE, Gilbert R, Risk MJ (1989) Macrofauna of Canadian arctic fjords. Mar. Geol. 85:331-358

Day RH et al. (2013) The Offshore Northeastern Chukchi Sea, Alaska: a Complex High-Latitude Ecosystem. Cont Shelf Res 67:147-165

Dunton KH (1984) An annual carbon budget for an Arctic kelp community. In: Barnes P, Schell D, Reimnitz E (eds) The Alaskan Beaufort Sea: Ecosystems and Environments. Academic Press Inc., Orlando, pp 311-325

Dunton KH, Schonberg SV (2000) The benthic faunal assemblage of the Boulder Patch kelp community. In: Truett J, Johnson S (eds) The natural history of an Arctic oil field. Academic Press, San Diego, pp 372-397

Dunton KH, Goodall JL, Schonberg SV, Grebmeier JM, Maidment DR (2005) Multi-decadal synthesis of benthic–pelagic coupling in the western arctic: role of cross-shelf advective processes. Deep Sea Res Part II 52:3462-3477

Dunton KH, Weingartner TJ, Carmack EC (2006) The nearshore western Beaufort Sea ecosystem: circulation and importance of terrestrial carbon in arctic coastal food webs. Prog Oceanogr 71:362-378

Dunton KH, Schonberg SV, McTigue N (2009) Characterization of benthic habitats in Camden Bay (Sivulliq Prospect and Hammerhead Drill Sites), Beaufort Sea Alaska. Shell Exploration and Production Company, Anchorage

Dunton KH, Schonberg SV, Cooper LW (2012) Food web structure of the Alaskan nearshore shelf and estuarine lagoons of the Beaufort Sea. Estuaries Coasts 35:416-435

Feder HM, Iken K, Blanchard AL, Jewett SC, Schonberg S (2011) Benthic food web structure in the southeastern Chukchi Sea: an assessment using 13 C and 15 N analyses. Polar Biol 34:1-12

Feder HM, Naidu AS, Jewett SC, Hameedi JM, Johnson WR, Whitledge TE (1994) The northeastern Chukchi Sea: benthos-environmental interactions. Mar Ecol Prog Ser 111:171-190

Feder HM, Jewett SC, Blanchard A (2005) Southeastern Chukchi Sea (Alaska) epibenthos. Polar Biol 28: 402–421. doi:10.1007/s00300-004-0683-4

Frost KJ, Lowry LF (1983) Demersal fishes and invertebrates trawled in the northeastern Chukchi and western Beaufort Seas 1976-1977. U.S. Department of Commerce NOAA Tech Rep NMFS-SSRF-764

Goñi MA, O'Connor AE, Kuzyk ZZ, Yunker MB, Gobeil C, Macdonald RW (2013) Distribution and sources of organic matter in surface marine sediments across the North American Arctic margin. J Geophys Res C Oceans 118:4017-4035

Graeve M, Kattner G, Piepenburg D (1997) Lipids in Arctic benthos: does the fatty acid and alcohol composition reflect feeding and trophic interactions? Polar Biol 18:53-61

Grebmeier JM, Cooper LW, Feder HM, Sirenko BI (2006a) Ecosystem dynamics of the Pacific-influenced northern Bering and Chukchi seas in the Amerasian Arctic. Prog Oceanogr 71:331-361

Grebmeier JM et al. (2006b) A major ecosystem shift in the northern Bering Sea. Science 311:1461-1464

Grebmeier JM (2012) Shifting patterns of life in the Pacific Arctic and sub-Arctic seas. Annu Rev Mar Sci 4:63-78

Gunderson DR, Ellis IE (1986) Development of a plumb staff beam trawl for sampling demersal fauna. Fish. Res 4:35-41

Haahtela I (1990) What do Baltic studies tell us about the isopod *Saduria entomon* (L.)? Ann Zool Fennici 27:269-278

Hearon G, Dickins D, Ambrosius K, Morris K (2009) Mapping sea ice overflood using remote sensing: Smith Bay to Camden Bay. DF Dickins Associates, Coastal Frontiers Corporation, Aerometric, and The Geophysical Institute, University of Alaska, Alaska

Hufford GL (1973) Warm water advection in the Southern Beaufort Sea August-September 1971. J Geophys Res 78:2702-2707

Iken K, Bluhm B, Dunton K (2010) Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. Deep Sea Res Part II 57:71-85

Jørgensen LL, Ljubin P, Skjoldal HR, Ingvaldsen RB, Anisimova N, Manushin I (2015) Distribution of benthic megafauna in the Barents Sea: baseline for an ecosystem approach to management. ICES J Mar Sci. 72:595-613

Konar B, Iken K (2005) Competitive dominance among sessile marine organisms in a high Arctic boulder community. Polar Biol 29:61-64

Konar B (2007) Recolonization of a high latitude hard-bottom nearshore community. Polar Biol 30:663-667

Link H, Chaillou G, Forest A, Piepenburg D, Archambault P (2013) Multivariate benthic ecosystem functioning in the Arctic-benthic fluxes explained by environmental parameters in the southeastern Beaufort Sea. Biogeosciences 10: 5911-5929

Loeng H et al. (2005) Marine systems. In: Symon C, Arris L, Heal B (eds) Arctic climate impact assessment. New York, pp 439-538

Logerwell E, Rand K, Weingartner TJ (2011) Oceanographic characteristics of the habitat of benthic fish and invertebrates in the Beaufort Sea. Polar Biol 34:1783-1796. doi: 10.1007/s00300-011-1028-8

Macdonald RW, Solomon SM, Cranston RE, Welch HE, Yunker MB, Gobeil C (1998) A sediment and organic carbon budget for the Canadian Beaufort Shelf. Mar Geol 144:255-273

Macdonald TA, Burd BJ, Macdonald VI, van Roodselaar A (2010) Taxonomic and feeding guild classification for the marine benthic macroinvertebrates of the Strait of Georgia, British Columbia.

Mahoney AR, Eicken H, Gaylord AG, Gens R (2014) Landfast sea ice extent in the Chukchi and Beaufort Seas: The annual cycle and decadal variability. Cold Reg Sci Technol 103:41-56

Maslanik J, Fowler C, Stroeve J, Drobot S, Zwally J, Yi D, Emery W (2007) A younger, thinner Arctic ice cover: Increased potential for rapid, extensive sea-ice loss. Geophys Res Lett 34: L24501. doi:10.1029/2007GL032043

Mathis JT, Pickart RS, Hansell DA, Kadko D, Bates NR (2007) Eddy transport of organic carbon and nutrients from the Chukchi Shelf: Impact on the upper halocline of the western Arctic Ocean. J Geophys Res C Oceans. doi: 10.1029/2006JC003899

Mayer M, Piepenburg D (1996) Epibenthic community patterns on the continental slope off East Greenland at 75 degrees N. Mar Ecol Prog Ser 143:151-164

McLaughlin FA, Carmack EC, Ingram RG, Williams W, Michel C, (2006) Oceanography of the Northwest Passage. In: Robinson AR, Brink K (eds) The Sea, New York, pp 1213-1244

Naidu AS (1974) Sedimentation in the Beaufort Sea: A synthesis. In: Marine Geology and Oceanography of the Arctic Seas. Springer, New York, pp 173-190

Naidu AS, Burrell DC, Hood DW, Dygas JA (1975) Texture, clay mineralogy, and chemistry of bottom sediments, western Beaufort Sea, Arctic Ocean. Geol S Am S 151:49-58. doi:10.1130/SPE151-p49

Naidu AS, Cooper LW, Finney RW, Macdonald RW, Alexander C, Semiletov IP (2000) Organic carbon isotope ratios ($d^{13}C$) of Arctic Amerasian Continental shelf sediments. Int J Earth Sci 89:522-532

Nikolopoulos A, Pickart RS, Fratantoni PS, Shimada K, Torres DJ, Jones EP (2009) The western Arctic boundary current at 152 W: Structure, variability, and transport. Deep Sea Res Part II 56:1164-1181

Packer DB, Watling L, Langton RW (1994) The population structure of the brittle star *Ophiura sarsi* Lütken in the Gulf of Maine and its trophic relationship to American plaice (*Hippoglossoides platessoides* Fabricius). J Exp Mar Biol Ecol 179:207-222

Parsons TR (1984) A manual of chemical and biological methods for seawater analysis. Pergamon Press, New York

Pickart RS (2004) Shelfbreak circulation in the Alaskan Beaufort Sea: Mean structure and variability J Geophys Res C: Oceans. doi: 10.1029/2003JC001912

Pickart RS, Spall MA, Moore G, Weingartner TJ, Woodgate RA, Aagaard K, Shimada K (2011) Upwelling in the Alaskan Beaufort Sea: Atmospheric forcing and local versus non-local response. Prog Oceanogr 88:78-100

Pickart RS, Schulze LM, Moore G, Charette MA, Arrigo KR, van Dijken G, Danielson S (2013) Long–term trends of upwelling and impacts on primary productivity in the Alaskan Beaufort Sea. Deep Sea Res Part I. doi: doi:10.1016/j.dsr.2013.05.003

Piepenburg D, Schmid MK (1996) Brittle star fauna (Echinodermata: Ophiuroidea) of the Arctic northwestern Barents Sea: composition, abundance, biomass and spatial distribution. Polar Biol 16:383-392

Piepenburg D (2005) Recent research on Arctic benthos: common notions need to be revised. Polar Biol 28:733-755

Piepenburg D et al. (2011) Towards a pan-Arctic inventory of the species diversity of the macro-and megabenthic fauna of the Arctic shelf seas. Mar Biodivers 41:51-70

Rand KM, Logerwell EA (2011) The first demersal trawl survey of benthic fish and invertebrates in the Beaufort Sea since the late 1970s. Polar Biol 34:475-488

Ravelo AM, Konar B, Trefry JH, Grebmeier JM (2014) Epibenthic community variability in the northeastern Chukchi Sea. Deep Sea Res Part II 102: 119-131. doi:10.1016/j.dsr2.2013.07.017i

Reimnitz E, Kempema E (1984) Pack ice interaction with Stamukhi Shoal, Beaufort Sea, Alaska. In: Barnes P, Schell D, Reimnitz E (eds) The Alaskan Beaufort Sea. Academic Press Inc., Orlando, pp 159-181

Reimnitz E, McCormick M, McDougall K, Brouwers E (1993) Sediment export by ice rafting from a coastal polynya, Arctic Alaska, USA. Arct Alp Res 25:83-98

Renaud PE, Morata N, Ambrose WG, Bowie JJ, Chiuchiolo A (2007) Carbon cycling by seafloor communities on the eastern Beaufort Sea shelf. J Exp Mar Biol Ecol. doi:349:248-260 doi:10.1016/j.jembe.2007.05.021

Roy V, Iken K, Archambault P (2014) Environmental drivers of the Canadian Arctic megabenthic communities PLoS One 9:e100900 . doi: 10.1371/journal.pone.0100900

Sandberg E, Bonsdorff E (1990) On the structuring role of *Saduria entomon* (L.) on shallow water zoobenthos. Ann Ann Zool Fennici 27:279-284

Schumacher BA (2002) Methods for the determination of total organic carbon (TOC) in soils and sediments. Ecological Risk Assessment Support Center, Las Vegas

Starmans A, Gutt J, Arntz WE (1999) Mega-epibenthic communties in Arctic and Antarctic shelf areas. Mar Biol 135:269-280

Strobel CJ et al. (1995) Environmental Monitoring and Assessment Program (EMAP) Laboratory Methods Manual Estuaries vol 1. Science Applications International Corp., Narragansett

von Appen WJ, Pickart RS (2012) Two Configurations of the Western Arctic Shelfbreak Current in Summer. J Phys Oceanogr 42:329-351

Weingartner TJ, Cavalieri DJ, Aagaard K, Sasaki Y (1998) Circulation, dense water formation, and outflow on the northeast Chukchi shelf. J Geophys Res 103:7647-7661

WoRMS Editorial Board (2015) World Register of Marine Species. Available from http://www.marinespecies.org at VLIZ. Accessed 2015-03-17

Table 2.7. PERMANOVA analysis and pairwise comparison of means for the effect of region and depth on the epibenthic community abundance and biomass on the Alaska Beaufort Sea shelf. df: degrees of freedom. SS: sum of squares. **P(perm) ≤0.001 and *P(perm) ≤0.01.

Data	Factors or levels	df	SS	Pseudo-F or t-value	P(perm)
Abundance	Region	1	20,326	14.79	0.0001**
	Depth	2	54,710	19.91	0.0001**
	Region x Depth	2	15,940	5.80	0.0001**
	Shallow: East vs West			2.03	0.0046*
	Mid-depth: East vs West			3.62	0.0001**
	Deep: East vs West			3.59	0.0001**
	East: Mid-depth vs Shallow			3.42	0.0001**
	East: Mid-depth vs Deep			2.36	0.0001**
	East: Shallow vs Deep			3.91	0.0001**
	West: Mid-depth vs Shallow			3.83	0.0001**
	West: Mid-depth vs Deep			3.52	0.0001**
	West: Shallow vs Deep			5.71	0.0001**
Biomass	Regions	1	15,967	7.88	0.0001**
	Depths	2	51,258	12.65	0.0001**
	Region x Depth	2	15,814	3.90	0.0001**
	Shallow: East vs West			1.32	0.1441
	Mid-depth: East vs West			2.99	0.0001**
	Deep: East vs West			2.69	0.0002**
	East: Mid-depth vs Shallow			2.60	0.0001**
	East: Mid-depth vs Deep			2.36	0.0002**
	East: Shallow vs Deep			2.71	0.0007**
	West: Mid-depth vs Shallow			3.34	0.0001**
	West: Mid-depth vs Deep			2.62	0.0001**
	West: Shallow vs Deep			4.16	0.0001**

Table 2.8. Mean values for diversity indices, mean number of taxa and total number of stations by geographic domains. Standard deviations are shown in parenthesis.

Geographic domain	Number of stations	Mean number of taxa	Index		
			Margalef	Shannon	Pielou
Eastern Shallow	7	13 (8)	2.86 (0.50)	1.57 (0.34)	0.52 (0.12)
Eastern Mid-depth	19	25 (8)	3.81(0.71)	1.56 (0.66)	0.49 (0.20)
Eastern Deep	6	21 (3)	2.5 (1.11)	1.30 (0.56)	0.61 (0.26)
Western Shallow	10	9 (4)	2.62 (0.84)	1.30 (0.42)	0.41 (0.10)
Western Mid-depth	14	31 (5)	4.19 (0.69)	1.81 (0.41)	0.54 (0.11)
Western Deep	15	25 (7)	1.95 (1.39)	0.81 (0.62)	0.36 (0.22)

Table 2.9. Two-way crossed ANOVA values for the tree diversity indices Margalef, Shannon and Pielou. Only significant values for Tukey test (95% confidence level) shown for each index. df: degrees of freedom. SS: sum of squares. **p value ≤0.001, *p value ≤0.01 and ·p value ≤0.1.

Index	Factors or levels	df	SS	F-value	p value	
Margalef	Depth	2	43.01	27.31	0.0001	**
	Region	1	0.00	0.00	0.9497	
	Depth x Region	2	2.66	1.69	0.1926	
	Mid-depth vs Deep				0.0001	**
	Shallow vs Mid-depth				0.0001	**
Shannon	Depth	2	4.80	8.42	0.0006	**
	Region	1	0.08	0.30	0.5879	
	Depth x Region	2	1.73	3.04	0.0549	·
	Western Shallow vs Eastern Mid-depth				0.0079	*
	Western Shallow vs Western Mid-depth				0.0004	**
Pielou	Depth	2	0.07	1.28	0.2858	
	Region	1	0.08	2.73	0.1036	
	Depth x Region	2	0.24	4.07	0.0215	*
	Western Shallow vs Eastern Shallow				0.0567	·

Table 2.10. Taxa selected by BVSTEP analyses for each geographic domain, using abundance data. In bold taxa selected for the same depth category across regions. Taxa marked with an asterisk were present exclusively in the western region.

Geographic domain	Number of taxa selected	Correlation Value	Sig. level (%)	Taxa
Eastern Shallow	6	0.945	0.1	**Amphipoda**, ***Saduria* spp.**, Pandalidae, *Leptasterias* spp., *Ophiocten sericeum, Psolus* spp.
Eastern Mid-depth	9	0.953	0.1	*Admete* spp., *Buccinum elatior, Similipecten greenlandicus, Tachyrhynchus* spp., *Sabinea septemcarinata*, **Pandalidae**, *Ophiocten sericeum, Psolus* spp., *Urasterias lincki*
Eastern Deep	1	0.771	0.9	*Ophiacantha bidentata*
Western Shallow	4	0.947	0.1	**Amphipoda**, *Sabinea septemcarinata,* ***Saduria* spp.**, *Stegophiura nodosa**
Western Mid-depth	9	0.959	0.1	*Retifusus roseus, Argis* spp., *Pagurus* spp., **Pandalidae**, *Spirontocaris* spp., *Ctenodiscus crispatus, Stegophiura nodosa*, Ophiura sarsii, Strongylocentrotus pallidus*
Western Deep	8	0.950	0.1	*Argis* spp., *Ctenodiscus crispatus, Leptasterias* spp. *Ophiopholis aculeata*, Ophiura robusta, Ophioscolex glacialis, Ophiura sarsii, Amphiodia craterodmeta**

Table 2.11. Characteristic taxa selected by BVSTEP analyses for each geographic domain using biomass data. In bold taxa selected for the same depth category across regions. Marked with an asterisk are the taxa that were present exclusively in the western region.

Geographic domain	Number of taxa selected	Correlation Value	Sig. level (%)	Taxa
Eastern Shallow	3	0.949	0.1	Amphipoda , ***Saduria* spp.**, *Psolus* spp.
Eastern Mid-depth	7	0.950	0.1	*Buccinum elatior,* ***Neptunea* spp.,** *Similipecten greenlandicus,* ***Pagurus* spp.**, *Sabinea septemcarinata, Psolus* spp., *Urasterias lincki*
Eastern Deep	5	0.957	9.7	*Chionoecetes opilio,* ***Ophiacantha bidentata***, *Ophiocten sericeum, Strongylocentrotus pallidus,* ***Stomphia* spp.**
Western Shallow	2	0.955	0.1	***Saduria* spp.**, Pandalidae
Western Mid-depth	12	0.951	0.1	***Neptunea* spp.**, *Hyas coarctactus*, ***Pagurus* spp.**, *Labidochirus splendescens**, Pandalidae, *Ctenodiscus crispatus, Ophiura sarsii, Psolus* spp., *Strongylocentrotus pallidus, Stomphia* spp., Bryozoa, *Thenea muricata*
Western Deep	6	0.951	0.1	*Ctenodiscus crispatus, Gorgonocephalus* spp., ***Ophiacantha bidentata***, *Ophiura sarsii, Actiniaria,* ***Stomphia* spp.**

Table 2.12. Mean value and standard deviations (SD) of the environmental parameters included in the BioEnv analysis for each geographic domain (Primer v6). Depth (m), bottom water temperature (T, °C), bottom water salinity (S, ‰), bottom water pH, bottom water chlorophyll *a* (BW chl *a*, μg/l) and bottom water phaeophytin (BW phaeo., μg/l), Sediment organic matter (Org. matter, % dry weight), sediment chlorophyll *a* (Sed. chl *a* , μg/cm^3), sediment phaeopigments (Sed. phaeo., μg/cm^3), gravel (%), sand (%), mud (%), sediment water content (Sed. water, %), sediment total nitrogen (TN, %), sediment total organic carbon (TOC, %), adjusted carbon to nitrogen ratio (C/N), seafloor categories (range 0-3; (0: only soft sediments, 1: cobble, 2: boulders, 3: cobble and boulders).

Env. Variables	Western						Eastern					
	Shallow		Mid-depth		Deep		Shallow		Mid-depth		Deep	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Depth	19.1	3.6	58.4	14.7	183	14.7	20	1.9	41.1	11.7	172.2	20.3
T	3.2	0.9	2.9	1.4	-0.3	0.6	1.3	0.5	-0.6	0.7	0.04	0.7
S	31.3	0.2	31.7	0.2	33.9	0.8	31.6	0.1	31.9	0.3	34.2	0.9
pH	8.2	0.0	8.2	0.0	8.0	0.1	8.2	0.0	8.1	0.1	8.1	0.0
BW chl *a*	0.3	0.2	0.2	0.2	0.1	0.1	0.2	0.2	0.8	0.8	0.1	0.1
BW phaeo.	0.2	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.5	0.4	0.0	0.0
Org. matter	3.3	1.5	4.4	0.9	5.6	1.2	3.5	2.5	3.2	0.8	4.4	0.9
Sed. chl *a*	2.2	2.4	2.3	1.2	4.3	1.5	2.4	2.1	2.5	1.2	1.8	1.1
Sed. phaeo.	1.6	0.8	5.0	1.8	7.6	3.1	1.8	2.2	4.0	2.1	5.3	2.5
Gravel	0.6	1.7	6.5	13.5	8.6	17.4	2.6	5.6	12.0	17.5	16.6	21.4
Sand	35.5	31.5	23.7	12.4	17.5	7.6	40.7	28.4	34.6	11.3	25.2	8.5
Mud	63.7	31.1	69.6	17.8	73.6	21.2	56.6	31.1	53.2	18.5	57.9	15.4
Sed. water	31.7	7.3	41.3	9.1	47.7	11.1	25.4	7.7	34.5	12.9	36.6	5.5
TN	0.1	0.1	0.2	0.0	0.2	0.1	0.1	0.1	0.1	0.1	0.2	0.0
TOC	1.4	0.7	1.4	0.4	1.5	0.5	0.9	0.9	0.9	0.4	1.2	0.1
C/N	8.4	1.9	8.1	0.8	7.9	1.0	8.9	2.3	7.3	1.2	7.2	0.4
Seafloor categories	0.2	0.4	0.6	0.8	0.4	0.5	1.4	1.4	1.3	1.1	1.3	0.7

Table 2.13. Principal component analysis (PCA) of normalized environmental variables selected by BioEnv analysis (Primer V6). Cumulative variation for three PCs amounts to 83.8%. Selected variables are bottom water pH, sediment phaeopigments (Sed. phaeo., μg/cm^3), bottom water salinity (S, ‰), sand (%), bottom water temperature (T, °C), sediment organic matter (Org. matter, % dry weight).

	PC1	PC2	PC3
Eigenvalues	2.98	1.52	0.55
% Variation	49.40	25.20	9.20
Eigenvectors			
pH	0.49	-0.26	0.04
Sed. phaeo.	-0.47	0.01	-0.77
S	-0.43	0.11	-0.28
Sand	0.27	0.63	-0.19
T	0.35	-0.54	0.54
Org. matter	-0.41	-0.48	-0.10

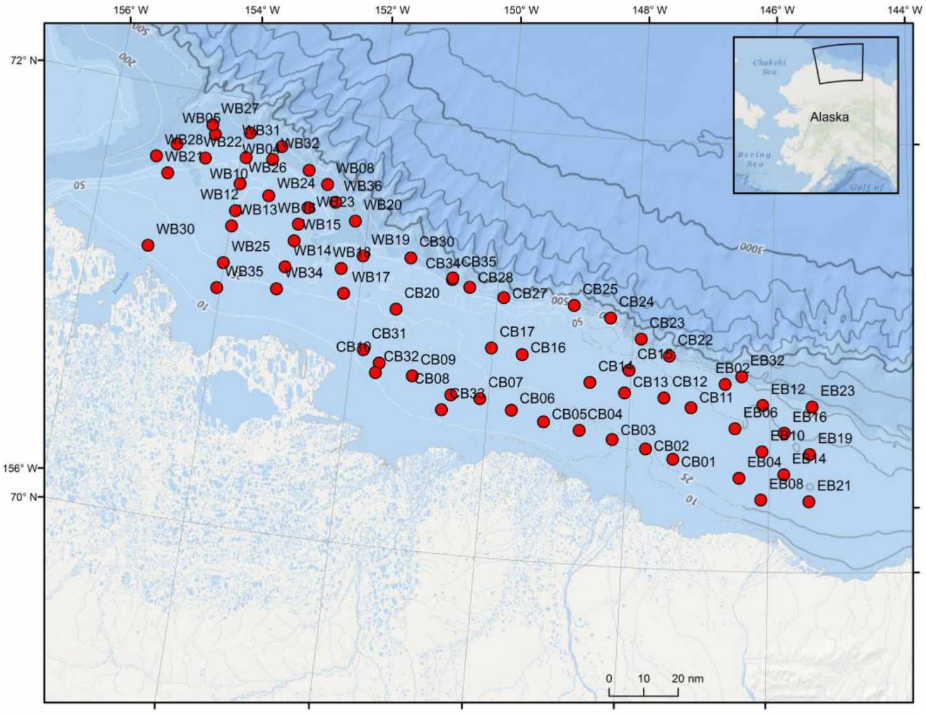

Figure 2.7. Stations sampled for epibenthic invertebrates during the Beaufort Sea Marine Fish Monitoring in the Central Beaufort Sea research cruise in 2011.

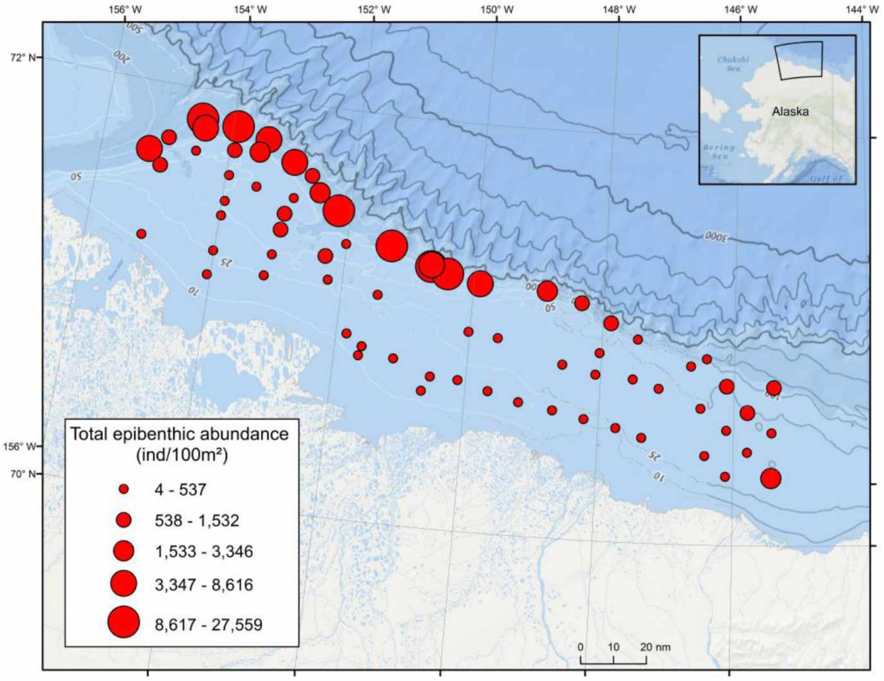

Figure 2.8. Abundance of epibenthos. Stations represented by scaled circles of total abundance (expressed in individuals in 100m²) by station.

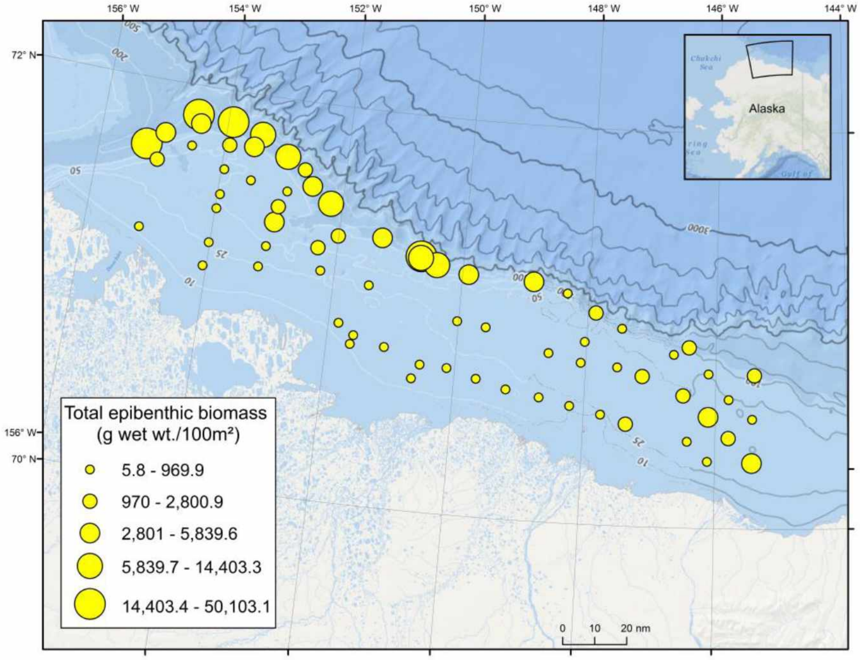

Figure 2.9. Biomass of epibenthos. Stations represented by scaled circles of total biomass (expressed in grams of wet weight in 100m²) by station.

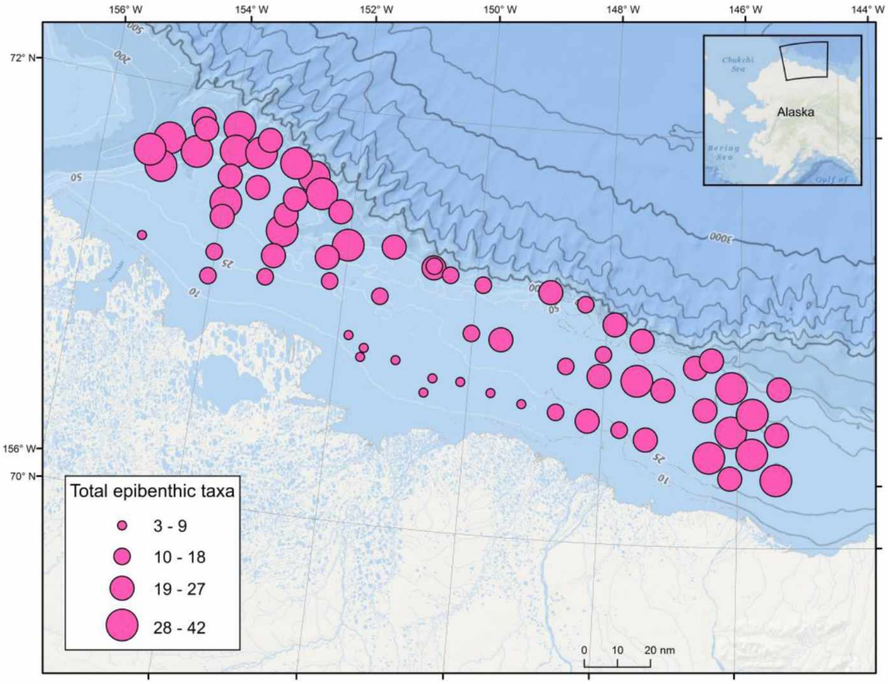

Figure 2.10. Total epibenthic taxa. Stations represented by scaled circles of number of taxa present by station.

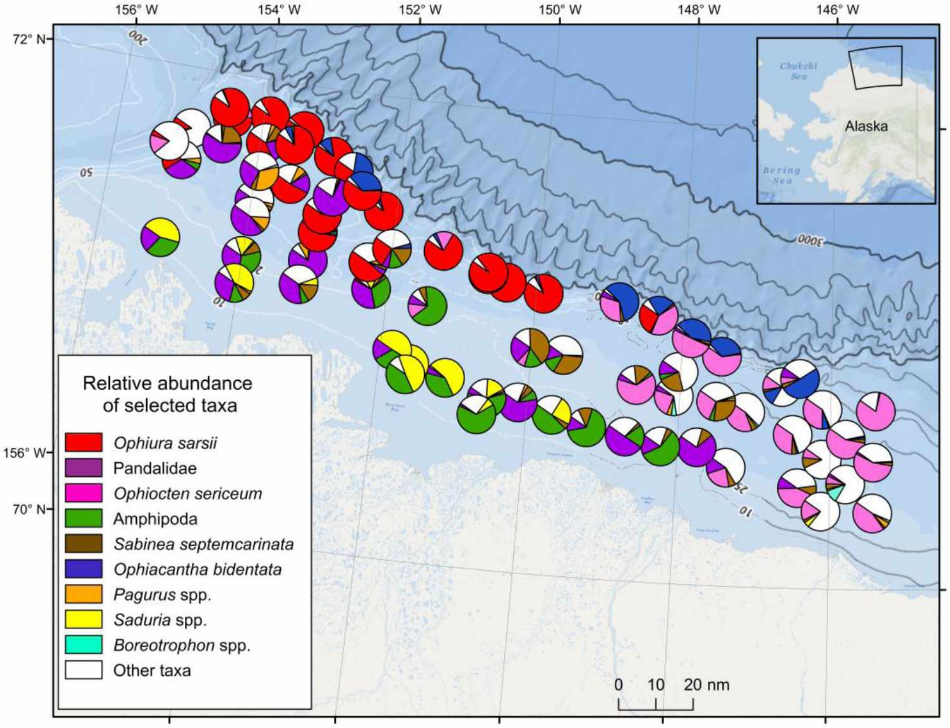

Figure 2.11. Relative epibenthic abundance per station. Each chart is showing the relative abundance of the selected taxa by BVSTEP procedure at each station.

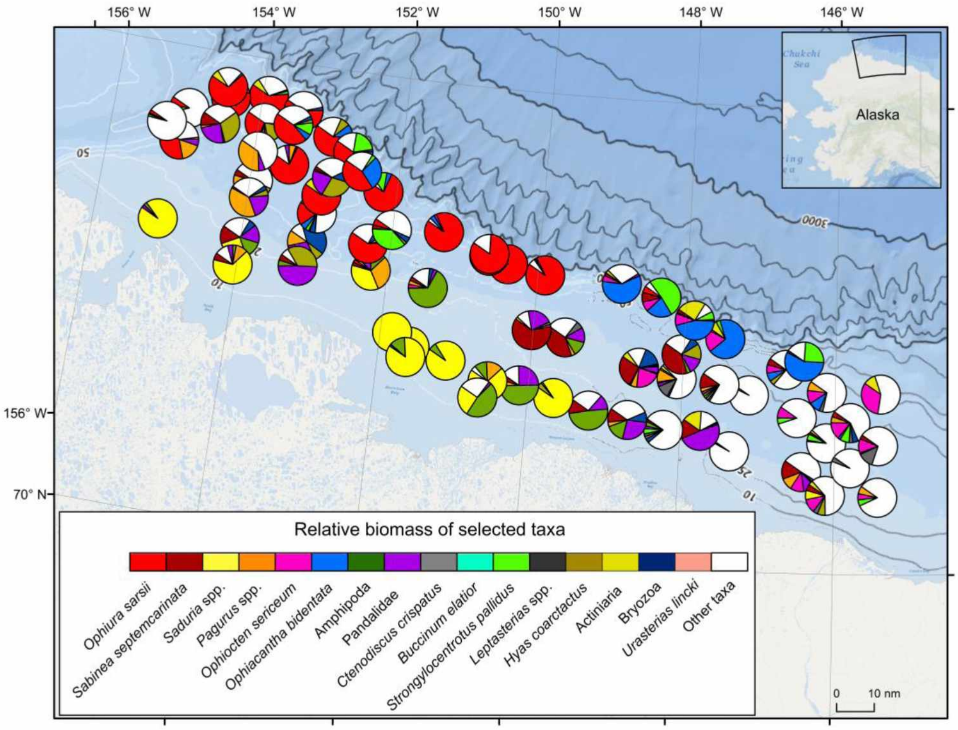

Figure 2.12. Relative epibenthic biomass per station. Each chart is showing the relative biomass of the selected taxa by BVSTEP procedure at each station.

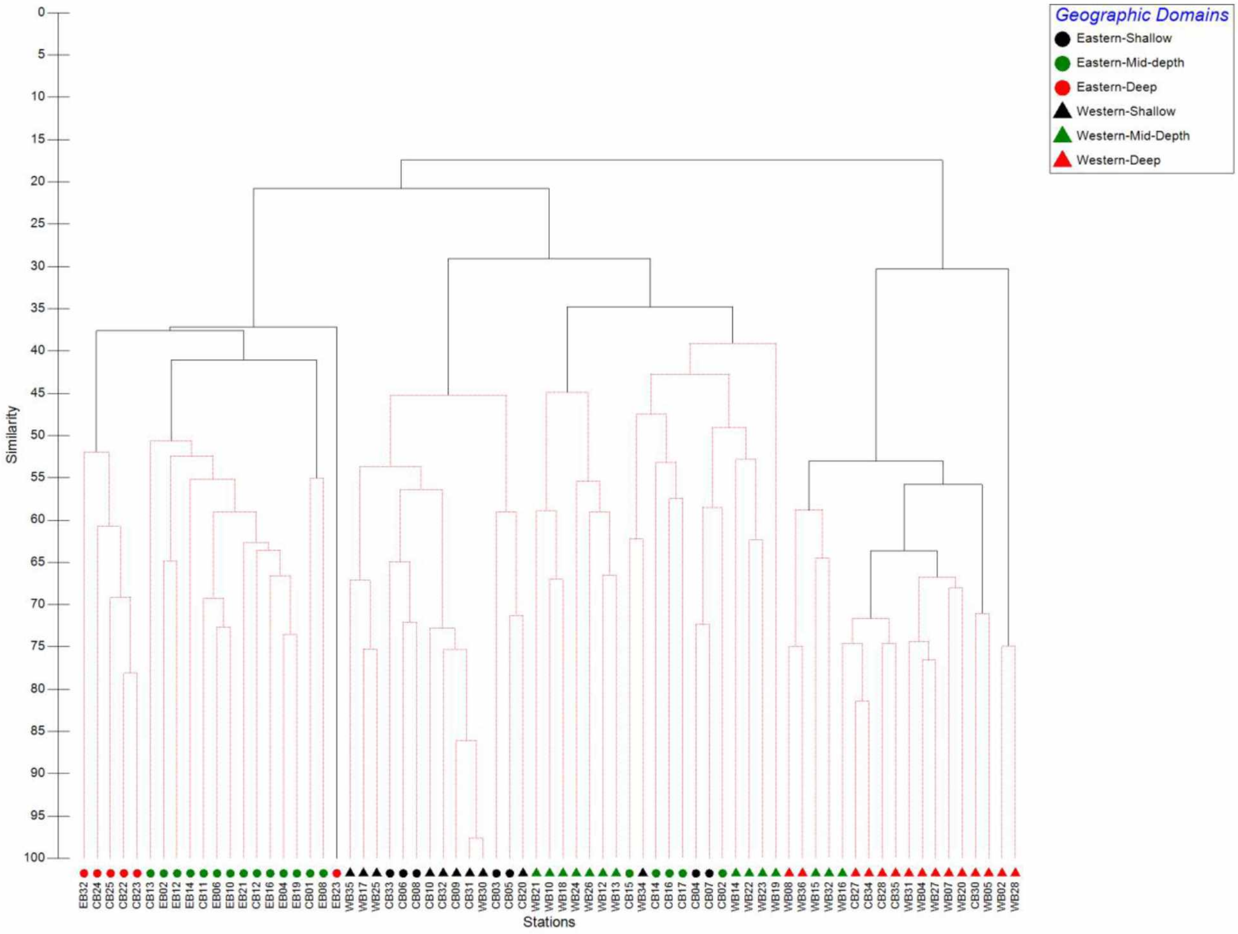

Figure 2.13. Cluster analysis of all stations based on a Bray-Curtis resemblance matrix of relative abundance per trawl and square root transformed data (Primer V6). Red dotted line represents groupings with no statistical significance defined by the SIMPROF test (Primer V6). Stations are symbolized and color coded by geographic domains.

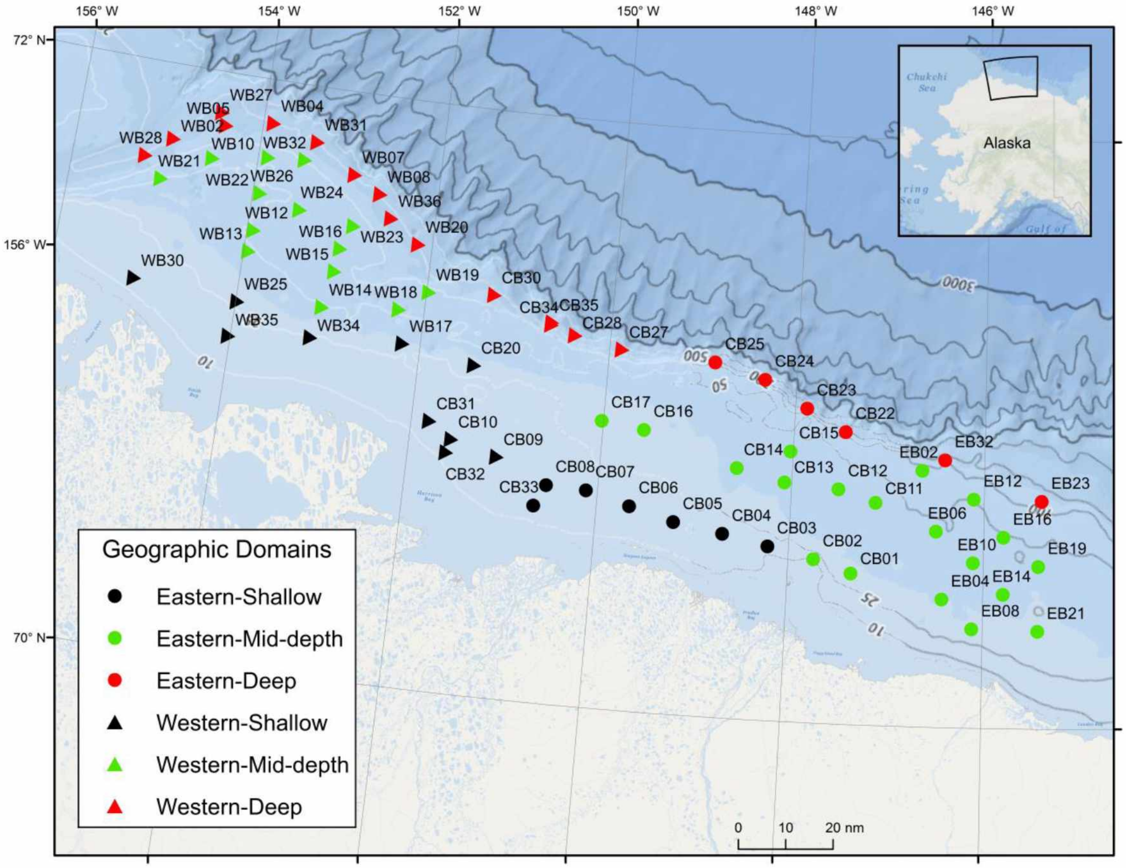

Figure 2.14. Defined geographic domains. Epibenthic trawl stations symbolized and color coded by geographic domain.

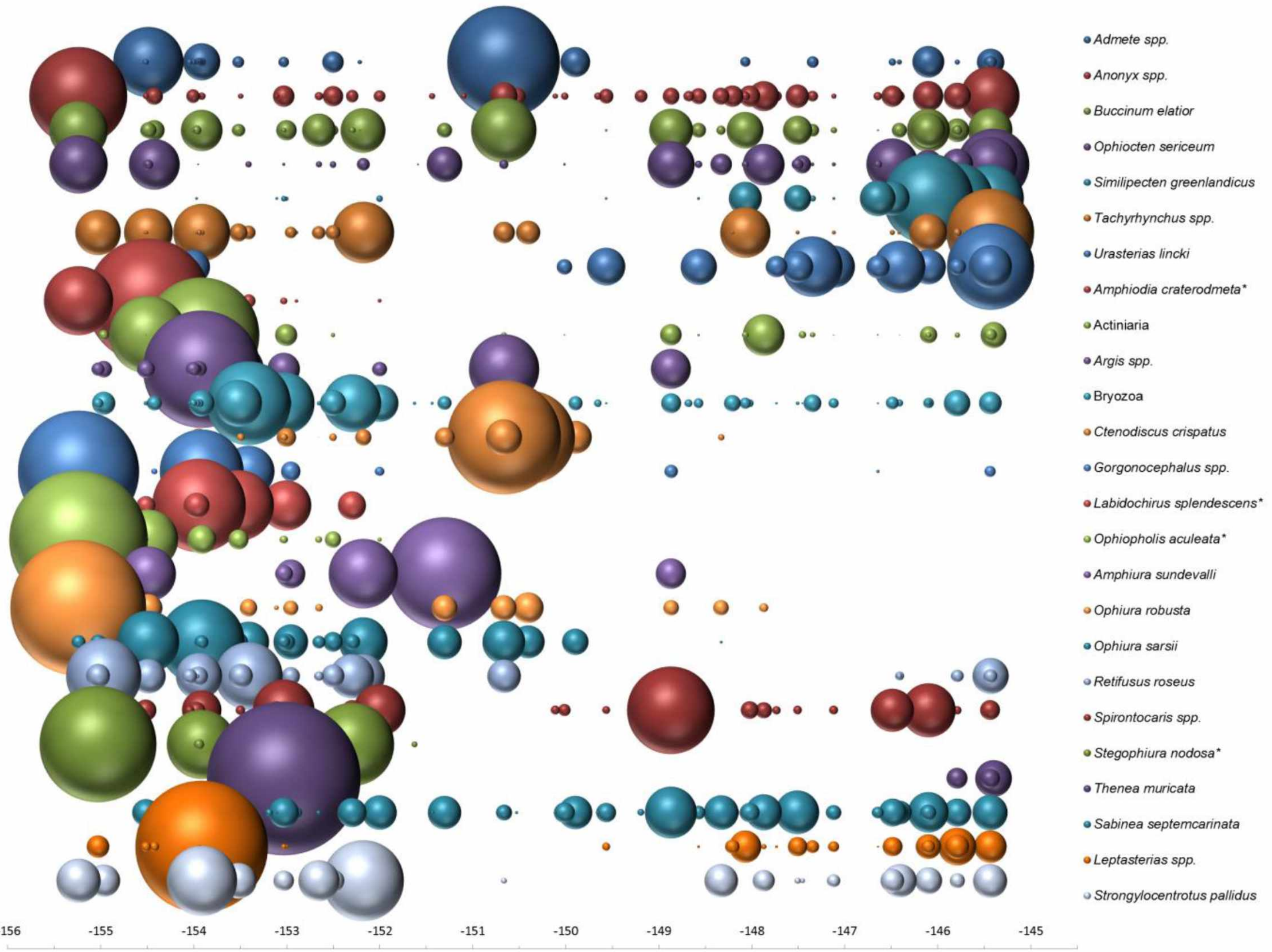

Figure 2.15. Range of distribution along the longitudinal extent of the study area for taxa selected in BVSTEP analysis by geographic domains. The first seven taxa were selected exclusively for the eastern region, the following 14 were selected exclusively for the western region and the last three were selected in the eastern and western regions for different depth groups. Each bubble is a station and the size of the bubble represents the taxon's relative biomass (bubble size range from 90% to <0.001% of the taxon's total biomass). Marked with an asterisk are the taxa that were only present exclusively in the western region.

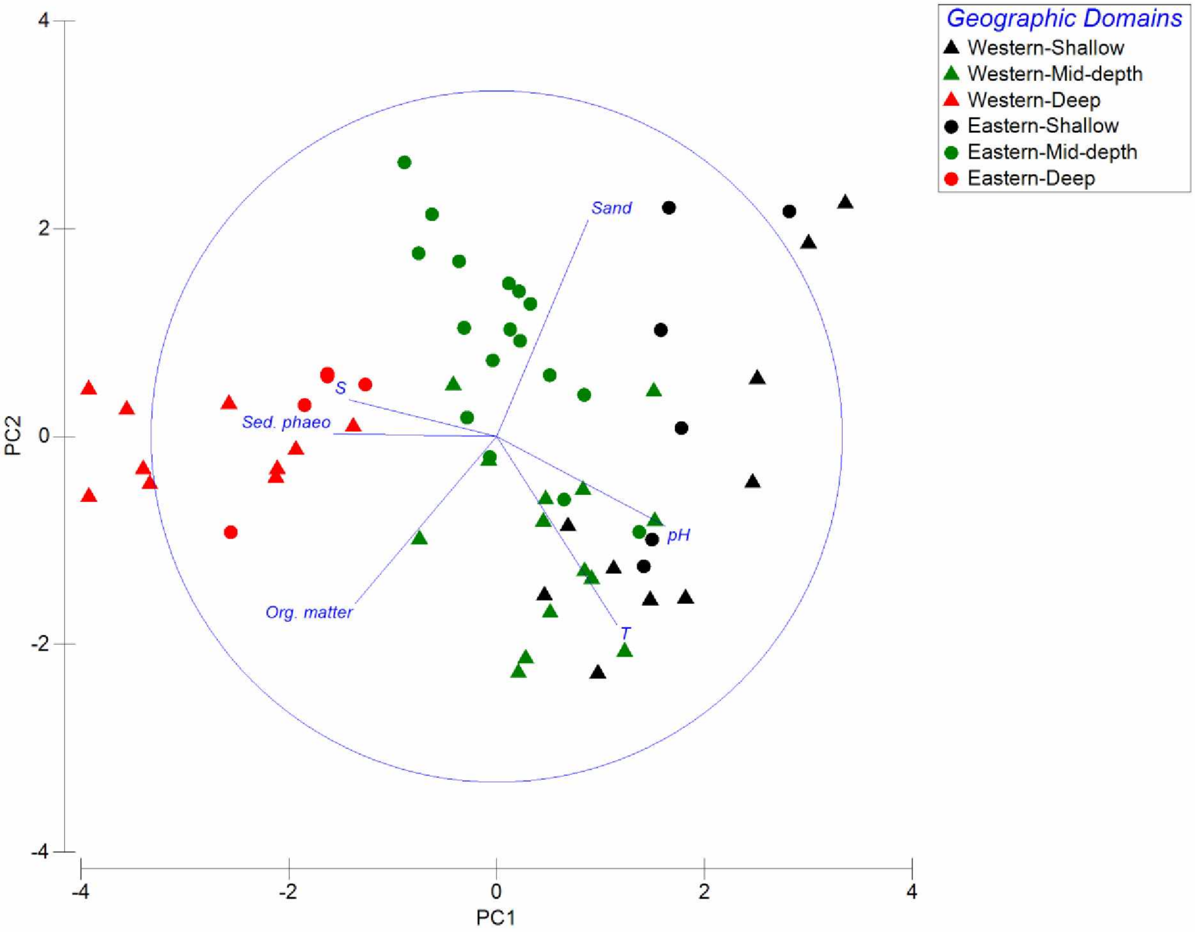

Figure 2.16. Principal Component Analysis (PCA) plot (Primer V6). Stations are symbolized by geographic domains and show the multivariate similarity among stations for the combination of environmental variables selected by BIOENV analysis (Primer V6). Vectors represent the direction and strength of each environmental variable to the total station distribution (Eigenvector values in Table 2.7).

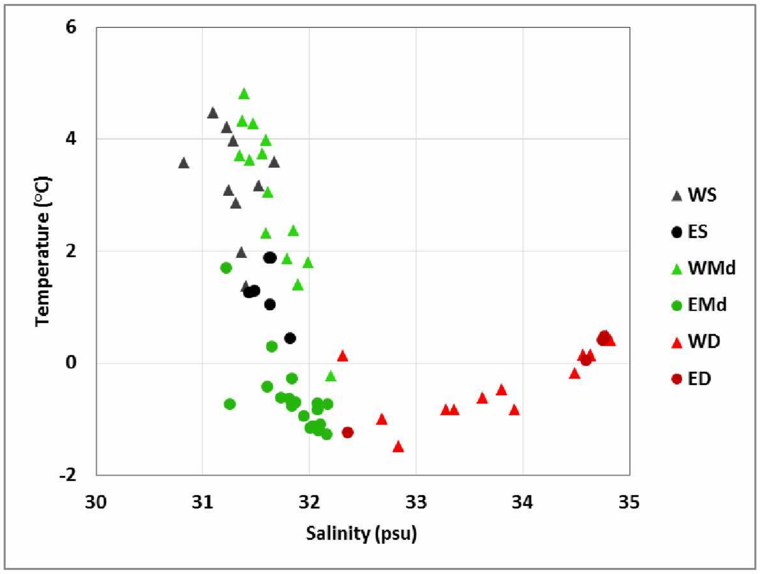

Figure 2.17. Bottom water temperature-salinity correlation for each station coded by geographic domain. Western shallow (WS), eastern shallow (ES), western mid-depth (WMd), eastern mid-depth (EMd), western deep (WD) and eastern deep (ED).

2.6 Appendix

Table 2.A. Stations sampled during the 2011 Alaska Beaufort trawl survey. Station names (-GC: stations sampled for gear comparison, -R: replicated station using the same gear as original sample), trawl beginning position, depth (meters), gear type (PSBT: plumb-staff beam trawl, PSBT-A: modified plumb-staff beam trawl), date sampled, and *a posteriori* defined region and depth group for each station.

Station	Latitude	Longitude	Depth	Gear type	Date Sampled	Region Group	Depth Group
EB21	70.3315	-145.4430	52	PSBT	8/17	Eastern	Mid-depth
EB23	70.7739	-145.4070	127	PSBT	8/17	Eastern	Deep
EB12	70.7782	-146.1099	68	PSBT	8/18	Eastern	Mid-depth
EB14	70.4561	-145.7967	39	PSBT	8/18	Eastern	Mid-depth
EB16	70.6503	-145.7977	56	PSBT	8/18	Eastern	Mid-depth
EB19	70.5520	-145.4381	33	PSBT-A	8/18	Eastern	Mid-depth
EB04	70.4360	-146.4200	35	PSBT-A	8/19	Eastern	Mid-depth
EB06	70.6667	-146.4938	45	PSBT-A	8/19	Eastern	Mid-depth
EB08	70.3367	-146.1104	30	PSBT	8/19	Eastern	Mid-depth
EB10	70.5619	-146.1066	41	PSBT	8/19	Eastern	Mid-depth
CB11	70.7583	-147.1254	48	PSBT-A	8/20	Eastern	Mid-depth
EB02	70.8725	-146.6500	64	PSBT-A	8/20	Eastern	Mid-depth
EB32	70.9101	-146.4159	126	PSBT	8/20	Eastern	Deep
CB01	70.5145	-147.3533	28	PSBT	8/21	Eastern	Mid-depth
CB02	70.5970	-147.7415	26	PSBT-A	8/21	Eastern	Mid-depth
CB12	70.7989	-147.5143	41	PSBT-A	8/21	Eastern	Mid-depth
CB22	70.9950	-147.4627	184	PSBT-A	8/21	Eastern	Deep
CB04	70.6262	-148.6868	13	PSBT-A	8/22	Eastern	Shallow
CB13	70.8133	-148.0767	43	PSBT-A	8/22	Eastern	Mid-depth
CB14	70.8528	-148.5788	36	PSBT-A	8/22	Eastern	Mid-depth
CB23	71.0686	-147.8788	183	PSBT-A	8/22	Eastern	Deep
CB24	71.1592	-148.3365	180	PSBT-A	8/22	Eastern	Deep
CB03	70.5928	-148.2158	23	PSBT-A	8/23	Eastern	Shallow
CB05	70.6548	-149.1974	19	PSBT-A	8/23	Eastern	Shallow
CB06	70.6970	-149.6623	19	PSBT-A	8/23	Eastern	Shallow
CB15	70.9201	-148.0300	33	PSBT-A	8/23	Eastern	Mid-depth
CB16	70.9602	-149.5722	33	PSBT-A	8/23	Eastern	Mid-depth
CB25	71.2073	-148.8749	179	PSBT-A	8/23	Eastern	Deep
CB27	71.2184	-149.9031	163	PSBT-A	8/24	Western	Deep
CB28	71.2520	-150.4104	103	PSBT-A	8/24	Western	Deep

CB07	70.7384	-150.1203	19	PSBT-A	8/24	Eastern	Shallow
CB17	70.9791	-150.0197	30	PSBT-A	8/24	Eastern	Mid-depth
CB20	71.1149	-151.4424	20	PSBT-A	8/25	Western	Shallow
CB08	70.7432	-150.5349	19	PSBT-A	8/25	Eastern	Shallow
CB09	70.8136	-151.1057	18	PSBT-A	8/26	Western	Shallow
CB10	70.8556	-151.5946	17	PSBT-A	8/26	Western	Shallow
CB31	70.9089	-151.8422	17	PSBT-A	8/26	Western	Shallow
WB17	71.1594	-152.2214	24	PSBT-A	8/26	Western	Shallow
WB19	71.3442	-152.0087	90	PSBT-A	8/26	Western	Mid-depth
CB30	71.3610	-151.3092	183	PSBT-A	8/27	Western	Deep
WB08	71.6546	-152.6614	183	PSBT-A	8/27	Western	Deep
WB20	71.5015	-152.1839	184	PSBT-A	8/27	Western	Deep
WB23	71.5343	-152.9027	60	PSBT-A	8/28	Western	Mid-depth
WB24	71.5634	-153.5034	53	PSBT-A	8/28	Western	Mid-depth
WB07	71.7110	-152.9747	183	PSBT-A	8/28	Western	Deep
WB31	71.8005	-153.4167	183	PSBT-A	8/28	Western	Deep
WB10	71.7238	-153.9227	53	PSBT-A	8/29	Western	Mid-depth
WB12	71.4710	-153.9570	52	PSBT-A	8/29	Western	Mid-depth
WB15	71.3723	-153.0386	79	PSBT-A	8/29	Western	Mid-depth
WB16	71.4517	-153.0111	65	PSBT-A	8/29	Western	Mid-depth
WB26	71.5988	-153.9508	49	PSBT-A	8/29	Western	Mid-depth
WB22	71.6912	-154.5217	51	PSBT-A	8/30	Western	Mid-depth
WB04	71.8418	-153.9206	184	PSBT-A	8/30	Western	Deep
WB05	71.8086	-154.4321	155	PSBT-A	8/30	Western	Deep
WB27	71.8512	-154.4951	178	PSBT-A	8/30	Western	Deep
WB30	71.2433	-155.1354	13	PSBT-A	8/31	Western	Shallow
WB13	71.3977	-153.9775	43	PSBT-A	8/31	Western	Mid-depth
WB21	71.5933	-155.0366	48	PSBT-A	8/31	Western	Mid-depth
WB02	71.7344	-154.9747	183	PSBT-A	8/31	Western	Deep
WB28	71.6624	-155.2461	183	PSBT-A	8/31	Western	Deep
WB25	71.2221	-154.0137	23	PSBT-A	9/1	Western	Shallow
WB34	71.1379	-153.1948	25	PSBT-A	9/1	Western	Shallow
WB35	71.1017	-154.0514	18	PSBT-A	9/1	Western	Shallow
WB14	71.2457	-153.1169	41	PSBT	9/1	Western	Mid-depth
WB32	71.7340	-153.5261	83	PSBT-A	9/1	Western	Mid-depth
CB32	70.8096	-151.6320	16	PSBT-A	9/2	Western	Shallow
WB18	71.2730	-152.3036	51	PSBT-A	9/2	Western	Mid-depth

WB36	71.5773	-152.5094	154	PSBT-A	9/2	Western	Deep
CB34	71.2805	-150.6733	183	PSBT-A	9/3	Western	Deep
CB35	71.2883	-150.6699	223	PSBT-A	9/3	Western	Deep
CB33	70.6780	-150.7046	16	PSBT-A	9/3	Eastern	Shallow
WB32-R	71.7329	-153.5032	80	PSBT-A	8/28		
WB21-GC	71.5943	-154.9852	45	PSBT	8/31		
WB13-GC	71.3973	-153.9954	40	PSBT	9/1		
WB14-GC	71.2467	-153.1024	38	PSBT	9/1		
WB31-R	71.7967	-153.4090	180	PSBT-A	9/1		
WB18-GC	71.2867	-152.2603	48	PSBT	9/2		
WB07-R	71.7137	-152.9786	180	PSBT-A	9/2		
CB33-GC	70.6802	-150.6911	13	PSBT	9/3		
CB33-R	70.6732	-150.7012	15	PSBT-A	9/3		
CB34-R	71.2782	-150.6530	180	PSBT-A	9/3		
CB35-R	71.2875	-150.6599	220	PSBT-A	9/3		

Table 2.B. List of epifaunal taxa encountered during the 2011 Alaska Beaufort Sea shelf research cruise. Taxon identification was performed by the authors and the following taxonomist: Nora Foster (NRF Taxonomic Services, USA; Mollusca), Kenneth Coyle (University of Alaska Fairbanks, USA; Amphipoda), Gordon Hendler (Natural History Museum of Los Angeles County, USA; Ophiuroidea), Chritopher Mah (Smithsonian National Museum of Natural History, USA; Asteroidea), Linda Cole Smithsonian National Museum of Natural History, USA; Ascidacea), Carlos Angulo-Preckler (University of Barcelona, Spain; Porifera). Taxon names were verified using WoRMS (WoRMS Editorial Board 2015).

Phylum	Taxa	Station of voucher collection or field identification
Arthropoda	Amphipoda	EB02, EB04, CB03, CB10, WB08, WB12
	Arctolembos arcticus	EB21
	Argis spp.	EB21, CB25
	Chionoecetes opilio	CB23
	Cirripedia	CB15
	Hyas coarctatus	CB03
	Labidochirus splendescens	WB24
	Lebbeus groenlandicus	WB14
	Nototropis smitti	EB21
	Pagurus spp.	CB03
	Pandalidae	EB21
	Paralithodes platypus	CB25, WB07
	Pycnogonida	CB29, EB23
	Sabinea septemcarinata	EB21, CB25
	Saduria entomon	CB08
	Saduria sabini	CB08, CB01
	Sclerocrangon boreas	WB23
	Spirontocaris arcuata	WB23
	Spirontocaris phippsii	EB21
	Spirontocaris spinus	CB25
	Stegocephalidae	EB21
	Synidotea spp.	WB20
	Synidotea bicuspida	EB21
	Weyprechtia heuglini	CB05
Brachiopoda	Brachiopoda	CB30
Bryozoa	*Alcyonidium* (Paralcyonidium) *vermiculare*	WB32
	Alcyonidium disciforme	CB20
	Alcyonidium spp.	WB07, CB08, WB07
	Bryozoa	WB19, WB32, EB06, EB01, WB19, CB01, EB06

	Flustra spp.	WB07, CB01
Chordata	*Acidia obliqua*	CB23, CB04
	Ascidiacea	CB03
	Chelyosoma spp.	CB03, WB10
	Halocynthia spp.	EB12
	Pelonaia corrugata	WB14
	Styela rustica	EB12
	Trididemnum spp.	WB18
Cnidarian	*Actinauge* spp.	EB21, EB32
	Actiniaria	EB14, EB23, CB01, WB22
	Alcyonacea	CB23, EB12
	Gersemia spp.	EB06
	Hydrozoa	CB01, WB12, CB04
	Staurozoa	CB15
	Stomphia spp.	EB21, EB23
	Urticina spp.	WB31
Echinodermata	*Amphiodia craterodmeta*	CB29
	Amphiura sundevalli	CB29, CB25
	Antedonidae	CB23, CB25, CB27
	Crossaster papposus	EB21
	Ctenodiscus crispatus	CB24
	Holothuroidea	WB08
	Gorgonocephalus arcticus	EB23
	Gorgonocephalus eucnemis	EB23
	Henricia sanguinolenta	WB32
	Leptasterias arctica	WB22
	Leptasterias groenlandica	EB21
	Lophaster furcifer	EB04, CB23
	Ocnus glacialis	EB21
	Ophiacantha bidentata	CB23, EB21, WB32, EB12
	Ophiocten sericeum	CB25
	Ophiopholis aculeata	WB27, WB19
	Ophiura robusta	CB23, CB25, WB07
	Ophiura sarsii	CB24
	Pontaster tenuispinus	EB23
	Poraniomorpha tumida	EB12, EB23
	Psolus peronii	EB21

	Pteraster militaris	WB15
	Pteraster obscurus	CB11
	Solaster stimpsoni	CB29
	Stegophiura nodosa	WB23
	Strongylocentrotus pallidus	EB21
	Urasterias lincki	CB01
Mollusca	*Admete* spp.	CB30
	Admete viridula	EB23, WB27, CB02
	Amicula vestita	WB32, CB30
	Beringius spp.	WB04, WB16
	Boreotrophon spp.	WB27, WB04, EB23, CB13
	Buccinum angulosum	WB07, EB21, EB12
	Buccinum scalariforme	EB23
	Buccinum glaciale	WB31
	Buccinum glaciale	WB32
	Buccinum polare	WB07
	Buccinum scalariforme	EB21
	Chlamys behringiana	WB16
	Clinopegma magnum	WB04
	Colus sabini	EB23
	Cryptonatica affinis	CB08
	Curtitoma conoidea	CB30
	Curtitoma decussata	CB30
	Curtitoma novajasemljensis	CB01
	Cylichna alba	EB21, CB01
	Cylichna occulta	CB20
	Dendronotus sp.	CB23
	Habevolutopsius attenuatus	WB02
	Hermissenda crassicornis	EB10
	Iphione sp.	EB08
	Lacuna turneri	CB03
	Lepeta caeca	EB06, CB28, WB32
	Limneria undata	EB14
	Euspira pallida	EB21
	Margarites costalis	EB23
	Margarites giganteus	CB20
	Musculus niger	WB04

	Muusoctopus sibiricus	CB23
	Neptunea communis	WB13
	Neptunea spp.	CB01
	Neptunea ventricosa	CB13
	Nodulotrophon coronatus	CB13
	Oenopota elegans	CB01
	Onchidiopsis spp.	EB12
	Onchidorididae	EB14
	Pandora glacialis	EB14
	Plicifusus kroeyeri	EB21, WB20
	Pyrulofusus deformis	CB01, EB23, EB19
	Retifusus roseus	EB21, WB07
	Rossia pacifica	EB23
	Similipecten greenlandicus	EB21
	Solariella varicosa	EB10
	Stenosemus albus	EB06, WB22
	Tachyrhynchus spp.	EB21
	Tritonia spp.	CB23
	Velutina coriacea	EB21
	Velutina velutina	EB12
	Volutopsius fragilis	EB23
	Volutopsius norwegicus	WB07
	Volutopsius spp.	EB23
Platyhelminthes	Platyhelminthes	EB12, EB14
Porifera	*Halichondria* (Eumastia) *sitiens*	CB03
	Myxilla (Burtonanchora) *lacunosa*	WB18
	Polymastia spp.	EB21, EB23
	Porifera	CB03
	Semisuberites cribrosa	CB11
	Thenea muricata	EB23

CHAPTER 3: What lies beneath the ice: relating seasonal sea ice patterns with benthic shelf fauna in the Alaska Arctic[1]

Abstract

Sea ice, as one of the most prominent features of the Arctic Seas, provides habitat for sympagic primary and secondary producers, which in turn provide food to the benthos. The seasonality of sea ice affects processes that influence export production, such as vertical mixing in the water column and changes in the depth of the photic zone, which in turn affect the quantity and quality of food deposited to the benthos. To date, the impact that sea ice variables (e.g., ice cover, persistence of the ice edge, and the phenology of ice retreat and growth) may have on Arctic benthic communities has been poorly quantified. The main objective of this analysis was to evaluate the relationship between the spatial variability in infaunal and epifaunal benthic community composition, biomass, and feeding guilds with the spatial variability in the patterns of the seasonality of sea ice. Benthic community data from 102 stations were gathered throughout the Alaska Beaufort and Chukchi Sea shelves, between 2009-2011. Passive microwave sea ice concentration data were used to compute variables meant to reflect the variability in the patterns of the seasonality of sea ice. Linear regressions resulted in 10 significant correlations between the number of benthic taxa, total station biomass, and each of the sea ice variables evaluated (from a total of 30 possible correlations). Multivariate analysis resulted in moderate and low correlation values between sea ice variables and taxonomic community composition based on biomass in the Beaufort Sea and Chukchi Sea. Sea ice variables were not more highly correlated with communities classified by feeding guilds in either region. The inclusion of sea ice variables to multivariate analysis using hydrographic variables (bottom water temperature, salinity), food availability and sediment type better explained variation in benthic community biomass. The patterns of the seasonality of sea ice did not have a direct effect on benthic communities, but rather provides a proxy for seasonal changes in wind driven currents, upwelling and riverine input on benthic community variability. Given its coarse resolution and insensitivity to ice thickness and snow depth, the passive microwave-derived sea ice data is a poor predictor of sympagic-benthic coupling. However, many of the environmental drivers relevant to

---

[1] Ravelo, A.M., Konar, B., Grebmeier, J.M., Mahoney, A.R. (In review) What lies beneath the ice: relating seasonal sea ice patterns with benthic shelf fauna in the Alaskan Arctic. Deep Res Part II Top Stud Oceanogr

benthic communities are hard to record *in situ* year round, and sea ice variables reflect changes in many of these environmental variables. Despite the shortcomings of passive microwave derived sea ice variables, their inclusion to the commonly used list of predictors of benthic commuity structure can improve our ability to explain benthic community patterns and their relation to the changing Arctic environment

3.1 Introduction

Alaskan Arctic shelves are characterized by areas of variable benthic standing stock and an overall dominance of invertebrate biomass over fish biomass (Feder et al., 2005; Rand and Logerwell, 2011; Ravelo et al., 2015, 2014). The seasonally high water column primary production that characterizes the Pacific Arctic shelves is reflected in the overall high benthic biomass and relatively low pelagic secondary production (Grebmeier et al., 2006a). In the Chukchi Sea, benthic biomass is comparable to other highly productive regions, with maximum values of >4000 g wet wt. m^{-2} for infauna and 217 g wet wt. m^{-2} for epifauna (Bluhm et al., 2009; Grebmeier et al., 2006a; 2015; Denisenko et al. 2015). On the western Alaskan Beaufort shelf, epibenthic invertebrates made up to 94% of the total benthic standing stock; with maximum epibenthic biomass estimates as high as 50,103.1 g wet wt. 100 m^{-2} (Rand and Logerwell, 2011; Ravelo et al., 2015). The predominance of benthic invertebrates over fish biomass is also reflected in the abundant higher trophic organisms, such as spectacled eiders, bearded seals, grey whales, and walrus that depend on bivalves, benthic amphipods, crab and polychaetes as main prey items (Bluhm and Gradinger, 2008; Cooper et al., 2013; Coyle et al., 2007; Schonberg et al., 2014). Besides being a food source, benthic organisms play an important role in bioturbation, and through organic carbon remineralization they contribute to the total benthic energy turnover (Piepenburg and Schmid, 1996; Renaud et al., 2007). Many Arctic benthic invertebrates are long lived and relatively stationary (Bluhm et al., 1998; Carroll et al., 2009; Gage, 2003). From patterns of species distribution and biomass, we can infer spatial patterns of persistent environmental conditions, as well as monitor for enviromental changes.

Despite being spatially variable, Arctic shelf systems are generally characterized by a tight relation between primary production and benthic food supply (Ambrose and Renaud, 1995; Dunton et al., 2005; Grebmeier and Barry, 1991; Piepenburg et al., 1997). Throughout the winter season, the ice-covered continental shelves are replenished with nutrients that are rapidly depleted as the ice-edge algal bloom forms in the spring (Stein and MacDonald, 2004). As sea ice melts, large amounts of sympagic algae sink rapidly to the benthos and provide fresh food to benthic consumers

(Ambrose et al., 2005; McMahon et al., 2006; Renaud et al., 2007). In addition to sympagic production, algal blooms in the ice-covered Pacific Arctic occur early in the season, before zooplankton biomass can significantly graze down the fresh phytoplankton material exported to the benthos (Grebmeier et al., 1988).

The most visible effect of climate change on the Arctic shelves is the spatial reduction of perennial sea ice, along with the early retreat and late formation of annual sea ice (Comiso et al., 2008; Stroeve et al., 2012). On Arctic shelves, changes in thickness, extent and persistence of sea ice can have a profound effect on biological processes and ecosystem functioning (Grebmeier, 2012; Lohrer et al., 2013). Through a longer phytoplankton growth season, the reduction of sea ice in Arctic waters is a main contributor to increased phytoplankton production, which is projected to increase over 3-fold from past decades if the Arctic becomes ice-free in spring (Arrigo et al., 2008). Along with an increase in phytoplankton production, pelagic secondary production may also benefit from longer ice-free seasons (Arrigo and van Dijken, 2015; Matsuno et al., 2011). The strong dependence of benthic communities on the early season primary production could force a shift from specialized feeders to more opportunistic benthic detritivores (Søreide et al., 2013). Changes in water column productivity will affect the quality and quantity of food deposited to the benthos, potentially changing the distribution of organisms based on their feeding strategies (Carmack and Wassmann, 2006; Grebmeier et al., 2006a; Wassmann et al., 2011).

One of the most distinct environmental characteristics of Arctic shelves is the seasonal formation and retreat of sea ice. With the onset of winter, the ocean loses heat to an increasingly cold atmosphere, allowing the formation of ice crystals and eventually sea ice floes. Although most Arctic shelves are annually covered by a combination of drifting pack ice offshore and landfast ice nearshore, the regional phenology of sea ice formation and retreat are largely defined by a combination of geographic, oceanographic and atmospheric features. The Alaskan Arctic is composed of two shelves, the Chukchi and Beaufort Seas, which differ greatly in their physical features. The Chukchi Sea is a wide shallow shelf (mostly <50 m), bordered latitudinally by land masses and delimited by the Bering Strait to the south. The Chukchi Sea is thus the only conduit of Pacific originated water into the Arctic Ocean (Carmack and Wassmann, 2006). In this region, sea ice retreats in response to the combination of atmospheric forcing and the inflow of warm water traveling north through Bering Strait, leaving the shelf mostly ice free during the summer months and limited to first-year ice the following winter (Frey et al., 2015; Mahoney, 2012; Woodgate et al., 2010). In contrast, the Alaskan Beaufort Sea has a shallow and narrow interior shelf that slopes down to the Canadian Basin (>3,000 m) in less than 100 km from shore (Norton and Weller, 1984). In the summer, many rivers discharge freshwater onto the Alaskan Beaufort Sea shelf, including the Mackenzie River, east of the Canadian border. Along the slope, the Alaskan Beaufort Sea receives inflowing modified Pacific water though Barrow Canyon and Atlantic water from the Arctic-wide cyclonic boundary current (Carmack and Macdonald, 2002; Nikolopoulos et al., 2009). The Beaufort Gyre, due to its anti-cyclonic movement, carries multiyear sea ice south and on to the shelf (Pritchard, 1984; Reimnitz and Kempema, 1984). These characteristics, along with other physical factors, determine the differences in the phenology of sea ice in each of the two regions. Recent research has focused on the impact that long term changes in environmental variables (including, changes in ice cover) have on specific benthic species biomass and/or nutrient fluxes, and sediment oxygen uptake (Cooper et al., 2013; Link et al., 2013; Søreide et al., 2013). However, the effect that sea ice parameters, such as ice cover, onset of sea ice melt and persistence of ice edge may have on the structure and composition of benthic communities remains largely unknown.

Benthic assemblages on Arctic shelves vary spatially following meso-scale (10-100 km) environmental patterns, such as changes in water mass properties, sediment grain size, and presence of polynyas (Blanchard et al., 2013; Carroll and Ambrose, 2012; Piepenburg et al., 2000; Roy et al., 2014). Indirect determinants of commuity structure such as position (latitude and longitude) and depth are commonly used as proxies for these or other unresolved meso-scale community drivers. In many cases, these proxies have higher predictive power than environmental variables that may directly affect benthic organisms, such as water mass characteristics and indicators of food supply (examples in Bluhm et al., 2009; Ravelo et al., 2014; 2015). Poor spatial resolution and a lack of year-round *in situ* measurements have limited past analysis to use point-in-time values to correlate with benthic communities or total biomass. The high seasonal variability that benthic organisms experience in Arctic shelf systems cannot be represented with a single value. Moreover, assessing the implications that the changes in patterns of the seasonality of sea ice will have for benthic invertebrates throughout the Alaskan Arctic becomes impossible without first determining which environmental variables are driving these communities. Using these same epibenthic community data as presented here, two previous studies used a number of environmental variables collected *in situ* to explain the pattern of epibenthic community variability in the Chukchi and Beaufort Sea shelves (Ravelo et al., 2014; 2015). The present analysis expands the previous work by including sea ice as a possible explanatory variable of epibenthic and infaunal communities, and by contrasting the relationship between benthic community taxonomic composition and feeding guilds and sea ice variables.

The overarching goal of this project was to explore the potential links between the patterns of the seasonality of sea ice and benthic invertebrate community patterns on two Alaskan Arctic shelves. The hypotheses tested were: 1) the patterns of the seasonality of sea ice is a significant predictor of total benthic (infauna and epifauna) biomass and number of taxa on the Chukchi and Beaufort Sea shelves, 2) sea ice is a better predictor of community structure when communities are classified by feeding guilds as opposed to communities classified by taxa, and 3) the addition of sea ice variables to the commonly used variables increases the predictive power of environmental drivers of benthic community structure.

3.2 Methods

3.2.1 Benthos

Stations were sampled in the Chukchi and Beaufort Seas from 2009-2011 (Figure 3.1). Specifically, on the Chukchi Sea shelf, stations extended from 67.67° to 72.40 °N and 168.96° to 159.37°W and ranged in water depth from 23 to 50 m. The sampling design was determined via two methods: 1) a general randomized tessellation stratified design (GRTS), and 2) a spatially oriented, nearshore-to-offshore, south to north grid overlaying the GRTS design; these two methods were applied to cover long term monitoring stations and include new stations, specific to a new sampling effort. Epibenthic data were collected at 52 stations and infaunal data were collected at 39 stations during two summer cruises, end of July to mid-August of 2009 and 2010 (Figure 3.1). On the Beaufort Sea shelf, 50 epibenthic stations were sampled in August-September of 2011, spanning from 70.33°N and 145.41°W to 71.73°N and 155.32°W and ranging in water depths from 13 to 90 m. The sample design for this survey chose some stations to repeat previously sampled locations by other research projects, while other stations were defined with a spacing of approximately 0.5° latitude and 0.25° longitude with the goal to cover the majority of the along-shelf extent of the Alaskan Beaufort Shelf (Figure 3.1).

In the Chukchi Sea, epifaunal samples were collected at all stations using a 3.05 m plumb-staff beam trawl (PSBT) with a 7 mm mesh and a 4 mm codend liner (Gunderson and Ellis, 1986). A rigid 3 m pipe forward of the net held the mouth open for an effective swath of 2.26 m; the vertical opening of the net was approximately 1.2 m. For the Beaufort Sea, the same PSBT was used at eight stations, while a modified version of this trawl net (PSBT-A) for stations with very soft sediments was used at 42 stations. The gear modification consisted of the addition of rubber rollers on the bottom of the net, which allowed a more surficial swath of the gear over the seafloor (Abookire and Rose, 2005). There was no significant difference in the samples collected by the two gear types, tested by repeated samples at 10 sites (results published in Ravelo et al., 2015). In both seas, trawls were towed for 2 to 5 minutes on the sea floor with a vessel speed of 1 to 1.5 knots. Once onboard, epifaunal samples were rinsed in sieves (4 mm mesh size), sorted to the lowest possible taxonomic level, and wet weight was recorded (1 gram precision). Epifaunal organisms were mostly identified to genus, but in some cases to family or phylum. Taxa lists for the Chukchi and Beaufort seas are provided in Ravelo et al. (2014, 2015).

Infaunal samples were collected only in the Chukchi Sea at 39 stations using a single $0.1m^2$ van Veen grab following methods outlined in Grebmeier et al. (1989). Samples were sieved (1 mm mesh size) shipboard and preserved with 10% buffered seawater formalin for post-cruise taxonomic identification and wet biomass determinations at the Chesapeake Biological Laboratory (CBL). Infaunal organisms were identified to family for most groups, with dominant infauna by biomass sorted to genus and species, particularly bivalves. A list of the top three infaunal taxa per-station can be found in Grebmeier and Cooper (2012).

3.2.2 Sea ice

Sea ice concentration data were obtained from the Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data set, available through the National Snow and Ice Data Center archives (Cavalieri et al., 1996). The data were generated using the NASA Team algorithm developed by the Oceans and Ice Branch, Laboratory for Hydrospheric Processes at NASA Goddard Space Flight Center (GSFC). Daily fields of sea ice concentration, with 25 km spatial resolution, were compiled for each station sampled for benthos spanning 5 years back from the date the benthic samples were collected. A five year retrospective mean was used to smooth out anomalies in sea ice coverage. From the sea ice concentration data at each station sampled, the following sea ice variables were produced): 1) Date of sea ice return, 2) Date of sea ice retreat, 3) Days with no sea ice, 4) Days covered by sea ice, 5) Days with MIZ (marginal ice zone) and 6) Average seasonal sea ice concentration (Table 3.1). The conventional value of 15% sea ice concentration was used to define the limit of continuous sea ice in passive microwave data (Parkinson et al., 1999). A seven day moving average was applied when calculating the "Date of sea ice return" and "Date of sea ice retreat" to smooth large abrupt changes in sea ice concentration. When quantifying the "Days with MIZ", some stations remained with low and above zero sea ice concentration for most of the "open water season". In those cases, all days were categorized as MIZ until the "Date of sea ice return".

3.2.3 Environmental

Environmental variables for all stations were collected when each station was sampled for biological data. For the Chukchi Sea, bottom water salinity, temperature (°C) and pH were obtained at each station using a YSI sonde 6600V2-4 (Yellow Springs, Ohio, USA). The sonde was factory-calibrated for temperature prior to use, salinity and pH were recalibrated daily. For the Beaufort Sea, bottom water salinity, temperature, pH, chlorophyll *a* and phaeopigments were collected using a SeaBird 25 CTD equipped with Niskin bottles (average distance from the seafloor was 8 m, s.d. 7 m). Water samples were filtered and processed for chlorophyll *a* content following Parsons (1984). For both regions, surface sediments were collected from a 0.1 m^2 van Veen grab for chlorophyll *a* concentration, total organic carbon (TOC) and nitrogen content (TN), carbon to nitrogen ratios (C/N), and sediment grain size (detailed description in Cooper et al., 2002; Ravelo et al., 2015; Trefry et al., 2014). For the Beaufort Sea, surface sediment organic matter and sediment water content were also collected for each station (details in Ravelo et al., 2015).

3.3 Data analysis

3.3.1 Biological data

Different sampling methods were used for collection of epifaunal and infaunal samples, therefore these data were analyzed separately. For the first hypothesis, "sea ice is a significant driver of total benthic biomass and community composition in the Chukchi and Beaufort Sea shelves", the predictors of total biomass and total number of taxa were determined with linear regressions using R (www.r-project.org, V2.15.0). The assumptions of normality and homogeneity of variance were verified for each linear model using the diagnostic tools QQ plot and Durbin-Watson tests. Epifaunal biomass was standardized to kg wet weight in 100 m^2 and infaunal biomass was standardized to g wet weight per m^2 for regression analysis. The station Chuk1010 for Chukchi Sea epifauna and the Beaufort Sea stations EB21 and WB21 were extreme data points and therefore they were excluded from the linear regression analyses to meet the assumption of normality. For the second hypothesis, "Sea ice is a better predictor of benthic commuity structure when organisms are classified by feeding guilds as opposed to communities classified by taxa", benthic taxa were classified by feeding guilds, based on the available bibliographic information (Gaymer et al., 2001; Hobson et al., 1995; Iken et al., 2010; Macdonald et al., 2010). When no information about the feeding mode of a specific taxon was available in the literature, the feeding mode of the closest related group was used. To address the second and third hypothesis, multivariate analyses were performed. Drivers of benthic community biomass were determined by means of Bray-Curtis dissimilarity matrix using the BioEnv routine in PRIMER v6 (Clarke and Gorley, 2006). Multivariate analyses were performed with epifaunal community data standardized to the relative contribution per trawl (in percent). Proportional data are commonly used in multivariate analysis when the size of the sample is not fixed, such as the area trawled (Clarke and Warwick, 2001). All biomass data were square-root transformed prior to analyses. All maps presented were generated using ArcMap from ESRI software. Total biomass was projected onto maps by scaled circles, with breaks determined by Jenks' Natural Breaks.

3.3.2 Sea ice variables

For the Chukchi Sea, the variable "Average seasonal sea ice concentration" was excluded from analyses due to high colinearity with the variables "Date of sea ice retreat" and "Days covered by sea ice". For the Beaufort Sea shelf, the variable "Days with no sea ice" was excluded from the analyses due to high colinearity with the variable "Days with MIZ". All other variables for both regions had colinearity values below 90%. The variable "Days with MIZ" was log transformed to correct for skewedness in both the Chukchi and Beaufort Sea data sets. For all maps of sea ice variables, interpolations were calculated using the Inverse Distance Weighted (IDW) technique from the Spatial Analyst tools in ArcMap from ESRI software and the color gradients were defined by Jenks' Natural Breaks.

3.3.3 Environmental data

To examine correlations between different sets of environmental drivers and benthic communities, the BioEnv procedure in PRIMER was used (Clarke and Gorley, 2006). The environmental variables examined in both regions corresponded to two main categories, permanent and seasonally variable. For the Chukchi Sea, the permanent variables available were: the position variables, depth (m), latitude and longitude, and habitat descriptors: sediment grain size fractions 0-5 phi (0 phi is gravel, 1-4 phi correspond to various sand grain sizes and ≥5 phi is silt and clay). The seasonal variables used were: sediment chlorophyll *a* (mg/m^2), sediment total organic carbon (TOC, %) and sediment total organic nitrogen (TON, %), carbon to nitrogen weight ratio (C/N), bottom water salinity (ppt), bottom water temperature (°C) and bottom water pH. No station was excluded from the analysis due to missing data; however, sediment TON and sediment grain size ≥5 phi were excluded from analyses due to high colinearity with sediment TOC and both sediment grain size 3 phi and sediment TOC, respectively. All environmental variables were normalized prior to analysis.

The permanent variables for the Beaufort Sea consisted of position variables: depth (m), latitude and longitude, and habitat descriptors: sediment grain size fractions gravel, sand and mud (silt and clay), and sediment water content (%). The seasonal variables used were: sediment chlorophyll *a* (μg/cm^3) and sediment phaeopigment (μg/cm^3) concentration, sediment organic matter content (% dry weight), sediment total organic carbon (TOC, %) and sediment total organic nitrogen (TON, %) content, molar carbon-to-nitrogen ratio (C/N), bottom water chlorophyll *a* (μg/l) and bottom water phaeopigment content (μg/l), bottom water salinity (‰), bottom water temperature (°C) and bottom water pH (-). A total of 46 stations had a complete set of environmental variables and were included in the analyses. Sediment percent gravel was square-root transformed, while bottom water chlorophyll *a* and bottom water phaeopigments were natural log transformed to correct for skewedness. No variable had to be excluded due to high colinearity. All environmental variables were normalized prior to analysis.

3.4 Results

3.4.1 Sea ice

Sea ice variables extracted from the passive microwave sea ice concentration data confirmed that, on average, the stations sampled in the Chukchi Sea had an earlier date of sea ice retreat, a later date of sea ice return, more days with no sea ice, less days covered by sea ice and less average sea ice concentration from May to October than the ones in the Beaufort Sea (Table 3.2, Figure 3.A). The "Date of sea ice retreat" had a much larger range across all stations in the Chukchi Sea (57 days) in comparison to the Beaufort Sea stations (13 days) (Table 3.2, Figure 3.A). On average, sea ice retreated in a south to north trajectory in the Chukchi Sea (Figures 3.2A and 3.5A), while in the Beaufort Sea the sea ice retreat typically followed an east to west trajectory (Figures 3.3A and 3.5A). The "Date of sea ice return" also had a much larger range across stations in the Chukchi Sea (32 days) in comparison to the Beaufort Sea (18 days) (Table 3.2, Figure 3.A). The edge of the sea ice advanced approximately perpendicular to the coast in the Chukchi Sea (Figures 3.2B and 3.5B), while in the Beaufort Sea the ice edge advanced parallel to the coastline (Figures 3.3B and 3.5B).

The range of summer days with no sea ice was similar between the Chukchi and the Beaufort Seas (Table 3.2, Figure 3.A). In the Chukchi Sea, most southern stations had the most number of sea ice free days during the summer season, with the exception of one southern nearshore station that had comparatively much less ice free days (Figure 3.2C). In the Beaufort Sea, the number of ice-free days increased from nearshore to offshore (Figure 3.3C). There was a large difference in the range of days covered with sea ice across all stations of the Chukchi and the Beaufort Seas (Table 3.2, Figure 3.A). In the Chukchi Sea, nearshore stations had the least number of winter days covered by sea ice (Figure 3.2D); while in the Beaufort Sea, stations on the western side of the shelf had the least number of days covered by sea ice (Figure 3.3D). Both regions had similar ranges for the number of days with MIZ and highest mean values nearshore (Table 3.2, Figures 3.2E & 3.3E). The average seasonal sea ice concentration (from May to October) across all stations had a similar high-end value in the Chukchi and the Beaufort Seas, while the low-end value was much lower in the Chukchi Sea in comparison to the Beaufort Sea (Table 3.2, Figure 3.A). In the Chukchi Sea, northern stations had an average higher sea ice concentration from May to October (Figure 3.2F); while in the Beaufort Sea, the higher average sea ice concentrations were observed in the eastern near shore and western shelf area (Figure 3.3F).

To explore the inter-annual variability of sea ice in each region, an animation of the sea ice concentration for each day of the years encompassed in the analysis was projected over the entire study area ("Sea ice animation" provided as supplemental material online, Figure 3.B). In the Chukchi Sea, the greatest inter-annual variability was in the location of the onset of sea ice formation and retreat. In 2005, 2008 and 2010 sea ice retreat occurred off the northern coast at the same time, or even before, sea ice was retreating through Bering Strait. In contrast, in 2006 and 2009 sea ice retreat advanced from Bering Strait northward throughout the shelf and in 2007 sea ice retreat started from Bering Strait opening a narrow corridor that reached all the way to Barrow Canyon before breakup occurred on the rest of the shelf (Figure 3.5A). Similarly, sea ice formation in the Chukchi Sea varied between some years, advancing from northeast to southwest, while in other years, forming off the north coast and advancing towards the northwest before the pack ice advanced from the north and reached the shelf (Figure 3.5B). In the Alaskan Beaufort Sea, a progressively earlier onset of ice retreat from 2005 to 2010 and a prevalent direction of retreat from east to west were observed (Figure 3.5A). In terms of sea ice return for the Beaufort Sea study area, the variability among years was restricted to the latitude at which sea ice advancing from shore northwards met with pack ice advancing south (Figure 3.5B). Also from these observations, Figures 3.3A, 3.3B and Figure 3.A, it is clear that sea ice retreat and return over the Beaufort shelf occurred very rapidly, resulting in very little variation in "Date of sea ice return" and "Date of sea ice retreat" between years.

3.4.2 Sea ice-benthos linkages

Sea ice variables had some predictive value for biomass and number of taxa per station (Figure 3.4). The variable "Days with MIZ" was a significant predictor of epifaunal and infaunal biomass and number of taxa, with opposite relationships with the response variables in the Chukchi (Figures 3.4A-C) and Beaufort Seas (Figures 3.4D-E). Regression analysis showed a weak linear relationship between "Days with MIZ" and total benthic biomass, with <18% explained variability in both regions (Table 3.3). "Days with MIZ" was also a significant predictor of number of taxa for Chukchi Sea infauna and Beaufort Sea epifauna, explaining 12% and 27% of the variability, respectively (Table 3.3, Figures 3.4D & 3.4H). The variable "Date of sea ice return" was negatively correlated with infaunal total biomass and number of taxa in the Chukchi Sea (Figures 3.4F & 3.4G). This variable explained 11% of the variability in number of infaunal taxa and less than 1% of the variability of total biomass in the Chukchi Sea (Table 3.3). In contrast, the "Date of sea ice return" was positively correlated with epifaunal total biomass and number of taxa in the Beaufort Sea, with a highly significant relationship (Figures 3.4H & 3.4I). This variable explained 31% of the total epifaunal biomass and had a moderate correlation to the number of epifaunal taxa, explaining 60% of the variability in the Beaufort Sea (Table 3.3). The variable "Average seasonal sea ice concentration" was marginally a significant predictor of the number of epifaunal taxa in the Beaufort Sea, explaining less than 1% of the variability in number of taxa (Table 3.3, Figure 3.4J). The variables "Days with no sea ice" and "Days covered by sea ice" were not significant predictors of benthic total biomass or number of taxa in either region.

The epifaunal community in the Chukchi Sea had 11 feeding guilds, and the infauna had 16 guilds; while the Beaufort Sea epifauna had 15 guilds (Figure 3.B). The hypothesis, "sea ice is a better predictor of benthic commuity structure, when organisms are classified by feeding guilds as opposed to communities classified by taxa", was essentially not supported. Only for the Chukchi Sea epifauna was the correlation value marginally higher than for taxonomic classification, and the variable "Days covered by sea ice" was the only variable selected as a driver of commuity structure (the correlation value was 0.4 at 0.1% significance). When performing the same analysis with the community classified by taxa, three variables were selected as drivers of commuity structure at a correlation value of 0.38 (0.1% significance) (Table 3.4). Of the three variables selected, "Days covered by sea ice" and "Date of sea ice return" added the most to the correlation value, while the addition of "Days with MIZ" was a negligible increase of 0.005 in the correlation value. For the Chukchi Sea infauna, the variables "Days with MIZ", "Days covered by sea ice" and "Date of sea ice return" were selected (in order of importance) as drivers of community feeding guilds with a correlation value of 0.37 (0.1% significance). This correlation value is essentially the same value that resulted from the community classified by taxa, where the variables "Days covered by sea ice" and "Date of sea ice return" were selected as community drivers (Table 3.4). For the Beaufort Sea, the variables "Date of sea ice return" and "Date of sea ice retreat" were selected (in order of importance) as drivers of the community feeding guilds, with a correlation value of 0.23 (0.3% significance). Although this correlation value was significantly smaller than for the community taxa (0.53, 0.1% significance), the same sea ice variables were selected as drivers for both types of community classification (Table 3.4).

The final hypothesis "the addition of sea ice variables to the commonly used variables will result in more explanatory power of benthic commuity structure", was fully supported by the results of the BioEnv analyses for communities of both regions. The highest correlations of environmental drivers with benthic communities were obtained by including permanent, seasonally variable and sea ice variables into the analysis (Table 3.5). In comparison to seasonal variables, sea ice variables correlated better to epibenthic communities in Beaufort and Chukchi Seas; however, this was not the case for infaunal communities in the Chukchi Sea (Tables 3.3 and 4). In the analyses with all the environmental variables available, one sea ice variable was selected as a driver of benthic commuity structure along with the traditionally used variables in both regions (Table 3.5). For epifaunal communities in both regions, the weakest correlation values were obtained when using seasonal variables alone; these were 0.3 for Chukchi Sea and 0.35 for Beaufort Sea (both at a 0.1% significance).

3.5 Discussion

3.5.1 Univariate linear correlations

As one of the most prominent features of the Arctic Sea shelves, sea ice drives many oceanographic and biological processes, such as water column stratification, formation of dense winter water, and ice edge algal blooms. From our analysis, several of the sea ice variables examined were significantly correlated with benthic biomass and number of taxa per station. "Days with MIZ", "Date of sea ice return" and "Average seasonal sea ice concentration" were individually weak to moderate predictors of total benthic biomass or number of taxa in both regions. Thus far, past studies in the Chukchi and Beaufort shelves have not directly included these sea ice variables in the search for drivers of benthic community standing stock. Furthermore, these earlier studies reported few or no single environmental variable as a significant predictor of total biomass or number of taxa (Blanchard et al., 2013; Bluhm et al., 2009; Ravelo, unpublished data; Roy et al., 2014). This suggests that although sea ice variables showed weak linear relationships in this current study, these variables should still be considered when attempting to understand the environmental features driving benthic communities.

Out of the five sea ice variables analyzed for each region, "Days with MIZ" was the only significant predictor, using linear regressions, of benthic biomass and number of taxa per station (except epifauna in the Chukchi Sea) in both regions. The MIZ has the potential for increased phytoplankton production due to the stratification of nutrient rich waters associated with the onset of sea ice melt (Cooper et al., 2002; Sakshaug, 2004). Long persistence of the ice edge over an area may extend the time the underlying benthos receives MIZ production. However, in the Chukchi Sea the relationship between the "Days with MIZ", total station biomass and number of taxa was positive, while the relationship in the Beaufort Sea was negative. This difference between regions indicates that this variable is encompassing different processes that may promote or hamper benthic biomass and number of taxa in each region. Overall, the majority of stations had similarly low number of "Days with MIZ" with higher values concentrated nearshore. This pattern reflects the ice that remains longer along the Arctic shores in the form of landfast (or formerly landfast) ice (Mahoney et al., 2014). In the Beaufort Sea, in the vicinity of the 20 m isobath, pressure ridges in the ice reveal the forces driving the pack ice against the landfast ice by the counterclockwise motion of the Beaufort Gyre (Mahoney et al., 2007). These pressure ridges can become grounded and plow through the sediments, acting as a barrier for water flow from the nearshore to the rest of the shelf

(Carmack et al., 2015; Reimnitz and Kempema, 1984). Therefore, benthic communities in the nearshore environment are subject to large seasonal changes in salinity (from riverine input), along with physical disturbance from increased sedimentation and ice grounding, which negatively affect the total biomass and limits the number of taxa that are able to live in such environments (Barnes, 1999; Carmack et al., 2015; Conlan and Kvitek, 2005; Kasper and Weingartner, 2015; Ravelo et al., 2015). The nearshore epibenthic community is less diverse, and has lower standing stock than the rest of the shelf (Ravelo et al., 2015). The results of this analysis reflect well the direct impact of sea ice on the nearshore Alaskan Beaufort Sea.

Landfast ice in the Chukchi Sea is less extensive offshore than in the Beaufort Sea, leaving the nearshore stations sampled in the Chukchi Sea outside of the typical spatial extent of landfast ice (Mahoney, 2012; Mahoney et al., 2014). Therefore, any potential grounded ice would not directly affect the nearshore stations of the Chukchi Sea study region in the same way as the nearshore stations of the Beaufort Sea. While no direct causation confirms the enhanced biomass in areas of persistent sea ice or former fast ice, the influence of the Alaska Coastal Current (ACC) in the nearshore area of the Chukchi Sea may help explain this positive correlation. The ACC is characterized as swift, fresh and nutrient-depleted in comparison to other offshore water masses transiting the Chukchi Sea (Coachman et al., 1975; Weingartner et al., 2005). Prevailing northeasterly winds have the potentioal to reverse the northward circulation along the Alaska coast (Weingartner et al., 2013; Winsor and Chapman, 2004). Therefore, prevalence of sea ice on the coast of the Chukchi Sea may explain by the persistence of landfast ice after breakup occurs on the shelf. In addition, the subsequent entrainment of the former landfast ice in the coastal current may also increase the number of days with ice in the nearshore region. The prevailing winds may keep this ice from exiting the shelf, moving it up and down the coast and lingering longer over the nearshore stations. Previous research characterized benthic communities in the nearshore Chukchi Sea as strongly driven by the influence of the ACC, with mixed results as to whether or not this water mass enhances benthic biomass or abundance (Blanchard and Feder, 2014; Feder et al., 2007; Grebmeier et al., 1988; Ravelo et al., 2014). Along the nearshore areas of the NE Chukchi Sea, areas of high biomass of benthic prey for sea ducks were explained by local environmental forces, such as nearshore counter currents that create depositional zones, hydrographic fronts and upwelling (Lovvorn et al., 2015). The nearshore stations in this analysis had communities (infauna and epifauna) dominated by the sand dollar *Echinarachnius parma*, that in comparison with communities offshore (dominated by other organisms), yield much larger biomass (measured in wet weight) (Feder et al., 1994; Ravelo et al., 2014). The details of the link between the ACC (or other environmental drivers) and the nearshore community dominated by *E. parma* will be discussed with the results of the multivariate community analysis.

Excluding the nearshore stations, the variable "Days with MIZ" in the Chukchi shelf range was 1-14 days, which is most likely a very short period of time to have a significant influence on benthic biomass. Stations with slightly above average "Days with MIZ" wrapped around the south of the Hanna Shoal area, which is an important passageway for Bering Sea water coming through the Central Chanel (Weingartner et al., 2005). Summer sea ice encountered in this area may be transient flows remnant from break up, and in the same way benthic biomass in this area may be benefiting from lateral advection of allochthonous organic matter from the south (Grebmeier et al., 2015; Søreide et al., 2013). Moreover, recent research has highlighted the potential importance of phytoplankton under the ice, at distances exceeding 100 km from the ice edge, potentially reducing the importance of a MIZ directly above benthic hotspots (Arrigo et al., 2014; Lowry et al., 2014).

Of the four stations sampled directly on Hanna Shoal in the Chukchi Sea (45, 46, 108 and 109; Figure 3.1), only station 109 had above average "Days with MIZ". Past research has characterized the Hanna Shoal area as an important summer feeding ground for Pacific Walrus, who rely on lingering sea ice as resting platforms in the summer months (Grebmeier et al., 2006b, 2015; Jay et al., 2012; Wood et al., 2015). Over the past decade the reduction of sea ice over Hanna Shoal has forced changes in foraging behavior of Pacific Walrus, forcing large numbers to commute from the Hanna Shoal's feeding grounds to the northern Chukchi Sea coast to rest (Jay et al., 2012). It is likely that the reduced number of days with MIZ over Hanna Shoal in our data set is due to the inability of passive microwave sensors to discriminate open water from sea ice at concentrations below 15% (Comiso and Nishio, 2008). This limitation in the detectability of low sea ice concentrations with passive microwave sensors along with the course resolution (25 km^2 grid size), should be noted as an important limiting factor when relating changes in sea ice with ecosystem characteristics and processes at a local scale (1-10 km^2). Despite the variable "Days with MIZ" not accounting for the possible persistence of smaller ice flows over Hanna Shoal, the stations over Hanna Shoal in the five-year period of this analysis had a slower sea ice retreat than neighboring stations, which is consistent with the pattern described for this area (Frey et al., 2015; Martin and Drucker, 1997; Wood et al., 2015).

The variable "Date of sea ice return" was only marginally a significant predictor of total infaunal biomass and number of taxa in the Chukchi Sea; therefore the significance of those results may be disregarded. In contrast, the "Date of sea ice return" was a moderate predictor of epifaunal biomass and number of taxa in the Beaufort Sea. The epifauna in the Beaufort Sea have a strong depth gradient, showing an increase in biomass and number of taxa from shore towards the shelf break (Ravelo et al., 2015). The larger biomass near the shelf break in the Beaufort Sea and later date of sea ice return may be driven by the same environmental forces that are also associated with bathymetry. Therefore, there is also little evidence of a causal relationship between increased biomass and later sea ice return in the Alaskan Beaufort Sea (See discussion below on community analysis).

3.5.2 Multivariate community correlations

In the Chukchi Sea, the variables "Days covered by sea ice" and "Date of sea ice return" were significant drivers of benthic community composition for both epifauna and infauna. Even though the pattern of high and low station biomass and number of taxa differ between the epifauna and infauna for the Chukchi Sea shelf, this result shows the importance of winter sea ice cover and sea ice return as integrators of relevant environmental changes for benthic commuity structure as a whole. The area over the shelf with the least number of "Days covered by sea ice", between Pt. Hope and Pt. Barrow, corresponds to an area of recurring winter polynyas (Figure 3.2D) (Cavalieri and Martin, 1994; Stringer and Groves, 1991). In some areas in the Arctic, polynyas have been considered local hotspots for benthic biomass, by promoting high phytoplankton production that is tightly coupled with benthic biomass (Graeve et al., 1997; Piepenburg, 2005; Roy et al., 2014). In addition, wind driven polynyas are an important source of dense water formation of the Chukchi Sea, creating vertical mixing that can reach the benthos in shallow waters (Smith et al., 1990; Winsor and Chapman, 2002). Smaller sediment particles (silts and clay) may become entrained in shallow areas under polynyas, leaving behind coarser sediments (i.e., sand) (Eicken et al., 2005). The benthic communities found within this region are highly dominated by the sand dollar *Echinarachnius parma* (Ambrose et al., 2001; Feder et al., 1994; Ravelo et al., 2014). *Echinarachnius parma* is a suspension feeder that shows preference for intermediate sandy sediments and avoids finer silt and clay sediments (Harold and Telford, 1982; Telford et al., 1983). Past studies have linked the presence of *E. parma* with the ACC and specifically with the areas with sandy sediments along the Alaskan Chukchi coast (Feder et al., 1994; Grebmeier et al., 1989; Ravelo et al., 2014). The combination of coarser sediment grain size due to the action of the swift ACC and coastal polynyas, along with the potential enhanced primary production in the early spring and re-suspension of particles in the winter months, may provide the optimal environment for *E. parma* to thrive.

The onset of freeze-up on Arctic shelves determines, along with the end of any late season or fall water column productivity, important oceanographic changes, such as dense water formation (through brine rejection in the formation of sea ice) and destabilization of the water column. In the present analysis, the variable "Date of sea ice return" was a driver for epifaunal and infaunal community biomass by both feeding guilds and taxonomic composition in both regions (Table 3.4). As an inflow shelf, water masses entering the Chukchi Sea have a significant effect on the shelf ecosystem by transporting warmer water, nutrients and pelagic organisms into the region (Carmack and Wassmann, 2006; Woodgate et al., 2005). In areas with warmer water, such as the Central Channel and ACC water masses in the Chukchi Sea, fall freeze-up may take longer because more time is required for the ocean to lose heat (Mahoney, 2012; Stroeve et al., 2012; Woodgate et al., 2010). A distinct epibenthic assemblage in the Chukchi Sea, dominated by crustaceans and with higher diversity indices, has been linked to the influence of this Central Channel water (Ravelo et al., 2014). Through the present analysis we can infer that, along with the potential enhanced nutrient load, the relatively higher temperature of the Central Channel water mass that is influencing benthic commuity structure in the Chukchi Sea is reflected in the later date of sea ice return.

In contrast, benthic assemblages in the Alaskan Beaufort Sea follow depth and longitudinal gradients (Carey and Ruff, 1977; Frost and Lowry, 1983; Ravelo et al., 2015). Partial sea ice cover over the shelfbreak along with favorable easterly winds may promote upwelling events in this region (Schulze and Pickart, 2012). An increase in upwelling intensity and frequency in the past decades has been driven mainly by changes in large-scale atmospheric circulation patterns (Pickart et al., 2013). Upwelling of nutrient rich water in the spring, in addition to fall upwelling aided by the delayed pack-ice advance over the shelf, may explain the relatively higher benthic biomass and number of taxa on the shelf break (Ravelo et al., 2015). The sea ice regime in the Beaufort Sea is tightly linked with the clockwise rotating motion of the Beaufort Gyre driven by the prevailing easterly winds (Reimnitz et al., 1994). The slightly later sea ice return on the outer shelf of the Alaskan Beaufort Sea shelf is more likely a consequence of the later formation of pack ice off-shelf in recent years, and not related to upwelling of warm water (Markus et al., 2009; Schulze and Pickart, 2012). Therefore, even though sea ice formation and benthic assemblages in the Beaufort Sea correlate well, different processes are producing the similarity in these patterns.

In the Beaufort Sea, the ice edge retreated consistently and rapidly from east to west over the study area from 2007-2011 (Figure 3.5A). The intrusion of warm and fresh water from the Mackenzie River contributes significantly to the melting of sea ice over the in the Beaufort Sea shelf, and can delay the onset of freezing in the fall (Carmack et al., 2015). The process of freshwater induced break up can be enhanced by the prior fragmentation of ice flows by strong wind driven forces on the Beaufort Gyre in the early summer (Greskowiak, 2014). Recent research has linked an increase in strong easterly wind events over past decades with increased intrusion of Mackenzie shelf waters further into the Alaskan Beaufort Sea shelf and promoting an earlier sea ice retreat (Macdonald et al., 1999; Pickart et al., 2013). Alaskan Beaufort Sea epibenthic communities vary following a longitudinal gradient, showing two significantly different communities in the east and western most areas of the shelf (Ravelo et al., 2015). The dominance of the brittle star species *Ophiocten sericeum* in the eastern Alaskan Beaufort shelf is one example of the influence of the Mackenzie River in the east. *Ophiocten sericeum* is found in small numbers in other areas of the Pacific Arctic, but often dominates in areas highly influenced by riverine input, such as in the Laptev and Kara Seas (Fetzer and Deubel, 2006; Piepenburg and Schmid, 1997). The declining influence of Pacific originated waters over the Alaska Beaufort Sea shelf is also evidenced by the absence of the dominant Chukchi Sea brittle star, *Ophiura sarsii* east of 148°W (Ravelo et al., 2015). In this case, the sea ice melt over the Alaskan Beaufort shelf and the pattern in species distribution can both be tied to larger processes influencing the water mass distribution, as well as the direction and intensity of Mackenzie River inflow in the region.

A community strongly represented by suspension feeders, which depend on vertical export for food, could indicate an area of strong benthic–pelagic coupling, as opposed to a community dominated by scavengers or predators. In the Beaufort Sea region epibenthic suspension feeders accounted for nearly 40% of the total biomass, while in the Chukchi Sea this feeding guild represented only 10% of the total biomass. In the Beaufort Sea, the same environmental variables that were strong drivers of community taxa were weak drivers of the community feeding guilds. Therefore, the sea ice variables defined in this analysis show little relation with the export of food to the benthos. In the Chukchi Sea, the sea ice variables had equal or slightly better correlation with epibenthic feeding guilds than community taxa for both benthic groups (infauna and epifauna). The classification of community organisms by feeding guilds is accompanied by a reduction in the number of "community components". In our analysis, benthic organisms had a much finer taxonomic resolution in the Beaufort Sea (genus and species) than those in the Chukchi Sea (family and genus) (Figure 3.B). The large reduction in "community components" when reclassifying the community by feeding guilds in the Beaufort Sea may be the cause for the reduction in the correlation value of sea ice drivers with community feeding guilds. In the Chukchi Sea, sea ice variables were already modest predictors of commuity structure, therefore reducing the number of "community components" may have not affected the correlation in the same way as in the Beaufort Sea. The different level of classification in each region, while not the main culprit, may have aided to the different outcomes these analyses produced in the Chukchi and Beaufort Seas.

The present analysis builds on two previous studies seeking to understand the driving forces, seasonally variable and permanent, influencing benthic commuity structure in the Alaskan Chukchi and Beaufort Seas. From those studies we learned that epibenthic community structure was strongly driven by gradients in longitude and depth (Ravelo et al., 2014; 2015). Infaunal organisms were strongly driven by sediment grain size, in addition to depth and position (Grebmeier et al., 1989). Variables such as depth, latitude and longitude are often used as proxies for environmental variables that have a direct influence on benthic organisms (McArthur et al., 2010). In many cases, these proxies have higher correlation values than biologically relevant variables, such as bottom water temperature, and indicators of food supply and quality (Post et al., 2006). However, if these surrogates do not have a clear relation with the local environmental patterns (i.e., changes in water mass, upwelling zones and polynyas) with clear biological meaning, the pursuit for understanding patterns of benthic communities and potential effects of climate change remains unresolved (Bluhm et al., 2009; Roy et al., 2014). For the two previous studies using these epibenthic data, the indirect determinants of commuity structure could be linked to the spatial distribution of important water masses and seasonal oceanographic features in each region (Ravelo et al., 2014; 2015). For the present study we ran the analysis of environmental drivers separately for seasonally variable and relatively permanent variables for each region. We confirmed that *in situ* measurements of water masses and local food availability alone were very weakly correlated with benthic community data (Table 3.5). The cause of these weak correlation values may be related to the nature of the NE Chukchi and Alaska Beaufort Seas, where bottom water characteristics are constantly subject to short-term changes in the direction and location of water masses, as well as upwelling events, especially in the open water season. In other regions with more homogeneous water mass influence, such as the northern Bering Sea and southern Chukchi Sea, "point in time" measurements may reflect better the seasonal conditions these organisms experience. However, the wide range of bottom water characteristics organisms experience throughout the year in Arctic shelf systems must be significant and remains difficult to encompass with a single value.

The advantage of using sea ice as a proxy for biologically relevant environmental drivers is that seasonal changes in sea ice can be directly linked with water mass dynamics (dense water formation, vertical mixing, particle resuspension, stratification, light attenuation and seafloor scouring, etc.) that are relevant to benthic organisms (Barnes et al., 1984; Eicken et al., 2005; Frey et al., 2011; Winsor and Chapman, 2002; Woodgate et al., 2005). Furthermore, sea ice, unlike depth and position, responds to environmental changes over time. Many of the effects of climate change in the Arctic are reflected in the changes in sea ice characteristics and its seasonality. Even though the the loss of summer sea ice extent or overall sea ice thickness (other than in the nearshore areas) may not directly affect benthic organisms, changes in water temperature, direction and intensity of wind-driven currents, increases in upwelling and riverine influence, changes in nutrient regimes, etc., do directly affect benthos, and sea ice may provide a quantitative way of assessing those effects.

3.6 Summary

From the five years of sea ice data included in this analysis, important inter-annual variability in the location of the formation and retreat of sea ice was observed in the Chukchi Sea; while the Beaufort Sea shelf showed a temporal trend of progressively earlier sea ice retreat from east to west. The large spatial and temporal variability of sea ice formation and retreat in the Chukchi Seas shown in our analysis concurs with the established knowledge of the complex interactions between the prevailing winds, water circulation and input of warm water that affect sea ice dynamics in these regions (Frey et al., 2015; Reimnitz and Kempema, 1984; Smith et al., 1990; Stringer and Groves, 1991). Furthermore, many other regionally important factors that have not been included in this analysis may be playing much larger roles than the ones listed above. For example, in the Chukchi Sea system, open water production provides over 95% of the annual organic carbon; in addition phytodetritus advected northward adds to the latitudinal supply of carbon to the benthos, decoupling to some extent the impact of less water column production in the North Chukchi Sea (Arrigo and van Dijken, 2015; Grebmeier et al., 2015). As a consequence, sea ice variables in the Chukchi Sea had less predictive power than the Beaufort Sea shelf. The benthic organisms included in this study are long lived and many are relatively immobile (Bluhm et al., 1998; Carroll et al., 2009; Gage, 2003). Therefore, the organisms collected at each station were not a "snapshot" of the communities found at that time and under those environmental conditions, but rather a time-integrated representation of the favorable conditions that allowed for those organisms to persist in that location. Passive microwave derived sea ice variables provide a means of including quantitative values that represent integrated large-scale seasonal environmental conditions. This study illustrates how the inclusion of sea ice variables can enhance our understanding of the complex interplay of environmental forces that create the myriad of habitats that allow the patchy distribution, the hotspots for biomass and diversity of Alaska Arctic benthic communities.

Acknowledgements

The authors are very grateful to Alaska Space Grant for providing funding to AMR. This study was made possible in part by samples collected under two grants from the Bureau of Ocean Energy Management (BOEM) Cooperative Agreement M10AC 2004 "Beaufort Sea Marine Fish Monitoring in the Central Beaufort Sea" Department of the Interior, BOEM and Contract number M08PC20056 as part of the Chukchi Sea Offshore Monitoring in Drilling Area (COMIDA) Project and the BOEM Alaska Environmental Studies Program. We are grateful to D. Prenki, H. Crowly and K. Wedemeyer (BOEM) for their role in project planning. We are especially grateful for the planning, assistance and long hours at work from the chef scientists of these expeditions, Ken Dunton from the University of Texas, Lee Cooper from the University of Maryland and Brenda Norcross from UAF. The data collections would have not been possible without the efforts of the captains and crew of the Alpha Helix, Moana Wave and Norsmen II research vessels. This analysis benefited from environmental data collected by John Treffry and team from the Florida Institute of Technology, Lee Cooper, Brenda Norcross's Fisheries Oceanography Lab at UAF, Katrin Iken from UAF and Bodil Bluhm from the University of Tromsø. The authors would like to thank Bodil Bluhm, Peter Winsor from UAF and Christian Zimmerman from the US Geological Survey for their valuable comments on earlier versions of this manuscript. A special thanks to Marc Oggier for assistance with Figure 3.5 and sea ice animation.

References

Abookire, A.A., Rose, C.S., 2005. Modifications to a plumb staff beam trawl for sampling uneven, complex habitats. Fish Res 71, 247–254.

Ambrose, J.W.G., Clough, L., Tilney, P., Beer, L., 2001. Role of echinoderms in benthic remineralization in the Chukchi Sea. Mar Biol 139, 937–949.

Ambrose, J. W.G., Quillfeldt, C., Clough, L., Tilney, P., Tucker, T., 2005. The sub-ice algal community in the Chukchi sea: large- and small-scale patterns of abundance based on images from a remotely operated vehicle. Polar Biol 28, 784–795. doi:10.1007/s00300-005-0002-8

Ambrose, J.W.G., Renaud, P.E., 1995. Benthic response to water column productivity patterns: evidence for benthic-pelagic coupling in the Northeast Water Polynya. J Geophys Res 100, 4411–4421.

Arrigo, K.R., Perovich, D.K., Pickart, R.S., Brown, Z.W., van Dijken, G.L., Lowry, K.E., Mills, M.M., Palmer, M.A., Balch, W.M., Bates, N.R., Benitez-Nelson, C.R., Brownlee, E., Frey, K.E., Laney, S.R., Mathis, J., Matsuoka, A., Greg Mitchell, B., Moore, G.W.K., Reynolds, R.A., Sosik, H.M., Swift, J.H., 2014. Phytoplankton blooms beneath the sea ice in the Chukchi sea. Deep Sea Res Part II Top Stud Oceanogr 105, 1–16. doi:10.1016/j.dsr2.2014.03.018

Arrigo, K.R., van Dijken, G.L., 2015. Continued increases in Arctic Ocean primary production. Prog Oceangr 136, 60-70.

Arrigo, K.R., van Dijken, G.L., Pabi, S., 2008. Impact of a shrinking Arctic ice cover on marine primary production. Geophys Res Lett 35, L19603. doi:10.1029/2008GL035028

Barnes, D.K., 1999. The influence of ice on polar nearshore benthos. J Mar Biol Assoc UK 79, 401–407. doi:10.1017/S0025315498000514

Barnes, P.W., Rearic, D.M., Reimnitz, E., 1984. Ice gouging characteristics and processes, in: Barnes, P.W., Reimnitz, E. and Schell, D.M. (Ed.), The Alaskan Beaufort Sea: Ecosystems and Environments. Academic Press Inc., San Diego, pp. 185–212.

Blanchard, A.L., Feder, H.M., 2014. Interactions of habitat complexity and environmental characteristics with macrobenthic community structure at multiple spatial scales in the northeastern Chukchi Sea. Deep Sea Res Part II Top Stud Oceanogr 102, 132–143. doi:10.1016/j.dsr2.2013.09.022

Blanchard, A.L., Parris, C.L., Knowlton, A.L., Wade, N.R., 2013. Benthic ecology of the northeastern Chukchi Sea. Part I. Environmental characteristics and macrofaunal community structure, 2008–2010. Cont Shelf Res 67, 52–66. doi:10.1016/j.csr.2013.04.021

Bluhm, B.A., Gradinger, R., 2008. Regional variability in food availability for Arctic marine mammals. Ecol Appl 18, 77–96.

Bluhm, B.A., Iken, K., Mincks Hardy, S., Sirenko, B.I., Holladay, B.A., 2009. Community structure of epibenthic megafauna in the Chukchi Sea. Aquat Biol 7, 269–293. doi:10.3354/ab00198

Bluhm, B.A., Piepenburg, D., von Juterzenka, K., 1998. Distribution, standing stock, growth, mortality and production of *Strongylocentrotus pallidus* (Echinodermata: Echinoidea) in the northern Barents Sea. Polar Biol 20, 325–334.

Carey, J.A.G., Ruff, R.E., 1977. Ecological studies of the benthos in the western Beaufort Sea with special reference to bivalve molluscs, in: Dunbar, M.J. (Ed.), Polar Oceans. Arctic Institute of North America, Calgary, pp. 505–530.

Carmack, E.C., Macdonald, R.W., 2002. Oceanography of the Canadian Shelf of the Beaufort Sea: a setting for marine life. Arctic 55, 29–45.

Carmack, E.C., Wassmann, P., 2006. Food webs and physical–biological coupling on pan-Arctic shelves: Unifying concepts and comprehensive perspectives. Prog Oceanogr 71, 446–477. doi:10.1016/j.pocean.2006.10.004

Carmack, E.C., Winsor, P., Williams, W., 2015. The contiguous panarctic Riverine Coastal Domain: A unifying concept. Prog Oceanogr 139, 13-23. doi:10.1016/j.pocean.2015.07.014

Carroll, M.L., Ambrose, W.G., 2012. Benthic infaunal community variability on the northern Svalbard shelf. Polar Biol 35, 1259–1272. doi:10.1007/s00300-012-1171-x

Carroll, M.L., Johnson, B.J., Henkes, G.A., McMahon, K.W., Voronkov, A., Ambrose Jr, W.G., Denisenko, S.G., 2009. Bivalves as indicators of environmental variation and potential anthropogenic impacts in the southern Barents Sea. Mar Pollut Bull 59, 193–206.

Cavalieri, D.J., Martin, S., 1994. The contribution of Alaskan, Siberian, and Canadian coastal polynyas to the cold halocline layer of the Arctic Ocean. J Geophys Res 99, 18343-18362.

Cavalieri, D.J., Parkinson, C.L., Gloersen, P., Zwally., H., 1996. Sea Ice Concentrations from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data. Arctic, full record. doi:10.5067/8GQ8LZQVL0VL

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User manual/tutorial.

Clarke, K.R., Warwick, R.M., 2001. A further biodiversity index applicable to species lists: Variation in taxonomic distinctness. Mar Ecol Prog Ser 216, 265–278. doi:10.3354/meps216265

Coachman, L.K., Aagaard, K., Tripp, R.B., 1975. Bering Strait: the regional physical oceanography. Univ of Washington Pr, Seattle.

Comiso, J.C., Nishio, F., 2008. Trends in the sea ice cover using enhanced and compatible AMSR-E, SSM/I, and SMMR data. J Geophys Res Ocean 113, 1–22. doi:10.1029/2007JC004257

Comiso, J.C., Parkinson, C.L., Gersten, R., Stock, L., 2008. Accelerated decline in the Arctic sea ice cover. Geophys Res Lett 35, L01703. doi:10.1029/2007GL031972

Conlan, K. E., Kvitek, R. G., 2005. Recolonization of soft-sediment ice scours on an exposed Arctic coast. Mar Ecol Prog Ser 286, 21-42.

Cooper, L.W., Grebmeier, J.M., Larsen, I.L., Egorov, V.G., Theodorakis, C., Kelly, H.P., Lovvorn, J.R., 2002. Seasonal variation insedimentation of organic materials in the St. Lawrence Island polynya region, Bering Sea. Mar Ecol Prog Ser 226, 13–26.

Cooper, L.W., Sexson, M.G., Grebmeier, J.M., Gradinger, R., Mordy, C.W., Lovvorn, J.R., 2013. Linkages between sea-ice coverage, pelagic–benthic coupling, and the distribution of spectacled eiders: Observations in March 2008, 2009 and 2010, northern Bering Sea. Deep Sea Res Part II Top Stud Oceanogr 94, 31–43. doi:10.1016/j.dsr2.2013.03.009

Coyle, K.O., Bluhm, B., Konar, B., Blanchard, A., Highsmith, R.C., 2007. Amphipod prey of gray whales in the northern Bering Sea: Comparison of biomass and distribution between the 1980s and 2002-2003. Deep Sea Res Part II Top Stud Oceanogr 54, 2906–2918.

Dunton, K.H., Goodall, J.L., Schonberg, S. V, Grebmeier, J.M., Maidment, D.R., 2005. Multi-decadal synthesis of benthic–pelagic coupling in the western arctic: role of cross-shelf advective processes. Deep Sea Res Part II Top Stud Oceanogr 52, 3462–3477.

Eicken, H., Gradinger, R., Gaylord, A., Mahoney, A., Rigor, I., Melling, H., 2005. Sediment transport by sea ice in the Chukchi and Beaufort Seas: Increasing importance due to changing ice conditions? Deep Sea Res Part II Top Stud Oceanogr 52, 3281–3302. doi:10.1016/j.dsr2.2005.10.006

Feder, H.M., Jewett, S.C., Blanchard, A., 2005. Southeastern Chukchi Sea (Alaska) epibenthos. Polar Biol 28, 402–421. doi:10.1007/s00300-004-0683-4

Feder, H.M., Jewett, S.C., Blanchard, A.L., 2007. Southeastern Chukchi Sea (Alaska) macrobenthos. Polar Biol 30, 261–275. doi:10.1007/s00300-006-0180-z

Feder, H.M., Naidu, A.S., Jewett, S.C., Hameedi, J.M., Johnson, W.R., Whitledge, T.E., 1994. The northeastern Chukchi Sea: benthos-environmental interactions. Mar Ecol Prog Ser 111, 171–190.

Fetzer, I., Deubel., H., 2006. Effect of river run-off on the distribution of marine invertebrate larvae in the southern Kara Sea (Russian Arctic), J Mar Syst 60, 98-114

Frey, K.E., Moore, G.W.K., Cooper, L.W., Grebmeier, J.M., 2015. Progress in Oceanography Divergent patterns of recent sea ice cover across the Bering , Chukchi , and Beaufort seas of the Pacific Arctic Region. Prog Oceanogr 136, 32–49. doi:10.1016/j.pocean.2015.05.009

Frey, K.E., Perovich, D.K., Light, B., 2011. The spatial distribution of solar radiation under a melting Arctic sea ice cover. Geophys Res Lett 38, L22501. doi:10.1029/2011GL049421

Frost, K.J., Lowry, L.F., 1983. Demersal fishes and invertebrates trawled in the northeastern Chukchi and western Beaufort Seas 1976-1977, U.S. Department of Commerce NOAA Technical Report NMFS-SSRF-764.

Gage, J.D., 2003. Growth and production of *Ophiocten gracilis* (Ophiuroidea: Echinodermata) on the Scottish continental slope. Mar Biol 143, 85–97.

Gaymer, C.F., Himmelman, J.H., Johnson, L.E., 2001. Distribution and feeding ecology of the seastars Leptasterias polaris and Asterias vulgaris in the northern Gulf of St Lawrence, Canada. J Mar Biol Assoc UK 81, 827. doi:10.1017/S0025315401004660

Graeve, M., Kattner, G., Piepenburg, D., 1997. Lipids in Arctic benthos: does the fatty acid and alcohol composition reflect feeding and trophic interactions? Polar Biol 18, 53–61.

Grebmeier, J.M., 2012. Shifting Patterns of Life in the Pacific Arctic and Sub-Arctic Seas. Ann Rev Mar Sci 4, 63–78.

Grebmeier, J.M., Barry, J.P., 1991. The influence of oceanographic processes on pelagic-benthic coupling in polar regions: A benthic perspective. J Mar Syst 2, 495–518.

Grebmeier, J.M., Bluhm, B.A., Cooper, L.W., Danielson, S.L., Arrigo, K.R., Blanchard, A.L., Clarke, J.T., Day, R.H., Frey, K.E., Gradinger, R.R., Kędra, M., Konar, B., Kuletz, K.J., Lee, S.H., Lovvorn, J.R., Norcross, B.L., Okkonen, S.R., 2015. Ecosystem characteristics and processes facilitating persistent macrobenthic biomass hotspots and associated benthivory in the Pacific Arctic. Prog Oceanogr 136, 92–114. doi:10.1016/j.pocean.2015.05.006

Grebmeier, J.M., Cooper, L.W., Feder, H.M., Sirenko, B.I., 2006a. Ecosystem dynamics of the Pacific-influenced northern Bering and Chukchi seas in the Amerasian Arctic. Prog Oceanogr 71, 331–361.

Grebmeier, J.M., Feder, H.M., McRoy, C.P., 1989. Pelagic-benthic coupling on the shelf of the Northern Bering and Chukchi Seas. II. Benthic community structure. Mar Ecol Ser 51, 253–268.

Grebmeier, J.M., McRoy, C.P., Feder, H.M., 1988. Pelagic-benthic coupling on the shelf of the Northern Bering and Chukchi Seas. I. Food supply source and benthic biomass. Mar Ecol Ser 48, 57–67.

Grebmeier, J.M., Overland, J.E., Moore, S.E., Farley, E. V, Carmack, E.C., Cooper, L.W., Frey, K.E., Helle, J.H., McLaughlin, F.A., McNutt, S.L., 2006b. A major ecosystem shift in the northern Bering Sea. Science 311, 1461–1464.

Greskowiak, J., 2014. Tide-induced salt-fingering flow during submarine groundwater discharge. Geophys Res Lett 41, 6413–6419. doi:10.1002/2014GL061184

Gunderson, D.R., Ellis, I.E., 1986. Development of a plumb staff beam trawl for sampling demersal fauna. Fish Res 4, 35–41.

Harold, A., Telford, M., 1982. Substrate preference and distribution of the northern sand dollar, *Echinarachnius parma* (Lamarck). Rotterdam, pp. 243–249.

Hobson, K. a., Ambrose, W.G., Renaud, P.E., 1995. Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: insights from δ^{13}C and δ^{15}N analysis. Mar Ecol Prog Ser 128, 1–10. doi:10.3354/meps128001

Iken, K., Bluhm, B., Dunton, K., 2010. Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. Deep Sea Res Part II Top Stud Oceanogr 57, 71–85.

Jay, C. V, Fischbach, A.S., Kochnev, A.A., 2012. Walrus areas of use in the Chukchi Sea during sparse sea ice cover. Mar Ecol Prog Ser 468, 1–13.

Kasper, J.L., Weingartner, T.J., 2015. The spreading of a buoyant plume beneath a landfast ice cover. J Phys Oceanogr 45, 478–494. doi:10.1175/JPO-D-14-0101.1

Link, H., Chaillou, G., Forest, a., Piepenburg, D., Archambault, P., 2013. Multivariate benthic ecosystem functioning in the Arctic-benthic fluxes explained by environmental parameters in the southeastern Beaufort Sea. Biogeosciences 10, 5911–5929. doi:10.5194/bg-10-5911-2013

Lohrer, A.M., Cummings, V.J., Thrush, S.F., 2013. Altered sea ice thickness and permanence affects benthic ecosystem functioning in coastal Antarctica. Ecosystems 16, 224–236.

Lowry, K.E., van Dijken, G.L., Arrigo, K.R., 2014. Evidence of under-ice phytoplankton blooms in the Chukchi Sea from 1998 to 2012. Deep Sea Res Part II Top Stud Oceanogr 105, 105–117. doi:10.1016/j.dsr2.2014.03.013

Lovvorn, J.R., Rocha, A.R., Jewett, S.C., Dasher, D., Oppel, S., Powell, A.N., 2015. Limits to benthic feeding by eiders in a vital Arctic migration corridor due to localized prey and changing sea ice. Prog Oceanogr 136, 162-174.

Macdonald, R.W., Carmack, E.C., McLaughlin, F.A., Falkner, K.K., Swift, J.H., 1999. Connections among ice, runoff and atmospheric forcing in the Beaufort Gyre. Geophys Res Lett 26, 2223–2226. doi:10.1029/1999GL900508

Macdonald, T.A., Burd, B.J., Macdonald, V.I., van Roodselaar, A., 2010. Taxonomic and feeding guild classification for the marine benthic macroinvertebrates of the Strait of Georgia, British Columbia, Can Tech Rep Fish Aquat Sci 2874, iv-63.

Mahoney, A., Eicken, H., Shapiro, L., 2007. How fast is landfast sea ice? A study of the attachment and detachment of nearshore ice at Barrow, Alaska. Cold Reg Sci Technol 47, 233–255.

Mahoney, A.R., 2012. Sea ice conditions in the Chukchi and Beaufort Seas, U.S. Arctic Program Pew Environment Group.

Mahoney, A.R., Eicken, H., Gaylord, A.G., Gens, R., 2014. Landfast sea ice extent in the Chukchi and Beaufort Seas: The annual cycle and decadal variability. Cold Reg Sci Technol 103, 41–56. doi:10.1016/j.coldregions.2014.03.003

Markus, T., Stroeve, J.C., Miller, J., 2009. Recent changes in Arctic sea ice melt onset, freezeup, and melt season length. J Geophys Res 114, C12024. doi:10.1029/2009JC005436

Martin, S., Drucker, R., 1997. The effect of possible Taylor columns on the summer ice retreat in the Chukchi Sea. J Geophys Res 102, 10473. doi:10.1029/97JC00145

Matsuno, K., Yamaguchi, A., Hirawake, T., Imai, I., 2011. Year-to-year changes of the mesozooplankton community in the Chukchi Sea during summers of 1991, 1992 and 2007, 2008. Polar Biol 34, 1349–1360. doi:10.1007/s00300-011-0988-z

McArthur, M.A., Brooke, B.P., Przeslawski, R., Ryan, D.A., Lucieer, V.L., Nichol, S., McCallum, A.W., Mellin, C., Cresswell, I.D., Radke, L.C., 2010. On the use of abiotic surrogates to describe marine benthic biodiversity. Estuar Coast Shelf Sci 88, 21–32. doi:10.1016/j.ecss.2010.03.003

McMahon, K.W., Ambrose, W.G.J., Johnson, B.J., Sun, M-Y., Lopez, G.R., Clough, L.M., Carroll, M.L., 2006. Benthic community responses to ice algae and phytoplankton in Ny Alesund, Svalbard. Mar Ecol Prog Ser 310, 1–14.

Nikolopoulos, A., Pickart, R.S., Fratantoni, P.S., Shimada, K., Torres, D.J., Jones, E.P., 2009. The western Arctic boundary current at 152 W: Structure, variability, and transport. Deep Sea Res Part II Top Stud Oceanogr 56, 1164–1181.

Norton, D., Weller, G., 1984. The Beaufort Sea: background, history, and perspective, in: Barnes, P.W., Reimnitz, E. and Schell, D.M. (Eds.), The Alaskan Beaufort Sea: Ecosystems and Environments. Academic Press Inc., San Diego, pp.3-19.

Parkinson, C.L., Cavalieri, D.J., Gloersen, P., Zwally, H.J., Comiso, J.C., 1999. Arctic sea ice extends, areas, and trend, 1978-1996. J Geophys Res C Ocean 104, 20837–20856. doi:10.1029/1999JC900082

Parsons, T.R., 1984. A Manual of Chemical and Biological Methods for Seawater Analysis. Pergamon Press, New York.

Pickart, R.S., Schulze, L.M., Moore, G.W.K., Charette, M.A., Arrigo, K.R., van Dijken, G., Danielson, S.L., 2013. Long-term trends of upwelling and impacts on primary productivity in the Alaskan Beaufort Sea. Deep Sea Res Part I Oceanogr Res Pap 79, 106–121. doi:10.1016/j.dsr.2013.05.003

Piepenburg, D., 2005. Recent research on Arctic benthos: common notions need to be revised. Polar Biol 28, 733–755.

Piepenburg, D., Ambrose, W.G., Brandt, A., Renaud, P.E., Ahrens, M.J., Jensen, P., 1997. Benthic community patterns reflect water column processes in the Northeast Water polynya (Greenland). J Mar Syst 10, 467–482.

Piepenburg, D., Brandt, A., Juterzenka, K. Von, Schnack, K., Seiler, D., Witte, U., Spindler, M., 2000. Patterns and Determinants of the Distribution and Structure of Benthic Faunal Assemblages in the Northern North Atlantic, in: Schafer, P., Ritzau, W., Schluter, M., Thiede, J. (Eds.), The Northern North Atlantic:A Changing Environment. Springer, Berlin, pp. 179–198.

Piepenburg, D., Schmid, M.K., 1997. A photographic survey of the epibenthic megafauna of the Arctic Laptev Sea shelf: Distribution, abundance, and estimates of biomass and organic carbon demand. Mar Ecol Ser 147, 63–75.

Piepenburg, D., Schmid, M.K., 1996. Distribution, abundance, biomass, and mineralization potential of the epibenthic megafauna of the Northeast Greenland shelf. Mar Biol 125, 321–332.

Post, A.L., Wassenberg, T.J., Passlow, V., 2006. Physical surrogates for macrofaunal distributions and abundance in a tropical gulf. Mar Freshw Res 57, 469–483. doi:doi:10.1071/MF05182

Pritchard, R.S., 1984. Beaufort Sea ice motions, in: Barnes, P., Reimnitz, E., Schell, D.M. (Eds.), The Alaskan Beaufort Sea: Ecosystems and Environments. Academic Press Inc., San Diego, pp. 95–113.

Rand, K.M., Logerwell, E.A., 2011. The first demersal trawl survey of benthic fish and invertebrates in the Beaufort Sea since the late 1970s. Polar Biol 34, 475–488.

Ravelo, A.M., Konar, B., Bluhm, B.A., 2015. Spatial variability of epibenthic communities on the Alaska Beaufort Shelf. Polar Biol 38, 1783–1804. doi:10.1007/s00300-015-1741-9

Ravelo, A.M., Konar, B., Trefry, J.H., Grebmeier, J.M., 2014. Epibenthic community variability in the northeastern Chukchi Sea. Deep Sea Res Part II Top Stud Oceanogr 102, 119–131. doi:10.1016/j.dsr2.2013.07.017

Reimnitz, E., Dethleff, D., Nürnberg, D., 1994. Contrasts in Arctic shelf sea-ice regimes and some implications: Beaufort Sea versus Laptev Sea. Mar Geol 119, 215–225. doi:10.1016/0025-3227(94)90182-1

Reimnitz, E., Kempema, E.W., 1984. Pack ice interaction with Stamukhi Shoal, Beaufort Sea, Alaska, in: Barnes, P.W., Reimnitz, E., Schell, D.M. (Eds.), The Alaskan Beaufort Sea: Ecosystems and Environments. Academic Press, Inc, San Diego, pp. 159–181.

Renaud, P.E., Morata, N., Ambrose, W.G., Bowie, J.J., Chiuchiolo, A., 2007. Carbon cycling by seafloor communities on the eastern Beaufort Sea shelf. J Exp Mar Bio Ecol 349, 248–260. doi:10.1016/j.jembe.2007.05.021

Roy, V., Iken, K., Archambault, P., 2014. Environmental Drivers of the Canadian Arctic Megabenthic Communities. PLoS ONE 9, e100900. doi:10.1371/journal.pone.0100900

Sakshaug, E., 2004. Primary and secondary production in the Arctic seas, in: MacDonald, R.W., Stein, R. (Eds.), The Organic Carbon Cycle in the Arctic Ocean. Springer, Berlin, pp. 57–82.

Schonberg, S.V., Clarke, J.T., Dunton, K.H., 2014. Distribution, abundance, biomass and diversity of benthic infauna in the Northeast Chukchi Sea, Alaska: Relation to environmental variables and marine mammals. Deep Sea Res Part II Top Stud Oceanogr 102, 144-163. doi:10.1016/j.dsr2.2013.11.004

Schulze, L.M., Pickart, R.S., 2012. Seasonal variation of upwelling in the Alaskan Beaufort Sea: Impact of sea ice cover. J Geophys Res 117, C06022. doi:10.1029/2012JC007985

Smith, S.D., Muench, R.D., Pease, C.H., 1990. Polynyas and leads: An overview of physical processes and environment. J Geophys Res 95, 9461. doi:10.1029/JC095iC06p09461

Søreide, J.E., Carroll, M.L., Hop, H., Ambrose, W.G., Hegseth, E.N., Falk-Petersen, S., 2013. Sympagic-pelagic-benthic coupling in Arctic and Atlantic waters around Svalbard revealed by stable isotopic and fatty acid tracers. Mar Biol Res 9, 831–850. doi:10.1080/17451000.2013.775457

Stein, R., MacDonald, R.W., 2004. The organic carbon cycle in the Arctic Ocean. Springer, Berlin.

Stringer, W.J., Groves, J.E., 1991. Location and Areal Extent of Polynyas in the Bering and Chukchi Seas. Arctic 4, 164–171.

Stroeve, J.C., Serreze, M.C., Holland, M.M., Kay, J.E., Malanik, J., Barrett, A.P., 2012. The Arctic's rapidly shrinking sea ice cover: a research synthesis. Clim Change 110, 1005–1027. doi:10.1007/s10584-011-0101-1

Telford, M., Harold, A.S., Mooi, R., 1983. Feeding structures, behaviour, and microhabitat of *Echinocyamus pusillus* (Echinoidea: Clypeasteroida). Biol Bull 165, 745–757. doi:10.2307/1541476

Trefry, J.H., Trocine, R.P., Cooper, L.W., Dunton, K.H., 2014. Trace metals and organic carbon in sediments of the northeastern Chukchi Sea. Deep Sea Res Part II Top Stud Oceanogr 102, 18–31. doi:10.1016/j.dsr2.2013.07.018

Wassmann, P., Duarte, C.M., Agustí, S., Sejr, M.K., 2011. Footprints of climate change in the Arctic marine ecosystem. Glob Chang Biol 17, 1235–1249.

Weingartner, T., Aagaard, K., Woodgate, R., Danielson, S., Sasaki, Y., Cavalieri, D., 2005. Circulation on the north central Chukchi Sea shelf. Deep Sea Res Part II Top Stud Oceanogr 52, 3150–3174.

Weingartner, T., Dobbins, E., Danielson, S., Winsor, P., Potter, R., Statscewich, H., 2013. Hydrographic variability over the northeastern Chukchi Sea shelf in summer-fall 2008-2010. Cont Shelf Res 67, 5–22. doi:10.1016/j.csr.2013.03.012

Winsor, P., Chapman, D.C., 2004. Pathways of Pacific water across the Chukchi Sea: A numerical model study. J Geophys Res 109, C03002. doi:10.1029/2003JC001962

Winsor, P., Chapman, D.C., 2002. Distribution and interannual variability of dense water production from coastal polynyas on the Chukchi Shelf. J Geophys Res 107, 10.1029.

Wood, K.R., Bond, N.A., Danielson, S.L., Overland, J.E., Salo, S.A., Stabeno, P.J., Whitefield, J., 2015. A decade of environmental change in the Pacific Arctic region. Prog Oceanogr 136, 12–31. doi:10.1016/j.pocean.2015.05.005

Woodgate, R.A., Aagaard, K., Weingartner, T.J., 2005. A year in the physical oceanography of the Chukchi Sea: Moored measurements from autumn 1990-1991. Deep Sea Res Part II Top Stud Oceanogr 52, 3116–3149.

Woodgate, R.A., Weingartner, T., Lindsay, R., 2010. The 2007 Bering Strait oceanic heat flux and anomalous Arctic sea-ice retreat. Geophys Res Lett 37, L01602. doi:10.1029/2009GL041621

Table 3.1. Defining attributes of the six sea ice variables created for this analysis.

Variable	Definition
Date of sea ice return	The date sea ice concentration increased to >15%
Date of sea ice retreat	The date sea ice concentration decreased to <15%
Days with no sea ice	Number of days with 0% sea ice concentration (from the Date of sea ice retreat and until the Date of sea ice return)
Days covered by sea ice	Number of days with sea ice concentration >85%
Days with MIZ (marginal ice zone)	Number of days with sea ice +/- 15% (from the Date of sea ice retreat and until sea ice concentration became consistently zero)
Average seasonal sea ice concentration	The sea ice concentration from May to October

Table 3.2. Range, mean and standard deviation for each sea ice variable in the Chukchi and Beaufort Sea shelf regions. Standard deviation (sd)

Variable	Chukchi Sea		Beaufort Sea	
	Range	Mean (sd)	Range	Mean (sd)
Date of sea ice retreat	June 11 - Aug 7	July 9 (14 days)	July 6 -July 19	July 15 (4 days)
Date of sea ice return	Nov 4 - Dec 6	Nov 10 (45 days)	Oct 14 - Nov 1	Oct 25 (5 days)
Days with no sea ice	74 - 166	119 (21)	27 - 113	88 (28)
Days covered by sea ice	117 - 208	174 (22)	176 - 203	197 (6)
Days with MIZ	0 - 56	8 (9)	0 - 53	13 (17)
Average seasonal sea ice concentration	14% - 40%	27% (7)	38% - 44%	41% (1)

Table 3.3. Adjusted R^2 values for significant linear regressions between sea ice variables and Chukchi Sea epifauna and infauna, and Beaufort Sea epifauna.

Region	Response variable	Descriptor variable	Total Biomass	Number of Taxa
Chukchi Sea	Epifauna	Days with MIZ	0.17**	x
	Infauna	Days with MIZ	0.11*	0.12*
		Date of sea ice return	-0.06·	-0.11*
Beaufort Sea	Epifauna	Days with MIZ	-0.13**	-0.27***
		Date of sea ice return	0.31***	0.6***
		Average seasonal sea ice concentration	x	0.04·

·0.1 *0.05 **0.01 ***0.001

Table 3.4. Multivariate correlations between sea ice variables and benthic communities classified by taxa and feeding guilds

Region	Explanatory Variables	Class.	Corr. value	Sig. (%)	Number of variables selected	Selected Variables
Chukchi Sea	Epifauna	Taxa	0.38	0.1	3	Days covered by sea ice, Date of sea ice return, Days with MIZ
		Feeding guilds	0.4	0.1	2	Days covered by sea ice
	Infauna	Taxa	0.38	0.1	2	Days covered by sea ice, Date of sea ice return
		Feeding guilds	0.37	0.1	3	Days with MIZ, Days covered by sea ice, Date of sea ice return
Beaufort Sea	Epifauna	Taxa	0.53	0.1	2	Date of sea ice return, Date of sea ice retreat
		Feeding guilds	0.22	0.3	2	Date of sea ice return, Date of sea ice retreat

Table 3.5. BioEnv analyses for the Chukchi Sea and Beaufort Sea regions with different combination on variables included

Region	Response Variables	Explanatory Variables Included	Corr. value	Sig. (%)	Number of variables selected	Selected Variables
Chukchi Sea	Epifauna	Seasonal	0.3	0.1	2	TOC, B w salinity
		Permanent	0.37	0.1	2	Longitude, Depth
		All	0.53	0.1	4	Longitude, Sediment grain size 2 phi, Days covered by sea ice, TOC
	Infauna	Seasonal	0.41	0.1	3	TOC, B w salinity, C/N
		Permanent	0.43	0.1	3	Depth, Longitude, Latitude
		All	0.56	0.1	5	Depth, B w temperature, Sediment grain size 2 phi, TOC, Date of sea ice return
Beaufort Sea	Epifauna	Seasonal	0.35	0.1	5	Sed phaeopigments, B w temperature, Sed chla/phaeo, B w salinity, Sed organic matter
		Permanent	0.51	0.1	2	Depth, Longitude
		All	0.59	0.1	3	Date of sea ice return, Longitude, Depth

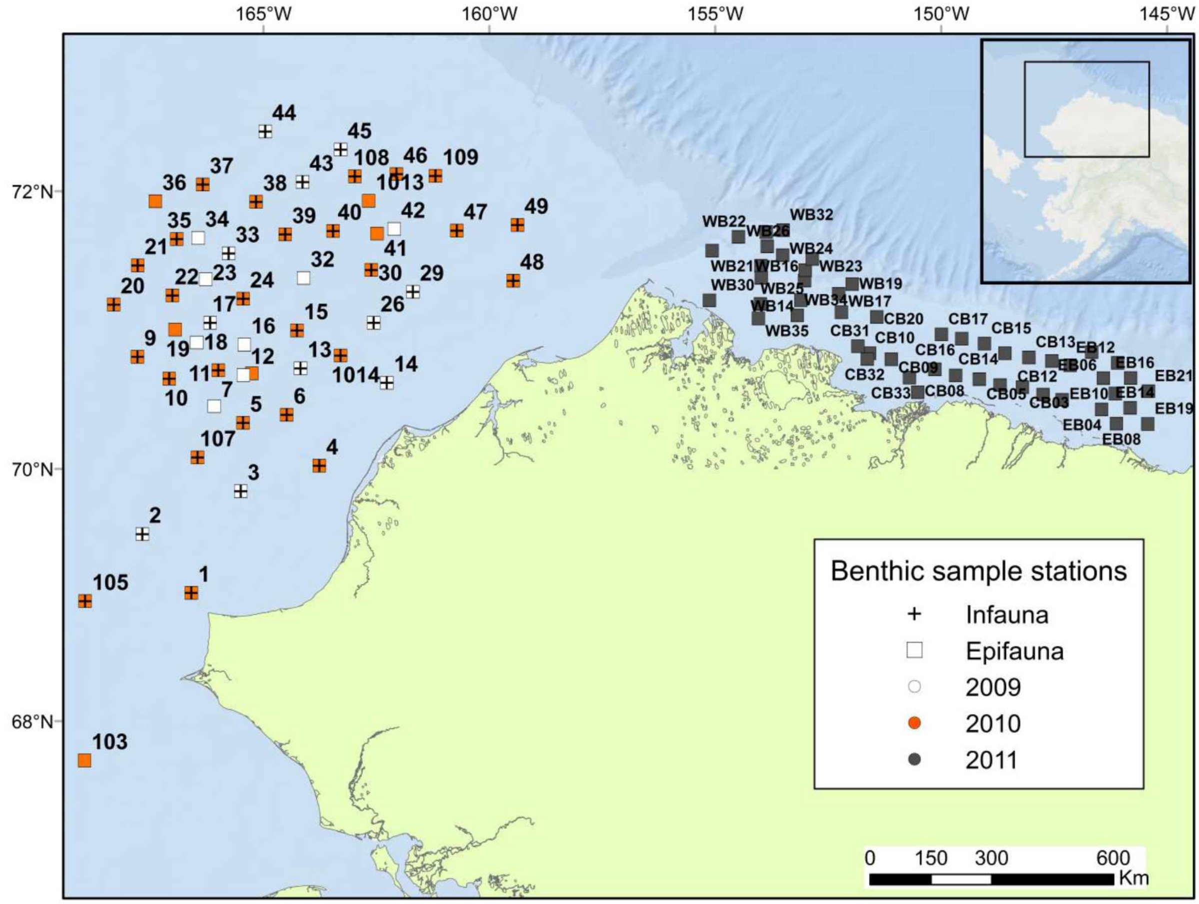

Figure 3.1. Benthic sample stations. In the Chukchi Sea study region, stations were sampled for epifauna and infauna in 2009 and 2010 and epifauna stations in the Beaufort Sea study region were sampled in 2011.

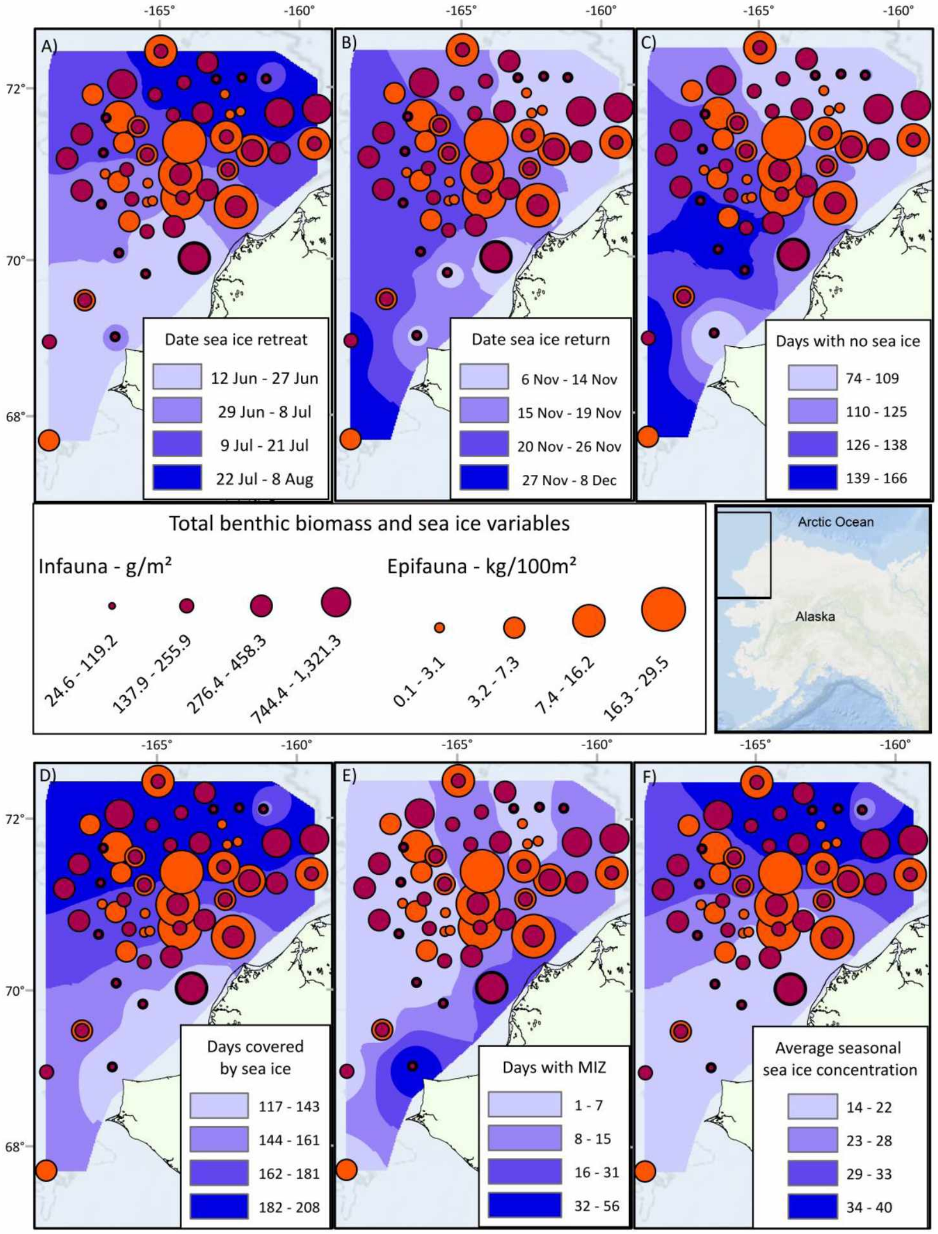

Figure 3.2. Sea ice variables, benthic biomass and number of taxa in the Chukchi Sea. Interpolation of mean values of each sea ice variable for the Chukchi Sea (2004-2009 and 2005-2010 depending on the year of biological sample collection), total station epifauna biomass (kg wet weight/100m2) and infaunal biomass (g wet weight/m2) for stations sampled in 2009 and 2010. A. Date of sea ice retreat. B. Date of sea ice return. C. Days with no sea ice. D. Days covered by sea ice. E. Days with MIZ (marginal sea ice zone, defined in methods). F. Average seasonal sea ice concentration. Sea ice interpolations determined by Inverse Distance Weighting with ArcMap. Values (biomass circle sizes and sea ice color gradient) represented by Jenks' Natural Breaks.

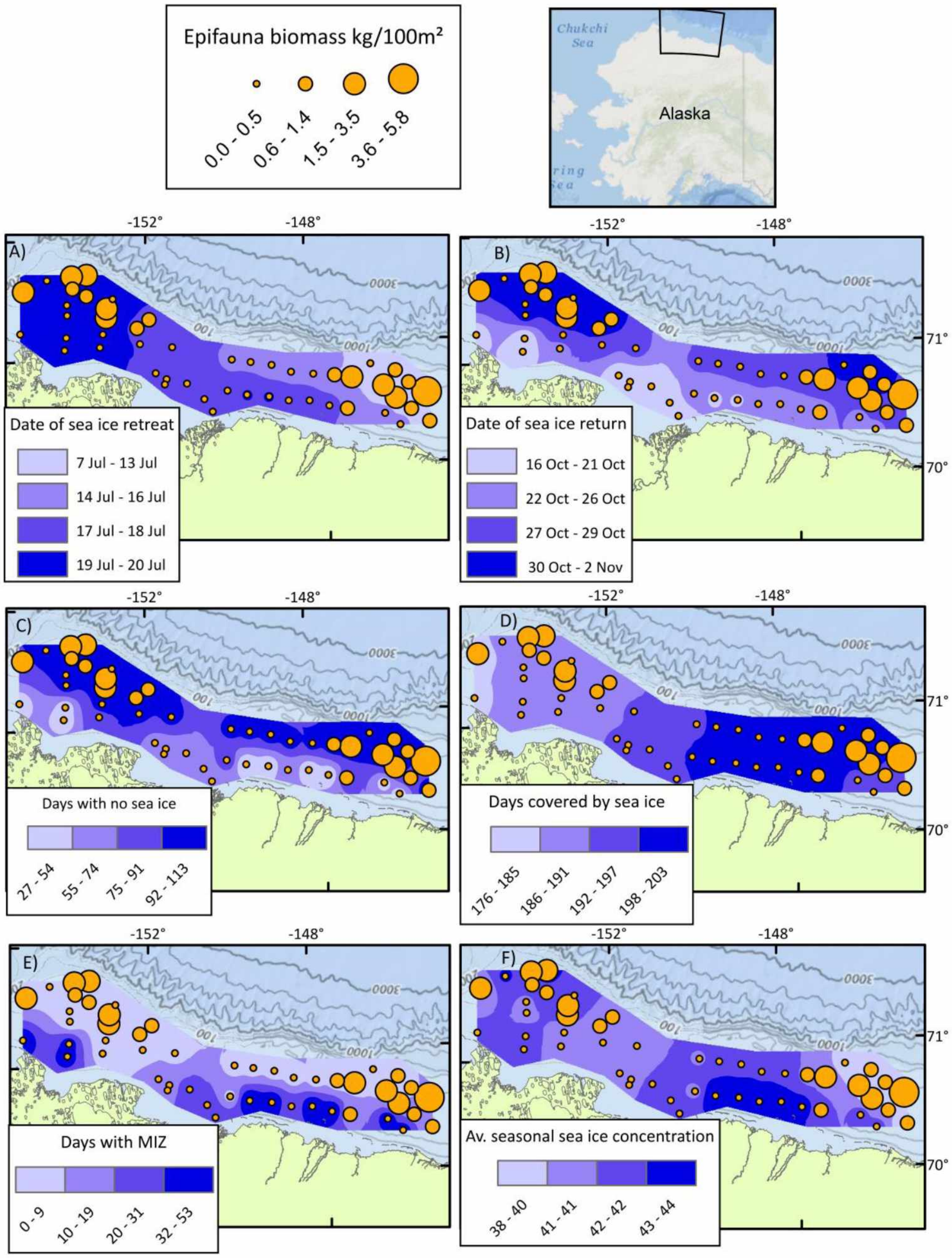

Figure 3.3. Sea ice variables, benthic biomass and number of taxa in the Beaufort Sea. Interpolation of mean values of each sea ice variable for the Beaufort Sea shelf (2006-2011) and total epibenthic station biomass (kg wet weight/100m²) sampled in 2011. A. Date of sea ice retreat. B. Date of sea ice return. C. Days with no sea ice. D. Days covered by sea ice. E. Days with MIZ (marginal sea ice zone). F. Average seasonal sea ice concentration. Average seasonal sea ice concentration. Sea ice interpolations determined by Inverse Distance Weighting with ArcMap. Values (biomass circle sizes and sea ice color gradient) represented by Jenks' Natural Breaks.

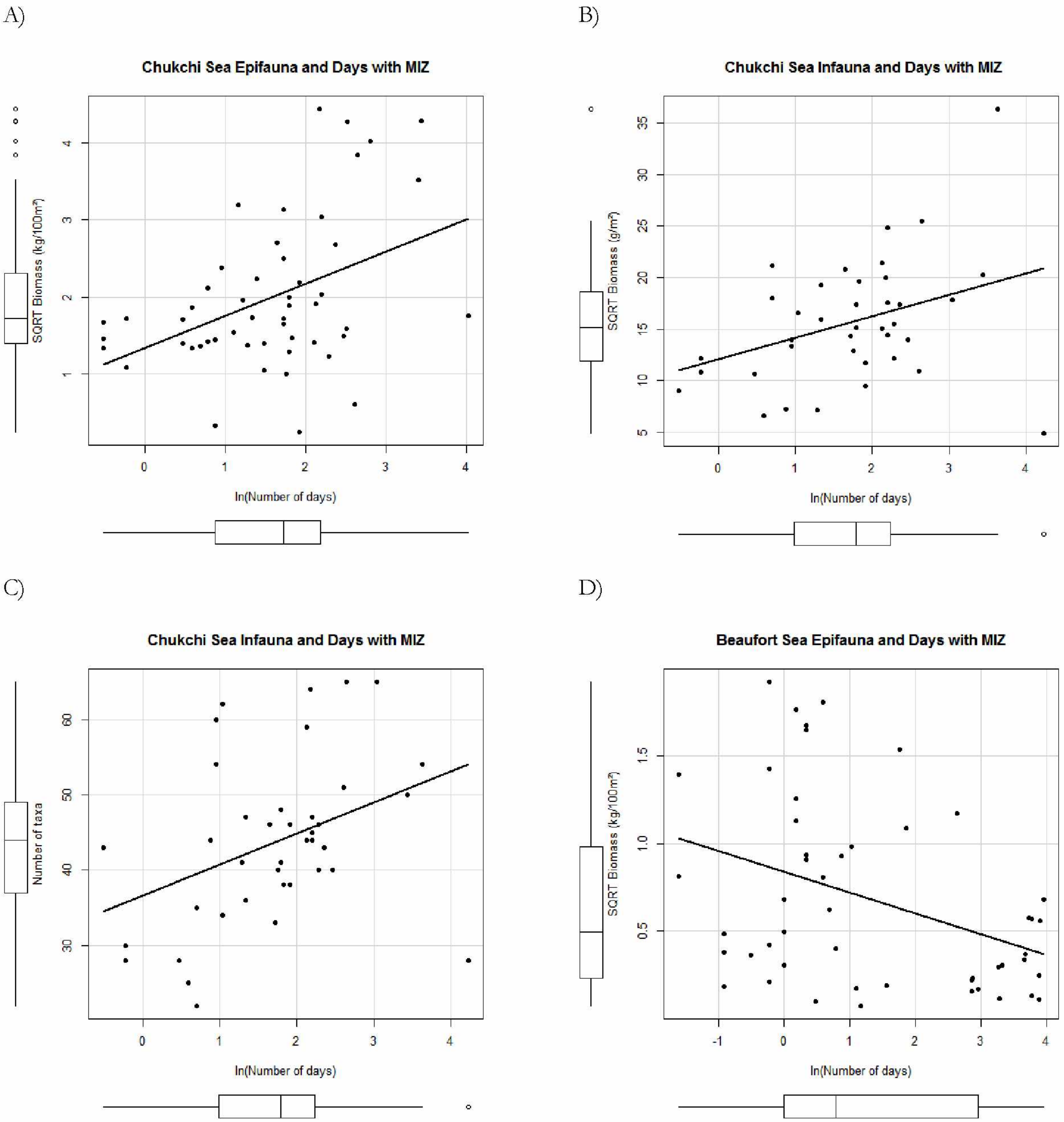

Figure 3.4. Statistically significant linear regressions between sea ice variables and benthos (stations biomass or number of taxa) in the Chukchi and Beaufort Seas. A. Chukchi Sea total epifaunal biomass (square-root transformed) regressed against Days with MIZ (marginal ice zone, ln transformed). B & C. Chukchi Sea total infaunal biomass (square-root transformed) regressed against Days with MIZ (marginal ice zone, ln transformed) and Date of sea ice return. D & E. Chukchi Sea total infaunal total taxa regressed against Days with MIZ (marginal ice zone, ln transformed) and Date of sea ice return. F & G. Beaufort Sea region epifaunal biomass (square-root transformed) regressed against the sea ice variables Date of sea ice return and Number of days with MIZ (marginal ice zone, ln transformed). H-J. Beaufort Sea region number of epifaunal taxa regressed against the sea ice variables Date of sea ice return, number of days with MIZ (marginal sea ice zone, ln transformed) and Average seasonal sea ice concentration (ln transformed).

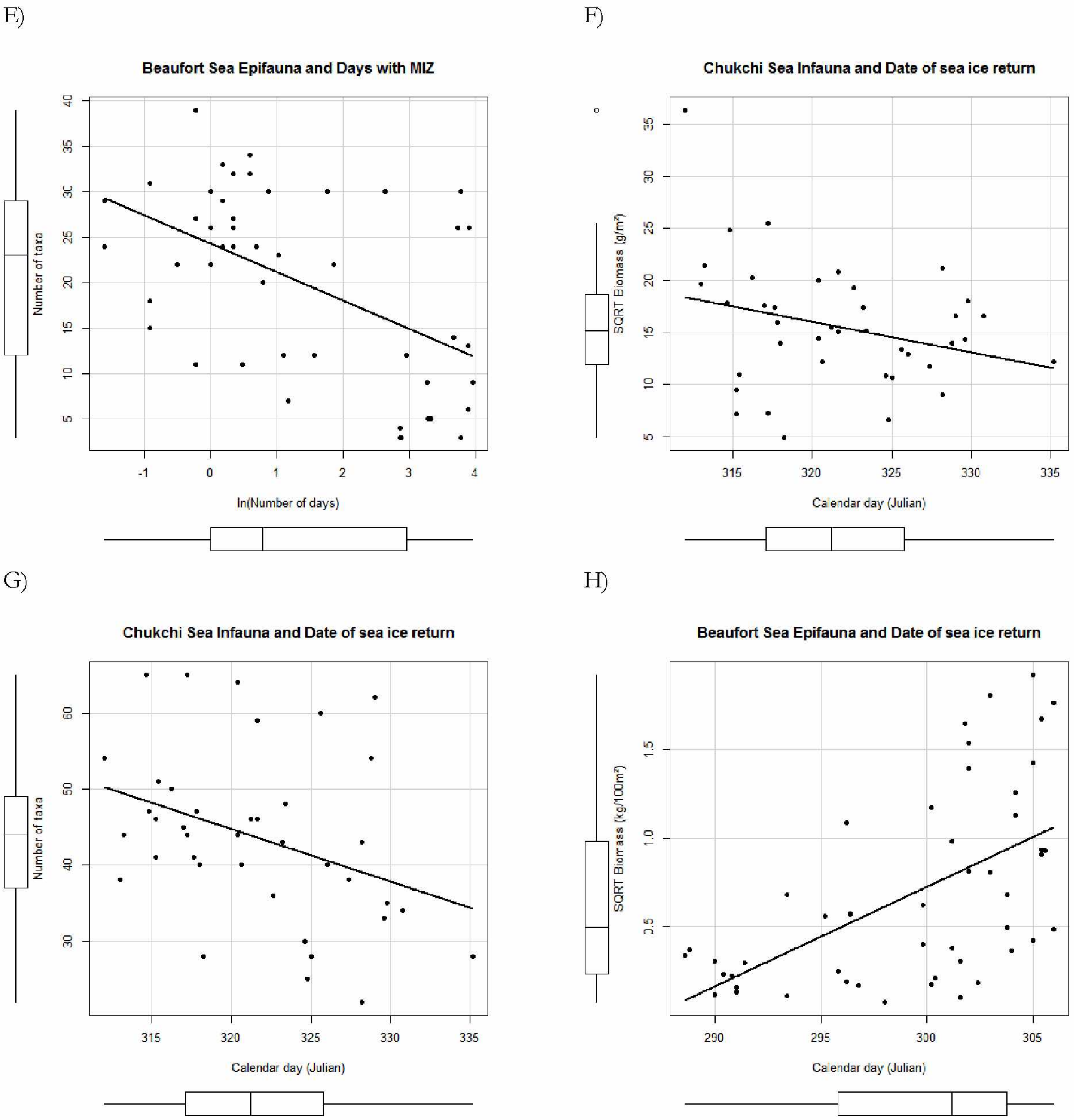

Figure 3.4. (cont.). Statistically significant linear regressions between sea ice variables and benthos (stations biomass or number of taxa) in the Chukchi and Beaufort Seas. A. Chukchi Sea total epifaunal biomass (square-root transformed) regressed against Days with MIZ (marginal ice zone, ln transformed). B & C. Chukchi Sea total infaunal biomass (square-root transformed) regressed against Days with MIZ (marginal ice zone, ln transformed) and Date of sea ice return. D & E. Chukchi Sea total infaunal total taxa regressed against Days with MIZ (marginal ice zone, ln transformed) and Date of sea ice return. F & G. Beaufort Sea region epifaunal biomass (square-root transformed) regressed against the sea ice variables Date of sea ice return and Number of days with MIZ (marginal ice zone, ln transformed). H-J. Beaufort Sea region number of epifaunal taxa regressed against the sea ice variables Date of sea ice return, number of days with MIZ (marginal sea ice zone, ln transformed) and Average seasonal sea ice concentration (ln transformed).

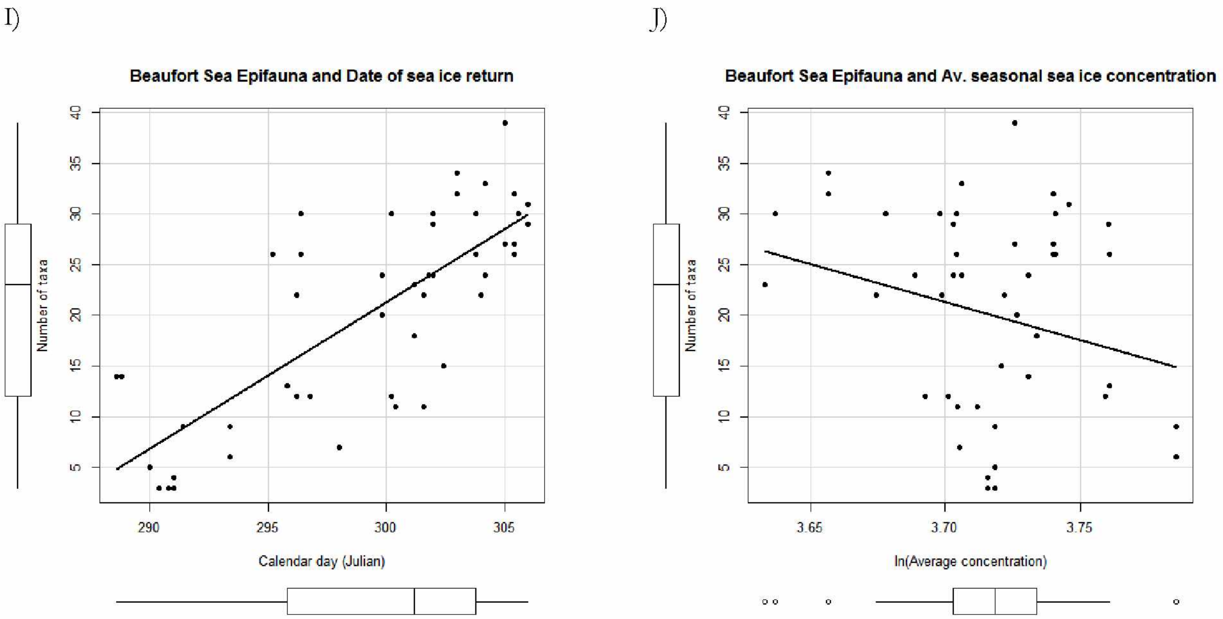

Figure 3.4. (cont.). Statistically significant linear regressions between sea ice variables and benthos (stations biomass or number of taxa) in the Chukchi and Beaufort Seas. A. Chukchi Sea total epifaunal biomass (square-root transformed) regressed against Days with MIZ (marginal ice zone, ln transformed). B & C. Chukchi Sea total infaunal biomass (square-root transformed) regressed against Days with MIZ (marginal ice zone, ln transformed) and Date of sea ice return. D & E. Chukchi Sea total infaunal total taxa regressed against Days with MIZ (marginal ice zone, ln transformed) and Date of sea ice return. F & G. Beaufort Sea region epifaunal biomass (square-root transformed) regressed against the sea ice variables Date of sea ice return and Number of days with MIZ (marginal ice zone, ln transformed). H-J. Beaufort Sea region number of epifaunal taxa regressed against the sea ice variables Date of sea ice return, number of days with MIZ (marginal sea ice zone, ln transformed) and Average seasonal sea ice concentration (ln transformed).

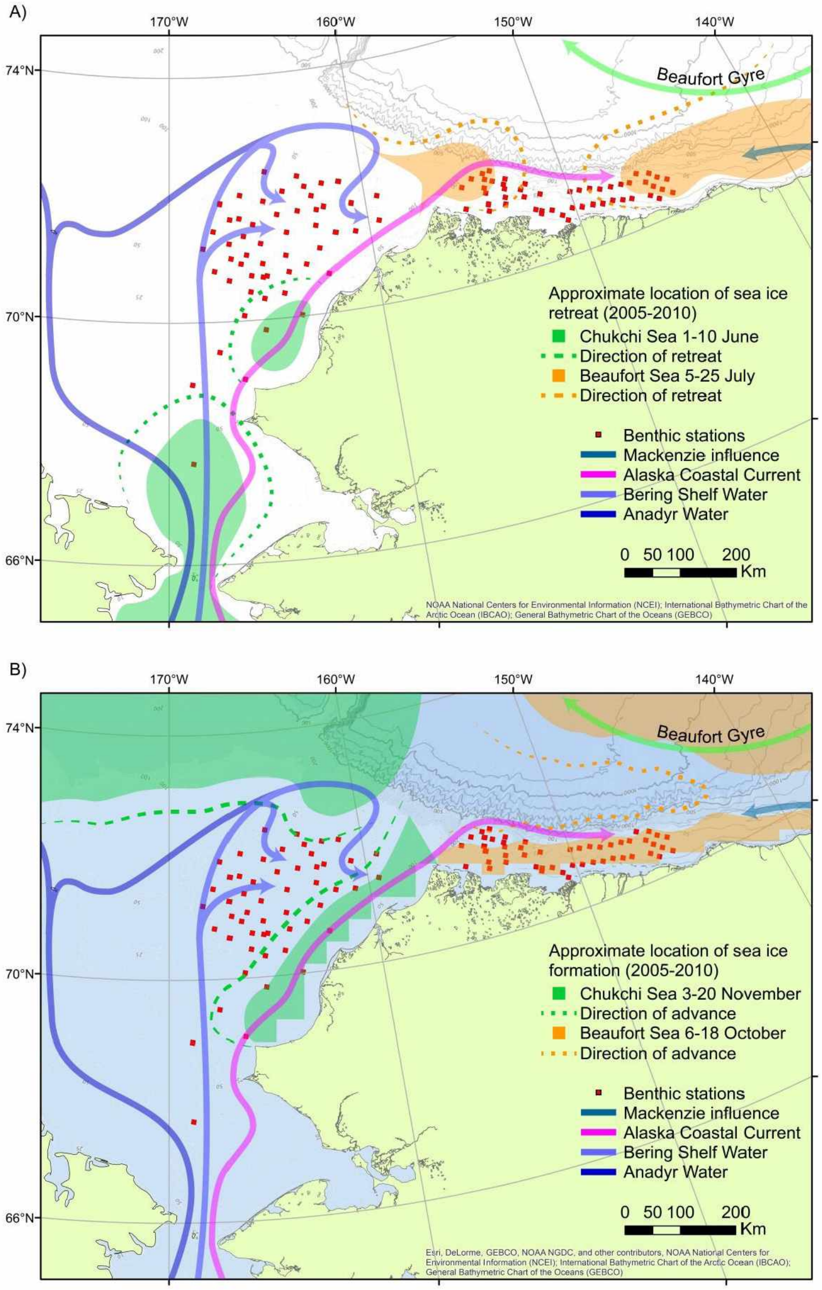

Figure 3.5. Approximate location of sea ice edge (shaded areas) and general direction of retreat (A) and formation (B) (dashed lines) for the years 2005 to 2010. The prevalent water mass trajectories and general direction are depicted by colored lines and arrows. A. The timeframe for observed edges for the Chukchi Sea was 1-10 of June and for the Beaufort Sea was 5-25 of July; the white in the background represents sea ice. B. The timeframe for observed edges for the Chukchi Sea was 3-20 of November and for the Beaufort Sea was 6-18 of October; the blue in the background represents open water. Figures designed by Marc Oggier

3.7 Appendix

Table 3.A. Feeding guild classification and number of taxa in each group for the Chukchi Sea epifauna and infauna, and the Beaufort Sea epifauna. "X" denotes no taxa in that category.

Feeding guilds			Chukchi Sea		Beaufort Sea
Food source	Feeding mode	Food type/size	Epifauna	Infauna	Epifauna
Epibenthic	Predator	macrofauna	X	X	1
		zooplankton	3	3	7
	Suspension/Filter		9	27	24
Surface	Chemosynthetic	Omnivorous	X	2	X
	Deposit		1	27	2
	Detritus		1	6	1
	Herbivorous	macrofauna	2	5	3
		microfauna	X	6	4
	Omnivorous	macrofauna	2	2	3
		microfauna	2	5	9
	Predator	macrofauna	23	6	55
		meiofauna	X	3	X
	Scavenger	macrofauna	X	1	1
	Suctorial parasite	macrofauna	1	X	1
	Suspension/Filter		X	12	3
Subsurface	Predator	macrofauna	2	5	2
		meiofauna	1	8	2
	Deposit		X	16	X

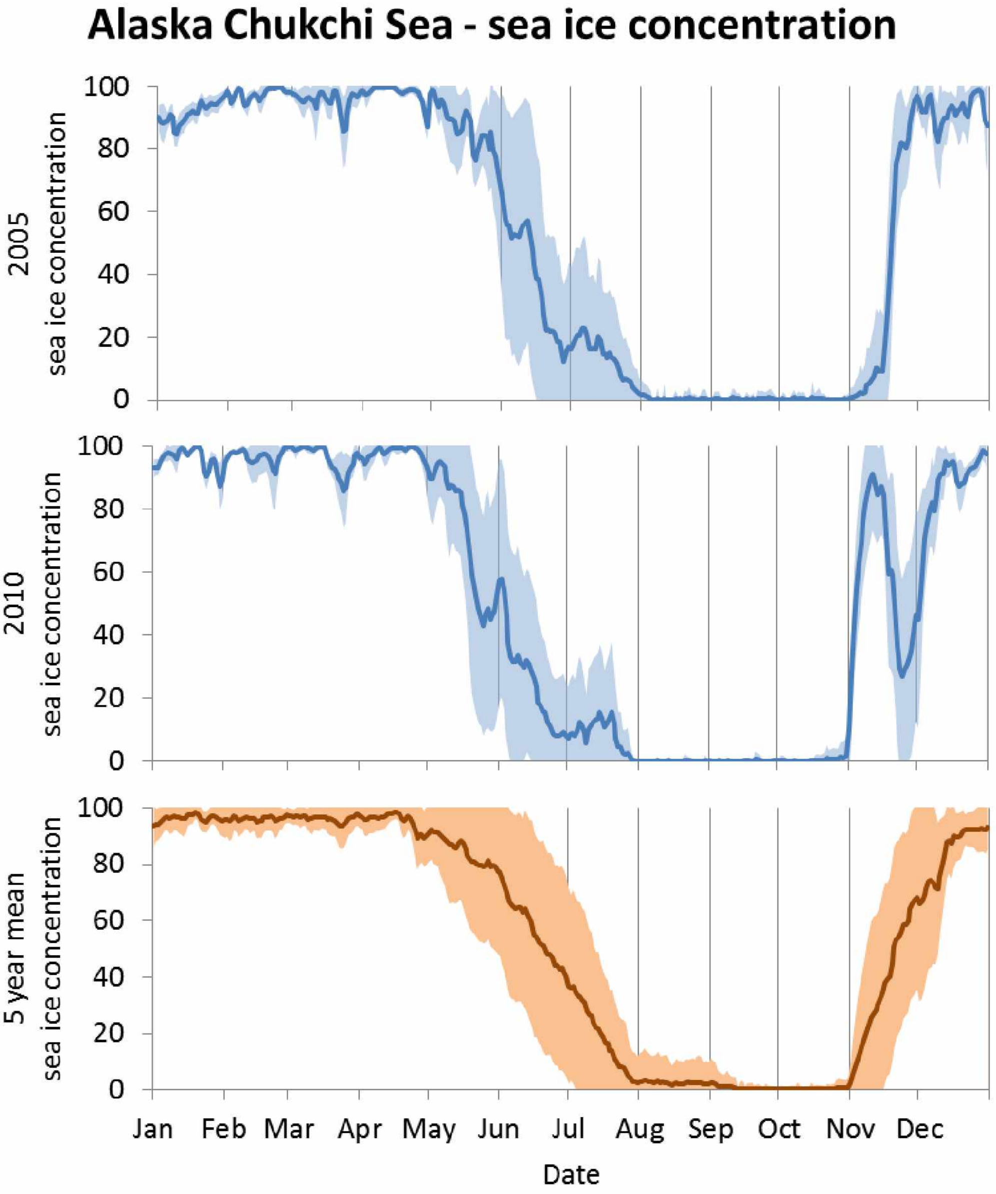

Figure 3.A-1. Regional daily average of sea ice concentration for the Chukchi Sea study region: average sea ice concentration and standard deviation for 2005, 2010 and the five-year average (2005 to 2009 and 2006 to 2010, depending on the year the station was sampled).

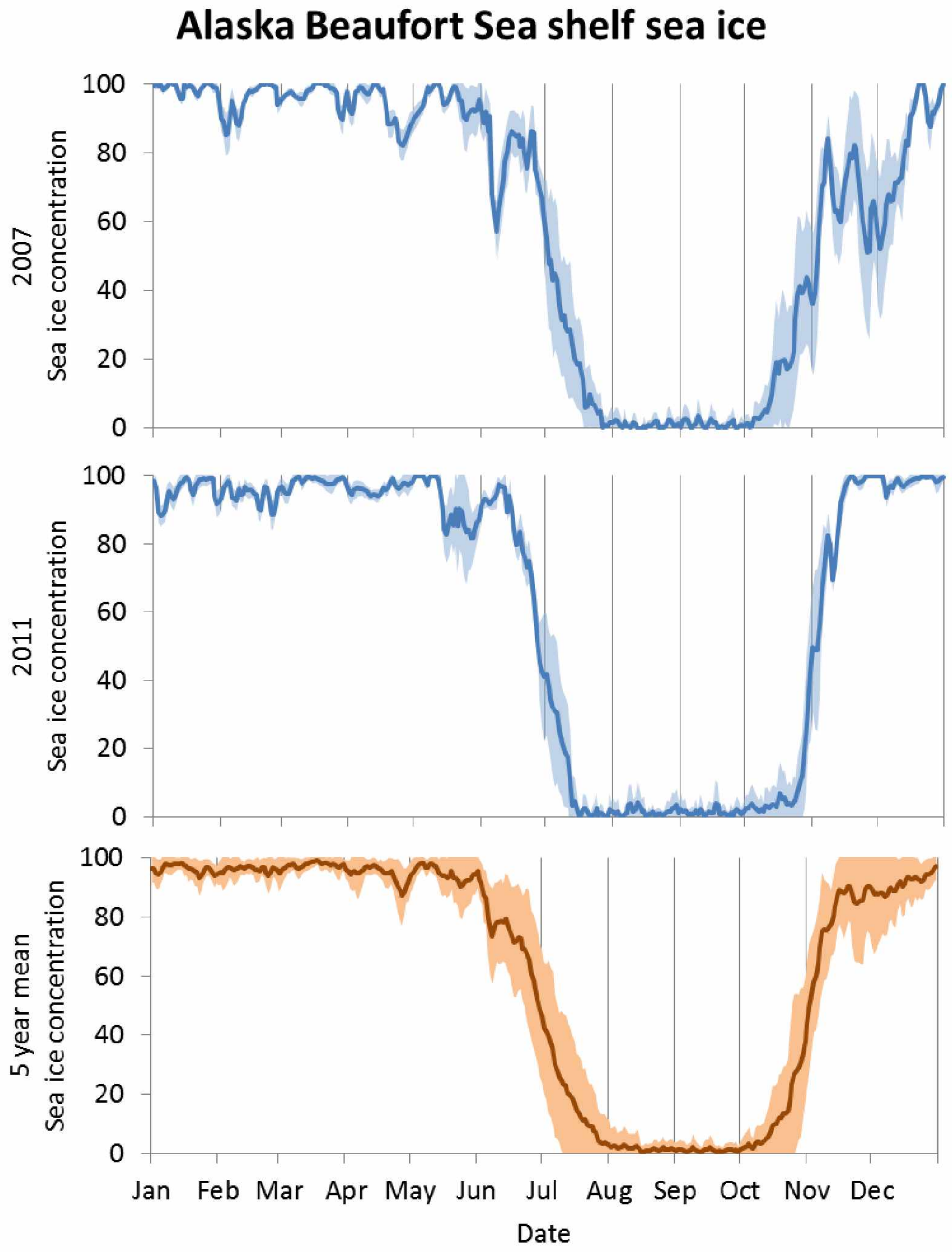

Figure 3.A-2. Regional daily average of sea ice concentration for the Beaufort Sea shelf study region: average sea ice concentration and standard deviation for 2007, 2011 and the five year average.

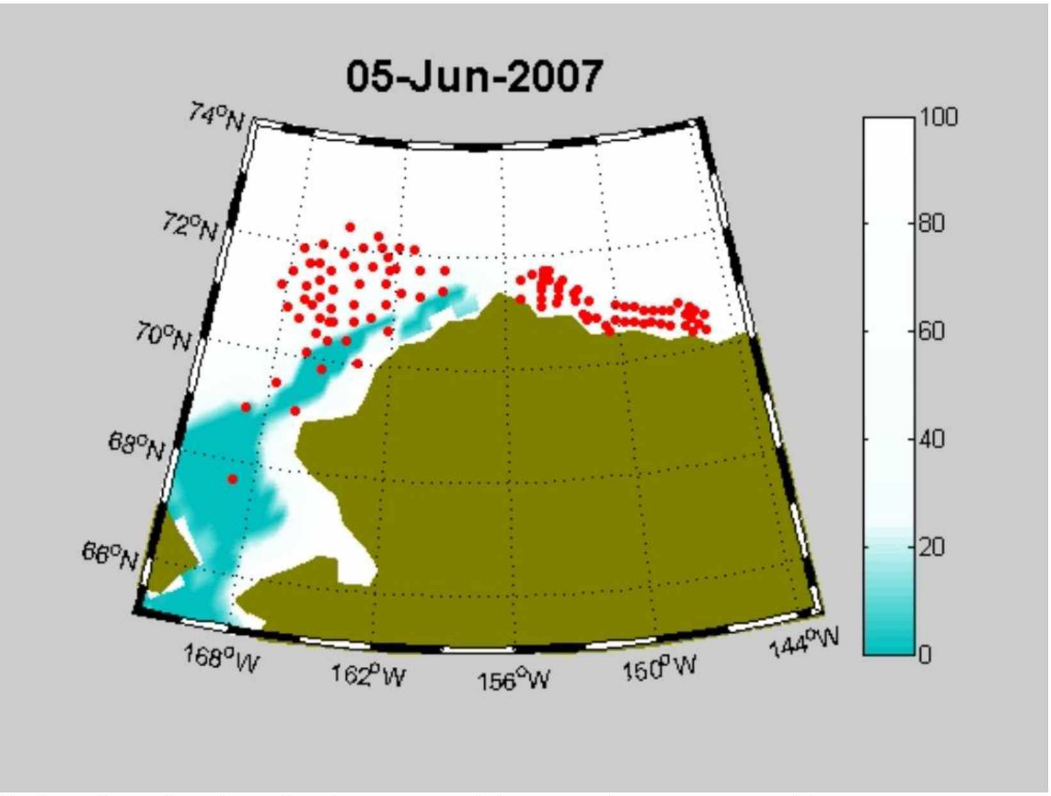

Figure 3.B. Snapshot of sea ice animation extracted from supplementary materials.

CHAPTER 4: Growth and production of the brittle stars *Ophiura sarsii* and *Ophiocten sericeum* (Echinodermata: Ophiuroidea) in the Alaskan Arctic[1]

Abstract

The slow growth and high longevity of polar marine species is largely determined by low temperatures and the extreme seasonality of food supply, which in turn define the energy turnover of the Arctic marine system. The general objective of this study was to determine the population growth pattern of the dominant shelf brittle star species *O. sarsii* and *O. sericeum* through age determination, individual production, and total turnover rates (P:B) in the Alaskan Arctic. In the summer of 2013, *O. sarsii* were collected in the northeastern Chukchi Sea (depth range 35 to 65 m), while *O. sericeum* were collected in the central Beaufort Sea (depth range 37 to 200 m). Growth curves for both species had similar shapes, showing initial fast growth, with an inflection period followed by a second phase of fast growth. Changes in the allocation of energy, aided by a possible change in diet, may be the mechanisms responsible for the observed age dependent growth rates. Asymptotic age was higher in *O. sarsii* than *O. sericeum*; however, both species had significantly higher maximum ages than temperate region congeners. Individual production was higher for *O. sarsii* than for *O. sericeum* by nearly an order of magnitude throughout the size spectra. Both species had equally low P:B ratios, similar to Antarctic species, but much lower ratios than tropical species. Such characteristics would suggest that the dense brittle star assemblages that characterize the Arctic shelf systems could have a recovery time from disturbance on the order of decades.

---

[1] Ravelo AM, Konar B, Bluhm B, Iken K (In prep) Growth and production of the brittle stars *Ophiura sarsii* and *Ophiocten sericeum* (Echinodermata: Ophiuroidea) in the Alaskan Arctic. Prepared for submission to Marine Biology

4.1 Introduction

Across the Arctic, brittle star assemblages can occur in high densities and account for a significant fraction of the total epibenthic biomass (Piepenburg 2000; Piepenburg 2005). Off the northeast Greenland coast, for example, brittle stars account for more than 95% of the epibenthic abundance (Piepenburg and Schmid 1996). The highly productive waters of many Arctic shelves promote areas of high brittle star abundance and biomass through tight benthic-pelagic coupling (Ambrose et al. 2001; Bluhm et al. 2009; Ravelo et al. 2014; Ravelo et al. 2015). Although brittle stars are important prey for crab and demersal fish, relatively low predator abundance and generally small fish size may be factors contributing to the high density of brittle stars in many Arctic regions (Tyler 1972; Aronson 1989; Packer et al. 1994; Rand and Logerwell 2010; Divine et al. 2015). The importance of these brittle star assemblages for carbon remineralization was recorded in the NE Chukchi Sea and central Beaufort Sea, where brittle stars were responsible for 25 to 41% of the total benthic respiration (Ambrose et al. 2001; Renaud et al. 2007).

On the Alaskan Arctic shelves, the two most abundant brittle star species are *Ophiura sarsii* and *Ophiocten sericeum* (Frost and Lowry 1983; Bluhm et al. 2009; Ravelo et al. 2014; Ravelo et al. 2015). Throughout the Alaskan Arctic, these two species only overlap in their distribution in the productive area of the western Beaufort Sea shelf and upper slope (Ravelo et al. 2014; Ravelo et al. 2015). The large bodied *O. sarsii*, with a maximum disc diameter of 40 mm, is a circumpolar species found as far south in the Pacific as 35° N (Piepenburg 2000). Throughout the Chukchi Sea shelf and western Beaufort Sea slope, *O. sarsii* outnumbers all other brittle star species, and locally all other epibenthic taxa, accounting for up to 71% of the average epibenthic abundance with 34 ind./m^2 per station (Ravelo et al. 2014). In the highly productive northeast Chukchi Sea, with an average biomass estimate for epibenthos of 62.7 g wet wt./m^2, brittle stars (mainly *O. sarsii*) accounted for 39% of that biomass (Ravelo et al. 2014). However, east of 148° W on the Beaufort Sea shelf, *O. sarsii* is not present and the dominant brittle star species is *Ophiocten sericeum* (Ravelo et al. 2015). The smaller-bodied *O. sericeum*, with a maximum disc diameter of 18 mm, is a circumpolar species found in various habitats north of 40° N and it is especially abundant on interior shelves, such as the central Beaufort shelf and Laptev Sea (Piepenburg et al. 1997; Piepenburg 2000; Roy et al. 2015; Ravelo et al. 2015). On the central Beaufort Sea shelf, the average abundance of epibenthic invertebrates per station was 4 ind./m^2, with *O. sericeum* accounting for nearly 40% of the total abundance of this region (Ravelo et al. 2015). Despite the wide distribution of these brittle star species, the local dominance over all other epibenthic taxa, the importance in carbon remineralization and the role as prey to fish and crabs, little is known of temporal stability, growth and production for these species in Arctic waters (Piepenburg 2000).

The life history of species is reflected in how fast they grow; accordingly, long-lived species tend to grow slower than short-lived species. The longevity and growth pattern of the inhabitants of a region can provide information regarding the carrying capacity, biological interactions, and stability of the marine system they inhabit (Carroll et al. 2011a; Dolbeth et al. 2012). For brittle stars, the determination of growth and age is possible through the measurement and quantification of growth bands in skeletal structure of their arm ossicles (Gage 1990a). Growth bands provide an accurate way of directly determining the age and growth structure of a population, as opposed to indirect growth estimates through modal analysis of size (disc diameter in brittle stars). The latter may be a faster alternative, but disc diameter is an inferior proxy for age, as it may vary within the same age class due to within-cohort variation of gonad development or arm regeneration (O'Connor and McGrath 1980; Sköld et al. 1994). More importantly, size may underestimate the true population age structure and provide inaccurate growth estimates, due to the stacking of many age classes into few size categories, especially in larger specimens with slower growth rates (Fujita and Ohta 1989).

The effects of low temperatures and the seasonality of food supply are reflected in the slower growth rate and larger body size of polar benthic invertebrates compared with lower latitude taxa (Brey and Clarke 1993; Bluhm et al. 1998; Sejr et al. 2002; Blicher et al. 2007). This also seems to hold true for brittle stars within the sub-family Ophiurinae in Antarctica and the Southern Ocean, where species examined revealed decreasing growth rate and increasing age with increasing latitude (Dahm 1999). The ongoing climate-associated changes on Pacific Arctic shelves that are particularly relevant to Arctic benthic organisms include the increase in water temperature and changes in water column primary productivity (Woodgate et al. 2010; Arrigo and van Dijken 2015). These changes may affect the metabolic rate, growth and production of benthic organisms, which in turn can alter benthic production and energy transfer to higher trophic levels. Currently, our sparse knowledge of these population parameters for Arctic benthic species, particularly brittle stars, limits our ability to model the energy flow through the Alaskan Arctic benthos and from making solid projections for future climate scenarios (Hoover 2013, Whitehouse et al. 2014).

Accordingly, the purpose of this study was to fill in this gap of knowledge, with the general objective of determining the population growth patterns through growth bands, size structure, productivity and total turnover rates of *O. sarsii* and *O. sericeum* in the Alaskan Chukchi and Beaufort seas. Given the high density of brittle stars in the Alaskan Arctic and subsequent potential for negative intra-specific interactions, such as competition for space and cannibalism, a faster growth rate in early stages after recruitment may allow a survival advantage as opposed to slower growing recruits. Therefore, we hypothesized 1) the growth curves of *O. sarsii* and *O. sericeum* have similar shapes, with an initial period of fast growth that decreases gradually with increasing body size until achieving asymptotic size at similar maximum ages. Because *O. sarsii* dominates in the highly productive Chukchi Sea region and is absent on the less productive eastern central Beaufort shelf, it is possible that the less productive region is not capable of sustaining a larger species with a higher energetic demand, such as *O. sarsii*. Therefore, the high densities of *O. sarsii* may not only be a function of the highly productive system in which it dominates, but also a product of high individual production (P) values. With this in mind, we formulated the following hypotheses, 2) *O. sarsii* has higher individual production values compared with *O. sericeum* individuals of the same size, and 3) *O. sarsii* has a higher P:B ratio than *O. sericeum*.

4.2 Methods

4.2.1 Study regions

The Chukchi Sea is an inflow shelf, bordered longitudinally by land masses and with the Bering Strait as the geographic feature that defines its southern limit. This southern connection makes the Chukchi Sea the only conduit of Pacific-origin water into the Arctic Ocean (Carmack and Wassmann 2006). The northeastern Chukchi Sea is highly productive, with integrated water column primary production of up to 500 mg chl/m^2 (Grebmeier et al. 2015). The nutrient rich water originates in the Pacific and Bering Sea and is then transported northward through the Bering Strait. This water movement supports high seasonal primary production on the Chukchi shelf, which in conjunction with low zooplankton grazing pressure translates into high deposition of organic matter to the benthos (Grebmeier et al. 2006; Grebmeier et al. 2015).

In contrast, the central Beaufort Sea has a shallow and narrow interior shelf that slopes down to the Canadian Basin (>3,000 m) in less than 100 km wide (Jakobsson et al. 2012). Along the slope from the west, inflowing modified Pacific water enters the Beaufort Sea though Barrow

Canyon and Atlantic water from the Arctic-wide cyclonic boundary current below the 200 m isobath (Carmack and Macdonald 2002; Nikolopoulos et al. 2009). The high benthic biomass on the Chukchi Sea shelf thereby extends into the western Beaufort Sea, supported by the inflow of highly productive waters of Pacific and Bering Sea origin (Logerwell et al. 2011; Ravelo et al. 2014). On the Canadian Beaufort Shelf, with the exception of areas of upwelling, low water column primary production is mostly limited by nutrients and light availability, resulting in a total annual estimate ranging from 12 to 16 g C/m^2 for this region (Naidu 1974; Carmack et al. 2004). Along with *in situ* and advected components of marine production, this region receives terrestrial carbon related to riveriene inflow and coastal errosion (Goñi et al. 2013). The seasonal discharge of many rivers, particularly the Colville and the Mackenzie Rivers, can affect large areas of the shelf with terrigenous organic matter, inorganic sediments and reduced salinity (Macdonald et al. 1999; Carmack and Wassmann 2006).

4.2.2 Sample collection

In both the Chukchi and Beaufort seas, brittle stars were collected using a 3.05 m plumb-staff beam trawl (PSBT) with a 7 mm mesh and a 4 mm codend liner (Gunderson and Ellis 1986); however, a modified version (PSBT-A) was used on very soft sediment stations in the Beaufort Sea (Abookire and Rose 2005). The trawl time ranged from 1 to 5 minutes on the seafloor at a vessel speed of 1 to 1.5 knots and the distance trawled ranged from 63 m to 383 m. *Ophiura sarsii* were collected at 20 stations in the NE Chukchi Sea at water depths ranging from 35 to 65 m during the August 2013 COMIDA-CAB Hanna Shoal cruise (Chukchi Sea Monitoring In Drilling Area-Chemical And Benthos). Sampling sites in the Chukchi Sea were selected by random generation using a hexagonal tessellation approach to ensure sites were randomly yet evenly distributed through the Hanna Shoal study area (Figure 4.1; Ravelo et al. 2014). *Ophiocten sericeum* were collected in August during the 2013 US-Canada Transboundary cruise in the central Beaufort Sea at 17 stations, with water depths ranging from 37 to 200 m (Bell et al. 2016). Sampling sites in the Beaufort Sea were in part chosen to repeat previously sampled locations by other research projects and additional sampling stations were selected at a spacing approximately 0.5° latitude and 0.25° longitude with the goal to cover the majority of the along-shelf extent of the central Beaufort Shelf (Figure 4. 1).

4.2.3 Age, size frequency and organic mass determination

At each station, all brittle stars were counted and a total weight recorded. For *O. sarsii,* 115 to 350 individuals were haphazardly selected from each station and disc diameters were measured. These measured individuals were then frozen and later processed at the University of Alaska Fairbanks (UAF). For *O. sericeum,* 95 to 380 individuals were collected from each station and then immediately frozen, due to time constraints in the field, and later processed at UAF. For both species, brittle star disc diameter was measured from the base of one arm to the opposite interradius (Hyman 1955), with an accuracy of 0.1 mm using digital calipers when possible and ImageJ software when the individuals were too small or fragile for handling (Abramoff et al. 2004).

Subsamples of the brittle stars used for size frequency distributions that showed no evidence of damage or regenerated arms were used for aging and organic mass (OM) content analysis. Regenerated arms can be easily distinguished by changes in coloration and/or size of the regenerated portion of the arm. To ensure an even representation of all sizes, 10-12 individuals were haphazardly selected for every 1 mm body size increment. Individuals at the extremes of the size spectrum (largest and smallest) were collected in addition to the described size frequency samples to increase the size range for aging and OM samples.

The determination of growth and age was performed through the measurement and quantification of annual growth bands in skeletal structure of the arm ossicles (Gage 1990a). Each arm ossicle is composed of a central articulating condyle and four surrounding fossae. The skeletal structure of the ossicle is composed of a three-dimensional meshwork called stereom. Changes in the microstructure of the stereom, from high density to low density, can be seen in a band pattern throughout the fossae (Figure 4.2). The seasonal periodicity of the stereom density was demonstrated with a temperate ophiuroid species, where high density stereom corresponded to slow growth typical of winter months and low density stereom corresponded to fast growth typical of summer months (Wilding and Gage 1995). Combining the two seasonal changes in stereom density would represent one year of growth and because the band patterns are consistent throughout the fossae, total age can be determined (Gage 1990b; Wilding and Gage 1995; Dahm and Brey 1998; Gage 2003). Evidence from other ophiuroid age studies indicate that as individuals grow, the stereom of the central part of the ossicle develops over the fossa, concealing the early growth bands of the larger individuals and, therefore, an age correction is necessary (Dahm and Brey 1998). Age correction was applied following the back calculation method described in Dahm and Brey (1998):

the first band of the smallest sized individuals, those with clearly no overgrown bands because the size of the visible band is greater than the concealing area, determined the size of the first growth band or age 1 (VB1max). Whenever the first visible growth band in larger individuals was larger than VB1max this was an indication that one or more age bands were hidden by the partly overgrown fossa. Successively, depending on the size of the first visible growth band (exceeding VB2max, VB3max or VB4max, etc.) with increasing individual size, more growth bands were added to the total count (2, 3 or 4, etc.).

The ossicles used for aging came from the base of four arms of each individual sampled (the fifth arm and disc were used for OM determination). Tissue was removed by soaking each arm in 5% sodium hypochlorite at 60°C for 10 to 60 minutes (depending on the size of the arm) and later washed with distilled water. The process of selecting and preparing the ossicles of each individual in the sample took place in three steps. First, up to ten ossicles from each individual, with no anomalous calcium carbonate growth or fossae damage, were selected using a dissecting scope. The ten ossicles were dyed using Alizarin red, after which the single best ossicle was selected, based on the clarity to distinguish growth bands, using a Leica stereo microscope with 6.3:1 zoom. Finally, the selected ossicle was mounted on a stub, and coated with gold for microstructure examination using a scanning electron microscope (SEM) at the Advanced Instrumentation Laboratory, UAF (Gage 1990a; Gage 1990b).

Ossicle growth measurements (using ossicle radius, R) were taken along a transect of the upper right or left fossa, determined by a 45° angle from the vertical axis that runs through the center of the ossicle (Figure 4.2A). Growth bands were measured along the same longitudinal axis from the center of the ossicle to where the stereom changed from fine pores to large pores (winter to summer season transition) (Figure 4.2B). All measurements were performed directly on each SEM image using ImageJ. Accuracy of growth band determination and count were assessed three times by the same person. First, growth bands were marked on all images, in a second round growth bands marked were reassessed and growth band extent was measured. A third quality control assessment was performed for each image before all measurement values were compiled.

Two growth models were applied to the corrected size-at-age data using the Virtual Handbook to Population Dynamics, which uses the iterative Fit by Excel-Solver based on the

NEWTON nonlinear fitting algorithm (Brey 2001). The models used were the Special von Bertalanffy growth function

$$DD_t = DD_\infty\left(1 - e^{-K(t-t_0)}\right) \tag{1}$$

and the Gompertz growth function:

$$DD_t = DD_\infty e^{-e^{-K(t-t^*)}} \tag{2}$$

where DD_t is the size at age t (in mm disc diameter), DD_∞ is the asymptotic size (in mm), K is a growth constant per year, and t_0 is the age at size zero (in years), while t^* is the age at the inflection point of the curve (in years).

Because of the difficulty of obtaining brittle stars with all arms intact, only one complete arm was used for OM content analysis in addition to the central disc. Total arm organic mass was calculated by multiplying the weight of the single arm processed by five. Arms were severed at the edge of the main disc with a scalpel to obtain only the disc organic mass content. The single complete arm and the disc were processed separately to obtain the OM weight. Disc and the single arm of each specimen were dried in an oven at 60° C for a minimum of 24 hours, after which they were incinerated for 10-12 hours in a muffle furnace at 500° C. All weights were recorded with a precision of 10 µg on a microscale. Organic mass value for each specimen was calculated as ash-free dry mass as follows:

$$OM = [DDW + (5ADW)] - [DAW + (5AAW)] \tag{3}$$

where DDW and ADW are the disc and single arm dry weight, respectively; DAW and AAW are the disc and arm ash weight, respectively.

The mass specific growth rate, MSGR (1/y), was calculated using the size-mass relationship and the parameters of the von Bertalanffy growth function:

$$MSGR = bK(DD_\infty - DD_i)/DD_i \tag{4}$$

where K is the growth parameter of the von Bertalanffy growth function, DD_∞ is the maximum or asymptotic size, DD_i is the mean-diameter of size class i (determined by the best fitted growth model for each species), and b is the slope of the size mass relationship.

The organic mass production for each size class (*i*), P*i* (g AFDM/y/m^2), was calculated as:

(5) $P_i = MSGR_i OM_i N_i$

where OM*i* and N*i* are the mean individual organic mass and the number of individuals in size class *i* standardized to m^2, respectively. The total annual production results in:

(6) $P = \sum Pi$

The total P:B (1/y) ratio was calculated from total production across all size classes (P, g AFDM/y/m^2) and the average biomass (g AFDM/m^2) of all stations. Because biomass in the field was measured in wet weight, a conversion factor was applied from the individual wet weight to organic mass, using the same subsample of the population used to determine individual OM. For *O. sarsii*, the conversion factor was 0.120421 g OM per g wet weight (N = 260), while for *O. sericeum* the conversion was 0.143318 g OM per g wet weight (N = 137).

4.3 Results

4.3.1 Age and growth

Out of the 256 *O. sarsii* ossicle samples imaged, 150 were clear enough to measure and quantify growth bands. Of the remaining 106 samples not included in the age analysis, 11% had anomalous calcium carbonate growth covering parts of the fossae, 72% had unclear growth bands, and 17% had other issues (i.e., edge of the fossa was damaged or the fossa edge was tilted back). From the 147 *O. sericeum* samples imaged, 98 were clear enough to measure and quantify growth bands. Of the remaining 49 samples that did not allow growth band quantification, 30% had anomalous calcium carbonate growth covering at least parts of the fossae, 64% had unclear growth bands, and 6% had other issues (as above). Outliers for both species were excluded for having significantly higher or lower numbers of growth bands in comparison with individuals of similar disc diameter (see SEM image examples in Figure 4.A and B). For *O. sarsii*, eight samples, ranging from 14 to 19 mm DD, were excluded from growth parameter calculations as outliers, reducing the total sample size to 142 samples. For *O. sericeum*, four samples, ranging from 2 to 13 mm DD, were excluded from growth parameter calculations as outliers, reducing the total sample size to 94 samples.

Corrected ages in *O. sarsii* ranged from 1 to 27 years. Age correction for *O. sarsii* resulted in the addition up to nine years to the visible growth bands of the largest individuals (Figures 4.3A and 4.3C). The corrected ages of *O. sericeum* ranged from 2 to 20 years. Visible age band readings were adjusted by adding up to six years in the largest individuals (Figure 4.3B and 4.3D). Body size-at-age determination was possible given the significant linear relation between body size and ossicle radius for both species ($p < 0.05$). For *O. sarsii*, increase in body size explained 98% of the increase in ossicle radius (Figure 4.4A). For *O. sericeum*, the increase in body size explained 97% of the increase in ossicle radius (Figure 4.4B).

The two growth models (Gompertz and specialized von Bertalanffy) had very high and similar R^2 for both species (Figure 4.5). However, for *O. sarsii* the Gompertz model resulted in the lower residual sum of squares, while for *O. sericeum,* the best fit resulted from the von Bertalanffy model (Table 4.1). According to the best fit model for each species, the asymptotic size was 40 mm for *O. sarsii* and 20 mm *O. sericeum* (Table 4.1, Figure 4.5). The growth rate computed with the best fit model for each species were very similar (*O. sarsii*, K = 0.077 and *O. sericeum* K = 0.065). The age at size 0 (von Bertalanffy model) was very similar for both species (*O. sarsii*, to = 0.65 and *O. sericeum* to = 0.50), while the age of inflection point of the Gompertz model was greater for *O. sarsii* (14 years) than for *O. sericeum* (10 years) (Table 4.1).

4.3.2 Individual production and turn-over rates

Body size of *O. sarsii* ranged from 1.8 to 30.9 mm and the mode of the population was 8.2 mm (N = 6,478) (Figure 4.6A). For *O. sericeum,* body size ranged from 1.1 to 14.9 mm disc diameter and the mode of the population was 2.9 mm (N = 3,683) (Figure 4.6B). The size distribution of both species appeared to be multimodal, with peaks including a large range of sizes. The very smaller sizes were absent or sparse from the population subsample, likely in part due to the trawl mesh size.

A total of 260 *O. sarsii* individuals were used for organic mass determination, ranging from 2.4 to 32.2 mm disc diameter. The following equation determined the organic mass to body size relationship with an $R^2 = 0.95$ (Figure 4.7A).

$$OM = 2\times10^{-4} DD^{2.3953} \qquad (7)$$

For *O. sericeum*, a total of 137 individuals were used for organic mass determination, ranging from 1.9 to 14.6 mm disc diameter. The following equation determined the organic mass to body size relationship with an $R^2 = 0.97$ (Figure 4.7B).

$$OM = 8 \times 10^{-6} DD^{3.4564} \quad (8)$$

The average station biomass for *O. sarsii* was 5.69 g wet wt./m^2 (sd: 4.41, range: 0.48 - 16.55) or 0.69 g OM/m^2 after conversion (N = 20 stations). The average abundance per station in the study region was 392 ind./100m^2 (sd: 451, range: 22 - 1,543). From the mass specific growth rate (MSGR), the total annual organic mass production and the production to biomass ratio amounted to 0.13 g/y/m^2 and 0.20/y, respectively (Table 4.2). Individual production increased with body size until it peaked at size class 23.3 mm and later remained constant at slightly lower values until the largest size class recorded (Figure 4.8A).

For *O. sericeum,* the average station biomass was 0.96 g wet wt./m^2 (sd: 1.35, range: 0.06 - 3.78) or 0.1413 g OM/m^2 (N = 14 stations). The average abundance per station in the study region was 680 ind./100 m^2, (sd: 1066, range: 11 - 4,030). From the MSGR, the total P and P:B amounted to 0.02 g/y/m^2 and 0.11 y^{-1}, respectively (Table 4.2). Individual production increased steadily with body size, until size class 10.2 mm where it remained relatively constant until the last size class recorded (Figure 4.8B).

4.4 Discussion

4.4.1 Age and growth

This analysis is the first to report on the age and growth of brittle stars from the Arctic. While the annual periodicity of growth bands has been validated for other high latitude echinoderms, this validation has not been undertaken for ophiuroids. From previous studies on the temperate ophiuroid *Ophiura ophiura*, strong evidence relates these bands to annual periodicity, where individuals collected in the winter months had a narrow band formed by high density stereom at the edge of their fossae, and specimens collected during the summer months had a wide band formed by low density stereom at the edge of this growth zone (Wilding and Gage 1995). In the present study, the vast majority of ossicles imaged had the edge of the fossae conformed by large pores (low density stereom). Considering all samples in this study were collected in mid to late August, these brittle stars would have been exposed to the high open water primary production season for a few months (Arrigo et al. 2014; Ravelo et al. in review). These results confirm that *O. sarsii* and *O. sericeum*, like other brittle star species, deposit low density stereom during the highly productive open water season of the Alaskan Arctic, though validation of the periodicity of growth increments remains necessary. Techniques such as mark-recapture or tank experiments using tetracycline or calcine staining, used to validate growth mark increments of fish, mollusks, sea urchins and other fauna, could be considered in future research focused on brittle stars (Gage 1991).

As was the case for other brittle star species, the number of visible growth bands in *O. sarsii* and *O. sericeum* had to be corrected due to overgrowth of the central stereom over the earlier growth bands (Dahm 1996; Gage et al. 2004). The age correction method used in this study was based on the back calculation method described for other ophiuroid species by Dahm and Brey (1998). With over 400 measured samples to assess and correct for age for both species combined, this method proved time consuming and somewhat subjective. The low number of replicate individuals for each visible growth band increment prevented testing the statistical significance of the corrected ages. Despite the shortcomings of this aging method, the estimated asymptotic sizes (40 mm DD for *O. sarsii* and 20 mm DD for *O. sericeum*) agreed with the maximum sizes recorded in the literature for both species (40 mm DD for *O. sarsii* and 18 mm DD for *O. sericeum*; Piepenburg 2000). This result, along with the high correlation of the growth models applied to the corrected age data, support the validity of back calculations of size at age applied to the size at age data. By increasing the number of individuals per size class sampled, future analyses could statistically corroborate the back calculated age increments; however, the increase in processing time and cost of a larger sample size may be substantial.

Based on the growth patterns of other brittle star species, we hypothesized that *O. sarsii* and *O. sericeum* would have similarly shaped growth curves, characterized by initial fast growth that decreases gradually with increasing body size, until achieving asymptotic size at similar maximum age. While the first part of this hypothesis was supported, both *O. sarsii* and *O. sericeum* had similarly shaped growth patterns; the growth curves did not follow the predicted size at age pattern for corrected and visible growth bands. Rather, growth of *O. sarsii* and *O. sericeum* followed an apparent oscillatory pattern, with an initial period of fast growth (approximately eight years), followed by a reduction in growth, resembling an inflexion period (four to five years) and, finally, a second period of accelerated growth with no clear asymptotic age. Despite the high correlation values of the growth models applied, the predicted growth did not conform well to the distribution of size by age; as a result growth was simultaneously over and under-estimated by the model outputs (Figure 4.5).

The growth pattern observed for both species could be a result of a combination of development strategies associated to predation pressure, the high seasonality of food supply and low temperatures also observed in other polar marine invertebrates (Clarke 1980; Brey 1991). The allocation of energy to fast growth in early life stages allows the smaller individuals of the population to escape high predation pressure (Gage 1990b). For example, significantly higher predation pressure was reported for the smaller sizes of *O. sarsii* (3-13 mm DD) by the flatfish American plaice (*Hippoglossoides platessoides*) in the north Atlantic even when larger size classes were available (Packer et al. 1994). As prey of fish and crab, larger brittle stars must allocate energy to arm regeneration due to cropping during non-fatal attacks; however, smaller brittle stars may be consumed entirely (O'Connor et al. 1986; Packer et al. 1994; Sköld and Rosenberg 1996; Divine et al. 2015). The combination of predation pressure on smaller sizes and the high seasonality of food supply for Arctic brittle stars could favor the allocation of energy exclusively to growth early in life. Alongside, reproductive processes require energetic expenses that results in reduced energy allocation to somatic growth in adults; therefore, it is common for marine invertebrates to experience reduced somatic growth with the onset of gonadal development and spawning (Brey 1991; Storero et al. 2010; Stevenson and Mitchell 2016).

To date no information exists on the size at maturity for Arctic brittle stars, including *O. sarsii* and *O. sericeum*; however, gametogenic analysis of the deep sea brittle star *Ophiomusium lymani*, showed that developed gonads were only present in individuals larger than the mid-size classes (Gage and Tyler 1982). While ophiuroids present many developmental strategies (i.e. planktotrophic and direct development), for species with planktonic larva, the number and size of the ova are directly related to the size of the individual (Hendler 1975). Therefore, allocating most energy to gonad production after a certain body size would optimize the reproductive outcome, which is especially important in regions, such as the Arctic shelves, with extreme seasonality in food supply. With increasing size, brittle stars may be able to allocate energy to both reproduction and growth, with a transitional period (the inflection in the growth curve) in which predation pressure is reduced and gonad production may be favored over somatic growth.

A shift in diet of organisms after the inflection phase (beyond 10 mm DD) may also contribute to the second phase of fast growth in both species. In deep-sea echinoids, stable isotope analysis traced different food sources in their somatic and reproductive tissue, suggesting a partition in the allocation of resources for growth and reproduction (Stevenson and Mitchell 2016). Though size-related shifts in diet have not been reported for Arctic brittle stars, O. *sarsii* and O. *sericeum* are non-specialized predator/scavengers at trophic level 2.7 and 2.9 respectively (Iken et al. 2010; Divine et al. 2015); therefore, an increase in body size would allow for an increase in prey size and overall energy yield (Macdonald et al. 2010).

Increased longevity and slow growth are characteristic of many polar invertebrate species, including echinoderms (Brey and Clarke 1993; Ambrose et al. 2006; Gusev and Jurgens-Markina 2012). Our results, along with being the first records of age for Arctic brittle stars, concur with the trend of higher maximum ages of polar *versus* subpolar, temperate and tropical species (Dahm 1993; Gage 2003; Sköld et al. 2001). The Antarctic brittle star *Ophiurolepis gelida* is the oldest aged brittle star at 33 years (after age correction) and 21 mm disc diameter (Dahm and Brey 1998). This maximum age is considerably higher than that of all other aged sub-Antarctic species (Dahm 1996). Maximum ages for the two sub-Arctic congeners of O. *sarsii*, *Ophiura albida* and *Ophiura ophiura*, were nine years at 9 mm and 15 mm disc diameter, respectively (Dahm 1993), which is considerably younger than the maximum 27 years found in our study. Compared with the maximum age of 20 years for O. *sericeum* (14 mm disc diameter), the sub-Arctic *Ophiocten gracilis* had a considerably lower maximum age of seven years at 10 mm disc diameter (Gage 2003). Recent analysis of growth rates along a latitudinal gradient showed a strong linear relationship between echinoid growth rates and temperature, with polar species growth falling significantly below the projected linear trend (Peck 2016). The high seasonality of food availability in polar regions has also been discussed as a major contributor to the reduced growth rate of benthic invertebrates inhabiting these regions (Brey and Clarke 1993; Blicher et al. 2007). Though the mechanisms for the increased longevity of polar organisms is not entirely clear, the combination of slow growth rates, larger body size and delayed maturity are known to play an important role in the extended life span of polar marine invertebrates (Pörtner et al. 2007).

4.4.2 Individual production and turn-over rates

With broadcast-spawning species such as O. *sarsii* and O. *sericeum* the expectation is to have a population formed by many small sized individuals and a gradual decrease in numbers of larger individuals (Gage 2003). In the present study, the lack of very small-sized individuals for both species may be due to the use of a trawl net with a 4-mm codend liner, which should exclude individuals with a disc diameter smaller than 4 mm. Some smaller sized individuals may still be retained with the accumulation of fine mud and silt in the trawl mesh, but not quantitatively sampled. This is especially true for regions heavily influenced by riverine input, such as the central Beaufort shelf, where *O. sericeum* samples were collected (Naidu 1974; Whitefield et al. 2015). Therefore, the absence of smaller sized individuals in the size frequency distributoin (especially for *O. sarsii*) could more likely be interpreted as a methodological bias and less so as the absence of new recruits.

In populations where recruitment is either very low or very infrequent and lifespans are long, the size distribution usually would show extreme negative skewness (Ebert 1983). This is not the case for the populations of *O. sarsii* and *O. sericeum* sampled in this study. Despite the lack of smaller sizes, the size frequency distribution of the two species shows a clear positive skewness. Though a modal analysis was not performed, small modal peaks, spanning 2-3 mm of body size, can be observed throughout the size frequency distribution of the two species. These smaller modal peaks may be representing recruitment events; however, defining size classes through size frequency distributions is difficult for slow growing species with large individual variability in growth due to the staking of size classes (Fujita and Ohta 1990). Another pattern observed in the size distribution of both species is the presence of larger modal peaks, spanning 5-10 mm of body size. The sizes with low frequency that are delineating the larger modes could represent particular periods of very low recruitment for both species. Interestingly, the sizes with the lowest frequency for both species (13-15 mm for *O. sarsii* and 10-11 mm for *O. sericeum*) correspond to individuals of approximately the same 13-18 age range.

In particular, for the Pacific Arctic, the lack of long-term and/or seasonal studies focused on meroplankton has limited our understanding of the supply side of benthic standing stock (Hopcroft et al. 2008). Without this information, it is difficult to relate the low or high frequencies of certain size classes in our size distributions to the periodicity of low recruitment events. High density of ophioplutei of *O. sericeum* in the Kara Sea in early September correlated well with the high density of adults found in that region (Fetzer and Deubel 2006). However, ophiuroid larvae were not found in high densities during a three-year sampling effort in our Beaufort Sea study region (C. Smoot, pers. comm.) or in the Chukchi Sea shelf (E. Ershova, pers. comm.), though those cruises all happened in late summer, perhaps after the recruits had settled. In addition, there is evidence that successful recruitment in polar environments can be sporadic (Brey et al. 1995; Blicher et al. 2007). The large Antarctic brittle star, *Ophionotus victoriae*, despite showing consistent timing of reproduction among years, had large inter-annual variation in reproductive effort over three years (Grange et al. 2004). Increasing this uncertainty, a study reviewing the gonad development and larval density of *O. sericeum* off northeast Greenland found that larval production occurred at a biannual rate (Thorson 1950; Pearse 1965). Consequently, it is possible that the sample collection performed in the Kara Sea encountered a large spawning event (Fetzer and Deubel 2006), and does not represent consistent annual reproductive effort. Without long-term time series data of meroplankton abundance, and gonad development in adults, it is impossible to determine the inter-annual variability in spawning and recruitment, especially if low spawning events occur many years apart. In addition to reproductive periodicity, high mortality of larvae and/or of newly settled recruits may also be an important factor contributing to the multimodal population size structure. The periodicity of reproduction effort and/or successful recruitment events is a key component for understanding the stability of these populations and energy allocations within these populations.

Annual production for *O. sarsii* peaked with individuals ranging 22-24 mm DD. These size classes, along with the 6-9 mm DD range, contributed most to population production. For *O. sericeum*, the smallest (< 4 mm DD) and largest (> 10 mm DD) size classes contributed the most to the production of the population. The pattern observed for *O. sericeum* agrees with that observed for the boreal species *Ophiura ophiura* and *O. albida*, where the contribution of production was related to the high density of smaller individuals and the high individual organic mass values in the larger size classes (Dahm 1993). The low frequency of smaller size classes of *O. sarsii* in our samples may be responsible for the intermediate sizes contributing a larger fraction of the population production. Had the smaller size classes been adequately represented in our samples of *O. sarsii*, the total value of population production may have been substantially greater. Furthermore, gonadal production and arm regeneration, though neglected in this study, certainly would subtract energy from growth, especially in the larger size classes. Considering we purposely excluded individuals with signs of arm regeneration, our values for growth and production may not reflect the extra energy cost many individuals experience in natural populations. This is especially true for large individuals with body sizes out of the target range of predators, who nevertheless remain vulnerable to attacks with their easily-severed arms. Therefore, it must be noted that the values of annual production presented here may underestimate to some degree total brittle star production.

In support of the second hypothesis, *O. sarsii* has higher individual production values compared with *O. sericeum* individuals of the same size. For both species, organic mass increased with increasing body size following the same exponential trend, also described for other brittle star species (Packer et al. 1994; Dahm 1993; Gage 2003). However, for a given size or age class, the individual production of *O. sarsii* was nearly an order of magnitude greater than the individual production of *O. sericeum* suggesting species-specific physiological characteristics; however, the magnitude of this difference may be enhanced by regional differences in productivity regimes in which each species was collected. Regional environmental forces can have a significant influence on benthic organism growth rates and production (Carroll et al. 2011a; Carroll et al. 2011b). *Ophiura sarsii* were collected in the highly productive northeast Chukchi Sea, where integrated water column chlorophyll *a* can reach 500 mg/m^2 (Grebmeier et al. 2015). Conversely, *O. sericeum* were collected on the less productive central Beaufort Sea shelf and upper slope, close to the Mackenzie River, with an annual primary production estimate of up to 16 g C m^{-2} (Carmack et al. 2004). This difference in water column productivity is also reflected in the benthic community biomass. The northeast Chukchi Sea benthic hotspots can reach > 4,000 g wet wt./m^2 in biomass for infauna and 644 g wet wt./m^2 for epifauna (Ravelo et al. 2014; Grebmeier et al. 2015; Denisenko et al. 2015). In contrast, the central Beaufort shelf epibenthic community, though diverse, has a recorded maximum biomass of 58 g wet wt./m^2 (Ravelo et al. 2015). Furthermore, high densities of both brittle star species are found on the shelfbreak of the Beaufort Sea in the vicinity of Barrow Canyon (Ravelo et al. 2015). This area sustains high benthic biomass and has been identified as a hotspot for feeding whales due to its high water column productivity (Okkonen et al. 2011). Individual production values match our knowledge of the productivity regimes of the NE Chukchi Sea and eastern Beaufort Sea. Future research assessing the individual production values of both species from individuals collected in the western Beaufort Sea region could provide insight into the differences in physiology and/or system carrying capacity for each species.

Our third hypothesis was supported by our results, in that *O. sarsii* had a higher turnover rate than *O. sericeum*. Both total annual production and P:B estimates for both species were comparable to values reported for Antarctic brittle star species and considerably lower than values reported for subpolar species. A comparison of biomass, annual production and P:B ratios for different regions shows this relationship for Antarctic and sub-Antarctic species as well (Table 4.2, updated from Table 4.5-26 in Dahm (1996)). As discussed above, environmental factors have a large influence on population abundance, biomass, growth and productivity. To date, changes in growth rate and productivity for the same brittle star species along temperature and food supply gradients has not been tested. Considering the near pan-Arctic shelf distribution and locally high densities of *O. sarsii* and *O. sericeum*, these species could be used as models for assessing the influence of different environmental characteristics on benthic population dynamics.

The premise for our second and third hypotheses was that the higher energetic demand of the larger *O. sarsii* excluded this species from inhabiting the Mackenzie influenced central Beaufort Sea. However, the absence of *O. sarsii* from the central Beaufort Sea may not only be attributed to low system production. Comparison with presence/absence data from 1970's trawl surveys reveal a distribution shift may have occurred for these two species over the past 40 years (Frost and Lowry 1983). Surveys performed from 2011 to 2014 in the central Beaufort Sea confirmed the absence of *O. sarsii* east of 148°W; where, in the 1970's this species was found as far as 141° W (Carey et al. 1974; Frost and Lowry 1984; Ravelo et al. 2015). This temporal change in distribution may be driven by long-term changes in wind driven water mass patterns along with the large influence of the Mackenzie River over the region (Whitefield et al. 2015). Long-term atmospheric data indicate that an increase in the prevalence and intensity of easterly winds in the central Beaufort shelf region has occurred over the past 40 years, causing more persistent and prolonged reversals of water flow from the Chukchi Sea entering the Beaufort Sea (Hufford 1973; von Appen and Pickart 2012; Pickart et al. 2013). Through these changes, not only is the transport of *O. sarsii* larvae from the Chukchi Sea population limited to the western Beaufort Sea, but it also favors the transport of *O. sericeum* larvae towards the west. Along with the reduction in transport of high nutrient waters from the Chukchi Sea into the Beaufort Sea shelf, an extensive intrusion of the Mackenzie inflow into the central Beaufort Sea has been observed in recent decades (Whitefield et al. 2015; Ravelo et al. in review). Furthermore, *Ophiocten sericeum* often dominates in interior shelves, such as in the Laptev and Kara Seas, characterized by riverine sources of carbon and reduced primary production (Piepenburg and Schmid 1997; Fetzer and Deubel 2006; Goñi et al. 2013). With increased freshening of the central Beaufort Sea shelf, this system may be transitioning into a more ideal environment for the less productive *O. sericeum* and less suitable for more productive species such as *O. sarsii*. Environmentally driven distribution shifts from more to less productive taxa can have large implications for higher trophic levels and energy flow throughout the marine system. Future studies linking environmental conditions with the survival strategies of dominant, pan-Arctic species such as *O. sarsii* and *O. sericeum,* may shed light on how different environmental conditions shape benthic communities, as well as how benthic systems may be changing under current and predicted climate scenarios.

4.5 Conclusion

The information presented through this research increases our understanding of the population dynamics of *O. sarsii* and *O. sericeum*, two of the most representative species of the Arcic shelf benthos. This study has demonstrated that the largest individuals were at least a decade older than temperate region congeners, therefore agreeing with the knowledge that polar species have slower growth rates and live longer than temperate region species.

The growth pattern of both *O. sarsii* and *O. sericeum* showed an inflection in growth, possibly related to life history mechanisms aimed to escape predation, optimize energy allocation to reproduction and increase energy intake with body size. Due to large variability in the size of age of the populations of both species, clear cohorts were not distinguishable from the size frequency data. However, large modal peaks spanning 5-10 mm of body size were quite clear and may be marked by low recruitment years. To complete our understanding of the stability of these brittle star populations over time, information is needed regarding the supply side of recruitment.

The two species investigated in this analysis differed greatly in maximum body size, maximum age and individual production values. The intrinsic physiological characteristics of each species are likely the cause of such differences. However, the difference between the two species may be enhanced by bottom up controls on growth and production specific to the region where each species was collected. In the Alaska Arctic, *O. sarsii* dominates the Chukchi Sea and western Beaufort Sea and is not present east of 148° W were *O. sericeum* dominates the shelf system. Therefore, the marked difference in the geographic distribution of the two species may be a consequence of their differences in energetic requirements, where unlike *O. sericeum*, *O. sarsii* is not able to successfully recruit in areas of lower productivity, higher terrigeneous sedimentation and fresh water input. Further research into the influence of water masses on larval distribution may shed light regarding the he current geographic distribution of the two species.

Acknowledgments

Samples for this analysis were collected during the 2013 COMIDA-CAB Hanna Shoal cruise (Chukchi Sea Monitoring In Drilling Area-Chemical And Benthos) and the US-Canada trans-boundary cruise, both funded by the US Department of the Interior, Bureau of Ocean Energy Management (BOEM), under Agreement Numbers M08PC20056 and M12AC00011. A. M. Ravelo would like to thank the North Pacific Research Board for supporting the sample processing and data analysis of this project and also the School of Fisheries and Ocean Sciences and the Advanced Instrument Lab at UAF for provided extra funds (Robert Byrd award) and a discounted rate for the use of the SEM. The authors are grateful for the hard work and dedication of the captains and crews of the USCC Healy and R/V Norseman II. Special thanks to Lauren Bell, Lorena Edenfield, Kimberly Powell, and Tanja Schollmeier for help with the collection of brittle stars. This manuscript and analysis benefited from the comments from Andrew Mahoney (UAF), Christian Zimmerman (United States Geological Survey) and Peter Winsor (UAF).

References

Abookire AA, Rose CS (2005) Modifications to a plumb staff beam trawl for sampling uneven, complex habitats. Fish Res 71:247–254

Abramoff MD, Magalhaes PJ, Ram SJ (2004) Image processing with ImageJ. Biophotonics Int 11:36–42

Ambrose WGJ, Caroll ML, Greenacre M, Thorrold SR, McMahon KW. (2006) Variation in *Serripes groenlandicus* (Bivalvia) growth in a Norwegian high-Arctic fjord: Evidence for local- and large-scale climatic forcing. Glob Chang Biol 12:1595–1607. doi: 10.1111/j.1365-2486.2006.01181.x

Ambrose WGJ, Clough L, Tilney P, Beer L (2001) Role of echinoderms in benthic remineralization in the Chukchi Sea. Mar Biol 139:937–949

Aronson RB (1989) Brittlestar beds: low-predation anachronisms in the British Isles. Ecology 70:856–865

Arrigo KR, Perovich DK, Pickart RS, Brown ZW, van Dijken GL, Lowry KE, Mills MM, Palmer MA, Balch WM, Bates NR, Benitez-Nelson CR, Brownlee E, Frey KE, Laney SR, Mathis J, Matsuoka A, Greg MB, Moore GWK, Reynolds RA, Sosik HM, Swift JH (2014) Phytoplankton blooms beneath the sea ice in the Chukchi sea. Deep Sea Res Part II Top Stud Oceanogr 105:1–16. doi: 10.1016/j.dsr2.2014.03.018

Arrigo KR, van Dijken GL (2015) Continued increases in Arctic Ocean primary production. Prog Oceanogr 136:60–70. doi: 10.1016/j.pocean.2015.05.002

Bell LE, Bluhm BA, Iken K (2016) Influence of terrestrial organic matter in marine food webs of the Beaufort Sea shelf and slope. Mar Ecol Prog Ser. doi:10.3354/meps11725

Blicher ME, Rysgaard S, Sejr MK (2007) Growth and production of sea urchin *Strongylocentrotus droebachiensis* in a high-Arctic fjord, and growth along a climatic gradient (64 to 77° N). Mar Ecol Prog Ser 341:89–102. doi: 10.3354/meps341089

Bluhm BA, Iken K, Mincks Hardy S, Sirenko BI, Holladay BA (2009) Community structure of epibenthic megafauna in the Chukchi Sea. Aquat Biol 7:269–293. doi: 10.3354/ab00198

Bluhm BA, Piepenburg D, von Juterzenka K (1998) Distribution, standing stock, growth, mortality and production of *Strongylocentrotus pallidus* (Echinodermata: Echinoidea) in the northern Barents Sea. Polar Biol 20:325–334

Brey T (1991) Population dynamics of *Sterechinus antarcticus* (Echinodermata: Echinoidea) on the Weddell Sea shelf and slope, Antarctica. Antarct Sci 3:251–256.

Brey T (2001) Population dynamics in benthic invertebrates. A virtual handbook. Version 01.2. In: http://www.thomas-brey.de/science/virtualhandbook

Brey T, Clarke A (1993) Population dynamics of marine benthic invertebrates in Antarctic and subantarctic environments: are there unique adaptations? Antarct Sci 5:253–266

Brey T, Pearse J, Basch L, McClintock J, Slattery M (1995) Growth and production of *Sterechinus neumayeri* (Echinoidea: Echinodermata) in McMurdo Sound, Antarctica. Mar Biol 124:279–292. doi: 10.1007/BF00347132

Carey JAG, Ruff RE, Castillo JG, Dickinson JJ (1974) Benthic ecology of the western Beaufort Sea continental margin: Preliminary results. In: Reed JC, Sayer JE (eds) Symposium on Beaufort Sea coastal and shelf research. The Arctic Institute of North America, San Francisco, pp 665–680

Carmack EC, Macdonald RW (2002) Oceanography of the Canadian Shelf of the Beaufort Sea: a setting for marine life. Arctic 55:29–45

Carmack EC, Macdonald RW, Jasper S (2004) Phytoplankton productivity on the Canadian Shelf of the Beaufort Sea. Mar Ecol Prog Ser 277:37–50

Carmack EC, Wassmann P (2006) Food webs and physical–biological coupling on pan-Arctic shelves: Unifying concepts and comprehensive perspectives. Prog Oceanogr 71:446–477. doi: 10.1016/j.pocean.2006.10.004

Carroll ML, Ambrose WG, Levin BS, Locke V, William L, Henkes GA, Hop H, Renaud PE (2011a) Pan-Svalbard growth rate variability and environmental regulation in the Arctic bivalve *Serripes groenlandicus*. J Mar Syst 88:239–251. doi: 10.1016/j.jmarsys.2011.04.010

Carroll ML, Ambrose WGJ, Levin BS, Ryan SK, Ratner AR, Henkes GA, Greenacre MJ (2011b) Climatic regulation of *Clinocardium ciliatum* (bivalvia) growth in the northwestern Barents Sea. Palaeogeogr Palaeoclimatol Palaeoecol 302:10–20. doi: 10.1016/j.palaeo.2010.06.001

Clarke A (1980) A reappraisal of the concept of metabolic cold adaptation in polar marine invertebrates. Biol J Linn Soc 14:77–92. doi: 10.1111/j.1095-8312.1980.tb00099.x

Dahm C (1999) Ophiuroids (Echinodermata) of southern Chile and the Antarctic: Taxonomy, biomass, diet and growth of dominant species. Sci Mar 63:427–432. doi: 10.3989/scimar.1999.63s1427

Dahm C (1996) Ökologie und Populationsdynamik antarktischer Ophiuroiden (Echinodermata). Berichte zur Polarforsch 194:1–289

Dahm C (1993) Growth, production and ecological significance of *Ophiura albida* and *O. ophiura* (Echinodermata: Ophiuroidea) in the German Bight. Mar Biol 116:431–437. doi: 10.1007/BF00350060

Dahm C, Brey T (1998) Determination of growth and age of slow growing brittle stars (Echinodermata: Ophiuroidea) from natural growth bands. J Mar Biol Ass UK 78:941–952

Denisenko S, Grebmeier J, Cooper L (2015) Assessing bioresources and standing stock of zoobenthos (key species, higher taxa, trophic groups) in the Chukchi Sea. Oceanography 28:146–157. doi: 10.5670/oceanog.2015.63

Divine LM, Bluhm BA, Mueter FJ, Iken K (2015) Diet analysis of Alaska Arctic snow crabs (*Chionoecetes opilio*) using stomach contents and $\delta^{13}C$ and $\delta^{15}N$ stable isotopes. Deep Res Part II Top Stud Oceanogr 1–13. doi: 10.1016/j.dsr2.2015.11.009

Dolbeth M, Cusson M, Sousa R, Pardal MA (2012) Secondary production as a tool for better understanding of aquatic ecosystems Can J Fish Aquat Sci 69: 1230–1253. doi:10.1139/F2012-050

Fetzer I, Deubel H (2006) Effect of river run-off on the distribution of marine invertebrate larvae in the southern Kara Sea (Russian Arctic). J Mar Syst 60:98–114. doi: 10.1016/j.jmarsys.2005.11.005

Frost KJ, Lowry LF (1983) Demersal fishes and invertebrates trawled in the northeastern Chukchi and western Beaufort Seas 1976-1977. U.S Department of Commerce NOAA Tech Rep NMFS-SSRF-764

Frost KJ, Lowry LF (1984) Trophic relationships of vertebrate consumers in the Alaskan Beaufort Sea. In: Barnes PW, Schell DM, Reimnitz E (eds) The Alaskan Beaufort Sea: ecosystems and environments. Academic Press Inc., pp 381–401

Fujita T, Ohta S (1989) Spatial structure within a dense bed of the brittle star *Ophiura sarsi* (Ophiuroidea: Echinodermata) in the bathyal zone off otsuchi, Northeastern Japan. J Oceanogr Soc Japan 45:289–300. doi: 10.1007/BF02123483

Fujita T, Ohta S (1990) Size structure of dense populations of the brittle star *Ophiura sarsi* (Ophiuroidea: Echinodermata) in the bathyal zone around Japan. Mar Ecol Prog Ser 64:113–122. doi: 10.3354/meps064113

Gage JD (1990a) Skeletal growth bands in brittle stars: microstructure and significance as age markers. J Mar Biol Ass UK 70:209–224

Gage JD (1990b) Skeletal growth markers in the deep-sea brittle stars *Ophiura ljungmani* and *Ophiomusium lymani*. Mar Biol 104:427–435.

Gage JD (2003) Growth and production of *Ophiocten gracilis* (Ophiuroidea: Echinodermata) on the Scottish continental slope. Mar Biol 143:85–97

Gage JD (1991) Skeletal growth zones as age-markers in the sea urchin *Psammechinus miliaris*. Mar Biol 217–228

Gage JD, Anderson RM, Tyler PA, et al. (2004) Growth, reproduction and possible recruitment variability in the abyssal brittle star *Ophiocten hastatum* (Ophiuroidea: Echinodermata) in the NE Atlantic. Deep Res Part I Oceanogr Res Pap 51:849–864. doi: 10.1016/j.dsr.2004.01.007

Gage JD, Tyler PA (1981) Re-appraisal of age composition, growth and survivorship of the deep-sea brittle star *Ophiura ljungmani* from size structure in a sample time series from the Rockall Trough. Mar Biol 64:163–172

Gage JD, Tyler PA (1982) Growth and reproduction of the deep-sea brittlestar *Ophiomusium lymani* Wyville Thomson. Oceanol Acta 5:73–83

Goñi MA, O'Connor AE, Kuzyk ZZ, Yunker MB, Gobeil C, Macdonald RW (2013) Distribution and sources of organic matter in surface sediments across the North American Arctic margin. J Geophys Res Ocean 118:1–19. doi: 10.1002/jgrc.20286

Grange LJ, Tyler PA, Peck LS, Cornelius N (2004) Long-term interannual cycles of the gametogenic ecology of the Antarctic brittle star *Ophionotus victoriae*. Mar Ecol Prog Ser 278:141–155. doi: 10.3354/meps278141

Grebmeier JM, Bluhm BA, Cooper LW, Danielson SL, Arrigo KR, Blanchard AL, Clarke JT, Day RH, Frey KE, Gradinger RR, Kędra M, Konar B, Kuletz KJ, Lee SH, Lovvorn JR, Norcross BL, Okkonen SR (2015) Ecosystem characteristics and processes facilitating persistent macrobenthic biomass hotspots and associated benthivory in the Pacific Arctic. Prog Oceanogr 136:92–114. doi: 10.1016/j.pocean.2015.05.006

Grebmeier JM, Cooper LW, Feder HM, Sirenko BI (2006) Ecosystem dynamics of the Pacific-influenced northern Bering and Chukchi seas in the Amerasian Arctic. Prog Oceanogr 71:331–361

Gunderson DR, Ellis IE (1986) Development of a plumb staff beam trawl for sampling demersal fauna. Fish Res 4:35–41

Gusev AA, Jurgens-Markina EM (2012) Growth and production of the bivalve *Macoma balthica* (Linnaeus, 1758) (Cardiida: Tellinidae) in the southeastern part of the Baltic Sea. Russ J Mar Biol 38:56–63. doi: 10.1134/S1063074012010063

Hendler G (1975) Adaptational significance of the patterns of ophiuroid development. Integr Comp Biol 15:691–715. doi: 10.1093/icb/15.3.691

Hoover CA (2013) Ecosystem model indicators for the Beaufort Sea Shelf Region of the Beaufort Sea. Can Data Rep Fish Aquat Sci 1249:vi–14

Hopcroft R, Bluhm B, Gradinger R (2008) Arctic Ocean Synthesis: Analysis of climate change impacts in the Chukchi and Beaufort Seas with strategies for future research. North Pacific Research Board, Fairbanks

Hufford GL (1973) Warm water advection in the southern Beaufort Sea August - September 1971. J Geophys Res 78:2702–2707

Hyman LH (1955) The invertebrates. 4. Echinodermata. McGraw-Hill, New York

Iken K, Bluhm B, Dunton K (2010) Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. Deep Sea Res Part II Top Stud Oceanogr 57:71–85

Jakobsson M, Mayer L, Coakley B, Dowdeswell JA, Forbes S, Fridman B, Hodnesdal H, Noormets R, Pedersen R, Rebesco M, Schenke HW, Zarayskaya Y, Accettella D, Armstrong A, Anderson RM, Bienhoff P, Camerlenghi A, Church I, Edwards M, Gardner JV, Hall JK, Hell B, Hestvik O, Kristoffersen Y, Marcussen C, Mohammad R, Mosher D, Nghiem SV, Pedrosa MT, Travaglini PG, Weatherall P (2012) The International Bathymetric Chart of the Arctic Ocean (IBCAO) Version 3.0. Geophys Res Lett 39:1–6. doi: 10.1029/2012GL052219

Logerwell EA, Rand KM, Weingartner TJ (2011) Oceanographic characteristics of the habitat of benthic fish and invertebrates in the Beaufort Sea. Polar Biol 1–14

Macdonald RW, Carmack EC, McLaughlin FA, Falkner KK, Swift JH (1999) Connections among ice, runoff and atmospheric forcing in the Beaufort Gyre. Geophys Res Lett 26:2223–2226. doi: 10.1029/1999GL900508

Macdonald TA, Burd BJ, Macdonald VI, van Roodselaar A (2010) Taxonomic and feeding guild classification for the marine benthic macroinvertebrates of the Strait of Georgia, British Columbia. Can Tech Rep Fish Aquat Sci 2874:iv–63

Naidu AS (1974) Sedimentation in the Beaufort Sea: a synthesis. In: Marine Geology and Oceanography of the Arctic Seas. Springer, Berlin, pp 173–190

Nikolopoulos A, Pickart RS, Fratantoni PS, Shimada K, Torres DJ, Jones EP (2009) The western Arctic boundary current at 152° W: Structure, variability, and transport. Deep Res Part II Top Stud Oceanogr 56:1164–1181. doi: 10.1016/j.dsr2.2008.10.014

O'Connor BDS, McGrath D (1980) The population dynamics of *Amphiura filiformis* (OF Müller) in Galway Bay, west coast of Ireland. Echinoderms Present past 218–222

O'Connor BDS, McGrath D, Keegan BF (1986) Demographic equilibrium: The case of an *Amphiura filiformis* assemblage on the west coast of Ireland. Hydrobiologia 142:151–158

Okkonen SR, Ashjian CJ, Campbell RG, Clarke JT, Moore SE, Taylor KD (2011) Satellite observations of circulation features associated with a bowhead whale feeding "hotspot" near Barrow, Alaska. Remote Sens Environ 115:2168–2174. doi: 10.1016/j.rse.2011.04.024

Packer DB, Watling L, Langton RW (1994) The population structure of the brittle star *Ophiura sarsi* Lutken in the Gulf of Maine and its trophic relationship to American plaice (*Hippoglossoides platessoides* Fabricius). J Exp Mar Bio Ecol 179:207–222. doi: 10.1016/0022-0981(94)90115-5

Pearse JS (1965) Reproductive Periodicities in Several Contrasting populations of *Odontaster validus* Koehler, a common Antarctic Asteroid. Biol Antarct Seas II Antarct Res Ser 5:39–85

Peck LS (2016) A Cold Limit to Adaptation in the Sea. Trends Ecol Evol 31:13–26. doi: 10.1016/j.tree.2015.09.014

Pickart RS, Schulze LM, Moore GWK, Charette MA, Arrigo KR, van Dijken G, Danielson SL (2013) Long-term trends of upwelling and impacts on primary productivity in the Alaskan

Beaufort Sea. Deep Sea Res Part I Oceanogr Res Pap 79:106–121. doi: 10.1016/j.dsr.2013.05.003

Piepenburg D (2005) Recent research on Arctic benthos: common notions need to be revised. Polar Biol 28:733–755

Piepenburg D (2000) Arctic brittle stars (Echinoredmata: Ophiuroidea). Oceanogr Mar Biol Annu Rev 38:189-256

Piepenburg D, Schmid MK (1996) Distribution, abundance, biomass, and mineralization potential of the epibenthic megafauna of the Northeast Greenland shelf. Mar Biol 125:321–332

Piepenburg D, Schmid MK (1997) A photographic survey of the epibenthic megafauna of the Arctic Laptev Sea shelf: Distribution, abundance, and estimates of biomass and organic carbon demand. Mar Ecol Prog Ser 147:63–75. doi: 10.3354/meps147063

Piepenburg D, Voss J, Gutt J (1997) Assemblages of sea stars (Echinodermata: Asteroidea) and brittle stars (Echinodermata: Ophiuroidea) in the Weddell Sea (Antarctica) and off Northeast Greenland (Arctic): A comparison of diversity and abundance. Polar Biol 17:305–322

Pörtner HO, Peck L, Somero G, B PTRS (2007) Thermal limits and adaptation in marine Antarctic ectotherms : an integrative view. Society 2233–2258. doi: 10.1098/rstb.2006.1947

Rand KM, Logerwell EA (2010) The first demersal trawl survey of benthic fish and invertebrates in the Beaufort Sea since the late 1970s. Polar Biol 34:475–488. doi: 10.1007/s00300-010-0900-2

Ravelo AM, Konar B, Bluhm BA (2015) Spatial variability of epibenthic communities on the Alaska Beaufort Shelf. Polar Biol 38:1783–1804. doi: 10.1007/s00300-015-1741-9

Ravelo AM, Konar B, Grebmeier JM, Mahoney AR (In review) What lies beneath the ice: relating seasonal sea ice patterns with benthic shelf fauna in the Alaskan Arctic. Deep Res Part II Top Stud Oceanogr

Ravelo AM, Konar B, Trefry JH, Grebmeier JM (2014) Epibenthic community variability in the northeastern Chukchi Sea. Deep Sea Res Part II Top Stud Oceanogr 102:119–131. doi: 10.1016/j.dsr2.2013.07.017

Renaud PE, Morata N, Ambrose WGJ, Bowie JJ, Chiuchiolo A (2007) Carbon cycling by seafloor communities on the eastern Beaufort Sea shelf. J Exp Mar Bio Eco 349:248-260

Roy V, Iken K, Archambault P (2015) Regional Variability of Megabenthic Community Structure across the Canadian Arctic. Arctic 68:180–192

Sejr MK, Sand MK, Jensen KT, Petersen JK, Christensen PB, Rysgaard S (2002) Growth and production of *Hiatella arctica* (Bivalvia) in a high-Arctic fjord (Young Sound, Northeast Greenland). Mar Ecol Prog Ser 244:163–169. doi: 10.3354/meps244163

Sköld M, Josefson A, Loo L-O (2001) Sigmoidal growth in the brittle star *Amphiura filiformis* (Echinodermata: Ophiuroidea). Mar Biol 139:519–526. doi: 10.1007/s002270100600

Sköld M, Loo L, Rosenberg R (1994) Production, dynamics and demography of an *Amphiura filiformis* population. Mar Ecol Prog Ser 103:81–90

Sköld M, Rosenberg R (1996) Arm regeneration frequency in eight species of ophiuroidea (Echinodermata) from European sea areas. J Sea Res 35:353–362. doi: 10.1016/S1385-1101(96)90762-5

Stevenson A, Mitchell JGF (2016) Evidence of nutrient partitioning in coexisting deep-sea echinoids, and seasonal dietary shifts in seasonal breeders: Perspectives from stable isotope analyses. Prog Oceanogr 141:44–59. doi: 10.1016/j.pocean.2015.12.004

Storero LP, Ocampo-Reinaldo M, González RA, Narvarte MA (2010) Growth and life span of the small octopus *Octopus tehuelchus* in San Matías Gulf (Patagonia): Three decades of study. Mar Biol 157:555–564. doi: 10.1007/s00227-009-1341-8

Thorson G (1950) Reproductive and larval ecology of marine bottom invertebrates. Biol Rev 25:1–45. doi: 10.1111/j.1469-185X.1950.tb00585.x

Tyler A (1972) Food resource division among northern, marine, demersal fishes. J Fish Res Bd Canada 29:997–1003

von Appen W-J, Pickart RS (2012) Two configurations of the Western Arctic Shelfbreak Current in summer. J Phys Oceanogr 42:329–351. doi: 10.1175/JPO-D-11-026.1

Whitefield J, Winsor P, McClelland J, Menemenlis D (2015) A new river discharge and river temperature climatology data set for the pan-Arctic region. Ocean Model 1–15

Whitehouse GA, Aydin K, Essington TE, Hunt Jr GL (2014) A trophic mass balance model of the eastern Chukchi Sea with comparisons to other high-latitude systems. Pol Biol 37:911-939

Wilding TA, Gage JD (1995) Skeletal growth markers in the brittle star Ophiura ophiura: Do they reflect a seasonal growth pattern. In: Emson R, Smith A, Campbell A (eds) Echinoderm Research. CRC Press, Balkema, Rotterdam, pp 283–291

Woodgate RA, Weingartner T, Lindsay R (2010) The 2007 Bering Strait oceanic heat flux and anomalous Arctic sea-ice retreat. Geophys Res Lett 37:L01602. doi: 10.1029/2009GL041621

Table 4.1. Growth models for *O. sarsii* and *O. sericeum*. Parameters for each model are, DD∞ is the asymptotic size (mm disc diameter), K the growth rate per year, t* the inflection point of the Gompertz curve and t_o the age at size 0 (years) of the von Bertalanffy model. The goodness of fit for each model is expressed in R^2 and RSS (residual sum of squares = Sum$(S-S')^2$) values.

	Model	DD∞	K	t* or t_o	R^2	RSS
Ophiura sarsii	Gompertz	40	0.077	14.00	0.91	817.99
	von Bertalanffy	48	0.030	0.65	0.88	1099.53
Ophiocten sericeum	Gompertz	23	0.085	10.00	0.95	69.44
	von Bertalanffy	20	0.065	0.50	0.96	57.63

Table 4.2. Published values for production, biomass and turnover rate of other brittle star species along with values from this study, updated from Dahm (1996) (Table 5-26). All weights are AFDW (ash free dry mass), where P is the annual production ($g/m^2/y$), B is the average biomass (g/m^2), P:B is the turnover rate (1/y) and mean body mass (mg of AFDW). (*) indicate averages of values published for several study sites.

Region	Species	Study region	Mean body mass	P	B	P:B	Source
Arctic	*Ophiura sarsii*	Chukchi Sea	30.00	0.13	0.69	0.20	this study
	Ophiocten sericeum	Beaufort Sea	3.00	0.02	0.14	0.11	this study
Antarctica	*Astrotoma agassizii*	Weddell and Lazarev Seas*	690.00	0.02*	0.28*	0.05*	Dahm (1996)
	Ophioceres incipiens	Weddell and Lazarev Seas*	20.00	0.11*	0.52*	0.20*	Dahm (1996)
	Ophionotus victoriae	Weddell and Lazarev Seas*	210.00	0.07*	0.39*	0.19*	Dahm (1996)
	Ophiurolepis brevirima	Weddell and Lazarev Seas*	90.00	0.05*	0.37*	0.14*	Dahm (1996)
	Ophiurolepis gelida	Weddell and Lazarev Seas*	30.00	0.30*	0.20*	0.14*	Dahm (1996)
Temperate to Sub-Arctic	*Amphiura chiajei*	North Atlantic - Irland	177.47	49.62	139.32	0.36	Munday and Keegan (1992)
	Amphiura filiformis	North Atlantic - Irland	30.00	31.50	21.00	1.50	O'Connor et al. (1986)
	Amphiura filiformis	Sweden - Gullmarsfjord	21.00	2.59	5.63	0.42	Skold et al. (1994)
	Ophiocten gracilis	North Atlantic - Rockall Trough	0.75	X	X	0.73	Gage and Tyler (1982a)
	Ophiocten gracilis	North Atlantic - Rockall Trough	X	0.26*	0.30*	0.86*	Gage (2003)
	Ophiomusium lymani	North Atlantic - Rockall Trough	1010.14	X	X	0.33	Gage and Brey (1994)
	Ophiothrix fragilis	North Atlantic - Bristol	42.80	31.43	17.30	1.82	George and Warwick (1985)
	Ophiura albida	North Sea	5.13	0.35	1.12	0.32	Dahm (1993)
	Ophiura ljungmani	North Atlantic - Rockall Trough	1.96	X	X	0.54	Gage and Tyler (1981)
	Ophiura ljungmani	North Atlantic - Rockall Trough	0.25	X	X	1.26	Gage and Brey (1994)

	Ophiura ophiura	North Sea	2.85	0.53	1.21	0.43	Dahm (1993)
	Ophiura ophiura	North Atlantic - Bristol	79.06	0.55	0.81	0.68	Warwick et al. (1978)
	Ophiura ophiura	North Atlantic - Bristol	7.87	0.11	0.24	0.50	Warwick and George (1980)
Sub-Antarctic	*Ophionotus hexactis*	South Georgia	48.75	3.39	7.45	0.45	Morison (1979)
Tropical	*Amphioplus coniortodes*	Atlantic - Florida	21.04	2.41	1.07	2.26	Singletary (1971)
	Micropholis gracillima	Atlantic - Florida	23.15	2.90	1.30	2.23	Singletary (1971)
	Ophionephtys limicola	Atlantic - Florida	70.82	5.60	2.41	2.33	Singletary (1971)

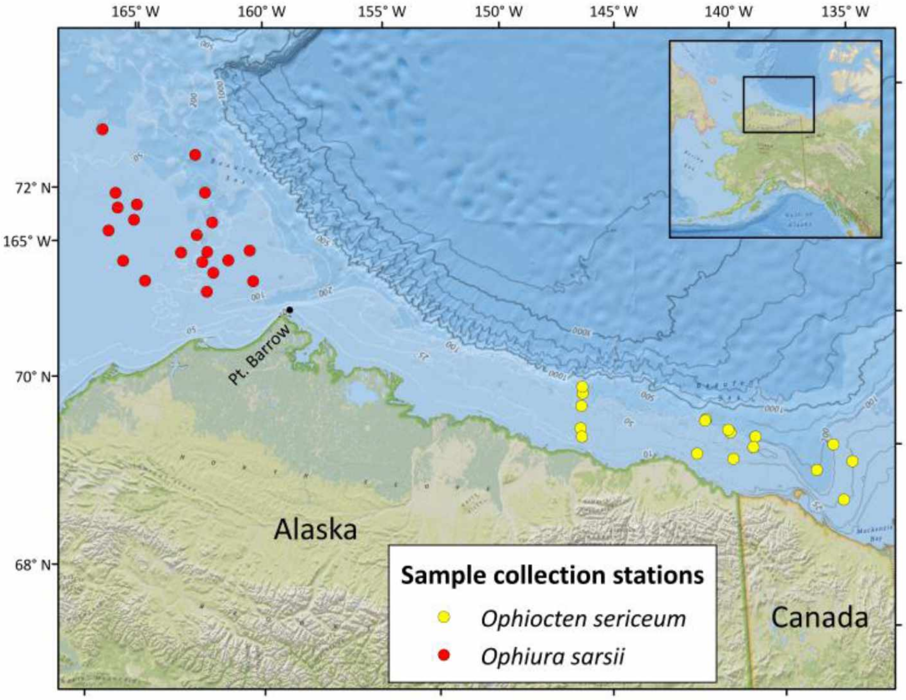

Figure 4.1. Collection sites for brittle stars, July-August 2013. Specimens of *Ophiura sarsii* were collected in the northeastern Chukchi Sea, and specimens of *Ophiocten sericeum* were collected in the central Beaufort Sea.

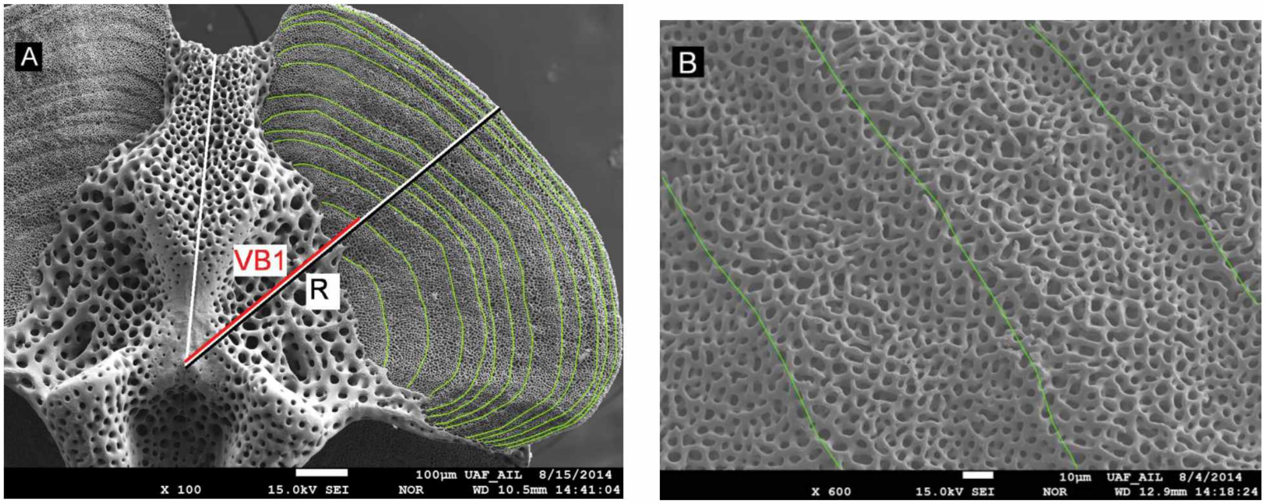

Figure 4.2. Scanning electron microscope image. A. *O. sarsii* ossicle with the 45° angle (white line) illustrating the longitudinal axis used to measure ossicle radius and count growth bands. Ossicle radius R (black line) was used to define the linear relation between ossicle and body size. All visible growth bands are highlighted and illustrate the intercept with measurement axis. Measurement of the first visible growth band that intercepts with measurement axis is labeled VB1 (red line). B. Magnified view of growth bands showing transition between fine pore stereom and large pore stereom on the fossae.

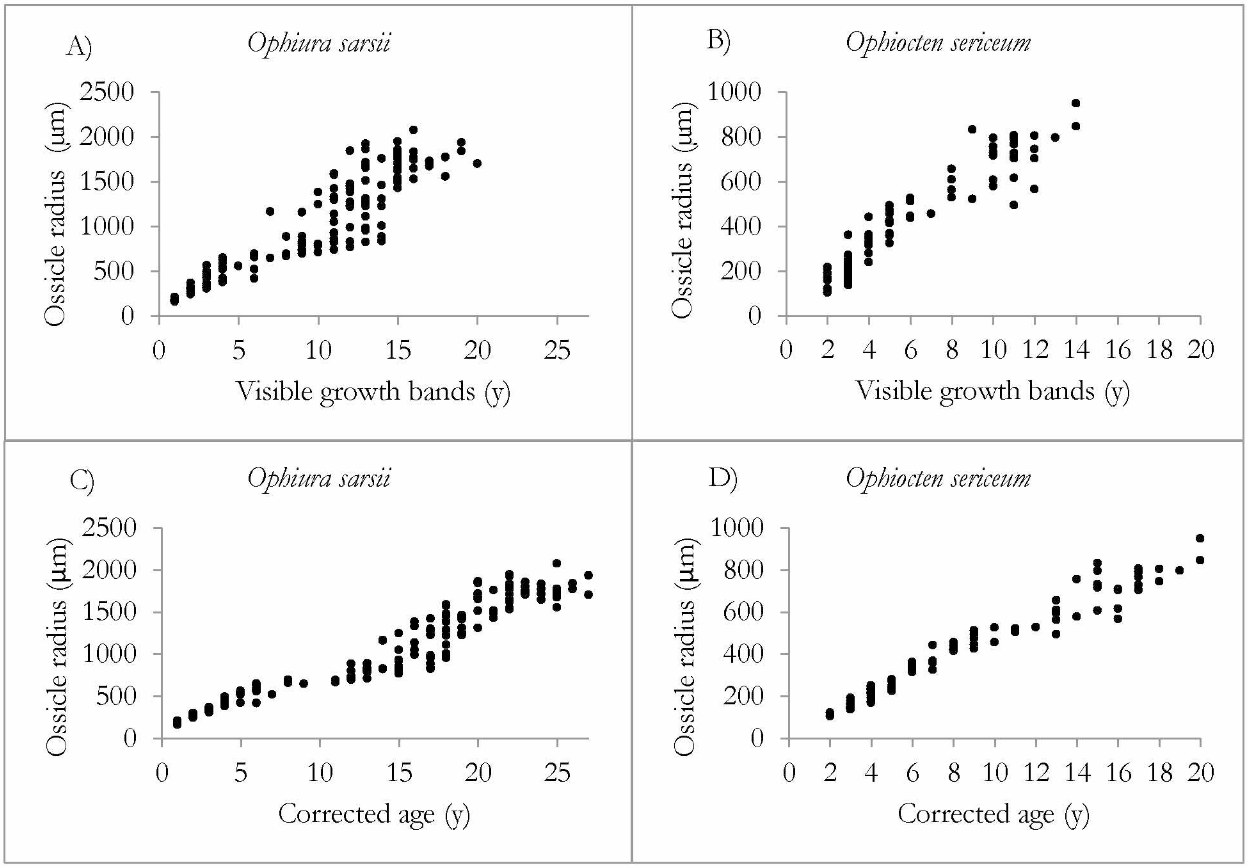

Figure 4.3. Ossicle radius (µm) as a function of the visible growth band of *Ophiura sarsii* (A) and *Ophiocten sericeum* (B). Body size (measured in disc diameter, mm) as a function of the corrected age of *O. sarsii* (C) and *O. sericeum* (D). For *O. sarsii* N =142 and for *O. sericeum* N =94.

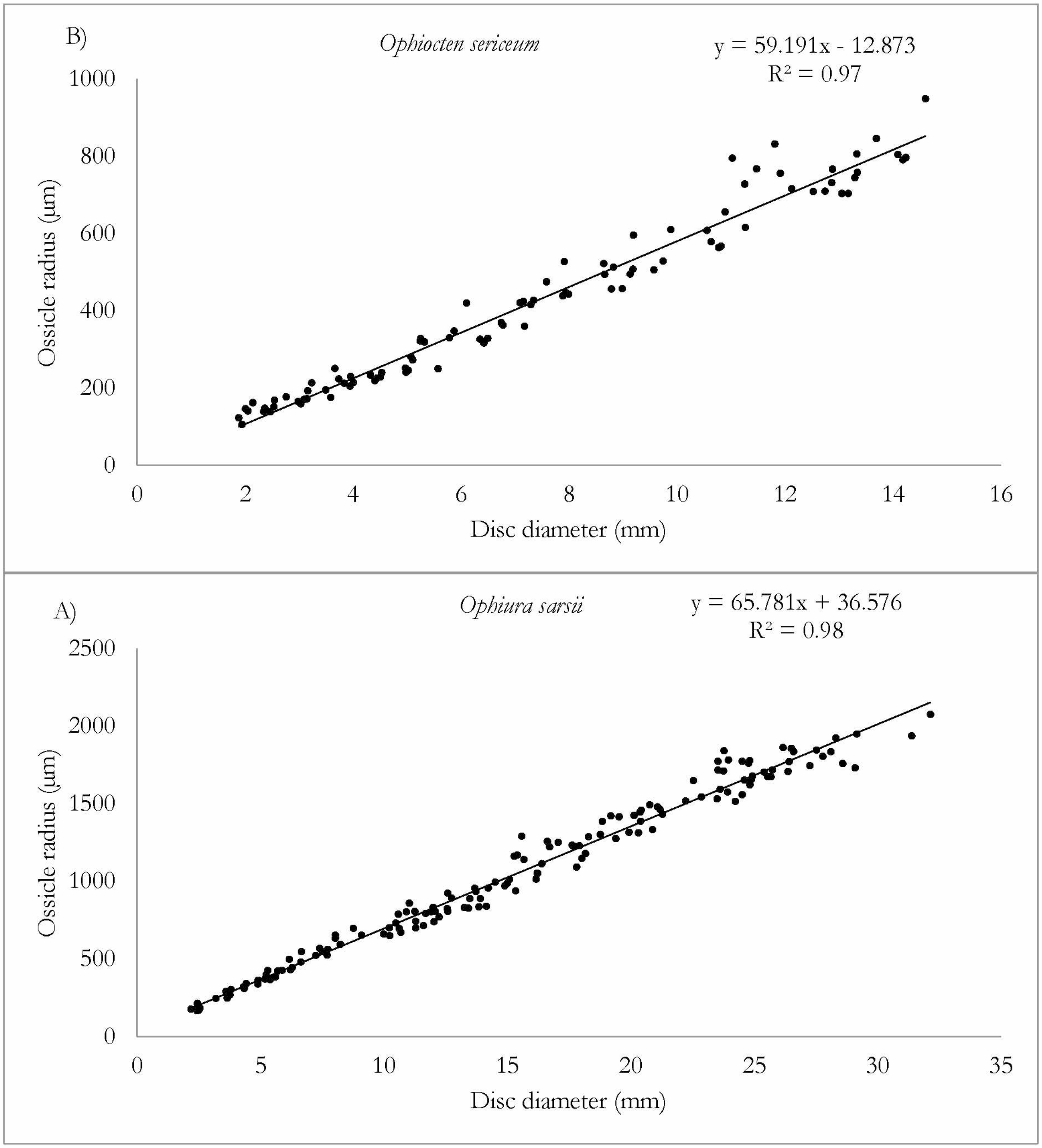

Figure 4.4. Linear relation between the ossicle radius and body size (disc diameter, mm) for (A) *Ophiura sarsii* (N = 150) and (B) *Ophiocten sericeum* (N = 98).

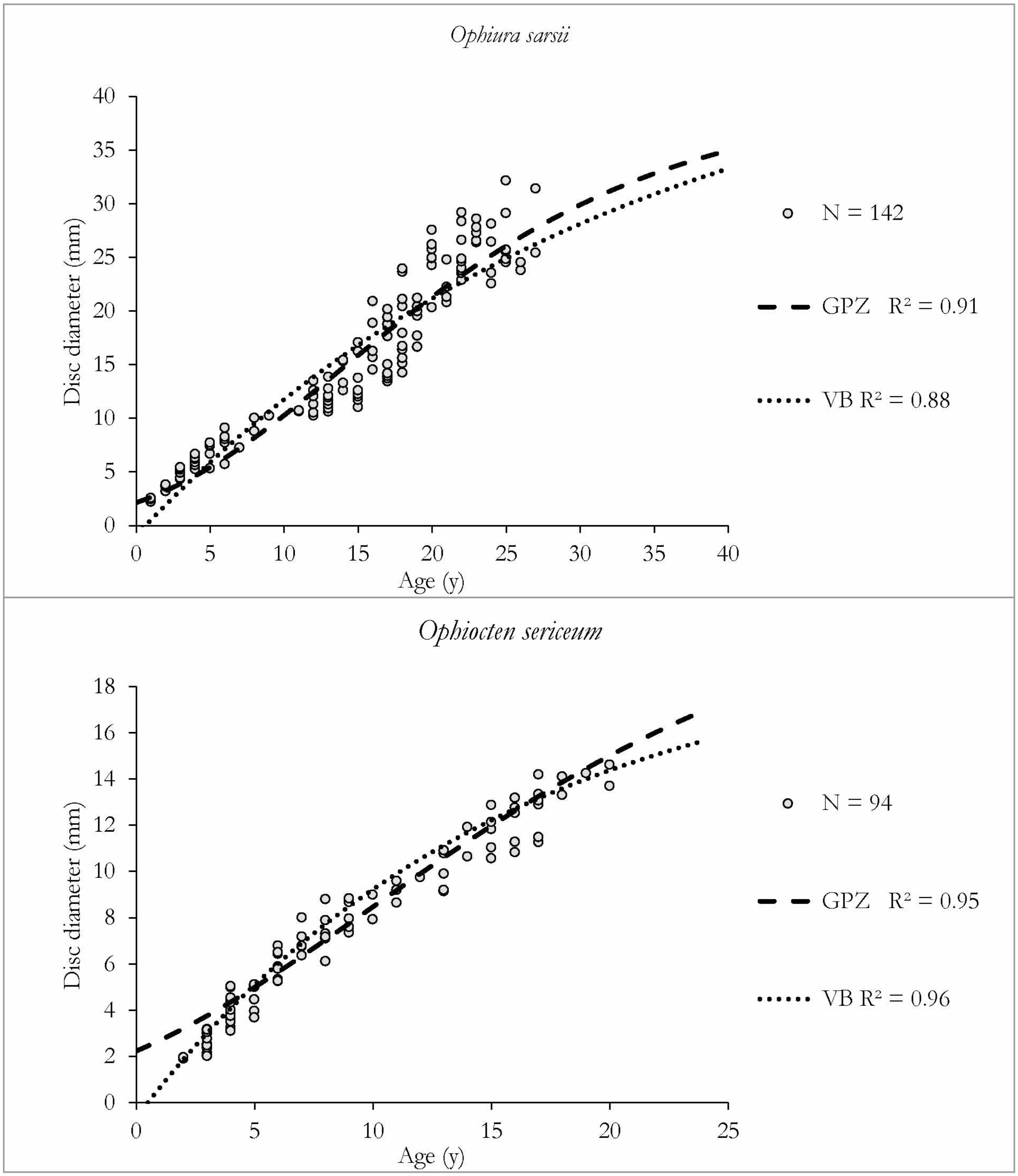

Figure 4.5. Fitted growth curves for body size (disc diameter, mm) as a function of corrected size at age data for (A) *Ophiura sarsii* and (B) *Ophiocten sericeum*. Gompertz growth curve (GPZ) marked with dashed line and von Bertalanffy growth curve marked with dotted line.

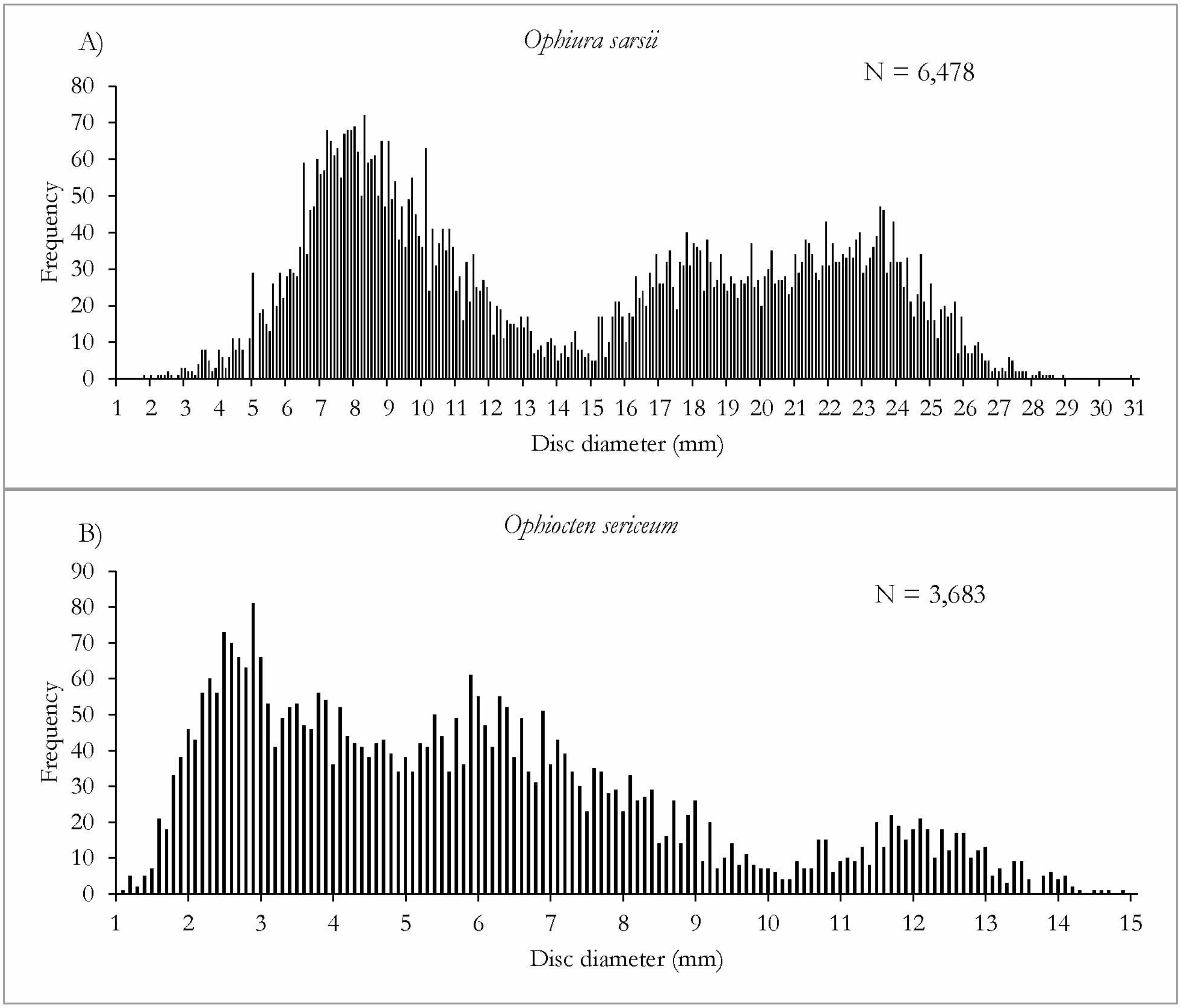

Figure 4.6. Absolute size frequency distribution for a representative subsample of the population of (A) *Ophiura sarsii* collected in the NE Chukchi Sea (N = 6,478) and (B) *Ophiocten sericeum* (N = 3,683) collected in the central Beaufort Sea.

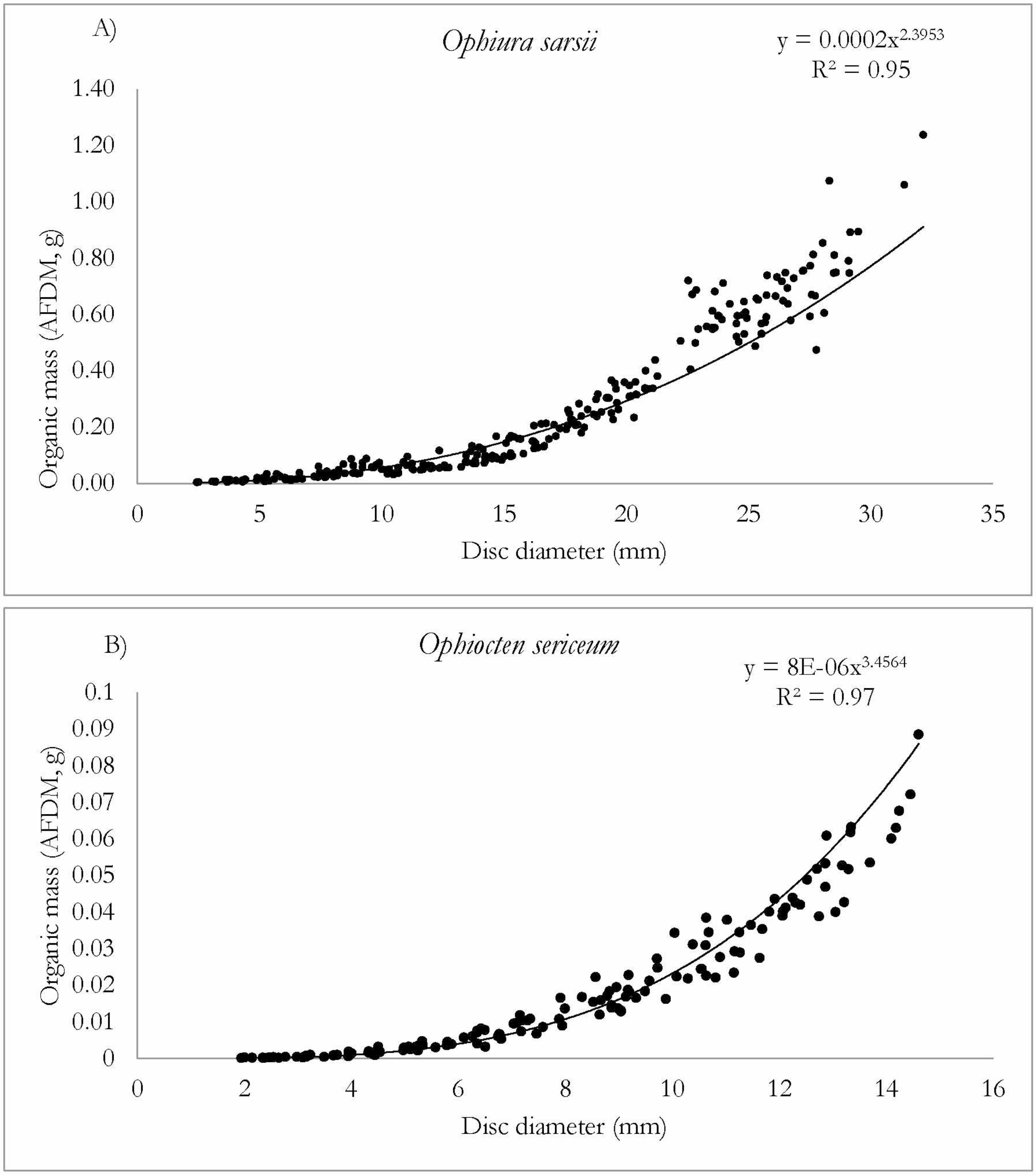

Figure 4.7. Organic mass content as a function of body size (disc diameter, mm) for (A) *Ophiura sarsii* (N =260) and (B) *Ophiocten sericeum* (N = 137). Ash free dry mass (AFDM) in g.

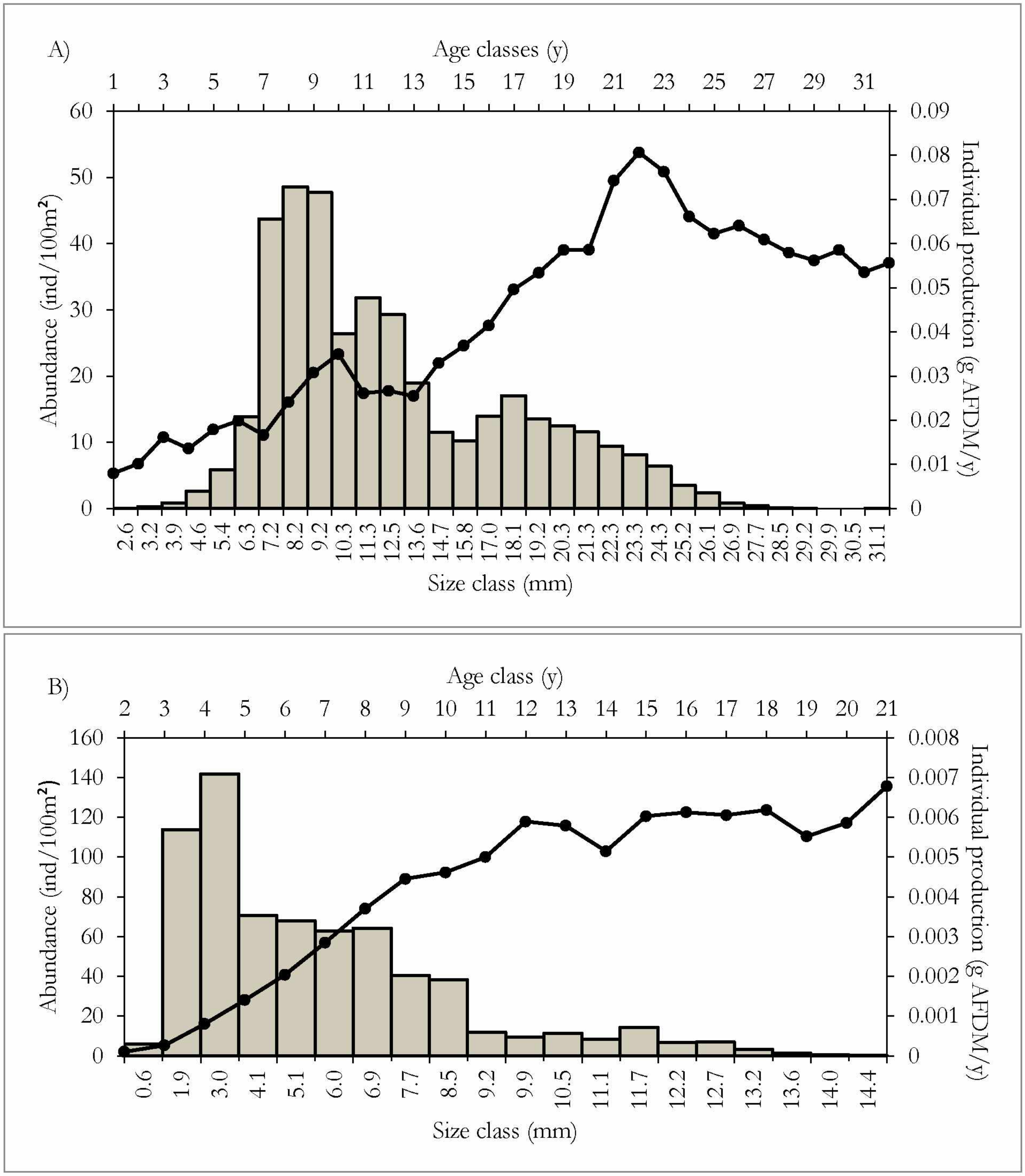

Figure 4.8. Distribution of size and age classes for the standardized abundance of the sampled population (bars, ind/100m^2) and individual production (line, g AFDM/y) for (A) *Ophiura sarsii* and (B) *Ophiocten sericeum*. Size and age classes were defined by the best fitted growth models for each species. Size as disc diameter in mm and age in years (y).

4.6 Appendix

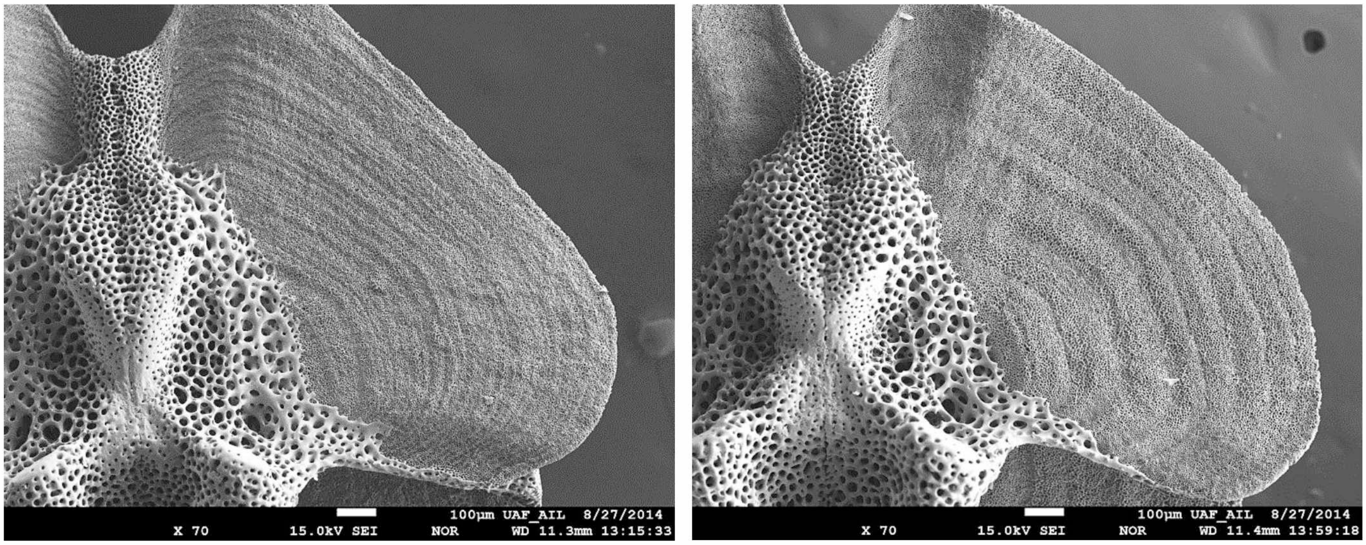

Figure 4.A. Images illustrate the top right fossae of two specimens of O. *sarsii* determined as outliers for age and growth analysis. These two images ilustrate the extreeme difference in growth rates of the two specimens. The specimen on the left had an estimated age after correction of 23 years (18.18 mm DD) and the specimen on the right an estimated age of 13 years after correction (18.04 mm).

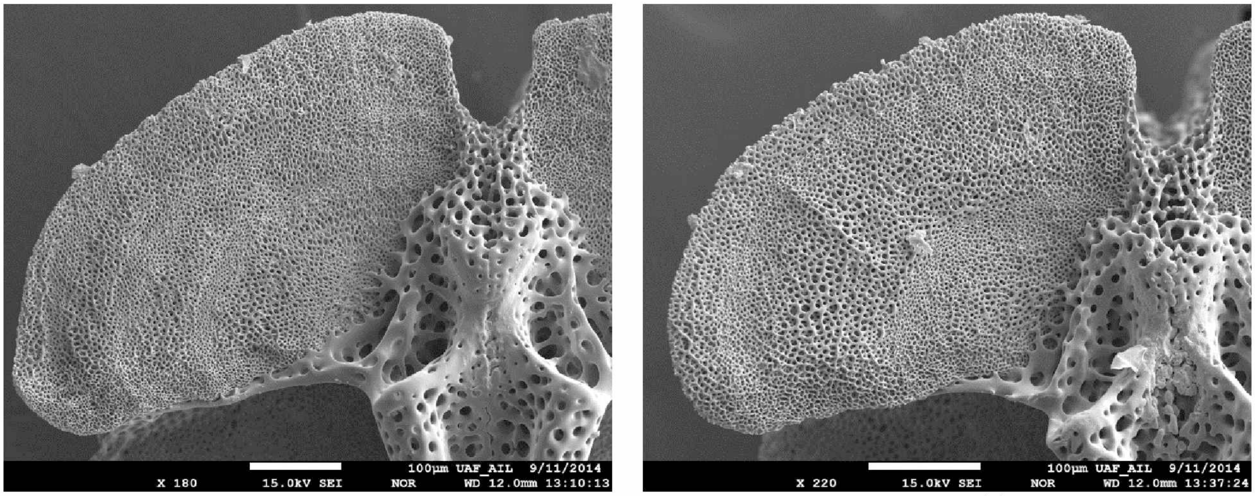

Figure 4.B. Images illustrate the top left fossae of two specimens of *O. sericeum*. The image on the left corresponds to a 8 years old individual after age correction at 8.8 mm DD, which is a growth rate consistent with other individuals of the same size. The image on the right illustrates an individual with either a very fast growth rate with 2 growth bands visible (age after correction this individual would be 5 years old) or this specimen is one of the many individuals in which not all growth bands are clearly discernable and therefore true age cannot be determined.

SUMMARY AND CONCLUSION

This analysis took place on the Alaskan Arctic shelves, where epibenthic invertebrates are a key element of the marine ecosystem. This research describes the patchy spatial distribution of epibenthic invertebrate communities across two Arctic shelves connected by ocean currents, the northeastern Chukchi and Beaufort Seas. Though this patchy distribution has been previously described in these seas, my research presents a novel examination of the epibenthos with extensive coverage throughout the Alaskan Arctic. Accordingly, my research demonstrated that communities throughout the Chukchi and Beaufort Sea shelves show large scale spatial patterns dominated by few, or even a single taxonomic group. Also, in both regions, areas of high and low abundance and biomass could be correlated with changes in taxonomic composition and environmental characteristics. Clusters of stations with high faunal similarity were best represented by either crustaceans or echinoderms, with the mid-depth regions of the Beaufort Sea represented by both major groups. This segregation highlights the importance of the specific environmental conditions necessary to provide the ideal habitat for each community. Ecosystem changes, such as increases in bottom water temperature, result in species and community distribution shifts, as well as increased presence of temperate species on Arctic shelves (Kortsch et al., 2012; Mueter and Litzow, 2008). Species range expansions into the Arctic and persistence over winter seasons have the potential to profoundly affect Arctic community compositions, by introducing new predation pressure and/or competition for resources. Through our knowledge of the physiological requirements of epibenthic taxa, it is possible to some extent to predict who will be the winners and losers of the future Arctic ecosystem. However, because there is not one single Arctic benthic community, projecting how the environmentally induced changes will affect epibenthic communities over large spatial scales becomes challenging.

In both Alaskan Arctic regions, epifauna communities at neighboring sample sites and within similar depths tended to be similar in taxonomic composition. This suggests that large scale environmental patterns are a major influence on the patterns of commuity structure. In the Chukchi Sea, communities varied following the trajectory of the major water masses in the region. Specifically, areas under the influence of the Bering Sea-Anadyr waters were dominated by various crustaceans and had the highest diversity values. Conversely, areas dominated by echinoderms were subject to known highly dynamic seasonal forces, such as wind driven current reversals and polynyas (Winsor and Chapman, 2002; Woodgate et al., 2015). The depth gradient in the Beaufort Sea was a strong determinant of commuity structure, likely because changes in bathymetry reflect important environmental processes varying with depth. Significantly different communities from nearshore to offshore and from east to west throughout the Beaufort Sea could be associated with various environmental forces, such as landfast ice, riverine input and water masses. Similarly, areas of high and low epibenthic biomass could be associated with large-scale environmental patterns. Areas with the highest epifaunal abundance and biomass in the Chukchi and Beaufort seas were dominated by echinoderms, particularly brittle stars. In both regions, brittle star dominated areas were located on each side of Barrow Canyon, highlighting the connectivity that exists between regions through high nutrient water masses (Brugler et al., 2014). The high brittle star biomass area in the Chukchi Sea coincides with an area of dense water formation due to recurrent wind driven polynyas during the ice covered season (Winsor and Chapman, 2002). These persistent environmental conditions may be creating a less favorable environment for other organisms, such as crustaceans, and therefore brittle stars escape the impacts of predators or potential competitors for resources (Aronson, 1989; Packer et al., 1994). In this way, environmental forces are not only creating adequate habitats for the community present, but are likely influencing biological interactions by excluding other organisms from those areas.

Through multivariate statistics, it is possible to visualize the spatial patterns of commuity structure and quantitatively match major environmental forces that contribute to those patterns. However, the quantitative match between community patterns and environmental drivers suffers from our limited ability to capture the complexity of the physical environment with the easily measurable variables. This limitation becomes especially evident when indirect variables describing location, such as latitude, longitude and depth are the strongest predictors of commuity structure. In both regions, longitude was the strongest determinant of epibenthic commuity structure, while biologically relevant variables (bottom water temperature, salinity, sediment organic matter, etc.) added little to the correlation values. This lack of explanatory power is likely in part because most of the biologically relevant variables are point in time measurements of the environment. Though these variables are measured *in situ* and provide an accurate view of the environmental conditions the organisms experience at the time of collection, the large seasonal changes that occur on Arctic shelves are not well reflected by these measurements.

One Arctic environmental characteristic that integrates large-scale environmental forces, acting in unison in space and time, is sea ice (Barber et al., 2015). In an effort to find additional explanatory variables of epibenthic commuity structure, I used passive microwave sea ice concentration data to compute variables describing sea ice phenology and duration. The six parameters considered in this analysis were: Date of sea ice retreat, Date of sea ice return, Number of days covered by sea ice, Number of days with no sea ice, Number of days with a marginal ice zone and Average sea ice concentration from May to October. Through these variables I was able to capture the documented different behavior of sea ice in the Chukchi and Beaufort Sea regions (Mahoney, 2012), highlighting the large differences in the physical environment of each region. Using multivariate analyses, the sea ice variables that had the strongest predictive power of epibenthic community biomass were the Number of days covered by sea ice in the Chukchi Sea; while in the Beaufort Sea the Date of sea ice retreat and Date of sea ice return were selected as the best predictors of commuity structure. In the Chukchi Sea, large inter-annual variability in the regional pattern of the formation and retreat of sea ice reduced the explanatory power of the sea ice variables for epibenthic commuity structure. Despite this caveat, this analysis provided yet another view of the complex interactions between the prevailing winds, water circulation and input of warm water that affect sea ice dynamics in this region. In contrast, in the Beaufort Sea, these sea ice variables integrated well the local recurring and seasonally variable drivers of epibenthic commuity structure, such as the influence of the Mackenzie River, the jet-stream current and upwelling events. The regular periodicity of these environmental forces and their strong effect on both the seasonality of sea ice and epibenthic communities resulted in high correlation values for sea ice and epibenthic community patterns.

In summary, though sea ice variables alone were not consistent predictors of epibenthic commuity structure across regions, they did provide a means for including quantitative values that represent integrated large scale environmental conditions. My research also highlights the complex interplay of the environmental forces that create the multitude of habitats that allow the patchy distribution of taxa, the hotspots for biomass, and varied diversity of Alaskan Arctic epibenthos. However, the detection of drivers of benthic commuity structure is far from complete and further research should focus on including more measures of environmental characteristics as well as of biological interactions.

As stated above, brittle star standing stock hotspots, mainly *Ophiura sarsii* and *Ophiocten sericeum*, are common throughout the Alaskan Arctic. The distribution of these two brittle star species in the study area, while extensive, only overlaps in the western Beaufort Sea shelf and upper slope. The regions where each species dominates differ greatly in oceanographic features and productivity regimes (Carmack et al., 2004; Grebmeier et al., 2015). Throughout the Chukchi Sea shelf and western Beaufort Sea slope, *O. sarsii* outnumber all other brittle star species, and locally all other epibenthic taxa. On the central Beaufort Sea shelf, *O. sericeum* accounted for nearly 40% of the total abundance of this region. Despite the prevalence of brittle stars throughout the Arctic, information regarding the age, growth, and productivity is lacking. In this first account of Arctic brittle star age, I found that the largest individuals of both species could live several decades and were markedly older than temperate region congeners. Inter-annual variability in the width of the annual growth marks suggests an environmental influence on the amount of growth that can be achieved by these individuals each year. Given the longevity of brittle stars in Arctic regions, annual growth could be used as a retrospective indicator of varying environmental conditions, similar to analysis performed using other Arctic fauna (Carroll et al., 2011; von Biela et al., 2011). Linking growth and individual production of brittle stars and other long-lived region-specific taxa to specific environmental conditions can help make solid projections of the productivity of the system under future climatic scenarios in the Arctic.

The distinct distribution patterns and differences in standing stock of the two brittle star species can be linked to differences in the total water column production of each region. *Ophiura sarsii* dominate in the highly productive northeast Chukchi Sea, where integrated water column chlorophyll *a* can reach 500 mg/m^2 (Grebmeier et al., 2015). Conversely, *O. sericeum* dominate on the less productive central Beaufort Sea shelf and upper slope, close to the Mackenzie River, with an annual primary production estimate of up to 16 g C m^{-2} (Carmack et al., 2004). This spatial relationship suggests different energetic requirements for each species and therefore a strong bottom-up control on the populations. Despite both species having equally low turnover rates, individual production was higher for *O. sarsii* than for *O. sericeum* by nearly an order of magnitude for equal body sizes. With regard to future scenarios, local changes in the oceanography and productivity regime throughout the Alaskan Arctic could therefore result in large changes in benthic production just through shifts in species distribution. For both species, the growth curves had similar shapes, showing initial fast growth, with an inflection period followed by a second phase of fast growth. As with many echinoderm species, changes in the allocation of energy, from growth to reproduction, may be the mechanisms responsible for the observed age dependent growth rates of the two brittle star species (Brey, 1991; Lawrence, 1987). The allocation of energy exclusively to somatic growth during the first 10 years after settlement may be related to the higher predation pressure on the smaller size individuals. Afterwards, once surpassed the critical size, gonad production and somatic growth may be accomplished. The longevity of these species, along with the large fraction of the populations of large body size, indicate that these brittle star assemblages do not experience short term fluctuations in population size. With observed and projected increasing water temperatures in the Arctic regions (Comiso, 2012), the potential introduction of new predators and increase in predation pressure cold increase the top-down control on these populations, with subsequent repercussions for the energy flow of the Arctic marine system.

Overall, my research has served to increase our understanding of the spatial patterns of epibenthic communities and the influence of environmental forces in the Chukchi and Beaufort Seas. This research has also highlighted areas in which more research is needed, especially considering the amplified effect of climate change in the Arctic marine environment (Comiso, 2012). Our current ability to model epibenthic community patterns and make future predictions is limited by the complexity of the ecosystems they inhabit and the number of biologically relevant drivers we have available for these analyses. Furthermore, understanding the stability and resilience of the Arctic ecosystems is not possible without a clear understanding of the biological-environmental interactions that exist in these systems combined with individual life histories and physiological tolerance ranges. Considering the longevity and slow growth of Arctic benthic invertebrates, presumably a long time must pass for the substantial biomass found on Arctic shelves to accumulate. This becomes especially important with current and projected resource development on Arctic shelves, where the recovery time after disturbance of these communities should take special consideration in any environmental impact assessments.

References

Aronson, R.B., 1989. Brittle star beds: low-predation anachronisms in the British Isles. Ecology 70, 856–865.

Barber, D.G., Hop, H., Mundy, C.J., Else, B., Dmitrenko, I.A., Tremblay, J.E., Ehn, J.K., Assmy, P., Daase, M., Candlish, L.M., Rysgaard, S., 2015. Selected physical, biological and biogeochemical implications of a rapidly changing Arctic Marginal Ice Zone. Prog Oceanogr 139, 122–150. doi:10.1016/j.pocean.2015.09.003

Brey, T., 1991. Population dynamics of *Sterechinus antarcticus* (Echinodermata: Echinoidea) on the Weddell Sea shelf and slope, Antarctica. Antarct Sci 3, 251–256.

Brugler, E.T., Pickart, R.S., Moore, G.W.K., Roberts, S., Weingartner, T.J., Statscewich, H., 2014. Seasonal to interannual variability of the Pacific water boundary current in the Beaufort Sea. Prog Oceanogr 127, 1–20. doi:10.1016/j.pocean.2014.05.002

Carmack, E.C., Macdonald, R.W., Jasper, S., 2004. Phytoplankton productivity on the Canadian Shelf of the Beaufort Sea. Mar Ecol Prog Ser 277, 37–50.

Carroll, M.L., Ambrose, W.G., Levin, B.S., Locke V, W.L., Henkes, G.A., Hop, H., Renaud, P.E., 2011. Pan-Svalbard growth rate variability and environmental regulation in the Arctic bivalve *Serripes groenlandicus*. J Mar Syst 88, 239–251. doi:10.1016/j.jmarsys.2011.04.010

Comiso, J.C., 2012. Large decadal decline of the arctic multiyear ice cover. J Clim 25, 1176–1193. doi:10.1175/JCLI-D-11-00113.1

Grebmeier, J.M., Bluhm, B.A., Cooper, L.W., Danielson, S.L., Arrigo, K.R., Blanchard, A.L., Clarke, J.T., Day, R.H., Frey, K.E., Gradinger, R.R., Kędra, M., Konar, B., Kuletz, K.J., Lee, S.H., Lovvorn, J.R., Norcross, B.L., Okkonen, S.R., 2015. Ecosystem characteristics and processes facilitating persistent macrobenthic biomass hotspots and associated benthivory in the Pacific Arctic. Prog Oceanogr 136, 92–114. doi:10.1016/j.pocean.2015.05.006

Kortsch, S., Primicerio, R., Beuchel, F., Renaud, P.E., Rodrigues, J., Lønne, O.J., Gulliksen, B., 2012. Climate-driven regime shifts in Arctic marine benthos. Proc Natl Acad Sci 109, 14052–14057.

Lawrence, J.M., 1987. Echinodermata, in: Pandian, T., Vemberg, F.J. (Eds.), Animal Energetics. Academic Press, Orlando, p. 340.

Mahoney, A.R., 2012. Sea ice conditions in the Chukchi and Beaufort Seas, U.S. Arctic Program Pew Environment Group.

Mueter FJ, Litzow, M.A., 2008 Sea ice retreat alters the biogeography of the Bering Sea Continental Shelf. Ecol Appl 18:309–320.

Packer, D.B., Watling, L., Langton, R.W., 1994. The population structure of the brittle star *Ophiura sarsi* Lütken in the Gulf of Maine and its trophic relationship to American plaice (Hippoglossoides platessoides Fabricius). J Exp Mar Bio Ecol 179, 207–222.

von Biela, V.R., Zimmerman, C.E., Moulton, L.L., 2011. Long-term increases in young-of-the-year growth of Arctic cisco *Coregonus autumnalis* and environmental influences. J Fish Biol 78, 39–56. doi:10.1111/j.1095-8649.2010.02832.x

Winsor, P., Chapman, D.C., 2002. Distribution and interannual variability of dense water production from coastal polynyas on the Chukchi Shelf. J. Geophys. Res. 107, 10.1029.

Woodgate, R., Stafford, K., Prahl, F., 2015. A Synthesis of Year-Round Interdisciplinary Mooring Measurements in the Bering Strait (1990–2014) and the RUSALCA Years (2004–2011). Oceanography 28, 46–67. doi:10.5670/oceanog.2015.57