DRIVERS OF FUNCTIONAL ECOLOGY OF THE ALASKAN ARCTIC EPIBENTHOS

By

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Abstract

This dissertation explored multiple facets of functional diversity for epibenthic invertebrate communities of Alaskan Arctic shelves. Functional diversity is the range of organismal traits within a community that determines ecosystem functioning. As a complement to taxonomic diversity, functional diversity reflects what species "do" as opposed to "who" they are, providing information on community-level ecosystem resilience and vulnerability. The Alaskan Arctic marine system is presently changing at an unprecedented rate, which impacts the biomass-rich benthos that is of great importance to upper trophic level fishes, birds, and marine mammals as a food source. In my first chapter, I tested the Biodiversity-Ecosystem-Functioning hypothesis that states ecosystem functioning increases with increasing diversity, using the functional composition of epibenthic communities on the Beaufort and Chukchi Sea shelves as case studies. Functional diversity generally followed taxonomic diversity patterns on both shelves; however, functional composition was more similar between the two shelf systems compared to taxonomic composition. Higher functional diversity on the Beaufort Sea shelf resulted from a more even distribution of functional traits, pointing to stronger resource partitioning and niche complementarity. This, in turn, suggests stronger maintenance of ecosystem function through more efficient nutrient cycling, energy turnover, and recovery from disturbances. In chapter 2, I applied the Community Assembly Theory that assumes species assemble in a non-random way due to a series of biotic and environmental filters using the same Chukchi and Beaufort seas epibenthic communities. Environmental conditions in the Chukchi Sea exerted a stronger environmental filter (i.e., stronger influence of cumulative environmental drivers) on epibenthic functional diversity, especially through gradients in temperature, depth, and mud, compared to weaker depth- and salinity-related filters in the Beaufort Sea. This suggests that the Beaufort Sea community may be less affected by climatic change compared to those in the Chukchi Sea. Strong environmental filtering in the Chukchi Sea can act as a barrier to invading taxa, who must possess a suite of functional traits that allows them to survive in the specific Arctic environment. Continued warming and declining sea ice are assumed to encourage poleward movements of boreal taxa, a process especially likely for taxa migrating from the Bering Sea into the Chukchi Sea. Thus, in the third chapter, I modeled future functional composition of epibenthic communities in the Northern Bering and Chukchi seas, based on past (2009-2019) and predicted environmental conditions under a warmer and fresher, “worst case” scenario for mid- and end-of-century timeframes. All regions exhibited functional changes over time associated with specific shifts in trait composition in each region; however, the magnitude of these functional shifts varied among time periods. The rate of functional changes suggests that Northern Bering Sea and Chukchi Sea communities may have already undergone a major transformation during the past decade, with fewer shifts expected by the mid-century. This dissertation employed a new approach of using functional traits to examine Arctic epibenthic community function and stability in relation to environmental conditions. It created a much-needed benchmark to assess regions of ecosystem vulnerability and resilience in the Alaskan Arctic.

Dedication

To my fiancé, Ty Rilleau, for his unfailing support through many life changes and his willingness to keep the embers of our Alaskan adventure alive.

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CHAPTER 1: INTRODUCTION

Ecosystem resilience in biological communities is measured by the level and degree that ecosystem function persists or recovers in response to perturbations, thus maintaining its original functionality (Oliver et al., 2015). Common measures of ecosystem resilience include biodiversity metrics, generally measured as taxonomic diversity, with higher biodiversity representative of stronger ecosystem resilience and function (Gunderson, 2000; and references therein). Higher biodiversity is assumed to lead to functional redundancy in a system where a larger number of species fulfilling similar functions (redundant species) buffer against the loss or decline of individual species, thus increasing overall system stability and resilience (e.g., Biggs et al., 2020). This idea is the basis for the Biodiversity-Ecosystem-Functioning hypothesis (BEF hypothesis; Loreau et al., 2001) that assumes higher diversity also leads to higher stability through increased resource partitioning (Loreau et al., 2001; Cardinale et al., 2009, 2012). This hypothesis, while rooted in taxonomy, assumes these highly diverse communities include species with diverse functional traits that allow them to exploit varied resources most effectively. More recently, these foundational ecological hypotheses about the interactions of biodiversity, ecosystem stability and resilience, and ecosystem function have been advanced by using functional traits as opposed to taxonomic identity to understand these relationships (de Bello et al., 2021; de Juan et al., 2022). Higher functional diversity stems from diverse expressions of biological traits (e.g., morphology, life history, and behavior attributes) and results in greater resource partitioning and movement of energy through ecosystems (McGill et al., 2006; Cadotte et al., 2011). For example, a diverse expression of morphologies in a community, such as laterally-compressed or upright, can inform about habitat formation or vulnerability to disturbance, respectively, directly affecting the stability of communities (Degen & Faulwetter, 2019). Consequently, using functional diversity in community ecology is fast gaining traction, including the marine realm (Beauchard et al., 2017; Degen et al., 2018), particularly in systems exposed to strong stressors from anthropogenic activity or climate change (de Bello et al., 2021).

One system that experiences climatic changes at an unprecedented rate is the Arctic Ocean (Rantanen et al., 2022). Arctic inflow shelves, regions that channel water and biota from temperate systems into the Arctic (Carmack & Wassmann, 2006), are particularly exposed to conditions, such as warming and freshening (Danielson et al., 2020). Much of the warming of the earth's atmosphere from the burning of fossil fuels is transferred to the world's oceans, and due to the phenomenon known as Arctic amplification (Serreze & Francis, 2006; Serreze & Barry, 2011), the Arctic is warming two to four times as fast as the rest of the world (Stroeve et al., 2012; Rantanen et al., 2022). Related, and a result of warming, Arctic shelf environmental changes include dramatic sea ice decline and changes to the timing of sea ice retreat (Polyakov et al., 2010; Huntington et al., 2020), decreased bottom water salinity (Danielson et al., 2020), increased vulnerability to ocean acidification (Feely & Chen, 1982; Byrne et al., 2010), and changes in primary productivity (Arrigo & van Dijken, 2015), among others. Biological communities in these Arctic shelf regions are adapted to the high-latitude environmental conditions, such as extremely cold water, sea ice coverage for much of the year, and highly seasonal primary production. For example, growth and reproduction of marine invertebrates are closely linked to the seasonal ice cover and primary production cycles (Brandner et al., 2017), while marine mammals depend on sea ice as a platform for rest (e.g., walrus, *Odobenus rosmarus divergens*; Fay, 1982) and/or hunting (e.g., polar bears, *Ursus maritimus*; Ferguson et al., 2000). In the case of bowhead whales Balaena mysticetus, timing of their migration with sea ice retreat follows timing of schools of krill occurrence (Citta et al., 2015; Moore et al., 2018). For Arctic peoples, cold temperatures and sea ice extent directly affect the timing and accessibility of subsistence hunting and fishing that coincides with many migratory marine mammal routes (Huntington et al., 2017). In short, sea ice structures the physical, biological, and cultural landscape of the maritime Alaskan Arctic, especially of the shallow shelf regions. Changes in this high-latitude environment have wide-reaching effects, from the productivity at the base of the food web that supports the dominant benthos of the shelf region to the humans that live in this area.

As the Arctic shelf systems continue to change, so will ecosystem function and diversity of benthic communities that are extremely important in the movement of energy throughout the Arctic food web. For example, benthic communities support a wide range of upper trophic level benthivorous animals, including demersal fishes (Whitehouse et al., 2017), bearded seals (*Erignathus barbatus*), gray whales (*Eschrichtius robustus*) and walruses (Fay, 1982), and diving birds (Lovvorn et al., 2003). Benthic communities play an important role in ecosystem functions, such as nutrient cycling (Kristensen & Kostka, 2013), energy turnover (Hall et al., 2009), benthic remineralization (Ambrose et al., 2001), and trophic transfers (Iken et al., 2010). Environmental changes of the Arctic shelf environment will lead to changes in habitat suitability for these benthic communities. The current timing of sea ice retreat creates habitat conditions that are characterized by strong pelagic-benthic coupling that supports high benthic biomass on shallow Arctic shelves (Grebmeier et al., 2006). When sea ice retreats poleward with the return of sunlight and solar radiation in the spring, sea ice melt promotes growth of sea ice algae and phytoplankton blooms, a product of a highly stratified water column from the meltwater-freshened surface waters (Grebmeier et al., 2015; Moore et al., 2018). These algal blooms exceed the consumption of zooplankton grazers in Arctic waters at that time, resulting in high-quality carbon export to the benthos and supporting it year-round through a food bank (Dunton et al., 2005; Grebmeier et al., 2006; Weems et al., 2012; Morata et al., 2020). Arctic species must also be able to inhabit these shelves year-round in subzero temperatures, under salinity fluctuations from sea ice melt and freeze and river discharge, and under the impact of terrestrial matter (Jørgensen et al., 1999; Piepenburg, 2005; Zinkann et al., 2021). However, while these conditions may seem "harsh" for biota to survive and can prevent non-indigenous species from establishing, the Arctic benthos is considered highly adapted to these conditions (Piepenburg, 2005). This allows the Arctic benthos to thrive in these Arctic conditions but also makes these taxa highly vulnerable to changes in the environment (Carroll & Carroll, 2003; Renaud et al., 2015).

In the Alaskan Arctic, the focus region of this dissertation, environmental changes associated with global warming are accelerated compared to the rest of the world (Rantanen et al., 2022; Shu et al., 2022). The Alaskan Arctic marine system includes the Northern Bering Sea west of Alaska and south of the Bering Strait, the Chukchi Sea to the northwest of Alaska, and the Beaufort Sea off Alaska's North Slope. The Chukchi Sea is an inflow shelf receiving net inflow of North Pacific waters and biota from the Bering Sea, through the narrow connection of the Bering Strait (Wood et al., 2015). The Beaufort Sea is an interior narrow shelf system (Carmack & Wassmann, 2006) that receives a mix of surface waters from the Chukchi Sea, river runoff from the Mackenzie River and other Arctic rivers, and upwelled Atlantic waters along its steep continental slopes (Pickart et al., 2013; Majewski et al., 2017). While each of these seas have their own environmental and benthic community characteristics, they also are connected. There is net flow from the Bering Sea into the Chukchi Sea (Overland & Roach, 1987), as well as a seasonal eastward flow from the Chukchi Sea onto the Beaufort Sea shelf across Barrow Canyon (Danielson et al., 2020). In the Northern Bering Sea, the cold pool, a supercooled bottom water layer that results from the previous winter's brine ejection during ice formation, traditionally forms an effective migration barrier for benthic invertebrates or demersal fish species between the Bering and the Chukchi seas (Mueter & Litzow, 2008; Thorson, 2019). Reduction of the cold pool in recent years has led to the extension of temperate or sub-Arctic water masses into the Arctic, a process called borealization (Polyakov et al., 2020). In response, species' habitats are also extending poleward (Fossheim et al., 2015), a process that is the focus of recent community studies (e.g., Mueter et al., 2021). Likewise, benthic communities in the Bering, Chukchi, and Beaufort Sea regions have been well-studied through many perspectives, including taxonomic diversity (Bluhm et al., 2009; Blanchard et al., 2013; Ravelo et al., 2014, 2015; Stevenson & Lauth, 2012), biogeography (Ravelo et al., 2020), trophic interactions (Iken et al., 2010; McTigue & Dunton, 2014), and a few recent forays into functional diversity (Rand et al., 2018; Liu et al., 2019; Logerwell et al., 2022). This dissertation expands on these previous works by delving deeper into benthic biodiversity. First, I established the basis of functional and taxonomic diversity of epibenthic communities in the Chukchi and Beaufort seas, then I investigated how functional diversity was driven by environmental influences on these two shelves. Lastly, using these building blocks of functional understanding, I investigated how benthic function and therefore ecosystem function and diversity, are likely to change in the future with respect to changing Arctic influences.

The first chapter of this dissertation specifically explored the BEF hypothesis for epibenthic communities in Arctic shelf systems. I investigated if functional diversity follows taxonomic diversity on the Chukchi and Beaufort Sea shelves epibenthic communities, thus comparing "what species do" with "who species are". A biological trait analysis was used to study epibenthic invertebrate functional composition and compare it with taxonomic diversity, both to each other and between the two shelves. Taxonomically different species can fill similar niches within a community based on similar functional traits, while conversely, similar species can fill different niches based on their functional traits (Hewitt et al., 2008; Krumhansl et al., 2016). This chapter further investigated how resource use and resource partitioning differed between the two shelf communities, based on biological traits instead of the more traditionally applied taxonomic lens.

The second chapter of my dissertation tested the Community Assembly Theory, which assumes that species possess a suite of traits that allow them to pass through a series of filters (e.g., dispersal limitation, biotic interactions, and environmental filtering), to establish regional and local communities (Keddy, 1992; Weiher & Keddy, 1995; Kraft et al., 2015). Conversely, these same filters can prevent some species from becoming part of the established community, if they do not possess traits that successfully pass these filters (Menegotto et al., 2019). Of these filters, environmental filtering can be measured through spatial and temporal correlative analyses of environmental influences on communities (Peck et al., 2004). Given strong environmental gradients on the Chukchi and Beaufort Sea shelves, I expected that functional composition would be most similar (low diversity) for epibenthic assemblages that were most heavily influenced by extreme environmental conditions (i.e., a strong environmental filter that results in high functional trait convergence). In contrast, I expected functional composition to be most dissimilar (high functional diversity) under more moderate environmental pressures (i.e., weak environmental filters that lead to high functional trait divergence). Additionally, trait-environment relationships were investigated to determine which functional traits were most structured by the environment; this allowed me to identify functional traits that would be most informative for future predictions of functional diversity in a changing Arctic.

The goal of the third chapter of my dissertation was to model epibenthic communities based on functional composition in the northern Bering and Chukchi seas, given expected changes in temperature and salinity by the middle and the end of this century. These changes in the environment can lead to the poleward movements of taxa, including commercially important ones, which has contributed much to the continued attention on Alaskan Arctic waters. For example, walleye pollock (*Gadus chalcogrammus*), Pacific cod (*Gadus macrocephalus*), Pacific salmon species (*Oncorhychus* spp.), and snow crab (*Chionoecetes opilio*) have all shifted their distributions poleward on the Alaskan Arctic shelves (Rand & Logerwell, 2011; Kolts et al., 2013; Nielsen et al., 2013; Stevenson & Lauth, 2019), evidence of borealization (Mueter et al., 2021). Unlike the European Arctic that has been heavily influenced by anthropogenic activities, such as commercial benthic fishing, the Alaskan Arctic provides a unique opportunity to model how benthic communities may change predominantly in response to climate perturbations. Therefore, instead of focusing on short-term human influences, we can focus on longer-term climate change effects on Arctic marine communities (Drinkwater et al., 2021). Using the connected system of the northern Bering and Chukchi seas, I investigated spatial and temporal patterns in epibenthic functional composition using joint species distribution models that accounted for the influence of functional traits (Tikhonov et al., 2020). Using the concept of environmental filtering, I used functional trait-environment relationships with bottom salinity and temperature from hindcast models for predictive mid- and end-of-the-century models of future epibenthic functional composition under the "fossil-fueled development", also known as the "worst case" scenario described by the Intergovernmental Panel on Climate Change (IPCC, 2019).

My thesis provides an in-depth analysis of Alaskan Arctic functional diversity, functional composition, and environmental correlates of epibenthic communities. I contributed novel knowledge of functional traits of taxa on the Bering, Chukchi, and Beaufort Sea shelves in relation to environmental conditions. I also contributed these trait data to the Arctic Traits Database (https://arctictraits.univie.ac.at/), an online and open-source tool for benthic ecologists. Each of my dissertation chapters built on each other to advance our understanding of Arctic benthic ecosystem function. This dissertation provides novel information to make informed predictions about which functional attributes will make temperate or sub-Arctic taxa competitively viable with current Arctic inhabitants.

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CHAPTER 2: COMPARISON OF FUNCTIONAL DIVERSITY OF TWO ALASKAN ARCTIC SHELF EPIBENTHIC COMMUNITIES[1]

Abstract

Alaskan Arctic shelf communities are currently experiencing dramatic changes that will likely affect ecosystem functioning of Arctic marine benthic communities. Here, functional diversity based on biological traits was used to assess differences and similarities in ecosystem functioning between two shelf systems that are geographically close but vary in many environmental influences: the Arctic Beaufort and Chukchi Sea epibenthic communities. We hypothesized that (1) patterns of functional composition and diversity metrics reflect patterns in taxonomic composition and diversity metrics in these two shelf communities; and (2) patterns in functional diversity metrics are distinct between the two shelves. We evaluated nine biological traits (body form, body size, feeding habit, fragility, larval development, living habit, movement, reproductive strategy, sociability) for 327 taxa in 2014 and 2015. For each trait, multiple modalities (specific expressions within a trait) were considered. Patterns in functional diversity metrics on both shelves reflected those in taxonomic diversity metrics. However, shelf communities were more similar in functional composition than taxonomic composition. Beaufort Sea communities had higher functional dissimilarity and functional evenness driven by differences in the modalities within body form, body size, larval development, and reproductive strategy. These traits primarily affect nutrient cycling, energy turnover, and recovery from disturbances, suggesting a stronger potential for future maintenance of ecosystem function and indicating a more even use of resources in the Beaufort Sea. The combination of functional and taxonomic diversity metrics enabled a comprehensive understanding of how ecological niche space is used and how epibenthic communities function in Alaskan Arctic shelf systems.

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[1] Sutton, L., Iken, K., Bluhm, B. A., & Mueter, F. J. (2020). Comparison of functional diversity of two Alaskan Arctic shelf epibenthic communities. *Marine Ecology Progress Series*, *651*, 1–21. https://doi.org/10.3354/meps13478divers

2.1 Introduction

Arctic ecosystems are changing rapidly as the Arctic is warming twice as fast as the rest of the planet (Stroeve et al. 2012), with continued decreases in sea ice extent (Carmack et al. 2016) and changes in primary production (Arrigo and van Dijken 2015, Frey et al. 2019). Ongoing shifts in the Arctic environment are associated with changes in marine community composition and ecosystem processes (Huntington et al. 2020, Waga et al. 2020). For example, environmental changes, such as changes in temperature or sea ice, can increase stress for Arctic species but create habitat conditions suitable for northward-moving boreal species, thus changing community composition (Mueter & Litzow 2008, Kortsch et al. 2015, Thorson et al. 2019). Alaskan Arctic shelves are known for regionally high productivity and tight pelagic-benthic coupling, leading to some of the most productive benthic shelf areas in the world (Grebmeier et al. 2006). Arctic benthic assemblages within the Beaufort and Chukchi Sea shelf communities are of great importance for these ecosystem processes as they support important food webs, which can channel anthropogenic or climatic perturbations to upper trophic levels (Iken et al. 2010, Divine et al. 2015a, Tu et al. 2015). These benthivorous upper trophic levels include ecologically and socially important bearded seals, walruses (Fay 1982, Oliver et al. 1983), demersal fishes (Whitehouse et al. 2016), crabs (Divine et al. 2015b), and birds (Lovvorn et al. 2003). Changes in benthic assemblages within shelf communities or in the energy pathways supporting these assemblages will, therefore, have effects on overall Arctic shelf ecosystem function.

Ecosystem function is broadly defined as the movement or storage of energy or material within an ecosystem (Bellwood et al. 2019). Benthic communities play important roles in ecosystem functions such as nutrient cycling (Grebmeier 1993, Kristensen 2000), energy turnover (Hall et al. 2009), trophic transfers (Iken et al. 2010, Kędra et al. 2015), remineralization (Ambrose et al. 2001), and resuspension of sediments (Snelgrove 1999, Snelgrove et al. 2000). Although different Arctic benthic shelf communities may share these general functions, adjacent communities such as on the Beaufort and Chukchi Sea shelves that differ distinctly in their oceanographic setting and primary production levels (Sakshaug 2004, Carmack & Wassmann 2006) can be expected to differ in the specific functional roles the benthos plays. The Chukchi

Sea is a shallow inflow shelf (sensu Carmack & Wassmann 2006), characterized by high nutrient influx from the Bering Sea, leading to high primary production. In contrast, the Beaufort Sea is a narrow interior shelf, which has lower primary production than the Chukchi Sea, driven by lower nutrient supplies from the Chukchi Sea to the western Beaufort shelf, upwelling from the shelf break, and high freshwater influx from the Mackenzie and Colville rivers (Carmack & Wassmann 2006, Hill et al. 2013, 2018, Grebmeier & Maslowski 2014). These differences in key environmental influences are suspected to play a role in driving patterns in taxonomic composition (e.g., Rand et al. 2018) and may also lead to differences in functional composition through differences in biological traits between the Beaufort and Chukchi Sea shelf benthic communities. This could result in different ecosystem functioning between the two shelves despite their proximity. Consequently, the responses and resilience (i.e., the ability of communities to maintain ecosystem function) of the benthic communities to perturbations will likely differ between the Beaufort and Chukchi Sea shelves.

Functional diversity within a geographical area can help explain and predict regional ecosystem functioning and ecosystem resilience to environmental change. The Beaufort and Chukchi Sea epibenthic communities can be functionally described by "what they do" based on specific functional traits of the taxa within the community rather than "who they are" purely based on taxonomy (Petchey & Gaston 2006). Hence, functional diversity is defined as the range of organismal traits of species within a community that, combined, determines ecosystem functioning (Tilman 2001, Bremner et al. 2006). Different taxa can play a similar functional role in a community based on their traits. Conversely, taxonomically similar organisms can have different functions within a community (Hewitt et al. 2008, Krumhansl et al. 2016). Differences in biological trait expression within a community will lead to differences in resource use because biological traits represent how taxa extract and move resources in their environment (McGill et al. 2006, Cadotte et al. 2011). In essence, functional diversity is the balance of the roles of taxa within communities through different traits and through redundancy or complementarity of shared traits that influence overall ecosystem functioning (Díaz & Cabido 2001).

Arctic marine communities are at particular risk of experiencing competitive disadvantages relative to invading boreal species. Although Arctic taxa typically occupy a narrow temperature range, modelling studies suggest these taxa may be resilient to environmental pressures, including high temperatures (Renaud et al. 2015, 2019). Therefore, there is a need to better understand the resilience of these Arctic shelf communities to ongoing changes in the environment. In a resilient system, a specific ecosystem function would be maintained even if one or several taxa were removed from the system. High functional redundancy, where the same biological traits are represented by several different species within a community, and high functional diversity, where many different traits are represented by taxa within a community, presumably lead to high ecosystem stability and increased resilience to change or disturbance (Hewitt et al. 2008).

The Biodiversity-Ecosystem-Functioning (BEF) hypothesis states that higher taxonomic diversity leads to improved ecosystem functioning through diversified resource use, which ultimately leads to higher ecosystem stability (Schulze & Mooney 1993, Loreau et al. 2001, Hooper et al. 2005, Cardinale et al. 2009, 2012). This theory is based in an understanding of biodiversity from a taxonomic perspective, which for epibenthos has been established in recent years for the Beaufort and Chukchi Sea shelf study areas (e.g., Feder et al. 2005, Bluhm et al. 2009, Blanchard et al. 2013, Ravelo et al. 2014, 2015, 2020). The underlying assumption of the BEF hypothesis is that higher taxonomic diversity also reflects higher functional diversity, but these assumptions are rarely explicitly tested. Support for this underlying assumption, for example, has been found for the macrobenthos in the Bering Sea (Kun et al. 2019). Despite a long-standing and ongoing debate in the marine ecology scientific community of this concept (Naeem et al. 1994), few studies have analyzed the relationship between taxonomic diversity and ecosystem function in Arctic benthic marine systems (but see Kokarev et al. 2017, Rand et al. 2018, Kun et al. 2019), systems that are prone to perturbations. We contend here that, if the BEF assumption is correct, functional diversity on the two Arctic shelf communities should follow the same patterns as taxonomic diversity, as functional diversity is based in biological traits that are defined by a species' identity. In addition, if functional diversity provides a complementary perspective to ecosystem functioning that taxonomy alone does not provide, then a more comprehensive understanding of ecosystem function can be expected when functional diversity is analyzed along-side taxonomic diversity. Therefore, given distinct environmental influences on the two shelves, we hypothesized that (1) differences in functional composition and diversity metrics in epibenthic shelf communities reflect patterns in taxonomic composition and diversity metrics; and (2) patterns in functional diversity metrics of Beaufort and Chukchi Sea epibenthic shelf communities are distinct from each other.

2.2 Methods

2.2.1 Study Sites

Epibenthic invertebrates were collected during four cruises in 2014 and 2015 on the US Beaufort and Chukchi Sea shelves (Figure 2.1). Here, we define each station as a representative assemblage of taxa within each shelf community. Beaufort Sea assemblages from 46 stations were studied during three research cruises: the US-Canada Transboundary Project 2014 sampled the central Beaufort Sea shelf, and the Arctic Nearshore Impact Monitoring in Development Area project III (ANIMIDA 2014, 2015) sampled the central and eastern Beaufort Sea shelf. Stations between 9 and 64 m bottom depth were included in this study. Chukchi Sea shelf assemblages from 67 stations were sampled during the Arctic Marine Biodiversity Observing Network survey in 2015 (AMBON 2015). These stations were sampled between 11 and 54 m bottom depth.

2.2.2 Sample Collection

Epibenthic invertebrate assemblages were sampled during all cruises towing a 3.05 m wide plumb-staff beam trawl with a 2.6 m wide and 1.2 m high mouth opening with a 7 mm mesh and a 4 mm codend liner (modified after Gunderson & Ellis 1986). Average trawl time at the bottom was 4-5 min at approximately 1.5-2 knots, depending on station depth and bottom conditions (see details in Iken et al. 2019). Biomass of all epibenthic invertebrates at each station was calculated as catch per unit effort by multiplying the estimated distance trawled by the width of the net and normalized to g wet weight per 1000 m^2. Bottom contact was determined using a time-depth recorder (Star Oddi). Invertebrates were identified onboard to the lowest feasible taxonomic level, and net wet weight of each taxon was recorded using digital hanging scales. Vouchers for taxa not identified in the field were fixed in either 10% formalin solution or 190-

proof ethanol for later identification with the help of taxonomic experts listed in the acknowledgement section. Taxon names followed those in WORMS (http://www.marinespecies.org) to standardize nomenclature.

2.2.3 Biological Traits Analysis

A dataset of biological traits was compiled for a total of 327 epibenthic taxa collected from both shelves. These data can be accessed via the supplementary material (Table S2.1) and with references via The Arctic Traits Database (https://www.univie.ac.at/arctictraits/). The Beaufort Sea community consisted of 246 taxa and Chukchi Sea community consisted of 247 taxa with 166 shared taxa within these shelves. Taxonomic resolution varied for these taxa, but was similar between the two shelf communities. The Beaufort Sea had 163 and Chukchi Sea had 172 taxa identified to species, 60 and 56 to genus, seven and five to family, four and five to class, seven and four to order, and the same five taxa were identified at the phylum level (Table S2.1). Taxonomic identifications were based on the same taxonomic expertise (see acknowledgements) so that the similar taxonomic resolution of the two sea shelf systems enabled an unbiased comparison of functional diversity based on biological traits. Biological traits analysis (BTA) functionally characterizes epibenthic organisms based on morphology, life history, and behavior. The BTA included a total of nine traits related to morphology (body form, body size, fragility, sociability), behavior (feeding habit, living habit, adult movement), and life history (larval development, reproductive strategy), following the definitions and categories in Degen and Faulwetter (2019) (Table 2.1). The biological traits matrix was assembled through a combination of qualitative traits based on observations and the authors' collective knowledge of Arctic invertebrates (morphological traits) and traits derived from extensive literature research (life history traits, behavioral traits). Where specific literature for a species was unavailable, traits were inferred from closely related species. Each trait was further separated into modalities to account for distinct categories within a trait that an organism could express (Table 2.1, S2.1).

The BTA was done with a fuzzy-coding approach, which allowed taxa to be assigned multiple modalities within a trait based on their affinity to those modalities (Chevenet et al. 1994, Bremner et al. 2006). Using a 0-3 scoring system, where 0 means no affinity and 3 is a high affinity to a modality, each taxon was assigned a number based on their affinity to each modality within a trait (Table S2.1, Chevenet et al.1994). Taxa with equal affinity to several modalities within a biological trait were assigned the same score for those modalities. All fuzzy-coded modality scores within a trait were then weighted so that they summed to 1 for each taxon and trait. The scores for all modalities across all traits created unique taxa biological trait profiles (taxa by trait matrix). These matrices were multiplied by the relative taxa biomass at each station (taxa by station matrix) to create fuzzy-coded community weighted means (CWM) for each station and trait. Therefore, the resulting station by trait matrix essentially highlighted the most common categorical modalities at each station, and therefore each assemblage, through biomass weighting (Table 2.2) (Garnier et al. 2007).

2.2.4 Shelf Comparisons of Functional and Taxonomic Diversity Metrics

Five functional diversity metrics were calculated for the Beaufort and Chukchi Sea shelf epibenthic assemblages to enable a community-level comparison (Table 2.2). Each of the functional diversity metrics represented a unique facet of overall functional diversity (Mason et al. 2005, Mouchet et al. 2010). These included functional dissimilarity (Rao's Quadratic Entropy [Rao's Q]), functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and functional redundancy (FRed: 1 – mean pairwise distances [MPD]) (Table 2.2). Functional dissimilarity (Rao's Q) compares how similar taxa biological trait profiles are to each other among assemblages (Rao 1982). Functional dissimilarity was complemented by functional metrics that described the available functional niche space (FRic) and how the space within a given niche was occupied among assemblages (FEve, FDiv) (Schleuter et al. 2010). As all traits were fuzzy-coded categorical variables, functional metrics of Rao's Q, FRic, FEve, and FDiv were based on a flexible distance-based framework (Laliberté & Legendre 2010). First, a Gower distance matrix among taxa was calculated using a trait by taxa matrix, followed by a principal coordinates analysis (PcoA). PcoA axes were then used as new 'trait values' to compute FRic, FEve, and FDiv for all stations (Laliberté & Legendre 2010). FEve used all PcoA axes whereas FRic and FDiv used the maximum number of PcoA axes allowed where the number of taxa was greater than the number of traits. FRed represents the degree to which taxa play similar roles in communities and was measured using the complement of mean pairwise distances (1 – MPD)

(Lawton & Brown 1993, Rosenfeld 2002, de Bello et al. 2016). All functional diversity metrics can range from 0 – 1, where zero indicates low functional diversity and 1 indicates the highest possible functional diversity.

Functional diversity metrics were compared to complementary taxonomic diversity metrics (Table 2.3). Rao's Q was compared to the Simpson taxonomic-based diversity index (Simpson 1949). Simpson diversity measures the chance that two individuals within a station are from the same taxon. The Simpson diversity index equals the maximum value of Rao's Q if all taxa were functionally completely different (i.e., each taxon represents unique functions) and Simpson index is, thus, commonly used in comparisons of functional and taxonomic diversity (Carmona et al. 2016). Margalef's richness index measures species richness while accounting for sampling effects and was compared to FRic. Finally, Pielou's evenness index was used to calculate species evenness and was compared to FEve.

All diversity metrics were compared between the Beaufort and Chukchi Sea shelf communities using a linear model of the form:

$$y = \alpha + \beta \times d + \varepsilon$$

where y is any of the diversity metrics, the intercept α corresponds to the mean value of index y for the Chukchi Sea, and d is a dummy variable with values d = 0 for the Chukchi Sea and d = 1 for the Beaufort Sea. Hence, the regression coefficient β corresponds to the mean difference in metric y between the Chukchi Sea and the Beaufort Sea. The error, ε, was modeled as a spatial random process with a correlation structure that exponentially declined with distance between stations to allow for spatial autocorrelation. This linear model form was chosen over a simple univariate test (e.g., ANOVA) due to the spatial nature of the residuals and the ability to account for spatial autocorrelation. Models were fit using a generalized-least-squares approach as implemented in the nmle package in R (Pinheiro et al. 2017). If the autocorrelation term did not significantly improve the model fit, metrics were compared using a simple linear model fit via least squares. To further investigate the relationship between the number of taxa and functional diversity on each shelf, Rao's Q was compared to Margalef's Index for the Beaufort and Chukchi Sea shelves using a non-linear generalized additive model (GAM).

2.2.5 Comparisons of Functional and Taxonomic Composition

Significant differences in functional (based on CWM) and taxonomic composition (based on taxon biomass) between the Beaufort and Chukchi Sea shelf assemblages were determined with analyses of similarity (ANOSIM) using a Gower distance matrix for functional composition and a Bray-Curtis dissimilarity matrix for taxonomic composition (Clarke & Warwick 1994). No transformation was performed on the functional composition matrix as this matrix was already fuzzy-coded for CWM. Taxon biomass data were square root transformed to balance the influence of rare and dominant taxa (Clarke & Warwick 1994). The ten most influential taxa on taxonomic composition were compared between the two shelves (similarity percentages analysis, SIMPER). These taxa were further compared between shelves in percent total biomass, frequency of occurrence, and average percent biomass per station. Furthermore, functional composition based on the proportion of modalities within biological traits was compared between the Beaufort and Chukchi Sea shelf communities using a fuzzy correspondence analysis (FCA; Chevenet et al.1994). To focus on biological traits that drove patterns in functional composition on each shelf, correlation ratios from the FCA were evaluated for the first two axes of the FCA. High correlation ratios indicate strong relationships of biological traits with the FCA axes. Following previous studies on biological traits (Conti & Schmidt-Kloiber 2014, Kokarev et al. 2017), we considered biological traits with correlation ratios > 0.1 as most representative of the variance captured by the FCA axes. All analyses evaluating differences in functional and taxonomic compositions were computed using the vegan package (Oksanen et al. 2017) in R version 4.0.2 (R Core Team 2017). Functional and taxonomic composition for each shelf were compared using the RELATE routine in the Primer V.7 software package (Clarke & Gorley 2015). Sufficient permutations were possible for all comparisons and statistical significance was set at p-values ≤ 0.05.

In addition to between-shelf comparisons, the relationships of functional and taxonomic structures were evaluated within each shelf using a multistep process of multivariate statistics.

First, we investigated which taxa and modalities best represented communities for each shelf using the BVSTEP analysis within the BEST routine in Primer V.7 (Clarke & Gorley 2015). Specifically, we investigated which subset of taxa or subset of modalities were necessary to maintain the original structures of taxonomic or functional composition and were, therefore, considered representative of the functional and taxonomic structure. These representative subsets of modalities and taxa were determined using a stepwise procedure based on at least 95% Mantel correlations. Subsequently, these subsets were considered as characteristic taxa and influential modalities. Resemblance matrices from these characteristic species and influential modalities were then compared using RELATE tests for each shelf separately.

2.3 Results

2.3.1 Functional and Taxonomic Diversity Metrics

All diversity metrics except for functional redundancy (FRed) had higher median values in the Beaufort Sea shelf community compared to the Chukchi Sea shelf community. However, only two functional diversity metrics (Rao's Q, FEve) and the corresponding taxonomic metrics (Simpson's diversity, Pielou's Evenness) were significantly higher in the Beaufort than Chukchi Sea shelf community (Figure 2.2, $p<0.01$). No spatial autocorrelation was detected for Rao's Q, FRic, Simpson diversity, and Pielou's Evenness, but was present in FEve, FDiv, Margalef's index, and FRed (Table 2.4). Fewer taxa were required to increase functional dissimilarity (Rao's Q) in the Beaufort Sea compared to the Chukchi Sea (Figure 2.3).

2.3.2 Comparison in Functional and Taxonomic Composition between Shelves

The Beaufort and Chukchi Sea epibenthic shelf communities moderately differed in functional composition, despite substantial overlap (ANOSIM: $R=0.292$, $p=0.001$, Figure 2.4a).
The first two FCA axes accounted for 42.36% of the total inertia with 24.70% explained by axis 1 and 17.66% explained by axis 2 (Figure 2.4a). The biological trait movement was mostly separated along axis 1, while the trait fragility was mostly separated along axis 2 (Figure 2.5). The biological traits body form, body size, larval development, and reproductive strategy were

strongly correlated with both axes with correlation ratios > 0.1 (Table 2.5, Figure 2.5). Within these biological traits that strongly correlated with both FCA axes, the Beaufort Sea shelf assemblages had proportionally higher biomasses of globulose (BF1) and laterally compressed (BF4) body forms, lecithotrophic (LD2) and direct development (LD3), small-medium sized (W2), and sexual brooder (RS4) modalities compared with Chukchi Sea assemblages (Figure 2.6). Conversely, the Chukchi Sea shelf assemblages had proportionally higher biomasses of dorso-ventrally compressed (BF3) and upright (BF5) body form, planktotrophic development (LD1), medium (W3) and medium-large size (W4), and sexual-external (RS2) modalities (Figure 2.6).

The Beaufort and Chukchi Sea epibenthic shelf communities also differed in taxonomic composition (ANOSIM, R=0.676, p=0.001, Figure 2.4b). The Beaufort Sea shelf contained 246 taxa and the Chukchi Sea shelf harbored 247 taxa with a total of 327 unique taxa combined for the two shelves. Of these total taxa, 166 taxa (51% of total) were shared between the Beaufort and Chukchi Sea shelf communities. The holothurian *Psolus peronii*, the scallop *Similipecten greenlandicus*, the brittle stars *Ophiocten sericeum* and *Ophiura sarsii*, the snow crab *Chionoecetes opilio*, the sand dollar *Echinarachnius parma*, the shrimp *Argis* sp., the basket star *Gorgonocephalus* sp., and the lyre crab *Hyas coarctatus* contributed most to differences in taxonomic composition between the two shelves (SIMPER, Table 2.6, Figure 2.4b). The two shelf communities differed strongly in the taxa that contributed most to biomass and frequency of occurrence (FO) per shelf. The Beaufort Sea shelf community was dominated in total biomass, average biomass per station, and FO by *P. peronii*, *S. greenlandicus* and *O. sericeum*. In contrast, the Chukchi Sea shelf community was dominated in total biomass and average biomass per station by *O. sarsii*, *C. opilio*, and *E. parma*, while FO was highest for *C. opilio*, *Argis* sp., and *H. coarctatus* (Table 2.6).

2.3.3 Comparison of Functional and Taxonomic Composition within each Shelf

Patterns in functional and taxonomic composition were significantly related to each other within both the Beaufort and Chukchi Sea shelf communities (RELATE test: rho=0.497, p=0.001 for Beaufort Sea; rho=0.619, p=0.001 for Chukchi Sea). Eight taxa best characterized the Beaufort

Sea shelf taxonomic structure (BVSTEP, Spearman's correlation coefficient: 0.952, p = 0.001, Figure 2.7a). These taxa were the amphipods *Acanthostepheia behringiensis* and *Paroediceros lynceus*, the cumacean *Diastylis goodsiri*, the seastars *Leptasterias groenlandica* and *Urasterias lincki*, the brittle star *O. sericeum*, the holothurian *P. peronii*, and the shrimp *Sabinea septemcarinata*. Six modalities contributed most to the Beaufort Sea functional structure (BVSTEP, Spearman's correlation coefficient: 0.951, p=0.001). These modalities were dorso-ventrally compressed (BF3), robust (F3), sessile (MV1), sexual brooding (R4), sexual-external reproduction (R2), and solitary (SO1). These influential modalities were well represented by the characteristic taxa (Figure 2.7a). In this matrix of characteristic taxa by modality, 48% of the possible taxa-modality pairings reflected some affinity to each other, often even high affinity. Resemblance matrices of the subset of characteristic taxa and the influential modalities for the Beaufort Sea were significantly related (RELATE; Rho=0.569, p=0.01).

A larger subset of taxa and modalities were needed in the Chukchi than the Beaufort Sea community to maintain taxonomic and functional structure. Twenty-eight taxa best characterized Chukchi Sea shelf taxonomic structure across all stations (BVSTEP, Spearman's correlation coefficient: 0.951, p=0.01; Figure 2.7b). Eleven modalities that most influenced the Chukchi Sea functional structure (BVSTEP, Spearman's correlation coefficient: 0.905 p= 0.001) were direct development (LD1), lecithotrophic development (LD2), fragile (F1), gregarious (SO2), solitary (SO1), laterally compressed (BF4), upright (BF5), medium size (W3), predator (FH4), sessile (MV1), and swimmer (MV4). Influential modalities in the Chukchi Sea were expressed to a lesser degree (39%) by the characteristic taxa and often at a lower affinity than in the Beaufort Sea (Figure 2.7b). Resemblance matrices of the subset of characteristic taxa and influential modalities for the Chukchi Sea were significantly related (RELATE; Rho=0.517, p=0.01).

2.4 Discussion

This study described the functional composition of the Beaufort and Chukchi Sea epibenthic shelf communities and explored the functional and taxonomic relationships between the two shelf systems. Overall, functional diversity patterns reflected those in taxonomic diversity on each shelf, supporting our first hypothesis. In addition, we found that the two shelves were functionally distinct, supporting our second hypothesis, albeit with much overlap in similar proportions of modalities between the two shelves. The biological traits that differed between shelves, especially those related to larval development, reproductive strategy, body size, and body form, can inform about energy flow and resource partitioning within each shelf as well as different community responses to changes and disturbances (Rand et al. 2018). The overlap in functional composition, but strong separation of taxonomic composition between the Beaufort and Chukchi shelves, suggests that different taxa fulfill similar functions in the two systems. Therefore, functional analyses provided complementary perspectives that related the taxonomic patterns to ecosystem function on these Arctic shelves. Specifically, we can use dominant biological traits to pinpoint which resources (e.g., available food or space) are most affected by changes or perturbations in the available niche space and how efficiently those niche spaces are occupied on these two shelf systems.

2.4.1 Comparison of Taxonomic and Functional Diversity Metrics

At the core of the Biodiversity-Ecosystem-Functioning (BEF) concept is the premise that higher taxonomic diversity leads to more efficient ecosystem functioning through higher interaction strength between taxa and their environment. The principle is that more species will use a more diverse set of resources in a system, ultimately increasing the stability of the system against perturbations (Schulze & Mooney 1993, Loreau et al. 2001, Hooper et al. 2005, Cardinale et al. 2009, 2012). In our study, taxonomic diversity (Simpson) and evenness (Pileou's) were significantly higher in the Beaufort Sea shelf assemblages compared to Chukchi Sea shelf assemblages, but there was no difference in taxonomic richness (Margalef's Index) between the two shelves. This similarity in taxonomic richness as well as in functional richness between the two shelf systems provided a unique opportunity to compare functional redundancy of the two shelves in similar taxonomic and functional space. Fewer modalities and fewer taxa were needed to describe the relationships between taxonomic and functional composition of the Beaufort Sea community (8 taxa, 6 modalities) compared to the Chukchi Sea community (28 taxa, 11 modalities; see Figure 2.7), reflecting a higher functional redundancy in the Chukchi Sea. Additionally, fewer taxa were required in the Beaufort Sea to increase functional dissimilarity compared to the Chukchi Sea at a given taxon richness. Together, these relationships point to lower functional redundancy and highly diverse biological trait profiles in the Beaufort Sea that tended to be dominated by single modalities within biological traits. High functional evenness in the Beaufort Sea indicated that most biological traits within assemblages were expressed evenly in functional space, albeit with individual taxa dominated by unique modalities. Likewise, the higher taxonomic evenness pointed to more evenly distributed biomass of taxa on the Beaufort Sea shelf. Our results show that, in general, functional diversity metrics measured on Alaskan Arctic shelf systems mirrored those of taxonomic metrics, following the hypothesized pattern of the BEF concept. Similar patterns between functional and taxonomic composition were found for the Bering Sea macrobenthos (Kun et al. 2019).

Given species are the building blocks of ecosystem function (Bellwood et al. 2019), functional diversity can pinpoint which characteristics, or traits, of species diversity influence ecosystem function (Tilman 2001). For example, we saw strong differences between shelves in body size, likely affecting the movement of energy across the shelves, and in larval development, reproductive strategy, and body form, all of which can inform about resistance to disturbances. This relationship between the two diversity approaches emphasizes the importance of using functional diversity as a complement to taxonomic diversity, especially on Arctic shelves (Rand et al. 2018), considering ecosystem function is likely to change with expected changes in taxonomic composition from climatic pressures (Renaud et al. 2015).

2.4.2 Functional Diversity Metrics

Epibenthic communities on both shelves were overall functionally similar as indicated by comparable FRic and FDiv. However, we also observed differences in functional dissimilarity (Rao's Q) between the epibenthos of the two shelf systems, which were driven by significant differences in FEve. Differences in FEve were reflected in the more even distribution of modalities for the influential biological traits of body form, body size, and larval development in the Beaufort Sea compared with the Chukchi Sea community. Differences in biological trait expressions within a community lead to differences in which resources are used within each community (McGill et al. 2006, Cadotte et al. 2011). Higher FEve and lower functional redundancy (although not significantly lower functional redundancy) in the Beaufort Sea community pointed to the use of a wider range of available resources within their respective niche space (Mason et al. 2005). For example, resource breadth for epibenthic shelf communities differs for substrate and food type. Sediments on the narrow Beaufort Sea shelf are a poorly sorted mix of gravel, sands, and muds, controlled by variable currents, river discharge, and ice rafting (Naidu 1974). In contrast, sediments on the broader Chukchi Sea shelf tend to be more uniform over larger regions in accordance to larger current systems (Grebmeier et al. 2015). Also, the Beaufort Sea shelf contains a diverse range of carbon sources as possible food sources for the benthos, including large amounts of terrestrial organic material from massive river discharge, marine phytoplankton, microphytobenthos, ice algal production, and macroalgal stands in the coastal Beaufort Sea (Dunton & Schell 1987, Bell et al. 2016, Harris et al. 2018). In contrast, there are fewer sources for macroalgae and terrestrial material on the Chukchi shelf. The higher FEve on the Beaufort shelf affords more opportunities to exploit such wider resource Availability. Higher FEve also reflects a strong potential for maintenance of ecosystem function with loss of species due to a high degree of niche complementarity (Hewitt et al. 2008). Greater niche complementarity usually leads to greater resource partitioning within communities (Finke & Snyder 2008). In contrast, the lower FEve in the Chukchi Sea community pointed to lower niche complementarity and, thus, a potential underutilization of resources (Mason et al. 2005). Higher functional redundancy in the Chukchi could also lead to underutilization of resources and is expected to increase with increasing temperatures through the borealization of the Chukchi Sea (Alabia et al. 2020). This scenario could lead to a system that is more vulnerable to invading species that would be able to capitalize on those available, underutilized resources (Tilman 2001). This is of particular importance to an inflow shelf such as the Chukchi Sea shelf, which receives species that are increasingly migrating northward from the Bering Sea in response to continued warming (Mueter & Litzow 2008, Stevenson & Lauth 2019, Thorson et al. 2019, Alabia et al. 2020).

2.4.3 Functional Trait Composition of Beaufort and Chukchi Sea Epibenthos

2.4.3.1 Trait similarities between the shelves

Composition of functional traits on the Beaufort and Chukchi Sea shelves was similar in many aspects as demonstrated through similar proportions of modalities within five biological traits. Shared trait composition should support similar ecosystem functioning (Lavorel & Garnier 2002). For example, benthic macrofaunal groups in the Baltic Sea clustered into groups based on shared biological trait composition that had similar effects on the ecosystem functions of stability and bioturbation (Villnäs et al. 2018, Kun et al. 2018). Similar modality composition between the Beaufort and Chukchi Sea shelves were seen in feeding habit, fragility, living habit, movement, and sociability. Many of these traits can be used to assess the vulnerability of benthic fauna to destructive forces and disturbances. Robustness of taxa, regeneration time, and position in the sediment have been used to assess benthic fauna vulnerable to disturbances such as the impact of predators (Weigel et al. 2016, Beauchard et al. 2017). Predator impacts may increase in Arctic shelf communities as ongoing and future habitat ranges of predatory species (e.g., Pacific and Atlantic cod) extend northward onto Arctic shelves (Rand & Logerwell 2011, Nielsen et al. 2013, Alabia et al. 2020). Such impacts could be further amplified if commercial fisheries were to move north into the Chukchi Sea from the Bering Sea, following demersal fish migrations (Christiansen et al. 2014). One could expect that the Beaufort and Chukchi Sea shelf systems would respond in a similar way to those disturbances based on their similar composition of many functional traits.

Within the shared biological traits of feeding habit and movement, specifically, deposit feeding habit and crawling movement can have strong impacts on ecosystem services such as sediment oxygenation, resuspension, and remineralization through downward and horizontal movements of detrital particles (Levinton 1995, Snelgrove 1999, Snelgrove et al. 2000, Queiros et al. 2013). For example, brittle stars are a dominant taxon across the Beaufort and Chukchi Sea shelves (Ravelo et al. 2015, 2017, Iken et al. 2019), and the prominent species (*Ophiocten sericeum* and *Ophiura sarsii*, respectively) generally express a similar biological trait profile. They are mostly deposit feeders, have medium/robust fragility, free-living habits, burrowing and crawling movement types, and solitary lifestyles. These distinctive modalities in ophiuroids affect carbon and nutrient cycling in a similar way in both Arctic shelf systems through bioturbation (Grebmeier 1993, Kristensen 2000, Ambrose et al. 2001, Kristensen et al. 2012).

2.4.3.2 Trait differences between the shelves

Strong differences existed in modality composition in four biological traits between the Beaufort and Chukchi Sea shelves: larval development, reproductive strategy, body size, and body form. These traits, to varying degrees, have been observed to drive variation in benthic ecosystem function in the North Sea (Bolam & Eggleton 2014) and the Arctic Ocean (Degen 2015, Kokarev et al. 2017, Rand et al. 2018). We suggest that these traits also contribute to differences in ecosystem functioning between the Beaufort and Chukchi Sea shelf communities.

The Chukchi Sea community had a higher proportion of planktotrophic larval development compared to the Beaufort Sea community. Planktotrophic larval development and sexual-external reproductive strategy provide epibenthic taxa with the ability to spread fast and far, which increases their ability to resist or recover after a disturbance (Węsławski et al. 2011). Planktotrophic larvae can spend days to months in the plankton phase because of their need to feed during development (Thorson 1950, Pechenik 1990, Buzhinskaja 2006). This planktonic duration is inversely correlated with temperatures, leading to typically longer times spent in the plankton for Arctic larvae (O'Connor et al. 2007, Ershova et al. 2019) due to reduced metabolic rates compared to regions with warmer water temperatures (Gillooly et al. 2002). For example, planktotrophic larval development time of two common crustaceans, the shrimp *Pandalus borealis* and the hermit crab *Pagurus bernhardus*, followed predicted exponential increases in larval duration with decreased temperature (O'Connor et al. 2007). Long larval development times, coupled with strong, large-scale advection driving a strong injection of larvae from the Bering Sea to the Chukchi Sea shelf (Ershova et al. 2019), allow Arctic taxa to efficiently colonize open space across large distances in the Chukchi Sea. In contrast, the Beaufort Sea shelf community, which does not possess a similar source of advected larvae, had high proportions of lecithotrophic and direct development. These development types either spend no time (direct development) or little time (lecithotrophic development) in the plankton, indicating a high level of preservation of local ecosystem processes mediated by these low-dispersal traits (Degen & Faulwetter 2019). These life history strategies may be an adaptation to the narrow Beaufort Sea shelf, likely reducing advective losses of larvae into unsuitable deep-sea habitats that could result from seasonally strong flow regimes (Pickart 2004). Also, direct or lecithotrophic development might be less affected by large-scale water column stressors. For example, high latitudes are particularly vulnerable to ocean acidification due to the naturally occurring low carbonate concentration derived from low water temperatures (Feely & Chen 1982, Feely et al. 1988, Byrne et al. 2010). These acidic conditions can be particularly detrimental to many of the pelagic early life stages of invertebrates (Long et al. 2013 a, b). Brooding species with direct development are likely less affected by ocean acidification due to maternal protection of the developing juveniles compared with species with planktotrophic larval development that spend extended time periods in those conditions (Lucey et al. 2015).

Body size has been referred to as the master or key trait because it affects numerous aspects of ecosystem functioning because of its many relationships with other traits (Degen et al. 2018). For example, body size is highly correlated with behavioral traits such as predatory feeding habits (Warwick 1984, Riede et al. 2010, Nordström et al. 2015), where larger-sized predators typically consume larger-sized prey (Riede et al. 2010). Indeed, we found a higher proportion of typical upper trophic level feeding habits (i.e., scavengers and predator) in the larger-sized Chukchi epibenthos. Body size can also influence nutrient cycling and energy turnover through metabolic rates (Hall et al. 2009). Nutrient cycling can be directly regulated by organisms, for example, through input of nitrogen to a system via excretion and ingestion and indirectly regulated through an organism's influence on microbial communities and primary production (Hall et al. 2009). In addition, communities with smaller-sized taxa (i.e., the Beaufort Sea community) will have a larger effect on energy turnover compared to those dominated by larger taxa because smaller taxa have higher metabolic, excretion, and turnover rates (e.g., shorter generation time) (Pearson & Rosenberg 1978, Brown et al. 2004, Hall et al. 2009). Larger mobile marine invertebrates such as in the Chukchi Sea are more likely to travel greater distances, which would move energy in the form of biomass across the shelves on a large scale, similar to the large-scale effects of dispersive larvae on ecosystem function discussed above. Higher metabolic, excretion, and turnover rates of smaller mobile invertebrates, coupled with smaller dispersal potential in the Beaufort Sea community, may retain energy more locally compared to the Chukchi Sea community. This essentially creates a system where taxa in the Beaufort Sea are more restricted to use the local resources available, where high FEve reflects more efficient use of all available resources by the functionally more dissimilar assemblages (high Rao's Q).

Body form is often related to ecological roles such as bioturbation and habitat formation that can lead to ecosystem stability (Degen & Faulwetter 2019). Taxa with specific body forms can be vulnerable to common disturbances, which may destabilize ecosystem function (Jørgensen et al. 2015, 2019, Degen et al. 2018, Degen & Faulwetter 2019). For example, pressure from some predators or trawling will likely affect upright body forms more than vermiform or dorso-ventrally compressed body forms because upright body forms have more above-ground exposure (Bremner et al. 2006, Jørgensen et al. 2019). Dorso-ventrally compressed body forms, in addition to vermiform body forms, increase bioturbation, which tends to foster ecosystem production and stability (Degen & Faulwetter 2019). Body form is more closely related to taxonomic identity than most other traits, i.e., biological traits are assigned to taxa that are typically identified based on morphological features (Beauchard et al. 2017). This close relationship between body form and taxonomy makes body form a contentious trait to include in functional diversity analyses (Beauchard et al. 2017). The inclusion of this trait has advantages and disadvantages due to the strong relationships that exist between body form-related traits and the taxa present in a region, which gives taxonomy disproportional weight in functional analyses. In our study, we saw this relationship between dominant body forms and taxonomy in both shelf systems. For example, the Chukchi Sea epibenthos was mostly dominated by the dorso-ventrally compressed body form, which was reflected in the frequent and high biomass-contributing species such as *Chionoecetes opilio*, *Echinarachnius parma*, and *Ophiura sarsii*. In contrast, the Beaufort Sea epibenthos was dominated by globulose, dorso-ventrally compressed, and laterally compressed body forms, which were represented by the frequent biomass contributors *Psolus peronii*, *Ophiocten sericeum*, and *Similipecten greenlandicus*, respectively (note that *S. greenlandicus* and other bivalves were functionally coded as laterally compressed based on morphology, not necessarily reflecting their position on the seafloor). Although a tight relationship with taxonomy did exist, we considered the inclusion of body form necessary to glean information on community vulnerability to such disturbances like trawling. The Chukchi Sea shelf, which is directly north of the Bering Sea, will likely see increased commercial interest, but may be more resilient to this type of disturbance if the shelf remains dominated by taxa that are dorso-ventrally compressed.

2.5 Conclusion

The current benchmark of functional and taxonomic diversity metrics and of functional and taxonomic composition of Beaufort and Chukchi Sea epibenthic communities provided here will aid in future shelf-wide or among-shelf ecosystem function comparisons in the Alaskan Arctic. In the rapidly changing Arctic, these benchmarks will support interpretation of long-term monitoring data. Currently, differences in specific biological traits (e.g., body form, body size, larval development, reproductive strategy) lead to differences in ecosystem function between the Beaufort and Chukchi Sea epibenthic shelf communities. These differences mirrored differences in taxonomic diversity, with the Beaufort Sea epibenthic community having significantly higher diversity. The combination of functional and taxonomic diversity metrics enables us to have a comprehensive understanding of how ecological niche space is currently used in Alaskan Arctic benthic shelf systems. Future studies should evaluate environmental influences on functional diversity as well as ecosystem function changes over time and space so we can predict how the ecology of the Arctic benthos is likely to change.

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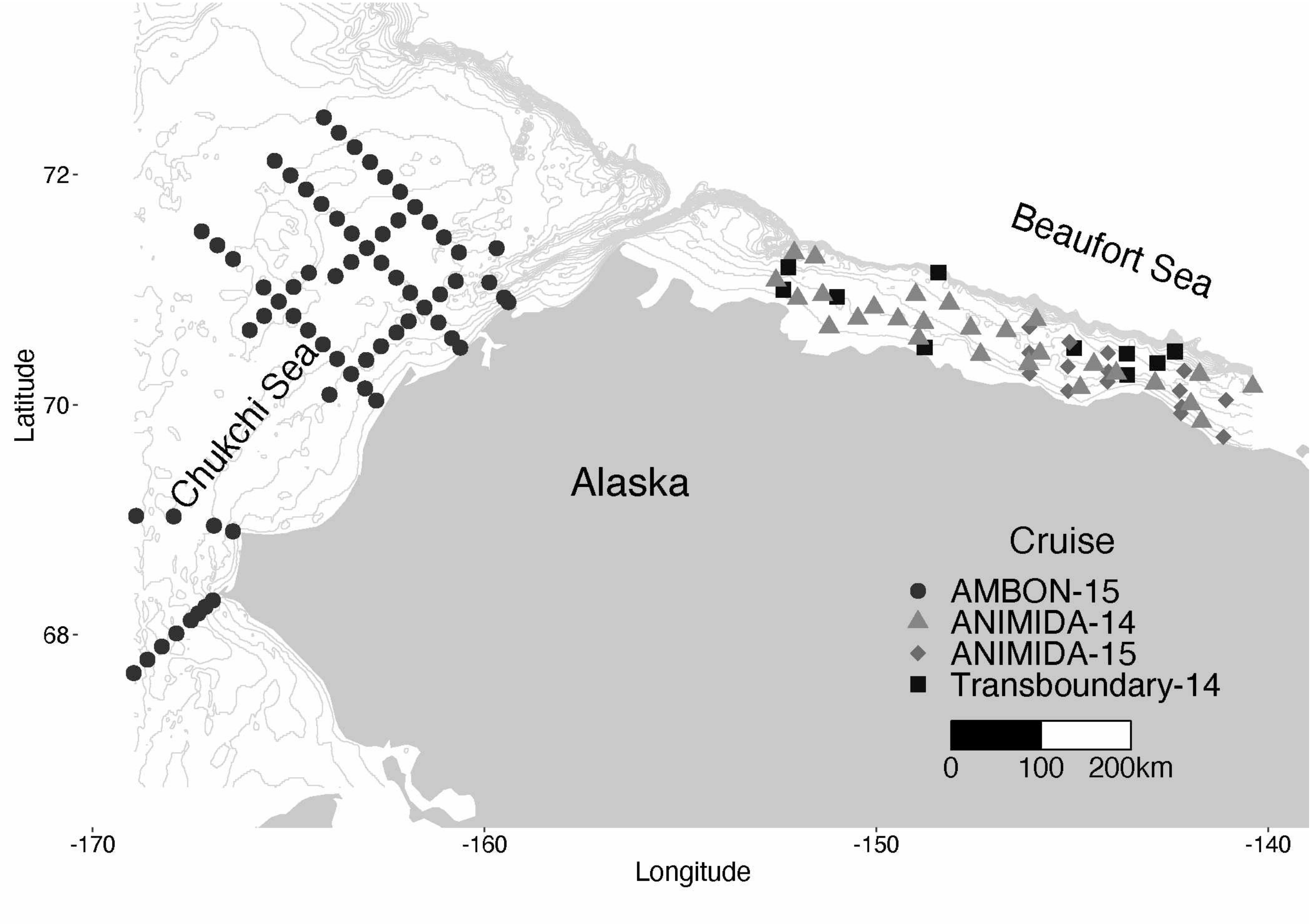


Figure 2.1. Stations sampled for epibenthic communities during four cruises in the Beaufort and Chukchi seas in 2014 and 2015. Stations are designated by symbols to different cruises. Depth contours in the study regions are shown in gray at 10 m intervals.

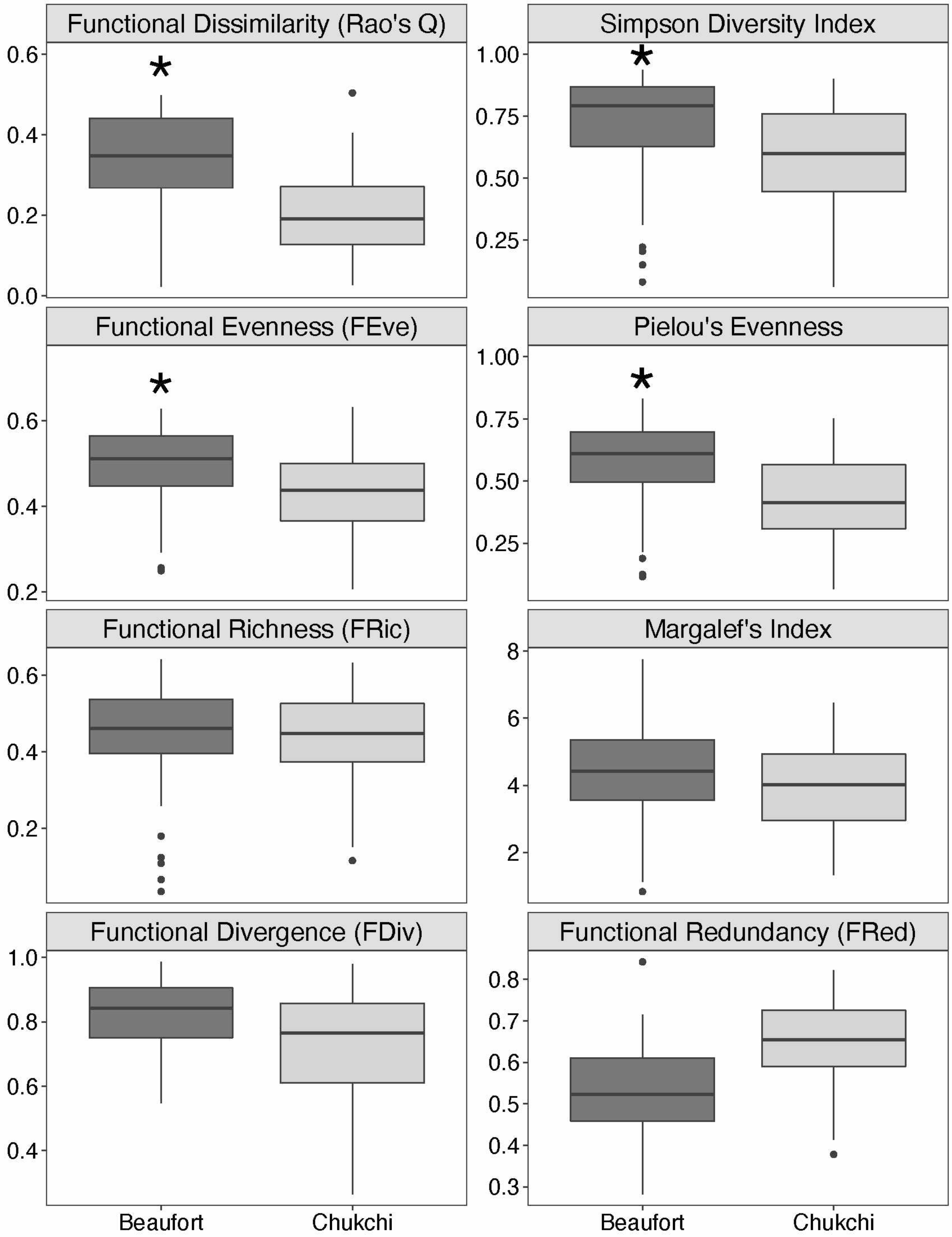


Figure 2.2. Diversity metrics for the Beaufort (dark gray) and Chukchi (light gray) Sea shelf epibenthic assemblages based on community weighted means for functional diversity indices and square root transformed biomass for taxonomic diversity indices. *indicates a significant difference between shelf assemblages (see Table 2.4).

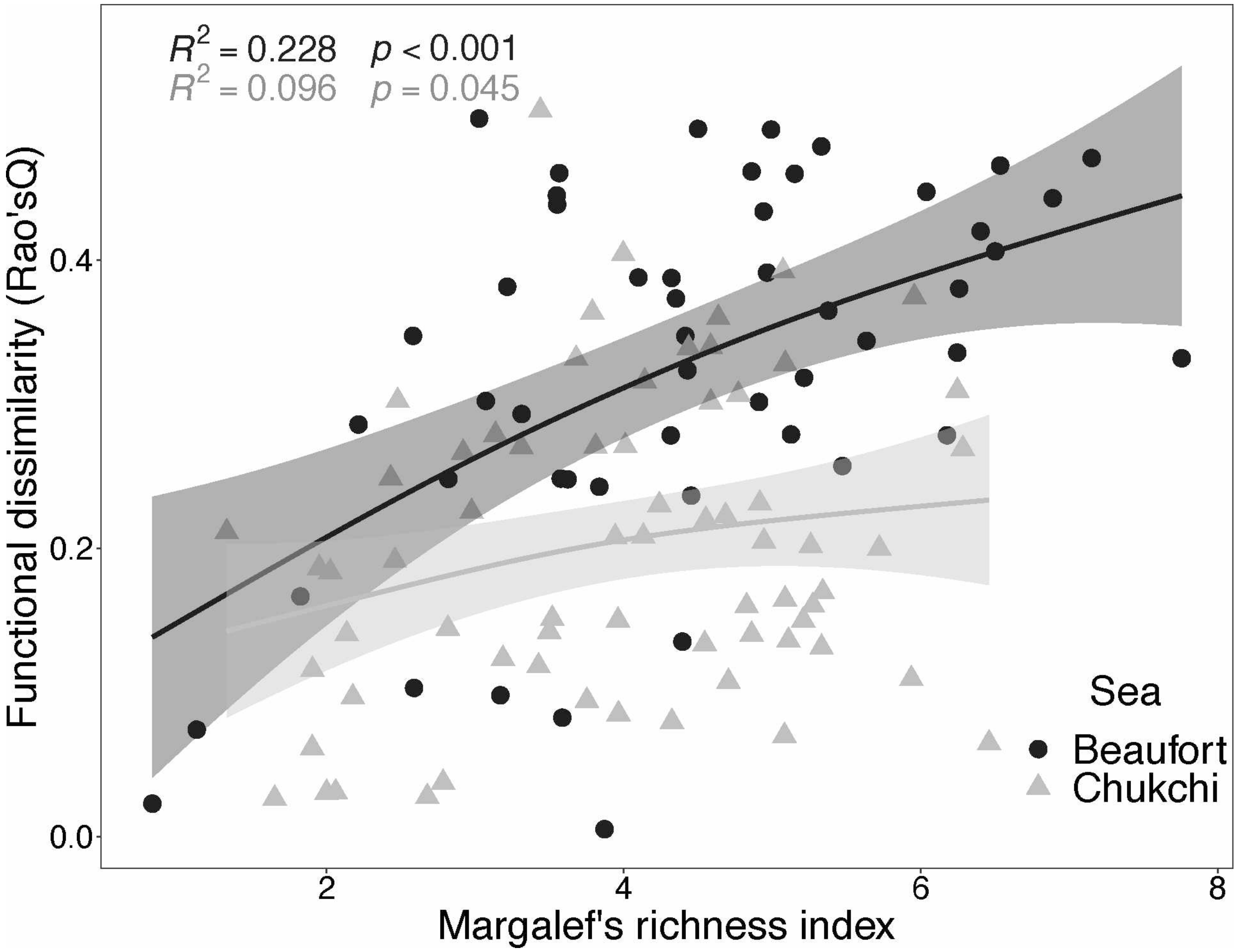


Figure 2.3. Functional dissimilarity (Rao's Q) in the Beaufort Sea (dark gray) and Chukchi Sea (light gray) as a function of species richness (Margalef's Index). Trends and confidence intervals estimated based on a generalized additive model (GAM)-smoother to visualize the general trends.

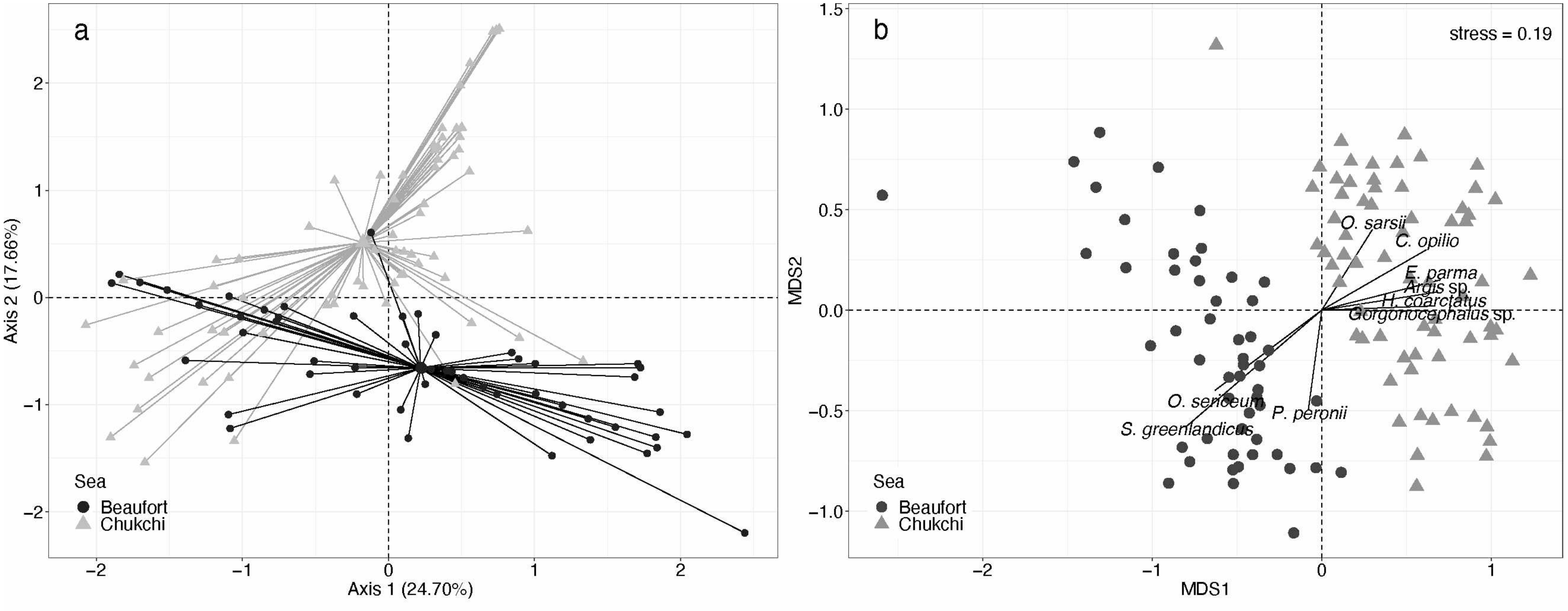


Figure 2.4. Fuzzy correspondence analysis of functional composition (a) and non-metric multidimensional scaling (nMDS) plot of taxonomic composition (b) of the Beaufort and Chukchi Sea shelf epibenthic communities. Each point represents a station in the Beaufort (dark gray) or Chukchi (light gray) Sea. Functional composition was based on the proportion of community-weighted-mean modalities expressed at each station while taxonomic composition was based on square root transformed biomass. Vectors in the FCA (a) represent the distance of stations to the centroid for each shelf system. Vectors in the nMDS (b) represent taxa that contributed most to differences in taxonomic composition between the two shelves (SIMPER analysis). The direction of vectors in the nMDS indicates where taxon biomass increased and influenced the ordination, and vector length indicates the strength of the pattern in taxon biomass along that direction

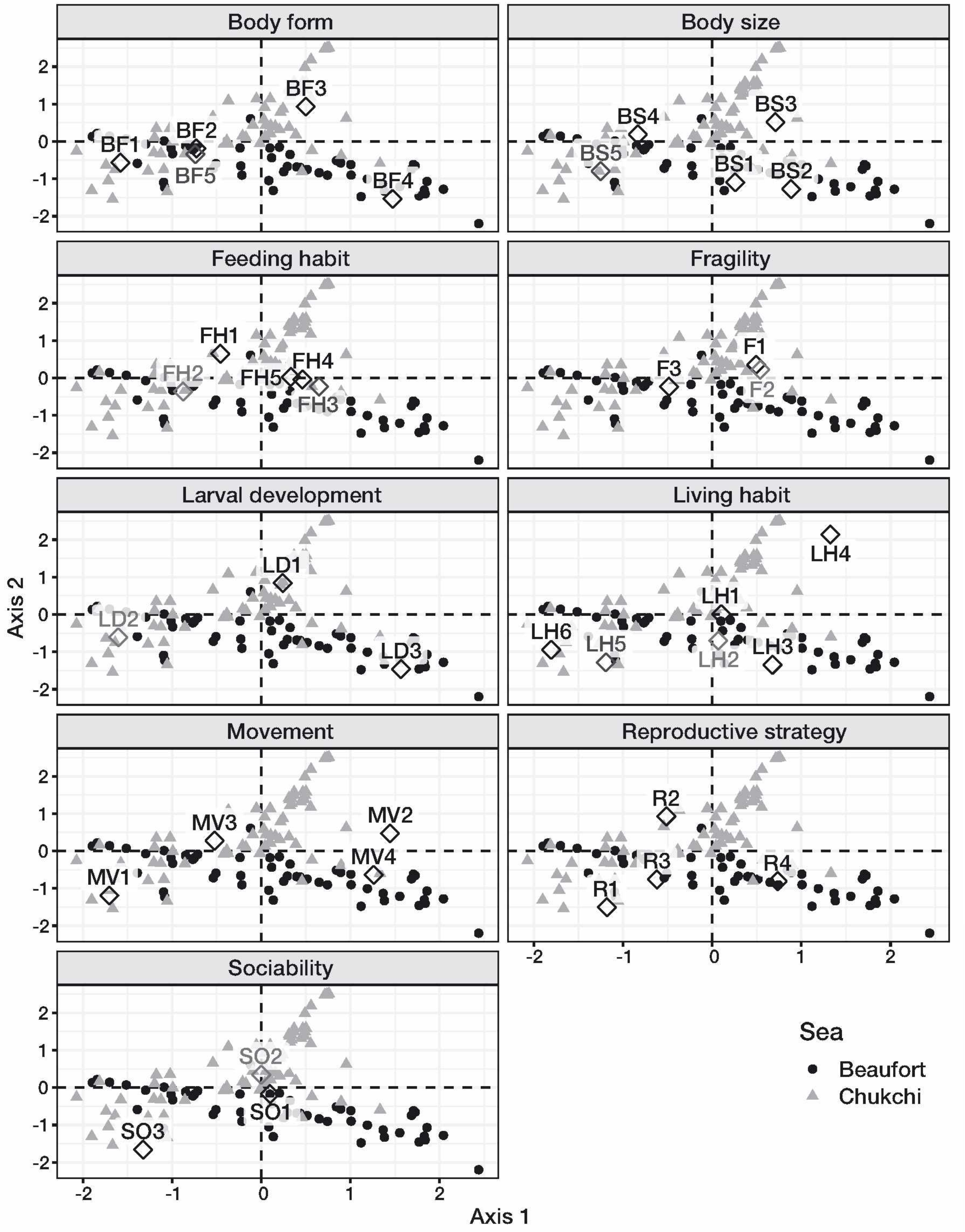


Figure 2.5. Fuzzy correspondence analysis plots of functional composition for stations from the Beaufort (dark gray) and Chukchi Sea (light gray) for all biological traits of epibenthic taxa. Vector length is representative of association strength and vector direction is indicative of influence on the ordination. For trait and modality definitions see Table 2.1.

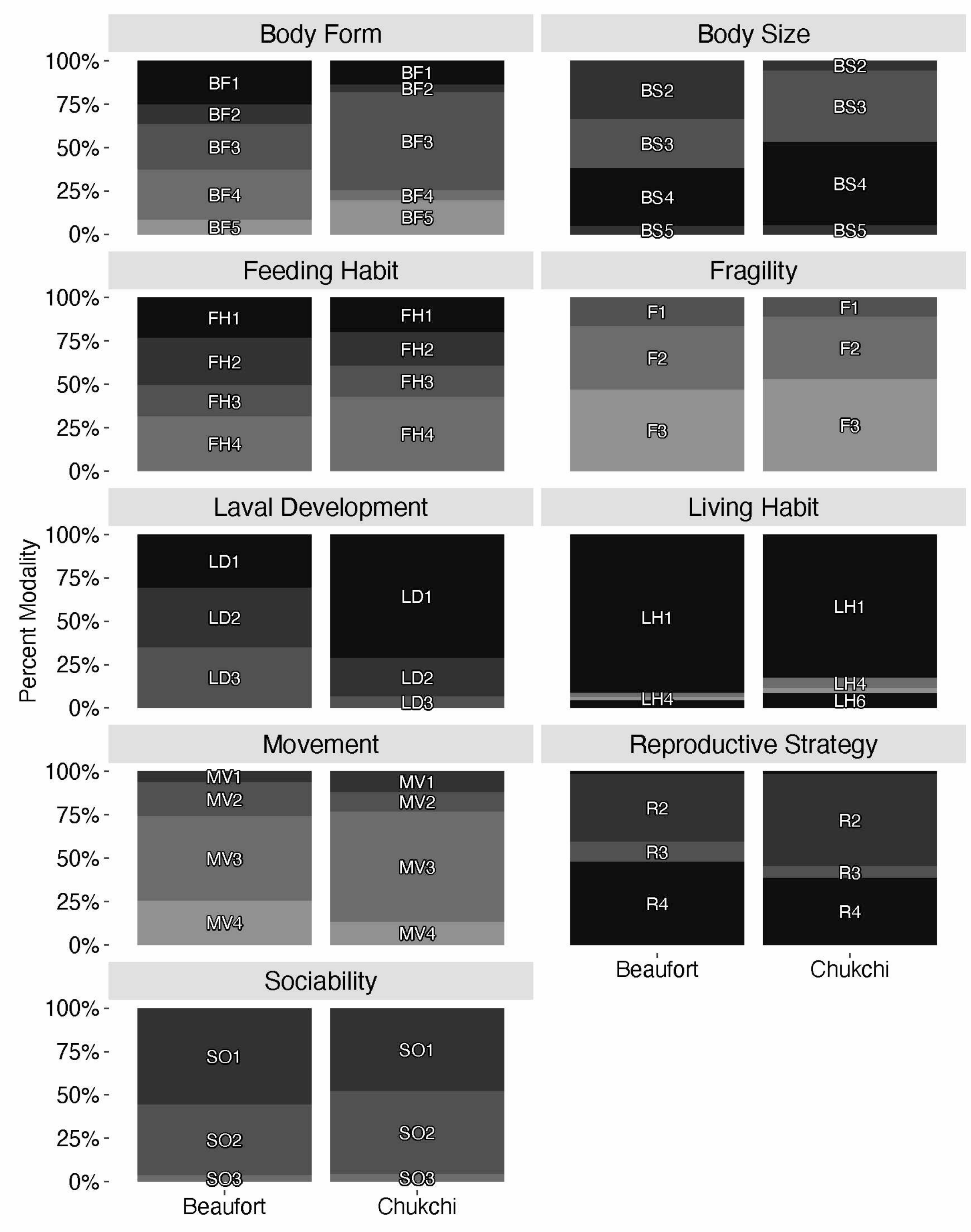


Figure 2.6. Stacked bar plots showing the percent of each modality within each biological trait for the Beaufort (left bars) and Chukchi (right bars) Sea shelf epibenthic communities. Only modalities that contributed greater than two percent of the total sea CWM biomass are shown. Modality abbreviations as in Table 2.4.

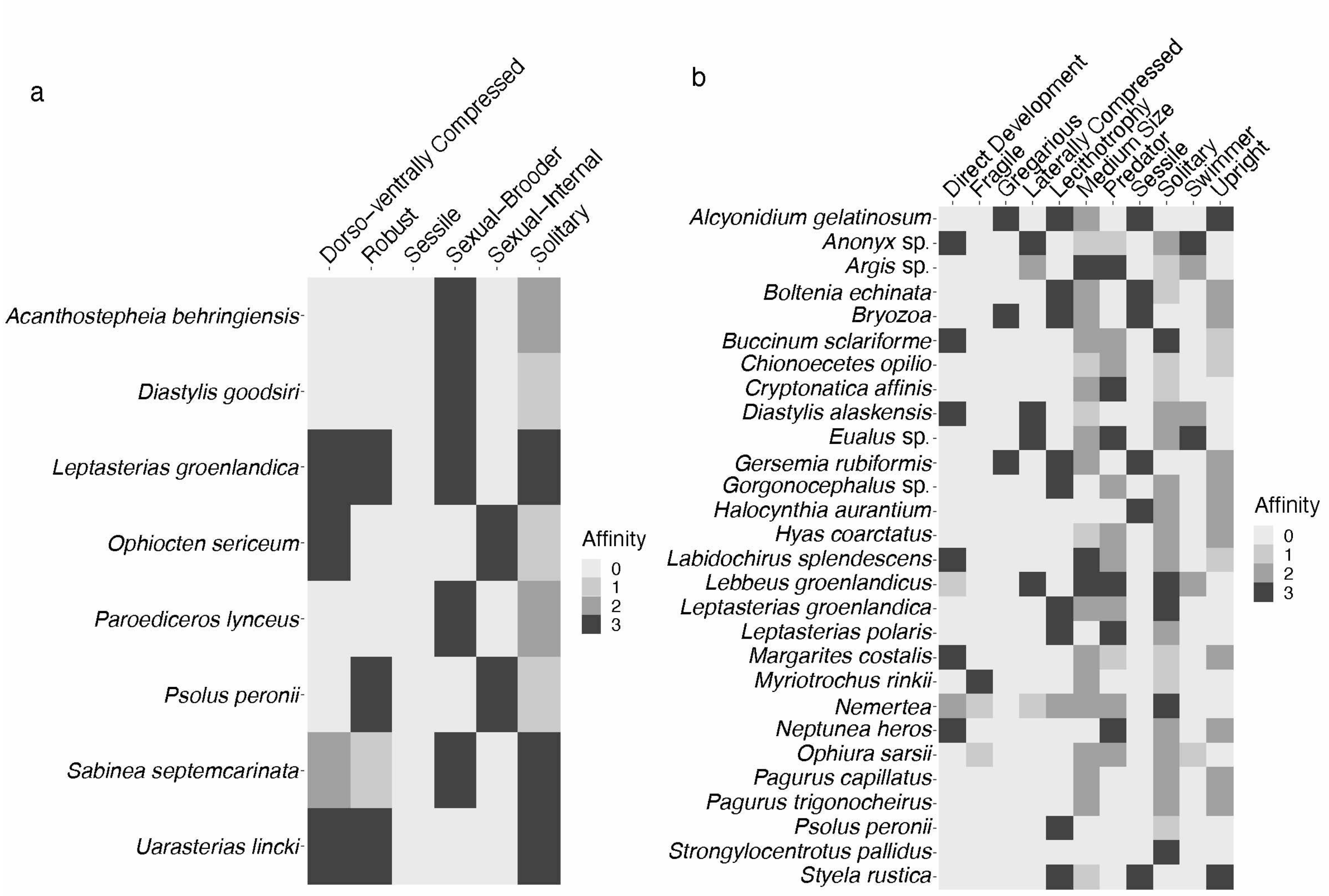


Figure 2.7. Matrix of pairwise affinities between characteristic taxa and influential modalities in the Beaufort Sea (a) and Chukchi Sea (b) based on BVSTEP analyses with Spearman's correlation coefficient > 0.95 and p ≤ 0.001. Shading represents a taxon's affinity for a given modality (from white = low affinity [0] to dark gray = high affinity [3]).

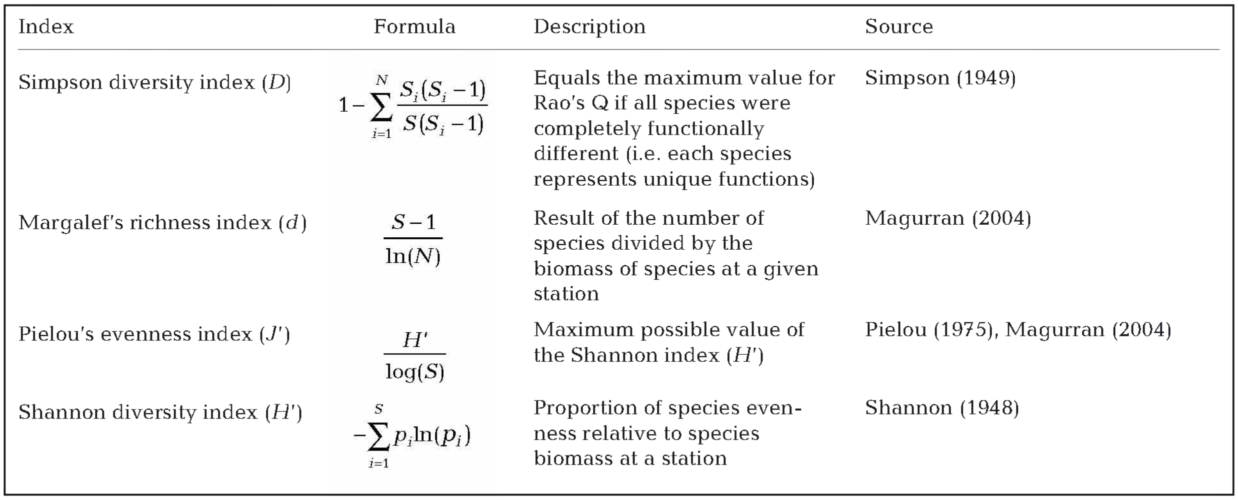
Table 2.1. Biological traits and modalities assembled for epibenthic invertebrates collected in the Chukchi and Beaufort seas, following Degen and Faulwetter (2019). Abb: Modality abbreviations used in figures.

Biological trait	**Modality**	**Abb.**	**Description**	**Ecological relevance**
Body Form	Globulose	BF1	Round	Ecological role of species (e.g., habitat forming) and/or vulnerability to mechanical disturbances
	Vermiform	BF2	Wormlike	
	Dorso-ventrally compressed	BF3	flattened/encrusting	
	Laterally compressed	BF4	Thin	
	Upright	BF5	Body forms upward from seafloor	
Size (wet weight in grams)	Small	BS1	0.01-0.1	Effect on productivity, energy flow, trophic and food web structure
	Small-medium	BS2	0.1-1.0	
	Medium	BS3	1.0-10	
	Medium-large	BS4	10-100	
	Large	BS5	>100.0	
Feeding Habit	Deposit feeder	FH1	Removal of detrital material from sediment	Indicative of hydrodynamic conditions and carbon transport
	Filter/suspension feeder	FH2	Filter food from the water column	
	Opportunist/scavenger	FH3	Scavenges food	
	Predator	FH4	Actively hunts live prey	
	Parasite	FH5	Feeds off other organisms	
Fragility	Fragile	F1	Easily damaged due to physical impacts	Sensitivity to physical and/or predatory disturbances
	Intermediate	F2	Moderately damaged due to physical impacts	
	Robust	F3	Unlikely damaged due to physical impacts	
Larval Development	Planktotrophic	LD1	Larvae feed and grow in water column	Ability to disperse, become invasive, or recover from disturbance
	Lecithotrophic	LD2	Larvae with yolk sac, pelagic for short periods	
	Direct development	LD3	No larval stage (eggs develop into juveniles)	
Living Habit	Free living	LH1	Not limited to any restrictive structure	Vulnerability to predation and perturbations, habitat facilitation, storage and movement of energy
	Crevice dwelling	LH2	Inhabiting coarse/rock or algal holdfasts	
	Tube dwelling	LH3	Tube lined with sand, mucus or CaCO3	
	Burrow dwelling	LH4	Species inhabiting burrows in the sediment	
	Epi/endo zoic/phytic	LH5	Biogenic species or algal holdfasts	
	Attached	LH6	Adherent to a substratum	
Movement	Sessile/none	MV1	No movement as adult	Movement of energy through nutrient cycling, carbon deposition, and maintain habitat stability
	Burrower	MV2	Movement in the sediment	
	Crawler	MV3	On surface via movement of appendages	
	Swimmer	MV4	Movement above the sediment	
Reproductive strategy	Asexual	R1	Budding	Ability to withstand disturbances and carbon transportation
	Sexual -external	R2	Eggs/sperm released into water	
	Sexual - internal	R3	Eggs deposited on substrate / internal fertilization	
	Sexual - brooder	R4	Eggs are brooded, larvae/mini-adult hatches	
Sociability	Solitary	SO1	Single individual	Sensitivity to disturbance and/or habitat forming
	Gregarious	SO2	Single individuals found in groups	
	Colonial	SO3	Living in permanent colonies	

Table 2.2. Summary of the functional indices used in this study where s is the total number of species, p_i and p_j are the relative biomass of species I and j, X_i is the fuzzy-coded trait value, $d_{ij,}$ is the dissimilarity in biological trait profiles for species I and j, dist(I,j) is the nearest neighbor minimum spanning tree (MST) distance for each pair of species (I, j), w_i and w_j are the proportional biomass of species I and j, T is the trait value (i.e., PcoA coordinates), n is the n^{th} trait value, Δd is the sum of biomass-weighted deviances from the center of gravity, $\Delta|d|$ is the absolute value of biomass-weighted deviances from the center of gravity, and $\overline{dG}$ is the mean distance to the center of gravity.

Metric	Equation	Description	Ecology	Source
Community weighted mean (CWM)	$\sum_{i=1}^{N} p_i X_i$	Sum of the relative biomass-weighted species' biological trait profiles at a station	Functional composition at each station	Garnier et al. (2007), Laliberté & Legendre (2010)
Functional dissimilarity (Rao's Q)	$\sum_{i=1}^{N}\sum_{j=1}^{N} d_{ij} p_i p_j$	Biomass-weighted sum of mean trait dissimilarities between individuals within a station	Dissimilarity of species' biological trait profiles within a station	Rao (1982), Ricotta et al. (2016)
Functional evenness (FEve)	$\dfrac{\sum_{i=1}^{N-1}\left(PEW_{I}, \frac{1}{N-1}\right) - \frac{1}{N-1}}{1 - \frac{1}{N-1}}$	Cumulative Gower distances between pairs of species represented by the minimum spanning tree (MST) branch lengths that links all species for each station based on species' biological trait profiles	Resource use from the entire range of resources available	Mason et al. (2005), Villéger et al. (2008)
Partial weighted evenness (PEW)	$\dfrac{EW_I}{\sum_{I=1}^{N-1} EW_I}$			
Weighted evenness (EW)	$\dfrac{dist(i,j)}{w_i + w_j}$			
Functional richness (FRic)	$(Ti_1 + (1-T)\, j_1,$ $Ti_2 + (1-T)\, j_2, \ldots,$ $Ti_n + (1-T)\, j_n)$	Total convex hull volume of each station in functional trait space as defined by the PCoA axes	Total niche space occupied by the station	Villéger et al. (2008)
Functional divergence (FDiv)	$\dfrac{\Delta d + \overline{dG}}{\Delta\lvert d\rvert + \overline{dG}}$	Distribution of the biomass-weighted distances of species from the station center of gravity in functional trait space	Degree to which species differentiate within the niche space of a station	Villéger et al. (2008), Laliberté & Legendre (2010)
Functional redundancy (FRed: 1 - MPD)	$1 - \dfrac{1}{\sum_{i>j}^{N} p_i p_j} \sum_{i>j}^{N} p_i p_j d_{ij}$	One minus the probability that species within a given station are equally and maximally different	Degree to which species play similar roles in communities	Rosenfeld (2002), Kembel et al. (2010), de Bello et al. (2016)

Table 2.3. Summary of the taxonomic-based metrics used in this study, where s_i is the biomass of species *i*, *S* is the total biomass of all species at each station, *n* is the number of species at each station, and p_i is the proportion of biomass of species *i* at a station relative to the total biomass of that station.



Index	Formula	Description	Source
Simpson diversity index (*D*)	$1-\sum_{i=1}^{N}\frac{S_i(S_i-1)}{S(S_i-1)}$	Equals the maximum value for Rao's Q if all species were completely functionally different (i.e. each species represents unique functions)	Simpson (1949)
Margalef's richness index (*d*)	$\frac{S-1}{\ln(N)}$	Result of the number of species divided by the biomass of species at a given station	Magurran (2004)
Pielou's evenness index (*J'*)	$\frac{H'}{\log(S)}$	Maximum possible value of the Shannon index (*H'*)	Pielou (1975), Magurran (2004)
Shannon diversity index (*H'*)	$-\sum_{i=1}^{S}p_i\ln(p_i)$	Proportion of species evenness relative to species biomass at a station	Shannon (1948)

Table 2.4. Metrics compared between the Beaufort and Chukchi Sea, model structure (with or without spatially autocorrelated residuals), estimated mean for the Beaufort Sea (intercept α), difference between Chukchi and Beaufort Sea means (β) and significance level for β. Significant differences ($p \leq 0.05$) in bold.

Metric	Spatial auto-correlation	α (CI)	β	Significance (H_0: $\beta = 0$)
Rao's Q	No	0.326 (0.294 – 0.358)	**-0.126**	**< 0.001**
Simpson	No	0.707 (0.644 – 0.771)	**-0.136**	**0.002**
FEve	Yes	0.493 (0.449 – 0.053)	**-0.056**	**0.053**
Pielou	Yes	0.588 (0.503 – 0.672)	**-0.137**	**0.020**
FRic	No	0.431 (0.392 – 0.470)	-0.003	0.827
Margalef	Yes	4.501 (3.858 – 5.145)	-0.768	0.078
FDiv	Yes	0.793 (0.651 – 0.936)	-0.123	0.464
FRed	Yes	0.553 (0.461 - 0.644)	0.228	0.276

Table 2.5. Correlation ratios of the biological traits for the first two FCA axes (RS, see Figure 2.4a). Biological traits (trait abbreviations as in Table 2.1) that accounted for the most variation in the FCA (correlation values [RS] >0.1) are shown in bold.

Trait	RS1	RS2
Body form (BF)	**0.26**	**0.21**
Body size (BS)	**0.17**	**0.11**
Fragility (F)	0.06	**0.12**
Feeding habit (FH)	0.09	0.03
Larval development (LD)	**0.30**	**0.22**
Living Habit (LH)	0.08	0.07
Movement (MV)	**0.26**	0.07
Reproductive strategy (RS)	**0.10**	**0.19**
Sociability (SO)	0.02	0.04
Variance	24.70%	17.66%
Eigenvalues	0.15	0.11

Table 2.6. Epibenthic taxa with the largest percent contribution to differences in taxonomic composition between the Beaufort and Chukchi Sea shelves, ordered from most contribution to least contribution. The cumulative percent of total biomass for influential taxa is shown.

Species	SIMPER results (%)		Total biomass (%)		Frequency of occurrence (%)		Average biomass per station when present (%)	
	Indiv. contrib.	Cum. contrib.	Chuk	Beau	Chuk n = 67	Beau n = 52	Chuk n = 67	Beau n = 52
Chionoecetes opilio	6.9	6.9	7.0	<0.1	94.0	7.7	1.4	0.1
Ophiura sarsii	6.9	13.8	22.5	0.5	50.8	7.7	8.4	2.1
Psolus peronii	5.2	19.0	6.0	41.1	26.9	51.9	4.3	24.7
Echinarachnius parma	3.9	22.9	33.0	0	11.9	0	52.4	0
Ophiocten sericeum	2.9	25.8	<0.1	11.1	6.0	80.8	0.1	4.3
Similipecten greenlandicus	2.5	28.3	0	7.3	0	78.9	0	2.9
Argis sp.	2.2	30.6	0.9	0.1	82.1	7.7	0.2	0.2
Gorgonocephalus sp.	2.2	32.8	2.8	<0.1	43.3	1.9	1.2	0.4
Hyas coarctatus	2.1	34.9	1.3	0.1	82.1	9.6	0.3	0.5
Number of taxa			247	246				
Total average biomass per station (g wet weight per 1000 m^2)			3849	16910				
Percent of total biomass			73.42	60.20				

2.6 Appendix

Table S2.1. Fuzzy coded values ranged from 0 (no affinity) to 3 (high affinity) for taxa in the first column. Traits are shown in the first row with modalities in the second row. Modality definitions are shown in Table 2.1.

	Body form					Body size					Feeding habit				Fragility			Larval development			Living habit						Movement				Reproductive strategy				Sociability		
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	1	2	3	1	2	3	1	2	3	4	5	6	1	2	3	4	1	2	3	4	1	2	3
Acanthonotozoma inflatum	0	0	0	3	0	1	2	0	0	0	0	0	1	2	0	1	2	0	0	3	3	0	0	0	0	0	0	0	2	2	0	0	0	3	2	2	0
Acanthonotozoma rusanovae	0	0	0	3	0	0	3	0	0	0	0	0	1	2	0	1	2	0	0	3	3	0	0	0	0	0	0	0	2	2	0	0	0	3	2	1	0
Acanthostepheia behringiensis	0	0	0	3	0	0	2	1	0	0	0	0	3	0	0	3	0	0	0	3	3	0	0	0	0	0	0	2	0	2	0	0	0	3	2	2	0
Acanthostepheia malmgreni	0	0	0	3	0	0	3	0	0	0	0	0	3	0	0	0	0	0	0	3	3	0	0	0	0	0	0	0	0	3	0	0	0	3	3	0	0
Actinaria	2	1	0	0	3	0	0	2	2	0	1	1	1	2	1	3	2	2	3	1	1	1	0	1	1	2	3	1	2	1	1	2	0	1	2	2	1
Adalaria sp.	2	0	1	0	0	0	2	1	0	0	0	0	0	3	0	3	0	0	3	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Admete solida	1	0	0	0	2	0	2	2	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Admete sp.	1	0	0	0	2	0	2	2	0	0	0	0	0	0	1	2	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Admete viridula	1	0	0	0	2	0	2	1	0	0	0	0	0	0	1	2	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Alcyonidium disciforme	1	0	2	0	0	0	2	2	0	0	0	3	0	0	0	3	0	0	3	0	3	0	0	0	0	0	3	0	0	0	1	0	0	2	0	0	3
Alcyonidium gelatinosum	0	0	0	0	3	0	0	2	2	1	0	3	0	0	0	2	1	0	3	0	0	0	0	0	1	2	3	0	0	0	1	0	0	2	0	0	3
Allantactis parasitica	3	0	0	0	0	0	0	2	1	0	0	0	2	1	3	0	0	0	3	0	0	0	0	0	3	0	2	0	1	0	0	3	0	0	2	1	0
Amicula vestita	0	0	3	0	0	0	0	2	1	0	3	0	0	0	0	3	0	0	3	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	2	1	0
Amphipoda	1	0	1	2	0	1	2	1	0	0	2	2	2	2	1	2	1	0	0	3	2	0	1	1	0	0	0	1	1	2	0	0	0	3	2	1	0
Amphiura sundevalli	0	0	3	0	0	0	3	0	0	0	0	3	0	0	3	0	0	3	0	0	0	0	0	3	0	0	0	3	0	0	0	3	0	0	1	2	0
Anomalisipho martensi	1	0	0	0	2	0	0	3	0	0	0	0	2	2	0	3	0	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Anomalisipho verkruezeni	1	0	0	0	2	1	1	2	0	0	0	0	2	2	0	2	1	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Anonyx sp.	0	0	0	3	0	0	2	1	0	0	0	0	2	1	0	3	0	0	0	3	3	0	0	0	0	0	0	0	0	3	0	0	0	3	2	2	0

Anthosactis janmayeni	1	0	0	0	2	0	0	3	0	0	0	0	0	3	0	3	0	0	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	0	2	1	0
Arcteobia anticostiensis	0	2	1	0	0	0	3	0	0	0	0	0	0	3	0	3	0	3	0	0	0	0	2	0	2	0	0	0	3	0	0	0	3	0	2	1	0
Arctolembos arcticus	0	0	0	3	0	0	2	1	0	0	3	0	0	0	1	2	0	0	0	3	0	0	3	0	0	0	0	2	0	2	0	0	0	3	3	0	0
Arctonoe vittata	0	2	1	0	0	0	3	0	0	0	3	0	0	0	1	2	0	3	0	0	1	0	0	0	2	0	0	0	3	0	0	3	0	0	3	0	0
Argis sp.	0	0	1	2	0	0	0	3	0	0	0	0	0	3	0	2	1	3	0	0	2	0	0	1	0	0	0	1	0	2	0	0	0	3	1	2	0
Ariadnaria borealis	1	0	0	0	2	0	2	1	0	0	0	3	0	0	0	3	0	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Arrhis luthkei	0	0	0	3	0	0	3	0	0	0	0	3	0	0	0	3	0	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	0	3	2	1	0
Arrhis phyllonyx	0	0	0	3	0	0	3	0	0	0	1	1	1	1	0	3	0	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	0	3	3	0	0
Ascidia callosa	1	0	0	0	2	0	0	1	2	1	0	3	0	0	2	1	0	3	0	0	0	0	0	0	0	3	3	0	0	0	0	3	0	0	1	2	0
Ascidiacea	2	1	2	0	2	0	0	2	1	0	0	3	0	0	1	2	1	1	2	1	1	0	0	0	1	2	3	0	0	0	1	2	0	2	1	2	2
Asterias amurensis	0	0	3	0	0	0	0	0	2	1	0	0	1	2	0	0	3	3	0	0	3	0	0	0	0	0	0	0	3	0	0	3	0	0	2	0	0
Atylus bruggeni	0	0	0	3	0	2	2	0	0	0	3	0	0	0	2	2	0	0	0	3	3	0	0	0	0	0	0	0	0	3	0	0	0	3	1	2	0
Atylus carinatus	0	0	0	3	0	0	3	0	0	0	3	0	0	0	2	2	0	0	0	3	3	0	0	0	0	0	0	0	0	3	0	0	0	3	2	2	0
Atylus smitti	0	0	0	3	0	1	2	0	0	0	3	0	0	0	2	2	0	0	0	3	3	0	0	0	0	0	0	0	0	3	0	0	0	3	2	2	0
Aulacofusus brevicauda	1	0	0	0	2	0	1	2	0	0	0	0	0	3	0	0	3	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Balanus sp.	1	0	0	0	2	1	2	2	2	0	0	3	0	0	0	0	3	3	0	0	0	0	0	0	1	2	3	0	0	0	0	0	0	3	1	2	0
Bathypolypus sp.	2	0	0	0	2	0	0	0	3	0	0	0	0	3	0	0	3	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	0	3	3	0	0
Beringius stimpsoni	1	0	0	0	2	0	0	1	2	0	0	0	2	2	0	2	2	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	2	1	0
Boltenia echinata	1	0	0	0	2	0	1	2	0	0	0	3	0	0	0	1	2	0	3	0	0	0	0	0	1	2	3	0	0	0	0	0	0	3	1	2	0
Boltenia ovifera	1	0	0	0	2	0	0	1	2	0	0	3	0	0	0	1	2	0	3	0	0	0	0	0	1	2	3	0	0	0	0	0	0	3	1	2	0
Boreoscala greenlandica	1	0	0	0	2	0	0	3	0	0	0	0	0	2	0	1	2	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Boreotrophon clathratus	1	0	0	0	2	0	1	2	0	0	0	0	0	3	0	3	0	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Boreotrophon cymatus	1	0	0	0	2	0	2	2	0	0	0	0	0	3	0	3	0	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Boreotrophon sp.	1	0	0	0	2	0	1	2	1	0	0	0	0	3	0	3	0	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Boreotrophon truncatus	1	0	0	0	2	0	2	2	1	0	0	0	0	3	0	3	0	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Brachiopoda	0	0	0	3	0	0	1	2	0	0	0	3	0	0	0	2	1	2	0	2	3	0	0	0	0	0	2	1	0	0	0	2	0	2	3	0	0
Bryozoa	1	0	1	0	2	0	1	2	2	0	0	3	0	0	0	2	1	0	3	0	1	0	0	0	1	2	3	0	0	0	1	0	0	2	0	0	3

Buccinum angulosum	2	0	0	0	1	0	0	1	2	0	0	0	2	2	0	0	3	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Buccinum ciliatum	2	0	0	0	1	0	0	3	0	0	0	0	2	2	0	3	0	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Buccinum glaciale	2	0	0	0	1	0	0	2	1	0	0	0	2	2	0	0	3	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Buccinum plectrum	2	0	0	0	1	0	2	2	2	0	0	0	2	2	0	0	3	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Buccinum polare	2	0	0	0	1	0	2	2	1	0	0	0	2	2	0	3	0	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Buccinum scalariforme	2	0	0	0	1	0	2	2	1	0	1	0	2	1	0	0	3	0	0	3	3	0	0	0	0	0	0	1	2	0	0	0	3	0	3	0	0
Buccinum solenum	2	0	0	0	1	0	1	2	2	0	0	0	2	2	0	0	3	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Buccinum sp.	2	0	0	0	1	0	2	2	1	0	1	0	2	2	0	1	2	0	0	3	3	0	0	0	0	0	0	1	2	0	0	0	3	0	3	0	0
Buccinum tenellum	2	0	0	0	1	0	0	3	0	0	0	0	2	2	0	0	3	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Bylgides promamme	0	2	1	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bylgides sarsii	0	3	0	0	0	0	2	0	0	0	0	0	0	3	1	2	0	3	0	0	0	0	0	2	2	0	0	0	2	1	0	3	0	0	1	2	0
Bylgides sp.	0	2	1	0	0	0	2	1	0	0	0	0	0	3	0	3	0	3	0	0	0	0	0	2	2	0	0	0	3	0	0	3	0	0	1	2	0
Calycidoris guentheri	1	0	2	0	0	0	2	1	0	0	0	0	0	3	0	3	0	3	0	0	3	0	0	0	0	0	0	0	0	3	0	0	3	0	3	0	0
Caprella	0	0	0	3	0	0	3	0	0	0	0	3	0	0	3	0	0	0	0	3	2	0	0	0	2	0	0	0	3	0	0	0	0	3	1	2	0
Ceradocus torelli	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	0	0	3	0	0	0	3	3	0	0
Cerianthus lloydi	2	0	0	0	1	0	0	3	0	0	0	0	0	3	0	3	0	3	0	0	0	0	3	0	0	0	0	3	0	0	0	3	0	0	1	2	0
Chelyosoma macleayanum	0	0	2	0	1	0	1	2	0	0	0	3	0	0	0	0	3	0	3	0	0	0	0	0	1	2	3	0	0	0	0	3	0	0	2	2	0
Chionoecetes opilio	0	0	2	0	1	0	0	1	2	0	0	0	1	2	0	0	3	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	1	2	0
Chlamys behringiana	0	0	0	3	0	0	0	0	3	0	0	3	0	0	0	0	3	3	0	0	3	0	0	0	0	0	0	0	0	3	0	3	0	0	1	2	0
Clinocardium ciliatum	2	0	2	0	0	0	2	1	0	0	0	3	0	0	0	0	3	3	0	0	3	0	0	0	0	0	0	3	0	0	0	3	0	0	3	0	0
Colus sabini	2	0	0	0	1	0	0	2	2	0	0	0	3	0	0	1	2	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	3	0	2	1	0
Colus sp.	2	0	0	0	1	0	0	2	2	0	0	0	3	0	0	1	2	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	3	0	2	1	0
Corella willmeriana	1	0	0	0	2	0	0	3	0	0	0	3	0	0	0	2	2	0	3	0	0	0	0	0	0	3	3	0	0	0	0	0	0	3	2	1	0
Coryphella sp.	1	0	2	0	0	0	3	0	0	0	0	0	0	3	0	3	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Crangon dalli	0	0	3	0	0	0	2	1	0	0	1	0	0	2	0	0	3	3	0	0	3	0	0	0	0	0	0	1	0	2	0	0	0	3	3	0	0
Crepidula sp.	1	0	2	0	0	0	3	0	0	0	0	3	0	0	0	3	0	1	0	2	1	0	0	0	0	2	0	0	3	0	0	2	2	0	1	2	0

Crossaster papposus	0	0	3	0	0	0	0	1	2	0	0	0	1	2	0	0	3	0	3	0	3	0	0	0	0	0	0	0	3	0	0	3	0	0	3	0	0
Cryptonatica affinis	3	0	0	0	0	0	0	2	1	0	0	0	0	3	0	3	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	1	2	0
Ctenodiscus crispatus	0	0	3	0	0	0	0	2	1	0	3	0	0	0	0	0	3	0	3	0	1	0	0	2	0	0	0	2	1	0	0	3	0	0	2	1	0
Curtitoma decussata	1	0	0	0	2	0	3	0	0	0	3	0	0	0	1	2	0	3	0	0	0	2	0	2	0	0	0	0	0	0	0	0	3	0	2	1	0
Curtitoma incisula	1	0	0	0	2	0	2	2	0	0	0	0	0	3	0	2	1	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	2	1	0
Curtitoma novajasemljensis	1	0	0	0	2	0	2	1	0	0	0	0	0	3	1	2	1	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	2	1	0
Curtitoma sp.	1	0	0	0	2	0	2	1	0	0	0	0	0	3	1	2	1	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	2	1	0
Curtitoma violacea	1	0	0	0	2	0	2	1	0	0	0	0	0	3	1	2	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	2	1	0
Cylichna alba	2	0	0	0	1	0	2	1	0	0	2	0	0	2	0	1	2	3	0	0	3	0	0	0	0	0	0	1	2	0	0	0	3	0	1	2	0
Cylinchnoides occultus	2	0	0	0	2	0	2	1	0	0	2	0	0	2	0	3	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	2	2	0
Dendrobeania sp.	0	0	0	0	3	0	2	2	3	0	0	3	0	0	0	3	0	0	3	0	0	0	0	0	1	2	3	0	0	0	1	0	0	2	0	0	3
Dendrodoa sp.	1	0	0	0	2	0	2	2	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	3	3	0	0
Dendronotus sp.	1	2	0	0	0	0	1	2	0	0	0	0	0	3	0	3	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Diaphana hiemalis	2	0	0	0	1	0	3	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diastylis alaskensis	0	0	0	3	0	0	2	1	0	0	3	0	0	0	0	3	0	0	0	3	3	0	0	0	0	0	0	0	1	2	0	0	0	3	2	2	0
Diastylis goodsiri scorpioides	0	0	0	3	0	0	3	0	0	0	2	2	2	1	0	3	0	0	0	3	3	0	0	0	0	0	0	0	0	3	0	0	0	3	1	2	0
Diastylis sp.	0	0	0	3	0	0	2	1	0	0	3	0	0	0	0	3	0	0	0	3	3	0	0	0	0	0	0	0	1	2	0	0	0	3	2	2	0
Diastylis spinulosa	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	3	0	0	0	3	3	0	0	0	0	0	0	0	1	2	0	0	0	3	2	2	0
Didemnum albidum	0	0	3	0	0	0	2	2	0	0	0	3	0	0	1	2	0	0	3	0	0	0	0	0	1	2	3	0	0	0	1	0	0	2	0	0	3
Distaplia alaskensis	0	0	3	0	0	0	2	1	0	0	0	3	0	0	1	2	0	0	3	0	0	0	0	0	0	3	3	0	0	0	1	0	0	2	0	0	3
Distaplia occidentalis	3	0	0	0	0	0	0	2	2	0	0	3	0	0	0	3	0	0	3	0	0	0	0	0	0	3	3	0	0	0	1	0	0	2	0	0	3
Dulichia spinosissima	0	0	0	3	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	3	0	0	2	0	1	0	0	0	2	1	0	0	0	3	3	0	0
Echinarachnius parma	1	0	3	0	0	0	0	2	1	0	2	2	0	0	0	2	1	0	0	2	2	0	0	2	0	0	0	3	0	0	0	3	0	0	1	2	0
Edwardsia sp,	0	3	0	0	0	0	0	3	0	0	3	0	0	0	1	2	0	1	2	0	0	2	0	1	0	0	1	2	0	0	1	2	0	0	1	2	0
Ericthonius sp.	0	0	0	3	0	0	3	0	0	0	0	3	0	0	0	3	0	0	0	3	0	0	3	0	0	0	0	0	1	2	0	0	0	3	3	0	0
Eteone spetsbergensis	0	3	0	0	0	0	3	0	0	0	1	0	0	2	1	2	0	0	3	0	1	0	0	2	0	0	0	3	0	0	0	0	0	3	3	0	0

Eualus sp.	0	0	0	3	0	0	2	2	0	0	0	0	0	3	0	1	2	3	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	3	2	2	0
Eucratea loricata	0	0	0	0	3	0	1	2	0	0	0	3	0	0	0	3	0	0	3	0	0	0	0	0	1	2	3	0	0	0	1	0	0	2	0	0	3
Eudistoma parvum	0	0	0	0	0	0	0	2	2	1	0	3	0	0	1	2	0	0	3	0	0	0	0	0	1	2	3	0	0	0	1	0	0	2	0	0	3
Eugyra sp.	3	0	0	0	0	0	3	0	0	0	0	3	0	0	1	2	0	0	0	3	3	0	0	0	0	0	3	0	0	0	0	0	0	3	3	0	0
Eunicidae	0	2	1	0	0	0	1	2	0	0	1	0	1	1	0	3	0	2	1	0	1	0	1	1	0	0	0	3	0	0	0	2	1	0	2	1	0
Eunoe depressa	0	2	1	0	0	0	1	2	0	0	0	0	0	3	0	3	0	3	0	0	1	0	0	0	2	0	0	0	3	0	0	0	0	3	3	0	0
Eunoe nodosa	0	2	1	0	0	0	0	3	0	0	0	0	0	3	1	2	0	3	0	0	2	0	0	0	1	0	0	3	0	0	0	0	0	3	3	0	0
Eunoe oerstedi	0	2	1	0	0	0	1	2	0	0	0	0	0	3	1	2	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	3	3	0	0
Eunoe sp.	0	2	1	0	0	0	1	2	0	0	0	0	0	3	1	2	0	3	0	0	2	0	0	0	1	0	0	1	1	0	0	0	0	3	3	0	0
Euphrosinidae	0	3	0	0	0	0	3	0	0	0	0	0	0	3	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Eupyrgus scaber	2	1	0	0	0	0	2	2	0	0	3	0	0	0	0	1	2	3	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	3	0	0
Eusirus cuspidatus	0	0	0	3	0	0	1	2	0	0	0	0	0	3	0	2	1	0	0	3	3	0	0	0	0	0	0	1	0	2	0	0	0	3	3	0	0
Euspira pallida	2	0	0	0	1	0	1	2	1	0	0	0	0	3	0	2	1	0	1	2	3	0	0	0	0	0	0	0	3	0	0	0	3	0	2	1	0
Evasterias echinosoma	0	0	3	0	0	0	0	0	0	3	0	0	0	3	0	0	3	3	0	0	3	0	0	0	0	0	0	0	3	0	0	3	0	0	2	1	0
Flabelligera mastigophora	0	3	0	0	0	0	0	3	0	0	3	0	0	0	2	1	0	0	0	3	2	2	0	0	0	0	0	3	0	0	0	0	0	3	3	0	0
Flabellina sp.	1	0	2	0	0	0	2	1	0	0	0	0	0	3	0	3	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Florometra	0	0	0	0	3	0	0	1	2	0	0	3	0	0	0	2	1	0	2	0	3	0	0	0	0	0	0	0	2	1	0	3	0	0	0	3	0
Gammaridae	0	0	0	3	0	1	2	1	0	0	2	1	0	0	0	2	1	0	0	3	0	0	3	0	0	0	0	0	3	0	0	0	0	3	2	1	0
Gastropoda	2	0	0	0	1	0	2	2	1	1	1	0	2	2	0	1	2	0	0	3	3	0	0	0	0	0	0	1	2	0	0	0	3	0	3	0	0
Gattyana amondseni	0	2	1	0	0	1	2	0	0	0	0	0	0	3	1	2	0	3	0	0	1	0	0	2	0	0	0	3	0	0	0	3	0	0	3	0	0
Gattyana ciliata	0	2	1	0	0	0	0	2	1	0	0	0	0	3	1	2	0	3	0	0	3	0	0	0	0	0	0	2	2	0	0	3	0	0	3	0	0
Gattyana cirrhosa	0	2	1	0	0	0	0	2	1	0	0	0	0	3	1	2	0	3	0	0	1	0	0	2	1	0	0	2	1	0	0	3	0	0	2	1	0
Gattyana sp.	0	2	1	0	0	0	0	2	1	0	0	0	0	3	1	2	0	3	0	0	2	0	0	2	1	0	0	2	1	0	0	3	0	0	2	1	0
Gaudichaudius iphionelloides	0	2	1	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gersemia rubiformis	1	0	0	0	2	0	2	2	0	0	0	3	0	0	0	3	0	0	3	0	0	0	0	0	0	3	3	0	0	0	0	0	0	3	0	0	3
Gorgonocephalus sp.	0	0	2	0	2	0	0	0	2	1	0	2	2	2	0	0	3	0	3	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	2	1	0
Granotoma albrechti	1	0	0	0	2	0	2	2	0	0	0	0	0	3	0	3	0	3	0	0	3	0	0	0	0	0	0	2	2	0	0	0	3	0	3	0	0

Halichondria sp.	1	0	1	0	1	0	2	2	2	2	0	3	0	0	0	3	0	0	3	0	0	0	0	0	2	1	3	0	0	0	1	0	0	2	0	0	3
Haliclona sp.	0	0	2	0	1	0	0	0	2	2	0	3	0	0	2	1	0	0	3	0	0	0	0	0	0	3	3	0	0	0	1	0	0	2	0	0	3
Haliclystus	0	0	0	0	3	0	2	2	0	0	0	3	0	0	0	2	1	0	2	0	3	0	0	0	0	0	0	0	2	1	0	3	0	0	0	3	0
Halirages nilssoni	0	0	0	3	0	0	3	0	0	0	0	3	0	0	0	2	1	0	0	3	3	0	0	0	0	0	0	0	0	3	0	0	0	3	3	0	0
Halocynthia aurantium	2	0	0	0	2	0	0	0	2	2	0	3	0	0	0	1	2	3	0	0	0	0	0	0	0	3	3	0	0	0	0	3	0	0	2	1	0
Harmothoe extenuata	0	2	1	0	0	0	3	0	0	0	0	0	0	3	1	2	0	3	0	0	1	0	0	2	1	0	0	3	0	0	0	0	0	3	2	1	0
Harmothoe imbricata	0	2	1	0	0	0	3	0	0	0	1	0	0	3	1	2	0	1	0	2	2	0	0	0	1	0	0	2	2	2	0	1	0	2	2	1	0
Harmothoe sp.	0	2	1	0	0	0	3	0	0	0	1	0	0	2	1	2	0	2	0	1	2	0	0	1	1	0	0	2	1	1	0	1	0	2	2	1	0
Henricia sanguinolenta	0	0	3	0	0	0	0	3	0	0	0	0	0	3	0	0	3	0	3	0	3	0	0	0	0	0	0	0	3	0	0	1	0	2	2	1	0
Henricia sp.	0	0	3	0	0	0	2	2	1	0	0	0	0	3	0	2	2	0	3	0	3	0	0	0	0	0	0	0	3	0	0	1	0	2	3	0	0
Henricia tumida	0	0	3	0	0	0	1	2	0	0	0	0	0	3	0	2	2	0	3	0	3	0	0	0	0	0	0	0	3	0	0	1	0	2	3	0	0
Heteropora sp.	0	0	0	0	3	0	1	1	2	2	0	3	0	0	0	2	1	0	3	0	0	0	0	0	0	3	3	0	0	0	1	0	0	2	0	0	3
Hexactinellida	0	0	0	0	3	0	2	2	0	0	0	3	0	0	1	1	1	0	3	0	0	0	0	0	0	3	3	0	0	0	1	0	0	2	2	1	0
Hiatella arctica	0	0	0	3	0	0	3	0	0	0	0	3	0	0	1	2	0	3	0	0	0	0	0	0	2	2	3	0	0	0	0	3	0	0	2	1	0
Hippomedon rylovi	0	0	0	3	0	0	3	0	0	0	0	0	2	1	1	2	0	0	0	3	3	0	0	0	0	0	0	0	2	2	0	0	0	3	2	1	0
Hippomedon sp.	0	0	0	3	0	0	3	0	0	0	0	0	2	1	1	2	0	0	0	3	3	0	0	0	0	0	0	0	2	2	0	0	0	3	2	1	0
Holothuroidea	2	2	0	0	0	0	2	2	0	0	2	2	0	0	1	1	2	1	2	0	2	0	0	1	0	0	0	1	2	0	0	2	0	1	2	2	0
Hormathia nodosa	1	0	0	0	2	0	0	0	3	0	0	0	0	0	0	1	2	0	1	2	0	0	0	0	0	3	2	0	1	0	0	0	0	3	2	2	0
Hyas coarctatus	0	0	2	0	2	0	0	1	2	0	0	0	2	2	0	0	3	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	2	1	0
Hydrozoa	0	0	0	0	3	1	1	2	1	0	0	1	0	2	1	2	0	0	2	1	0	0	0	0	1	2	3	0	0	0	2	1	0	2	1	1	2
Ischyrocerus latipes	0	0	0	3	0	0	2	1	0	0	0	3	0	0	0	3	0	0	0	3	1	0	2	0	0	0	0	0	0	3	0	0	0	3	2	2	0
Ischyrocerus sp.	0	0	0	3	0	0	3	0	0	0	0	3	0	0	0	3	0	0	0	3	1	0	2	0	0	0	0	0	0	3	0	0	0	3	2	2	0
Isopoda	0	0	3	0	0	0	3	0	0	0	0	0	1	2	0	0	3	0	0	3	3	0	0	0	0	0	0	2	0	1	0	0	0	3	2	1	0
Labidochirus splendescens	0	0	3	0	1	0	0	3	0	0	1	0	2	2	0	0	3	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	0	3	2	1	0
Lacuna crassior	2	0	0	0	1	0	2	1	0	0	3	0	0	0	1	2	0	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Lafoeina maxima	0	0	0	0	3	0	0	3	0	0	0	3	0	0	2	1	0	0	0	0	0	0	0	0	1	2	3	0	0	0	1	0	0	2	0	0	3
Latisipho hypolispus	1	0	0	0	2	0	0	2	1	0	0	0	2	2	1	2	1	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0

Lebbeus groenlandicus	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0	1	2	2	0	1	3	0	0	0	0	0	0	0	2	2	0	0	0	3	3	0	0
Lebbeus polaris	0	0	0	3	0	0	1	2	0	0	0	0	1	2	0	1	2	3	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	3	2	1	0
Lepeta caeca	2	0	2	0	0	0	2	1	0	0	3	0	0	0	0	2	1	3	0	0	3	0	0	0	0	0	0	0	3	0	0	3	0	0	2	1	0
Lepeta sp.	2	0	2	0	0	0	0	3	0	0	3	0	0	0	0	2	1	3	0	0	3	0	0	0	0	0	0	0	3	0	0	3	0	0	2	1	0
Leptasterias arctica	0	0	3	0	0	0	0	1	2	0	0	0	0	3	0	0	3	0	3	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	3	0	0
Leptasterias groenlandica	0	0	3	0	0	0	0	2	1	0	0	0	1	2	0	0	3	0	3	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	3	0	0
Leptasterias polaris	0	0	3	0	0	0	0	0	2	1	0	0	0	3	0	0	3	0	3	0	3	0	0	0	0	0	0	1	2	0	0	1	0	2	2	1	0
Leptasterias sp,	0	0	3	0	0	0	0	1	2	1	0	0	0	3	0	0	3	0	3	0	3	0	0	0	0	0	0	1	2	0	0	0	0	3	2	1	0
Lethasterias nanimensis	0	0	3	0	0	0	0	2	2	2	0	0	1	2	0	2	1	0	0	0	3	0	0	0	0	0	0	1	2	0	0	0	0	0	2	1	0
Limneria undata	2	0	0	0	1	0	2	2	0	0	0	0	0	3	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0	0	0
Lumbrineridae	0	3	0	0	0	0	2	1	0	0	2	0	2	2	2	1	0	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	3	0	3	0	0
Maera danae	0	0	0	3	0	0	3	0	0	0	3	0	0	0	2	2	0	0	0	3	0	0	3	0	0	0	0	2	0	2	0	0	0	3	3	0	0
Maera prionochira	0	0	0	3	0	1	2	0	0	0	3	0	0	0	2	2	0	0	0	3	0	0	3	0	0	0	0	2	0	2	0	0	0	3	3	0	0
Margarites costalis	1	0	0	0	2	0	1	2	0	0	2	0	0	1	0	3	0	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	1	2	0
Margarites groenlandicus	1	0	0	0	2	0	2	1	0	0	3	0	0	0	1	2	0	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	0	0	0
Margarites helicinus	1	0	0	0	2	0	2	1	0	0	2	0	0	1	0	3	0	0	0	3	2	0	0	0	1	0	0	0	3	0	0	0	3	0	1	2	0
Margarites sp,	1	0	0	0	2	0	2	1	0	0	2	0	0	1	0	3	0	0	0	3	2	0	0	0	1	0	0	0	3	0	0	0	3	0	1	2	0
Melaenis loveni	0	2	1	0	0	0	1	2	0	0	0	0	2	2	1	2	0	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	0	3	3	0	0
Melita dentata	0	0	0	3	0	0	2	1	0	0	3	0	0	0	0	2	1	0	0	3	0	0	0	0	0	0	0	2	0	2	0	0	0	3	2	1	0
melita quadrispinosa	0	0	0	3	0	0	2	2	0	0	0	3	0	0	0	3	0	0	0	3	1	0	0	0	1	2	2	1	0	0	0	0	1	2	0	3	0
Melita sp.	0	0	0	3	0	0	2	1	0	0	2	2	0	0	0	3	0	0	0	3	3	0	0	0	0	0	0	2	0	1	0	0	0	3	3	0	0
Melphidippa sp.	0	0	0	3	0	0	3	0	0	0	0	3	0	0	3	0	0	0	0	3	3	0	0	0	0	0	0	0	0	3	0	0	0	3	3	0	0
Metopa spitzbergensis	0	0	0	3	0	0	3	0	0	0	1	1	0	2	0	3	0	0	0	3	3	0	0	0	0	0	0	0	1	2	0	0	0	3	3	0	0
Metridium sp,	0	0	0	3	0	0	3	0	0	0	2	2	0	0	0	3	0	0	0	3	3	0	0	0	0	0	0	2	0	1	0	0	0	3	3	0	0
Molgula griffithsii	1	0	0	0	2	0	0	0	2	2	0	0	0	3	0	2	1	3	0	0	0	0	0	0	0	3	2	0	1	0	1	2	0	0	1	2	2
Molgula retortiformis	2	0	0	0	1	0	0	1	2	0	0	3	0	0	0	3	0	0	0	3	0	0	0	0	0	3	3	0	0	0	0	3	0	0	2	1	0

Molgula sp,	2	0	0	0	1	0	2	1	0	0	0	3	0	0	0	3	0	0	0	3	0	0	0	0	0	3	3	0	0	0	0	3	0	0	2	1	0
Monoculodes diamesus	2	0	0	0	1	0	2	1	0	0	0	3	0	0	0	2	2	0	3	0	0	0	0	0	0	3	3	0	0	0	0	3	0	0	3	0	0
Munnopsidae	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	3	2	0	0	2	0	0	0	2	0	1	0	0	0	3	3	0	0
Munnopsis typica	0	0	3	0	0	0	2	1	0	0	3	0	0	0	0	1	2	0	0	3	3	0	0	0	0	0	0	1	1	1	0	0	0	3	0	0	0
Musculus glacialis	0	0	3	0	0	0	3	0	0	0	0	3	0	0	0	2	1	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	0	3	3	0	0
Musculus niger	0	0	0	3	0	0	3	0	0	0	0	3	0	0	0	3	0	0	0	3	1	0	0	0	0	2	2	1	0	0	0	0	0	3	0	3	0
Musculus sp.	0	0	0	3	0	0	1	2	0	0	0	3	0	0	0	3	0	0	0	3	0	0	0	0	1	2	3	0	0	0	0	0	2	1	0	3	0
Myriotrochus rinkii	1	2	0	0	0	0	2	2	0	0	3	0	0	0	3	0	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	3	0	0	1	2	0
naticidae	2	0	0	0	1	0	1	2	1	0	0	0	0	3	0	2	1	2	1	1	3	0	0	0	0	0	0	0	3	0	0	0	3	0	2	1	0
Nemertea	0	2	0	1	0	0	1	2	0	0	0	0	1	2	1	2	0	2	2	2	2	2	0	0	2	0	0	1	2	0	1	2	0	2	3	0	0
Nemidia microlepida	0	2	1	0	0	0	3	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0
Neocrangon communis	0	0	2	1	0	0	1	2	0	0	0	0	0	3	0	0	3	0	0	3	2	0	0	1	0	0	0	0	0	3	0	0	0	3	3	0	0
Neohela monstrosa	0	0	1	2	0	0	3	0	0	0	2	1	0	0	0	3	0	0	0	3	0	0	0	3	0	0	0	2	0	1	0	0	0	3	1	2	0
Neoiphinoe coronata	1	0	0	0	2	0	1	2	0	0	0	2	0	0	0	3	0	2	1	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Neoiphinoe kroyeri	1	0	0	0	2	0	2	2	0	0	0	0	2	0	0	3	0	2	1	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Neopleustes pulchellus var euacanthus	2	0	0	0	1	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nephtys longosetosa	0	3	0	0	0	0	3	0	0	0	0	0	0	3	0	3	0	3	0	0	1	0	0	2	0	0	0	3	0	0	0	3	0	0	3	0	0
Nepthys ciliata	0	3	0	0	0	0	3	0	0	0	0	0	0	3	0	3	0	3	0	0	1	0	0	2	0	0	0	3	0	0	0	3	0	0	3	0	0
Nepthys sp.	0	3	0	0	0	0	1	2	1	0	0	0	0	3	0	3	0	3	0	0	1	0	0	2	0	0	0	3	0	0	0	3	0	0	3	0	0
Neptunea communis	1	0	0	0	2	0	0	2	2	0	0	0	0	3	0	0	3	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	2	1	0
Neptunea heros	1	0	0	0	2	0	0	0	2	1	0	0	0	3	0	0	3	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	2	1	0
Neptunea sp.	1	0	0	0	2	0	0	1	2	1	0	0	0	3	0	0	3	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	2	2	0
Nereis sp,	0	3	0	0	0	0	0	3	0	0	2	0	2	2	0	3	0	0	3	0	1	0	0	2	0	0	0	2	2	0	0	3	0	0	3	0	0
Nodulotrophon coronatus	1	0	0	0	2	0	0	3	0	0	0	0	0	3	0	3	0	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Nothria conchylega	0	3	0	0	0	0	2	1	0	0	1	0	1	1	1	2	0	0	0	0	1	0	2	0	0	0	0	0	3	0	0	0	0	3	1	2	0
Obesotoma japonica	2	0	0	0	1	0	1	2	0	0	0	0	0	3	0	3	0	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0

Obesotoma sp.	2	0	0	0	1	0	2	2	0	0	0	0	0	3	0	3	0	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Obesotoma tenuilirata	2	0	0	0	1	0	2	2	0	0	0	0	0	3	0	3	0	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Ocnus glacialis	1	2	0	0	0	0	0	2	1	0	2	2	0	0	0	3	0	0	3	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	1	2	0
Oenopota bicarinata	2	0	0	0	1	0	3	0	0	0	0	0	0	3	0	2	1	3	0	0	3	0	0	0	0	0	0	2	1	0	0	0	3	0	3	0	0
Oenopota declivis	2	0	0	0	1	0	3	0	0	0	0	0	0	3	1	2	0	3	0	0	3	0	0	0	0	0	0	2	1	0	0	0	3	0	3	0	0
Oenopota elegans	1	0	0	0	2	0	3	0	0	0	0	0	0	3	0	2	1	3	0	0	3	0	0	0	0	0	0	2	1	0	0	0	3	0	3	0	0
Oenopota harpa	2	0	0	0	1	0	2	1	0	0	0	0	0	3	0	2	1	3	0	0	3	0	0	0	0	0	0	2	1	0	0	0	3	0	3	0	0
Oenopota impressa	2	0	0	0	1	0	2	1	0	0	0	0	0	3	0	2	1	3	0	0	3	0	0	0	0	0	0	2	1	0	0	0	3	0	3	0	0
Oenopota pyramidalis	2	0	0	0	1	0	2	2	0	0	0	0	0	3	0	2	2	3	0	0	3	0	0	0	0	0	0	2	1	0	0	0	3	0	3	0	0
Oenopota sp.	2	0	0	0	1	0	2	1	0	0	0	0	0	3	1	2	1	3	0	0	3	0	0	0	0	0	0	2	1	0	0	0	3	0	3	0	0
Onchidiopsis sp,	3	0	0	0	0	0	0	0	1	2	0	0	0	3	1	2	0	3	0	0	2	0	0	0	1	0	0	0	3	0	0	3	0	0	2	1	0
Ophiacantha bidentata	0	0	3	0	0	0	1	2	0	0	2	2	0	0	1	2	0	0	3	0	2	0	0	0	1	0	0	0	3	0	0	3	0	0	1	2	0
Ophiocten sericeum	0	0	3	0	0	0	3	0	0	0	2	0	2	1	1	2	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	3	0	0	1	2	0
Ophiopholis aculeata	0	0	3	0	0	0	1	2	0	0	2	2	0	1	1	2	0	3	0	0	2	2	0	0	0	0	0	0	3	0	0	3	0	0	2	1	0
Ophiopleura borealis	0	0	3	0	0	0	2	2	0	0	2	2	0	0	1	2	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	1	2	0
Ophiura robusta	0	0	3	0	0	0	2	2	0	0	2	1	2	1	1	2	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	3	0	0	1	2	0
Ophiura sarsii	0	0	3	0	0	0	0	2	1	0	1	0	1	2	1	2	0	3	0	0	3	0	0	0	0	0	0	0	2	1	0	3	0	0	2	2	0
Ophiuroidea	0	0	3	0	0	1	1	2	1	0	1	1	2	2	1	2	0	3	0	0	3	0	0	0	0	0	0	0	2	1	0	3	0	0	2	2	0
Opisthobranchia	2	1	1	0	1	0	2	1	0	0	1	0	0	2	0	2	1	2	1	0	3	0	0	0	0	0	0	1	2	1	0	0	2	1	2	1	0
Orchomene pinguis	0	0	0	3	0	3	0	0	0	0	0	0	2	1	0	3	0	0	0	3	3	0	0	0	0	0	0	0	1	2	0	0	0	3	1	2	0
Orchomene sp,	0	0	0	3	0	0	3	0	0	0	0	0	2	1	0	3	0	0	0	3	3	0	0	0	0	0	0	0	1	2	0	0	0	3	1	2	0
Orchomenella minuta	0	0	0	3	0	0	3	0	0	0	1	0	2	0	0	3	0	0	0	3	3	0	0	0	0	0	0	2	0	1	0	0	0	3	3	0	0
Pagurus capillatus	0	0	2	0	2	0	0	2	1	0	2	0	2	0	0	1	2	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	2	1	0
Pagurus rathbuni	0	0	2	0	2	0	0	1	2	0	2	0	2	0	0	1	2	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	2	1	0
Pagurus sp,	0	0	2	0	2	0	0	2	1	0	1	0	2	0	0	1	2	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	2	1	0
Pagurus trigonocheirus	0	0	2	0	2	0	0	2	1	0	2	0	2	0	0	1	2	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	2	1	0

Pandalina sp,	0	0	0	3	0	0	2	2	0	0	0	0	1	2	0	1	2	3	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	3	3	0	0
Pandalus borealis	0	0	0	3	0	0	2	2	0	0	1	0	1	2	3	0	0	3	0	0	3	0	0	0	0	0	0	0	1	2	0	0	0	3	2	1	0
Pandalus goniurus	0	0	0	3	0	0	2	2	0	0	0	0	0	3	1	2	0	3	0	0	3	0	0	0	0	0	0	0	2	1	0	0	0	3	2	1	0
Pandora glacialis	0	0	0	3	0	0	1	2	0	0	0	3	0	0	2	1	0	0	3	0	3	0	0	0	0	0	0	2	2	0	0	0	3	0	2	1	0
Pannychia moseleyi	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paramphithoe cuspidata	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	1	0
Paramphithoe polyacantha	0	0	0	3	0	0	2	1	0	0	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	1	0
Paroediceros lynceus	0	0	0	3	0	0	2	1	0	0	0	3	0	0	2	1	0	0	0	3	2	0	0	1	0	0	0	2	0	1	0	0	0	3	2	2	0
Paroediceros propinquus	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pelonaia corrugata	0	3	0	0	0	0	0	2	1	0	0	3	0	0	0	1	2	0	0	3	3	0	0	0	0	0	3	0	0	0	0	3	0	0	3	0	0
Philine sp.	2	0	0	0	1	0	2	1	0	0	0	0	1	2	0	3	0	0	3	0	3	0	0	0	0	0	0	1	2	0	0	1	2	0	3	0	0
Photis sp.	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	3	0	0	0	3	1	0	2	0	0	0	0	0	0	3	0	0	0	3	3	0	0
Phyllodoce groenlandica	0	3	0	0	0	0	1	2	0	0	0	0	2	2	0	3	0	3	0	0	1	0	0	2	0	0	0	3	0	0	0	0	3	0	2	1	0
Phyllodocidae	0	3	0	0	0	0	2	1	0	0	0	0	0	3	0	3	0	3	0	0	1	0	0	2	0	0	0	2	2	1	0	0	3	0	2	1	0
Platyhelminthes	0	0	3	0	0	0	1	2	0	0	0	0	0	3	1	2	0	0	0	3	2	0	0	0	1	0	0	0	3	0	0	0	0	3	3	0	0
Pleustes cataphractus	0	0	0	3	0	0	3	0	0	0	1	0	1	2	0	1	2	0	0	3	3	0	0	0	0	0	0	0	0	3	0	0	0	3	3	0	0
Pleustes panopla	0	0	0	3	0	0	3	0	0	0	1	0	1	2	0	3	0	0	0	3	3	0	0	0	0	0	0	0	0	3	0	0	0	3	3	0	0
Plicifusus kroeyeri	1	0	0	0	2	0	0	2	2	0	0	0	0	3	0	2	2	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	2	1	0
Plicifusus sp.	1	0	0	0	2	0	0	3	0	0	0	0	0	3	0	2	2	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	2	1	0
Polymastia sp.	0	0	2	0	1	0	0	1	2	0	0	3	0	0	0	2	1	0	3	0	0	0	0	0	0	3	3	0	0	0	1	0	2	0	0	0	3
Polynoidae	0	2	1	0	0	0	1	2	0	0	1	0	1	2	1	2	0	2	0	1	2	0	1	1	1	0	0	2	2	1	0	2	1	2	2	1	0
Pontoporeia femorata	0	0	0	3	0	0	3	0	0	0	2	2	0	0	0	3	0	0	0	3	1	0	0	2	0	0	0	2	0	1	0	0	0	3	2	1	0
Porifera	1	0	2	0	2	0	1	2	2	1	0	3	0	0	1	2	1	0	3	0	1	0	0	0	1	2	3	0	0	0	1	1	1	1	1	1	2
Propebela arctica	1	0	0	0	2	0	3	0	0	0	0	0	0	3	0	3	0	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	1	2	0
Propebela nobilis	1	0	0	0	2	0	2	2	0	0	0	0	0	3	0	3	0	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	1	2	0
Propebela sp.	1	0	0	0	2	0	2	1	0	0	0	0	0	3	0	3	0	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	1	2	0

Protomedeia grandimana	0	0	0	3	0	0	3	0	0	0	1	2	0	0	0	3	0	0	0	3	0	0	3	0	0	0	0	2	1	0	0	0	0	3	3	0	0
Protomedia sp.	0	0	0	3	0	0	3	0	0	0	1	2	0	0	0	3	0	0	0	3	0	0	3	0	0	0	0	2	1	0	0	0	0	3	3	0	0
Pseudoliomesus ooides	1	0	0	0	2	0	2	2	0	0	0	0	1	2	0	2	1	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	0	0	0
Psolus peronii	2	1	0	0	0	0	0	0	3	0	2	2	0	0	0	0	3	0	3	0	3	0	0	0	0	0	0	0	3	0	0	3	0	0	1	2	0
Psolus phantapus	2	1	0	0	0	0	0	0	3	0	2	2	0	0	0	0	3	0	3	0	0	0	0	3	0	0	0	2	1	0	0	3	0	0	3	0	0
Pteraster jordani	0	0	3	0	0	0	0	0	3	0	1	0	2	2	0	0	3	0	3	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	3	0	0
Pteraster militaris	0	0	3	0	0	0	0	1	2	0	0	0	0	3	0	1	2	0	1	2	3	0	0	0	0	0	0	0	3	0	0	0	0	3	3	0	0
Pteraster obscurus	0	0	3	0	0	0	0	0	2	1	1	0	2	2	0	0	3	0	3	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	3	0	0
Pteraster sp.	0	0	3	0	0	0	0	1	2	1	1	0	2	2	0	0	3	0	3	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	3	0	0
Pycnogonidae	1	0	0	0	2	2	2	1	3	0	0	0	2	1	0	1	2	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Pyrulofusus deformis	0	0	1	0	2	0	0	0	3	0	0	0	0	3	0	3	0	3	0	0	3	0	0	0	0	0	0	0	2	1	0	0	0	3	2	2	0
Quasimelita formosa	0	0	0	3	0	0	2	1	0	0	2	1	0	0	0	3	0	0	0	3	3	0	0	0	0	0	0	0	0	3	0	0	0	3	3	0	0
Quasimelita quadrispinosa	0	0	0	3	0	0	3	0	0	0	2	2	0	0	0	3	0	0	0	3	3	0	0	0	0	0	0	2	0	1	0	0	0	3	3	0	0
Retifusus sp.	1	0	0	0	2	0	3	0	0	0	0	0	0	3	0	1	2	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Rhachotropis aculeata	0	0	0	3	0	0	1	2	0	0	0	0	0	3	0	3	0	0	0	3	3	0	0	0	0	0	0	0	0	3	0	0	0	3	2	1	0
Rhachotropis oculata	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	3	0	0	0	3	3	0	0	0	0	0	0	0	0	3	0	0	0	3	3	0	0
Rhegaster tumidus	0	0	3	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rozinante fragilis	0	0	0	3	0	0	3	0	0	0	2	0	1	0	0	3	0	0	0	3	3	0	0	0	0	0	0	0	0	3	0	0	0	3	3	0	0
Sabinea septemcarinata	0	0	2	1	0	0	0	2	1	0	0	0	0	3	0	2	1	3	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	3	3	0	0
Saduria entomon	0	0	3	0	0	0	0	2	1	0	0	0	1	2	0	0	3	0	0	3	3	0	0	0	0	0	0	2	0	1	0	0	0	3	2	1	0
Saduria sabini	0	0	3	0	0	0	0	2	1	0	0	0	2	1	0	0	3	0	0	3	3	0	0	0	0	0	0	2	0	1	0	0	0	3	3	0	0
Saduria sibirica	0	0	3	0	0	1	2	0	0	0	0	0	2	2	0	0	3	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	0	3	2	1	0
Sclerocrangon boreas	0	0	0	3	0	0	0	2	1	0	0	0	3	0	0	3	0	0	0	3	3	0	0	0	0	0	0	0	0	3	0	0	0	3	2	2	0
Scoletoma fragilis	3	0	0	0	0	0	1	2	0	0	2	0	0	2	0	0	0	0	3	0	1	0	0	2	0	0	0	3	0	0	0	0	0	0	0	0	0
Scoletoma sp.	3	0	0	0	0	0	1	2	0	0	2	0	0	2	0	0	0	0	3	0	1	0	0	2	0	0	0	3	0	0	0	0	0	0	0	0	0
Semisuberites cribrosa	0	0	0	0	3	0	1	2	0	0	0	3	0	0	0	2	1	0	3	0	0	0	0	0	0	3	3	0	0	0	0	0	0	0	0	0	3

Serripes groenlandicus	0	0	0	3	0	0	0	2	2	0	2	2	0	0	0	2	1	3	0	0	3	0	0	0	0	0	0	2	1	0	0	3	0	0	1	2	0
Serripes sp.	0	0	0	3	0	0	2	1	0	0	2	2	0	0	0	2	1	3	0	0	3	0	0	0	0	0	0	2	1	0	0	3	0	0	1	2	0
Sertularia sp. Thuiaria sp.	0	0	0	0	3	2	2	0	0	0	0	0	0	3	0	3	0	0	3	0	0	0	0	0	2	1	3	0	0	0	1	2	0	0	0	0	3
Similipecten greenlandicus	0	0	0	3	0	0	2	1	0	0	0	3	0	0	3	0	0	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	0	3	2	1	0
Socarnes bidenticulatus	0	0	0	3	0	0	0	3	0	0	0	0	3	0	0	3	0	0	0	3	3	0	0	0	0	0	0	0	0	3	0	0	0	3	1	2	0
Solariella obscura	2	0	0	0	1	0	3	0	0	0	1	0	0	2	1	2	0	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	1	2	0
Solaster sp.	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spinther sp.	0	0	3	0	0	0	2	1	0	0	0	0	0	1	1	2	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0	0
Spirontocaris sp.	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0	2	1	3	0	0	3	0	0	0	0	0	0	0	2	2	0	0	0	3	2	1	0
Stegocephalus ampulla	1	0	0	2	0	0	2	1	0	0	0	2	2	2	0	2	2	0	0	3	2	0	0	0	1	0	0	0	0	3	0	0	0	3	2	1	0
Stegocephalus inflatus	1	0	0	2	0	0	0	2	1	0	0	2	2	2	0	2	2	0	0	3	2	0	0	0	1	0	0	0	0	3	0	0	0	3	2	1	0
Stegocephalus sp.	1	0	0	2	0	0	2	2	0	0	0	2	2	2	0	2	2	0	0	3	2	0	0	0	1	0	0	0	0	3	0	0	0	3	2	1	0
Stegophiura nodosa	0	0	3	0	0	0	2	2	0	0	0	0	0	3	1	2	0	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	0	3	2	1	0
Stenosemus albus	0	0	3	0	0	0	3	0	0	0	3	0	0	0	0	2	1	0	3	0	2	0	0	0	1	0	0	0	3	0	0	3	0	0	3	0	0
Stomphia sp.	1	0	0	0	2	0	0	0	3	0	0	0	0	3	0	1	2	2	2	0	1	0	0	0	0	2	2	0	1	1	0	3	0	0	2	1	0
Strongylocentrotus pallidus	3	0	0	0	0	0	0	0	3	0	2	0	0	0	0	0	3	3	0	0	3	0	0	0	0	0	0	0	3	0	0	3	0	0	3	0	0
Styela rustica	0	0	0	0	3	0	0	1	2	0	0	3	0	0	0	2	1	0	3	0	0	0	0	0	2	2	3	0	0	0	0	3	0	0	0	3	0
Styela sp.	0	0	0	0	3	0	0	0	3	0	0	3	0	0	0	2	1	0	3	0	0	0	0	0	2	2	3	0	0	0	0	3	0	0	0	3	0
Suberites sp.	0	0	3	0	0	0	0	2	2	0	0	3	0	0	0	1	2	0	3	0	2	0	0	0	1	1	3	0	0	0	1	0	2	0	0	0	3
Syllis armillaris	0	3	0	0	0	2	2	0	0	0	1	0	0	2	1	2	0	3	0	0	3	0	0	0	0	0	0	2	1	0	0	3	0	0	3	0	0
Synidotea bicuspida	1	0	2	0	0	0	1	2	0	0	1	2	0	0	0	0	3	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	0	3	3	0	0
Synidotea sp.	1	0	2	0	0	0	2	2	0	0	1	2	0	0	0	0	3	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	0	3	3	0	0
Syrrhoe crenulata	0	0	0	3	0	0	3	0	0	0	0	3	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	0	0	3	0	0	0	3	3	0	0
Tachyrhynchus erosus	0	0	0	0	3	0	1	2	0	0	0	0	1	2	0	2	1	3	0	0	3	0	0	0	0	0	0	1	2	0	0	3	0	0	1	2	0
Tachyrhynchus sp.	0	0	0	0	3	0	3	0	0	0	0	0	0	3	0	2	1	3	0	0	3	0	0	0	0	0	0	1	2	0	0	3	0	0	1	2	0
Tanaidacea	0	0	0	3	0	0	3	0	0	0	1	0	0	1	0	3	0	0	0	3	1	1	1	1	0	0	0	2	1	0	0	0	0	3	3	0	0

Tecticeps sp.	0	0	3	0	0	1	2	0	0	0	0	0	3	0	0	0	3	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	0	3	2	1	0
Telmessus cheiragonus	0	0	2	0	2	0	1	0	2	0	0	0	0	2	0	0	3	0	0	3	2	0	0	1	0	0	0	0	3	0	0	0	0	3	3	0	0
Tmetonyx cicada	0	0	3	0	0	0	3	0	0	0	2	0	2	1	0	2	1	0	0	3	3	0	0	0	0	0	0	0	2	1	0	0	0	3	2	1	0
Trichotropis sp.	2	0	0	0	1	1	2	0	0	0	0	2	0	0	0	2	1	2	0	1	2	0	0	0	2	0	0	0	3	0	0	0	3	0	3	0	0
Triopha	2	1	1	0	1	0	3	0	0	0	1	0	0	2	0	2	1	3	0	0	3	0	0	0	0	0	0	1	2	1	0	0	3	0	2	1	0
Tritonia sp.	2	1	0	0	0	0	0	2	1	1	0	0	0	3	0	3	0	0	3	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Tubularia sp.	0	0	0	0	5	0	2	1	0	0	0	1	0	2	0	3	0	0	2	1	0	0	0	0	2	1	3	0	0	0	1	0	0	2	1	2	0
Unciola leucopsis	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	3	0	0	0	0	2	0	2	0	0	0	3	3	0	0
Urasterias lincki	3	0	0	0	0	0	0	0	2	2	1	0	2	2	0	0	3	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3	0	0
Urticina sp.	1	0	0	0	2	0	0	0	3	0	0	0	0	3	0	1	2	0	3	0	2	0	0	0	0	2	2	0	1	0	0	2	0	2	2	1	0
Velutina coriacea	2	0	0	0	1	0	3	0	0	0	0	0	0	3	1	2	0	3	0	0	2	0	0	0	1	0	0	0	3	0	0	0	3	0	2	1	0
Velutina laevigata	2	0	0	0	1	0	2	1	0	0	0	0	0	3	1	2	0	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	2	1	0
Velutina sp.	2	0	0	0	1	0	2	1	0	0	0	0	0	3	0	3	0	2	0	1	2	0	0	0	1	0	0	0	3	0	0	0	3	0	2	1	0
Velutina velutina	2	0	0	0	1	0	2	1	0	0	0	0	0	3	0	3	0	2	0	1	2	0	0	0	1	0	0	0	3	0	0	0	3	0	2	1	0
Volutopsius sp.	2	0	0	0	2	0	0	2	1	0	0	0	0	3	0	0	3	0	0	3	3	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Vulcanella sp.	3	0	0	0	0	0	0	0	2	1	0	3	0	0	0	3	0	0	3	0	0	0	0	0	0	3	3	0	0	0	0	3	0	0	0	0	3
Weyprechtia heuglini	0	0	0	3	0	0	2	1	0	0	0	2	1	0	0	3	0	0	0	3	3	0	0	0	0	0	0	0	0	3	0	0	0	3	3	0	0
Weyprechtia pinguis	0	0	0	3	0	0	2	1	0	0	1	1	1	0	0	3	0	0	0	3	3	0	0	0	0	0	0	0	0	3	0	0	0	3	3	0	0
Zoanthidea	0	0	0	3	0	3	0	0	0	0	1	0	2	0	3	0	3	0	0	0	0	0	0	0	3	3	0	0	0	2	1	0	0	1	0	3	0

CHAPTER 3: ENVIRONMENTAL FILTERING INFLUENCES COMMUNITY ASSEMBLY OF EPIBENTHIC COMMUNITIES[2]

Abstract

Community assembly theory states that species assemble non-randomly as a result of dispersal limitation, biotic interactions, and environmental filtering. Strong environmental filtering likely leads to local assemblages that are similar in their functional trait composition (high trait convergence) while functional trait composition will be less similar (high trait divergence) under weaker environmental filters. We used two Arctic shelves as case studies to examine the relationship between functional community assembly and environmental filtering using the geographically close but functionally and environmentally dissimilar epibenthic communities on the Chukchi and Beaufort Sea shelves. Environmental drivers were compared to functional trait composition and to trait convergence within each shelf. Functional composition in the Chukchi Sea was more strongly correlated with environmental gradients compared to the Beaufort Sea, as shown by a combination of RLQ and fourth corner analyses and community-weighted mean redundancy analyses. In the Chukchi Sea, epibenthic functional composition, particularly body size, reproductive strategy, and several behavioral traits (i.e., feeding habit, living habit, movement), was most strongly related to gradients in percent mud and temperature while body size and larval development were most strongly related to a depth gradient in the Beaufort Sea. The stronger environmental filter in the Chukchi Sea also supported the hypothesized relationship with higher trait convergence, although this relationship was only evident at one end of the observed environmental gradient. Strong environmental filtering generally provides a challenge for biota and can be a barrier for invading species, a growing concern for the Chukchi Sea shelf communities under warming conditions. Weaker environmental filtering, such as on the Beaufort Sea shelf, generally leads to communities that are more structured by biotic interactions, and possibly representing partitioning of resources among species from intermediate

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disturbance levels. We provide evidence that environmental filtering can structure functional community composition, providing a baseline of how community function could be affected by stressors such as changes in environmental conditions or increased anthropogenic disturbance.

3.1 Introduction

A central question of community ecology is why species from a regional pool form similar or distinct local species compositions (Weiher et al., 1998). In other words, what are the driving forces in the assembly of local biological communities? Three main filters have been proposed for species to pass through in order to be part of a local community based on their functional traits. These include dispersal limitation, biotic interactions, and environmental filters (Keddy, 1992; Pearson et al., 2018). This idea of filtering based on functional traits was first tested with terrestrial vegetation (Weiher et al., 1998; Götzenberger et al., 2012), terrestrial invertebrates (de Bello et al., 2009), and freshwater invertebrates (Conti et al., 2014), but has been used throughout all ecological systems in the framework of community assembly theory (Keddy, 1992; Weiher et al., 2011). This theory assumes species have a suite of measurable functional traits that allow them to persist in a given environment over time (Kraft et al., 2015). Conversely, community assembly theory assumes that a series of hierarchical filters can prevent a prospective species to enter a community if a species' functional traits would not perform well in the specific local ecosystem conditions (Keddy, 1992; Menegotto et al., 2019). The combined traits of community members should reflect the ability of communities to maintain ecosystem functions within a given environment (McGill et al., 2006; Sutton et al., 2020). If the functional traits represented by a local community do not optimally fill ecological niches and ecosystem functions, missing traits could predict the success of new species invasions (Webb et al., 2010; Pearson et al., 2018).

One of the primary filters of species into a local community is the environment. The relationship between abiotic conditions and functional traits can differ depending on the strength of environmental filtering occurring within a system (Blonder et al., 2015). While the effects of environmental filtering on community assembly can be seen worldwide in many different systems, the Arctic provides an excellent region to closely examine environmental filtering where narrow environmental ranges and highly seasonal conditions affect the species and their traits' ability to persist (Peck et al., 2004). Most Arctic shelves, including the Alaskan Arctic shelves, are considered benthic-driven systems where tight pelagic-benthic coupling, a result of the timing of sea-ice retreat, supports a high benthic biomass (Grebmeier et al., 2006). These benthic systems, in turn, support many higher trophic level fish (Whitehouse et al., 2017) and marine mammal consumers (Bluhm and Gradinger, 2008). Many Arctic epibenthic invertebrates are long-lived (e.g., Bluhm et al., 1998; Ravelo et al., 2017) and relatively slow moving as adults; they are, thus, mostly confined to local environmental conditions. Consequently, Arctic epibenthic invertebrates must express a range of functional traits that allow them to thrive in those local conditions (Sutton et al., 2020). Environmental variables acting as filters on Arctic benthic community assembly have been well studied from a taxonomic perspective (Bluhm et al., 2009; Blanchard et al., 2013; Ravelo et al., 2014; Grebmeier et al., 2015a) but few studies explicitly looked at these filters from a functional trait perspective (but see Rand et al., 2018; Jørgensen et al., 2019; Liu et al., 2019). Conversely, Arctic benthic taxa can be quite plastic in their environmental tolerance ranges and may be more robust to environmental changes than previously assumed (Renaud et al., 2015, 2019); this could lessen the influence of environmental filters. In light of the strong environmental changes due to climate impacts, specifically in the Arctic, as well as likely increased anthropogenic influence, there is urgency to better understand the relationship between benthic invertebrate functional traits and environmental conditions (Renaud et al., 2019).

We used two Alaskan Arctic shelves as case studies in which to test and compare the effect of environmental filtering on functional community assembly. The Alaskan marine Arctic comprises the Chukchi Sea to the west and the Beaufort Sea to the north (Figure 3.1), two regions that are geographically close but vary considerably in their environmental influences. The Chukchi Sea is a seasonally ice-covered, broad and shallow inflow shelf (Carmack and Wassmann, 2006). It is influenced by a diverse set of water masses entering through Bering Strait: the fresh and warm Alaska Coastal Current, and the Chukchi Shelf Currents that are cold and nutrient-rich (Danielson et al., 2020). These water masses and the food supply they provide have previously been linked to Chukchi Sea benthic community composition and biomass (Bluhm et al., 2009; Ravelo et al., 2014; Grebmeier et al., 2015b), benthic larval meroplankton distribution (Ershova et al., 2019), and benthic food web structure (Iken et al., 2010). In addition, Chukchi Sea epibenthic assemblages are also correlated with sediment grain size (Bluhm et al., 2009), which in turn is related to current speed of these water masses (Pisareva et al., 2015). Similar to the Chukchi Sea, the Beaufort Sea is also seasonally ice-covered, with much of the narrow shelf covered by landfast ice and pack ice (Mahoney et al., 2014). As an interior Arctic shelf, the Beaufort Sea is exposed to temperature and salinity ranges from downstream influences from the colder and fresher Alaska Coastal Current from the west (Danielson et al., 2020) and from warmer and saline upwelled water from the Beaufort Sea slope (Pickart et al., 2013; Bluhm et al., 2020). In addition, the Beaufort Sea shelf benthos is impacted by riverine input from the Colville and Mackenzie rivers (Weingartner et al., 2017), plus receives additional terrestrial organic material from coastal erosion (Divine et al., 2015; Doxaran et al., 2015). The Beaufort Sea shelf has a distinct depth gradient from on- to offshore, which reflects a gradient for landfast ice, and depth drops rapidly into a steep slope after the shelf break (Bluhm et al., 2020). These Beaufort Sea shelf characteristics have been previously correlated with patterns in taxonomic diversity of epibenthic (Ravelo et al., 2020) and zooplankton communities (Smoot and Hopcroft, 2017), and benthic food web structure (Divine et al., 2015; Bell et al., 2016). Here, we build on previous knowledge of these two shelf systems to investigate if and how environmental variables related to sediment properties (i.e., sediment grain size), food supply (i.e., sediment chlorophyll), and elements of hydrography (i.e., depth, salinity, temperature) affect the filtering of functional traits of epibenthic invertebrates both within each of the two shelves as well as how processes compare between the two shelves.

If filtering on these two shelves is indeed driven by strong gradients of distinct environmental conditions, we would expect the functional traits of local assemblages to be more similar at the more extreme values of these gradients. This means we expect local assemblages to express high local functional trait convergence at the more extreme values of the existing gradients. Across an environmental gradient, assemblages should exhibit a bell-shaped relationship between functional dissimilarity and environmental gradients (Muscarella and Uriarte, 2016; Denelle et al., 2019; Figure 3.2). For example, within the realized niche of the physiological range of many benthic invertebrates living in the Arctic, one might expect fewer functional traits to be competitive at either very low or very high temperatures, meaning that the traits of community members would exhibit high trait convergence at these more extreme values of the local environmental spectrum. Measuring trait convergence is a way to aggregate the complexities of different trait responses to environmental filtering into a single value; however, trait convergence can also inform further about the role of biological interactions and niche complementarity in a system after species and their traits have passed through the environmental filter (Pillar et al., 2009). In short, trait convergence not only represents the assembly of traits that were able to overcome the environmental filter, it also informs about the subsequent ecological sorting on the community level (Webb et al., 2010). Strong environmental filtering should provide less hospitable conditions for invading species unless the invaders possess the functional traits that are necessary to survive at the more extreme values of the local environmental gradients (Andersen et al., 2015). Alternatively, in locations where environmental filtering is relaxed, functional divergence within that local assemblage should increase, meaning the species are more dissimilar (more diverse) in their functional trait composition (Spasojevic and Suding, 2012). This weaker environmental filtering leads to increased niche complementarity, where species differ in their realized niches and resource partitioning allows species to coexist (MacArthur and Levins, 1967; Mason et al., 2005; Baltar et al., 2019).

The goal of this study was to investigate how environmental filtering influences functional composition and trait convergence within the community assembly framework. We use two geographically close but environmentally dissimilar Arctic epibenthic shelf systems as case studies to address four primary questions: (1) Is there a relationship between epibenthic functional trait composition and environmental gradients? (2) Is the strength of this environmental filtering similar on both the Chukchi and Beaufort Sea shelves? (3) If relationships between functional composition and environmental gradients exist, are they driven by the same trait modalities on the two shelves? (4) Do epibenthic communities follow the expected relationship of higher trait convergence with stronger environmental filtering within each shelf?

3.2 Materials and Methods

3.2.1 Study Sites and Sample Collection

Epibenthic taxa used in this study were collected from the Chukchi and Beaufort Sea shelves from research cruises in 2014 to 2015 (Figure 3.1). Stations in the Chukchi Sea were sampled as part of the Arctic Marine Biodiversity Observing Network survey in 2015 (AMBON, 2015). Stations in the Beaufort Sea were sampled as part of the US-Canada Transboundary Project 2014 and the Arctic Nearshore Impact Monitoring in Development Area project III (ANIMIDA, 2014, 2015). Bottom depth ranged from 11 to 54 m for the 67 stations in the Chukchi Sea and 10 to 64 m for the 46 stations in the Beaufort Sea. Epibenthic invertebrates were collected with a plumb-staff beam trawl with a mouth opening of 2.6 m wide and 1.2 m high as well as a 7 mm mesh and 4 mm codend liner (modified after Gunderson and Ellis, 1986). Environmental variables previously shown to influence epibenthic taxonomic composition (Bluhm et al., 2009; Blanchard et al., 2013; Ravelo et al., 2014, 2015) were collected at each station to reflect hydrography (depth, bottom water salinity, bottom water temperature; all from CTD profiles taken with a Seabird Model SBE911), sediment properties (percent gravel, sand, and mud), and food supply (sediment chlorophyll-a). Sediment properties and food supply were both sampled from top 1 cm sediments from van Veen grab samples, following analyses described in Grebmeier et al. (1989) and Cooper et al. (2012), respectively (also see Iken et al., 2019). Environmental variables for each shelf were standardized to a mean of zero and a variance of one, and a matrix of pairwise Euclidean distances between stations was created. Environmental variables were evaluated for collinearity via Pearson correlations. When collinearity existed [absolute value (Pearson) >0.70 see Supplementary Figure S3.1 for correlations of environmental variables] we chose one of the environmental variables. For example, percent sand was removed from the Chukchi Sea and Beaufort Sea models prior to analysis due high collinearity between percent sand and percent mud. Variability of environmental variables between the Chukchi and the Beaufort Sea was compared using a Levene's test. All environmental data are available through the MBON Data

Portal[3], the Alaska Ocean Observing System (AOOS) Data Portal[4], and the National Centers for Environmental Information (Kasper et al., 2017)[5].

3.2.2 Epibenthic Functional Composition

Epibenthic invertebrate functional composition was expressed through a combination of biological traits that describe the taxa's life history, morphology, and behavior, following commonly accepted definitions and categories (Degen and Faulwetter, 2019). Nine biological traits for a total of 327 taxa were assessed, with almost identical taxon richness in the Chukchi and Beaufort seas (n = 246, n = 245, respectively) at the same levels of taxonomic identification (Sutton et al., 2020). Each trait was categorized by modalities, which are specific categories within each trait (see Table 3.1). Modalities within each trait were assigned to each taxon using a fuzzy coding approach, where a minimum value of 0 indicated no affiliation with that modality and a maximum value of 3 indicated a strong affiliation of a taxon with a modality (Chevenet et al., 1994; Sutton et al., 2020). This process created unique biological trait profiles for all taxa, which were standardized between 0 and 1 to create a trait by taxon matrix (Q matrix). Trait information for all epibenthic taxa in this study can be accessed in Supplementary Material for this manuscript or via The Arctic Traits Database[6] for more detailed descriptions.

3.2.3 Relationships Between Functional Composition and Environmental Variables

The relationship between functional composition and environmental variables, expressed as covariance at each station, was tested with combinations of RLQ and fourth corner analyses (Dolédec et al., 1996; Legendre et al., 1997; Dray et al., 2014). RLQ is an ordination-based multivariate technique that relates a sites by environmental matrix (R-matrix) to a Q-matrix,

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[3] https://mbon.ioos.us/#search?type_group=all&tag|tag=ambon- projects&page=1
[4] https://portal.aoos.org/#module- metadata/af3a4323- b854- 4bce- 890e-793c02b24394/cd3ada75- 3897- 444f- 9d9c- 42f8840f1018
[5] https://www.ncei.noaa.gov/access/metadata/landing- page/bin/iso?id=gov.noaa. nodc:0162530
[6] https://www.univie.ac.at/arctictraits/

which are linked by a biomass-weighted species by site matrix (L-matrix; Dolédec and Chessel, 1994). It provides ordination scores that describe the relationship of linear combinations of trait modalities to environmental variables that are most covariant. A global significance value was obtained through Monte-Carlo tests via 4,999 permutations of the L matrix rows (stations; model 2) and L matrix columns (taxa; model 4) for each shelf and was used to assess if there was a significant relationship between functional composition and environmental conditions (Dray et al., 2014). Prior to the RLQ analysis for each shelf, separate correspondence analyses were performed for the fourth- root transformed L-matrix, and separate principal component analyses were performed for the standardized R-matrix and Q-matrix. The summary RLQ table, thus, compares the RLQ output to these separate ordinations to compare how much variance was preserved for each part of the RLQ.

Fourth corner analysis investigates the bivariate relationships of trait modalities to each environmental variable. When RLQ and fourth corner analyses are used in tandem, two associations are investigated: the first association investigates the significance of trait composition (individual modalities) to environmental gradients. The second association investigates the significance of environmental variables to trait composition (combination of modalities) (Dray and Legendre, 2008). To account for multiple testing, a false discovery rate correction was implemented for all RLQ and fourth corner analyses. We set a significance alpha value at 0.05 for all RLQ and fourth corner analyses to reduce our rate of type 1error. Significant modalities with the highest relative Pearson correlation values for each shelf with environmental axes from the RLQ-fourth corner were selected to further investigate spatial relationships in each shelf. Cut-off Pearson correlation values were chosen for modalities with absolute Pearson values >0.15 in the Chukchi Sea and modalities with absolute Pearson values > 0.10 in the Beaufort Sea, based on the overall range of Pearson correlation values for each shelf.

3.2.4 Trait Convergence

Trait convergence was evaluated using the measure of functional dispersion (FDis), where a lower dispersion value indicates more similar functional composition and, therefore, higher trait convergence of taxa at a station. To calculate FDis, the Q matrix was multiplied with a fourth root transformed, biomass-weighted L matrix to create a trait by station matrix (LQ matrix). The LQ matrix represented the functional composition at a station as community-weighted-means (CWM) (Lavorel et al., 2008; Sutton et al., 2020). Next, trait space for each station was calculated using a principal coordinate analysis (PcoA), where PcoA axes were used as the derived "traits" quantified from the CWM matrix (Laliberté and Legendre, 2010). FDis was then calculated as the mean distance of all taxa at a station to the biomass-weighted centroid of the stations in trait space (Anderson et al., 2006; Laliberté and Legendre, 2010). Average FDis was compared between the Chukchi and Beaufort epibenthic shelf communities using a generalized least squares (GLS) linear model while accounting for spatial autocorrelation:

$y=a_k+\varepsilon$ (1)

where y is FDis, the intercept α_k denotes the mean value of y for the Beaufort Sea (k = 1) and Chukchi Sea (k = 2). The error, ε, was modeled as a spatial random process with a correlation structure that declined exponentially with distance between stations to account for spatial autocorrelation. Models were fit using a generalized least squares approach (Pinheiro et al., 2020) when autocorrelation significantly improved the model; otherwise, ordinary least squares were used.

3.2.5 Trait Convergence and Environmental Gradients

The relationship between functional trait convergence and environmental gradients was tested by comparing the axes from CWM redundancy analyses (CWM-RDA, Nygaard and Ejrnaes, 2004) to our trait convergence metric (FDis) for each shelf. The reason for using CWM-RDA over the RLQ and fourth corner analyses to evaluate the relationship of functional dispersion to environmental gradients is that spatial coordinates could be included in the CWM-RDA model as a condition matrix of station latitude and longitude. Predictor variables in the CWM- RDA were represented by environmental variables that were retained after testing for collinearity (see above). We used the CWM-RDA axes that accounted for the majority of variance from the Chukchi Sea and Beaufort Sea, respectively, as proxies for overall environmental gradients (Lavorel et al., 2008). The relationships of FDis to these overall environmental gradients (i.e., CWM-RDA axes) were tested using a GLS model of FDis as a linear or quadratic function of the first two axes from the CWM-RDA, with autocorrelated residuals as in Equation (1). We chose quadratic relationships due to the expected bell-shaped relationship for environmental filtering (see Figure 3.2). The best model was represented by the lowest corrected AIC (AICc) that accounts for small sample size. In the Beaufort Sea, latitude and longitude were collinear with depth, so depth was removed from the CWM-RDA in the Beaufort Sea. Model outputs were considered significant at alpha = 0.05 for the relationship between RDA axes and environmental variables. All analyses were performed in R version 4.0.2 (R Core Team, 2020) using the ade4 (Dray and Dufour, 2007), vegan (Oksanen et al., 2020), FD (Laliberté and Legendre, 2010), and nlme (Pinheiro et al., 2020) packages.

3.3 Results

3.3.1 Functional Composition and Relationship to Environmental Conditions

Individual modalities had much closer relationships in pairwise comparisons with environmental variables in the Chukchi Sea compared to the Beaufort Sea where only two significant bivariate modality-environment relationships occurred (fourth-corner analysis, Figure 3.3). Temperature and mud in the Chukchi Sea had the most significant relationships with modalities, either positively or negatively (Figure 3.3A). Temperature had many positive relationships and only a few negative relationships with the modalities small/medium body size (BS2), fragile (F1), medium fragility (F2), and free-living (LH1). Percent mud was mostly negatively correlated with modalities except for the modalities free-living (LH1), crawler (MV3), and sexual-internal (R3). In the Beaufort Sea, depth was the only environmental variable with any significant relationship to modalities with two negative associations with the modalities medium/large (BS4) and lecithotrophic (LD2) (Figure 3.3B). These relationships were well expressed when RLQ and fourth-corner analyses were combined (Table 3.2).

When modalities were compared to environmental gradients along the RLQ axes, as opposed to individual environmental variables, the relationship between functional composition of epibenthic communities was globally significant for the Chukchi Sea ($p < 0.001$, inertia = 1.486) and for the Beaufort Sea ($p = 0.007$, inertia = 0.484) (Table 3.2). The RLQ analysis in the Chukchi Sea took a higher proportion of the variability for the three R, L, and Q matrices into account, indicating higher explanatory power compared to the Beaufort Sea (Table 3.2 and Supplementary Figure S3.2). The first RLQ axis of the Chukchi Sea represented the vast majority of the total cross-variance between traits and the environmental gradients with 91%, while only 5% was represented by the second axis (Figure 3.4A). The first RLQ axis in the Chukchi Sea represented a gradient of muddier and high chlorophyll-a content environmental conditions associated with negative R-loadings to more gravelly, and warmer conditions associated with positive R-loadings (RLQ analysis; Figure 3.4A). The first and second RLQ axes of the Beaufort Sea represented 82% and 9% of the of the total cross-variance between traits and the environmental gradients (Figure 3.4B). Based on the R-loadings, the first RLQ axis in the Beaufort Sea represented a gradient of shallow and fresher conditions associated with negative R-loadings to more saline and deeper conditions associated with positive R-loadings (RLQ analysis; Figure 3.4B). Environmental variable R-loadings of the RLQ analysis mirrored the significant associations between environmental variables and RLQ trait axes in both seas (RLQ and fourth corner analysis; $p < 0.05$; Figures 3.4A, B).

Fewer associations were present for the Chukchi Sea between modalities and environmental gradients (RLQ-axes) compared to bivariate associations of modalities and environmental variables (Figure 3.3) while the same associations were present in the Beaufort Sea (Figures 3.4C, D). The Chukchi Sea modalities with the strongest relationships with the first RLQ environmental axis included those from behavioral traits (feeding habit, living habit, movement) and body size (Figures 3.4A, C). Weaker relationships occurred with life history traits (larval development and reproductive strategy). Specifically, proportions of the modalities small/medium (BS2), free-living (LH1), crawler (MV3), and sexual-internal (R3) were negatively associated with RLQ environmental axis 1, representing increased proportions of these modalities with greater percent mud and chlorophyll-a and decreased proportions with temperature. Likewise, the proportion of the modalities medium/large (BS4), large (BS5), filter-feeding (FH2), lecithotrophic (LD2), attached (LH6), and sessile (MV1) were positively related to RLQ environmental axis 1, decreasing with percent mud and chlorophyll-a and increasing with warmer temperatures (Figures 3.4A, C). These associations well matched the spatial distribution of these environmental variables on the shelf, mostly in an on- to offshore pattern (Figures 3.5A, 3.6A). Similar to the bivariate associations between modalities and environmental variables, the modalities medium/large (BS4) and lecithotrophic (LD2) had positive associations with the first RLQ environmental axis in the Beaufort Sea (Figure 3.4D). The proportion of these modalities expressed at stations subsequently followed the depth and salinity gradients along the Beaufort Sea shelf (Figures 3.5B, 3.6A). All modality heatmaps can be found in Supplementary Figure S3.3.

3.3.2 Relationship Between Environmental Gradients and Trait Convergence

FDis in the Chukchi Sea decreased along an on- to offshore gradient, largely following a similar trajectory of temperature and opposite the trajectory of percent mud (Figure 3.6A). This represented higher trait convergence in the offshore and northern study region and higher trait divergence in onshore regions. Greater trait convergence on the Beaufort Sea shelf was found in the shallow western, nearshore stations, characterized by lower salinities, while trait divergence was greater at the deeper offshore and eastern sites (Figure 3.6A). Variability in both the environmental variables and in FDis differed between the Chukchi and Beaufort seas (Levene's test; $p < 0.05$; Supplementary Table S3.1). The Chukchi Sea had larger variability in percent sand, percent mud, temperature, and functional dispersion while the variability in depth was larger in the Beaufort Sea (Figure 3.6B). Mean FDis was not significantly different between the two seas ($p = 0.284$, adj. $R^2 = 0.009$; Figure 3.6B); however, the much larger variability in FDis in the Chukchi Sea indicated that stations there covered a greater range of trait convergence. This reflected a range of some stations with very similar functional composition to some stations with very dissimilar functional composition in the Chukchi Sea. In contrast, Beaufort Sea stations exhibited more consistent levels of higher trait divergence.

The relationship between FDis and environmental variables were assessed with CWM-RDA ordinations between functional composition and environmental variables after removing collinear associations (Supplementary Figure 3.1). The environmental matrix for the analysis included latitude and longitude to account for spatial autocorrelation. The overall CWM-RDA model was significant in the Chukchi Sea and mud, depth and temperature were significant terms in the model. RDA1 represented a gradient of warmer and larger sediment grain size associated with negative RDA1 values to cooler and muddier conditions with positive RDA1 values. The second RDA axis represented a gradient of deeper, muddier conditions associated with negative axis values to shallower and larger sediment grain size conditions associated with more positive values (Table 3.3 and Figure 3.7A). In the Beaufort Sea, two environmental variables, depth and salinity, were removed from the CWM-RDA due to their disproportionately strong influence on the model variance. The overall CWM-RDA was not significant in the Beaufort Sea and no environmental variables were significant in the model (Figure 3.7B). This was likely due to the high percentage of the variance explained by the conditioned (spatial associations) and unconstrained matrices (35 and 56%, respectively) compared to the variance that the constrained matrix explained (9%).

The relationship of FDis to significant environmental gradients expressed in CWM-RDA axes in the Chukchi Sea did not follow the expected bell-shaped relationship with the first axis and only very weakly with the second axis (Figures 3.7A, C, D). The best AIC selection model in the Chukchi Sea for FDis included both CWM-RDA axes (Figures 3.7C, D) and implied a negative (linear) relationship of FDis with the first axis (dominated by a gradient of warmer, low percent mud to cooler, muddier conditions) and a weak negative (quadratic) relationship with the second axis (representative of a gradient of deeper, muddier conditions to shallower, low percent mud conditions). In other words, functional trait convergence was greatest (low FDis) at high percent mud and smallest (high FDis) at warmer temperatures.

3.4 Discussion

This study explored whether and how the concepts of environmental filtering in community assembly theory applied to the functional composition of epibenthic communities using the Arctic Chukchi and Beaufort Sea epibenthic shelf communities as case studies. The Chukchi Sea, for the most part, had larger environmental gradients, and exhibited higher trait convergence in relation to environmental gradients compared to the Beaufort Sea. This provided evidence for the community assembly concept that aligns more extreme ends of an environmental gradient with fewer functional traits (higher trait convergence) (Figure 3.2) for the Chukchi Sea, although only part of this relationship was represented.

3.4.1 Drivers of Functional Composition and Environmental Variables

Environmental filtering, exhibited through the relationships of functional composition and environmental conditions, was evident on the Chukchi Sea but less so for the Beaufort Sea shelf. Functional composition on the Chukchi Sea shelf, namely several behavioral traits (i.e., feeding habit, living habit, movement) and body size, were correlated to some water mass characteristics (temperature) and sediment grain size, specifically percentage of mud. Sediment grain size is globally an important driver of soft-bottom benthic community composition and diversity (Snelgrove et al., 2001; Thrush et al., 2004) as well as on the Chukchi Sea shelf (Feder et al., 1994; Bluhm et al., 2009; Iken et al., 2019). Our results expand our understanding of this relationship beyond taxonomic composition to epibenthic functional traits in the study regions. Similarly, variation in sediment grain size has been linked to behavioral traits such as mobility and feeding habit in the Canadian Arctic (Krumhansl et al., 2016), as well as larval settlement selection along the eastern seaboard of the United States (Snelgrove et al., 1999). Sediment grain size can be a proxy for water flow intensity and deposition (Snelgrove and Butman, 1994). Patterns of distribution of finer sediments on the Chukchi Sea shelf are the result of variation in current velocities that carry finer sediment particles downstream of the Bering Strait, then deposit them in regions of reduced water flow such as in Hope Basin in the south-central Chukchi Sea and the northern and offshore regions of the shelf (Darby et al., 2009; Grebmeier et al., 2015b; Pisareva et al., 2015). Temperature and salinity are generally representative of dominant water masses; in the Chukchi Sea, these are most notably the mid-shelf cold, saline, and high-nutrient Chukchi Shelf Currents, while the Alaska Coastal Current (ACC) is warm, fresh, and low in nutrients (Danielson et al., 2020; Figure 3.1).

Areas with a high mud content on the Chukchi shelf were positively associated with small/medium body size, crawling movements, free-living habits, and sexual-internal reproductive strategy. These results are similar to the relationships of benthic traits and sediment grain size in the Canadian Arctic (Krumhansl et al., 2016) and seminal work on the US East Coast on the interaction between feeding habits and movement types with sediment grain size (Rhoads and Young, 1970). In the south-central Chukchi Sea, Hope Basin (Figure 3.1) is known for the especially high deposition rates of small particle sizes when water slows after transitioning the narrow Bering Strait. This deposition supplies ample food for deposit feeding clams, which in turn act as prey for many epibenthic invertebrates or marine mammals (Grebmeier et al., 2015a,b). The middle shelf in the northern Chukchi Sea was also particularly characterized by high percent mud in our study. This may be the result of converging water masses around Hanna Shoal, which leads to high deposition rates and reduced current flow (Blanchard et al., 2013; Weingartner et al., 2013), resulting in a shallow biological hotspot known to support many higher trophic levels (Young et al., 2017). The invertebrate movement type crawler and free-living habit that were most common in these areas are indicative of taxa that can easily move on fine-grained sediments, often pursuing predatory feeding habits (Grebmeier et al., 2006). These behavioral traits provide important ecosystem functions in muddy areas because crawling movement types and free-living habits foster bioturbation of the sediment, increasing oxygenation of the sediments and the resuspension of organic material (Snelgrove et al., 2000; Queiros et al., 2013). This especially benefits the lower trophic level food web. This effect can be seen in the fact that some of these areas coincide with "hotspots" in macrobenthic biomass that benefit from the deposition of fine-particle organic matter (Grebmeier et al., 2015b) but also high biomass of highly mobile epibethic invertebrates (Bluhm et al., 2009; Iken et al., 2019). At first glance, the strong association between sexual-internal reproduction (i.e., eggs deposited on the substrate and/or internal fertilization) is somewhat surprising given that egg laying tends to be more common on hard substrates. However, regions of high percent of mud in the Chukchi Sea also have high instances of gastropods, many of which can lay their egg masses on other gastropods or shells or as large, protected masses on top of the sediment (e.g., Naticidae, Buccinidae).

Lecithotrophic, larger, filter feeding, sessile, and attached living habit had a strong negative relationship with mud in the Chukchi Sea. Filter-feeding taxa are generally limited by such finer sediments as they tend to clog filter-feeding appendages (Rhoads and Young, 1970). This process forces filter feeders to allocate energy to clearing feeding apparatuses instead of growth and reproduction (Ellis et al., 2002). Many epifaunal filter-feeding taxa are sessile and, thus, require hard substrate for attachment (e.g., Almond et al., 2021), which would create better habitat suitability for this feeding type in the more coastal Chukchi Sea waters, where faster water flow creates coarser sediments (Pisareva et al., 2015). This may also explain the positive relationship of robust, filter-feeding, lecithotrophic taxa with increasing temperature, as the coastal Chukchi waters are also characterized by higher temperatures (Weingartner et al., 2005; Danielson et al., 2020), rather than a causal relationship between filter feeding with temperature per se. Although lecithotrophic larval development has previously been documented to follow warmer temperatures along the southern California and Florida coast (Goddard, 2004), the negative relationship to chlorophyll-a content is likely the result of taxa that can survive in areas of low food availability for their planktonic stage. Larger, more robust taxa in coastal Chukchi Sea regions may be more likely to withstand an increased risk of disturbance along the dynamic coastal environment.

The relationships of functional composition to environmental gradients were much weaker in the Beaufort Sea compared to the Chukchi Sea with few significant trait-environmental relationships driven mostly by depth and to a lesser degree, salinity. Depth has been identified as a driving force of functional traits in inflow Arctic shelves such as the Bering Sea (Liu et al., 2019) and the Barents Sea (Cochrane et al., 2012) and has long been suggested as a general key environmental variable to track functional traits (Costello et al., 2015). Depth increases unidirectionally with distance from shore across the narrow Beaufort Sea shelf; it often is considered a proxy for many environmental drivers (Jakobsson et al., 2012) such as salinity, temperature, and, in polar seas, influences of ice cover and scour. For example, in the shallower coastal Beaufort Sea, environmental conditions are especially related to the degree and extent of nearshore ice scouring (Mahoney et al., 2014), input of sediments and terrestrial matter from coastal erosion (Doxaran et al., 2015), and riverine influence from major rivers such as the Mackenzie and Colville rivers (Rachold et al., 2005). This highly dynamic coastal environment might select against modalities such as lecithotrophic, which was associated with deeper conditions. In deeper Beaufort shelf regions close to the shelf edge, physical disturbance may be less common but there is increased influx of nutrients and warmer water from upwelling from the deep slope that add environmental variability (Pickart et al., 2013). This allows for taxa to exploit more diverse resources and likely leads to the presence of taxa that have predominantly a larger body size and pelagic larvae such as ophiuroids, holothurians, or gastropods that thrive in more established soft-bottom Artic communities (Ravelo et al., 2020).

3.4.2 The Influence of Environmental Filters on Trait Convergence

We assumed that optimal suites of functional modalities of species should be more similar (higher trait convergence) at the more extreme local values of an environmental gradient and should be dissimilar (higher trait divergence) at more moderate levels of a local environmental gradient (Figure 3.2). Overall, we saw that environmental drivers in the Chukchi Sea with greater variability, i.e., covering a greater range of an environmental gradient, had a greater correlation with functional composition and trait convergence. Specifically, we found higher trait convergence toward the more extreme values of a gradient of percent mud and water mass characteristics. However, we did not see the expected relationship of higher trait divergence at more intermediate levels of percent mud and temperature. This may be a result of using ordinated environmental variables as the gradient, where the influence of one variable becoming more extreme may be offset by the effect of other variables. In the natural system, taxa with their functional traits are not exposed to individual environmental conditions but to this combination of conditions (Everatt et al., 2015). This suggests that while environmental filters exist and may affect individual trait modalities strongly, the responses of other modalities in this complex environment may continue to result in high trait dispersion.

If we postulate that multiple environmental variables can offset their effects on FDis, why did we then see high trait convergence (low FDis) at one end of the combined environmental gradient but not the other? We suggest that the specific environmental variables at play (grain size, temperature, and depth in the Chukchi Sea) only caused a sufficient filter at one end of the realized gradient, i.e., the actual conditions experienced on the shelf. For example, polar taxa in general are known to be highly adapted in their physiological tolerance to low temperatures (Peck et al., 2004). The higher temperatures experienced in the more coastal Chukchi waters may, therefore, present an effective environmental filter at the edge of the tolerance window, but the colder temperatures on the offshore shelf may not have been functionally limiting.

The relationship of the environmental gradients with trait convergence was not significant in the Beaufort Sea. Likely, the removal of the variable depth was a cause for non-significant relationships, which was the strongest variable in the RLQ analysis with traits. Since depth was highly correlated with latitude and longitude, it was removed to account for spatial autocorrelation. Depth across the Beaufort Sea shelf increases steadily to 100 m at the shelfbreak (Jakobsson et al., 2012) and depth-related patterns across the entire shelf depth range have been found in epibenthic taxonomic diversity (Ravelo et al., 2020). Given that functional composition patterns generally match those of taxonomic composition (Sutton et al., 2020), it is possible that changes in trait convergence may occur if deeper Beaufort Sea shelf regions would be included.

The lack of apparent environmental filtering on the Beaufort Sea shelf could also represent a system where biotic interactions act as a second filter that may shape community function more prominently rather than the environment. This interpretation matches well with our previous findings that epibenthic functional composition on the Beaufort shelf had higher functional dissimilarity and evenness than that in the Chukchi Sea (Sutton et al., 2020). This more balanced interplay of environmental and biological filters (Weiher et al., 2011) that we propose for the Beaufort Sea may promote higher trait divergence and the coexistence of many functional roles (Cornwell et al., 2006). The environmental conditions in the Beaufort Sea may be more representative of disturbances, such as seasonal ice-scouring and spring freshet, rather than continuous environmental gradients that would exert sufficient sustained (e.g., year-round) pressure to drive trait convergence. Intermediate disturbance regimes promote functional richness (Grime, 2006; Cadotte et al., 2011), where more diverse functional traits are used to exploit more diverse resources, a process known as disturbance-induced niche complementarity (Roxburgh et al., 2004). This niche complementarity resulting from intermediate disturbance is different from strong environmental filtering, where the latter would be limiting the functions that are able to thrive at the more extreme values of a local gradient, ultimately limiting niche complementarity (Valdivia et al., 2017).

3.5 Conclusion

The influence of environmental filtering on the functional community assembly was much more evident for the Chukchi Sea, although we did not see the expected bell-curve relationship of functional trait convergence in response to environmental gradients. In the Chukchi Sea as the system with stronger environmental filters, behavioral traits (i.e., feeding habit, living habit, movement) had the strongest associations to environmental gradients. These traits may, therefore, be good indicators of environmental filtering in regions that are experiencing strong changes of environmental conditions due to climate change such as the Arctic. In the Chukchi Sea, these changes include an increasing influx of warmer water from the North Pacific (Woodgate, 2018), conditions that may negatively affect smaller-sized taxa with characteristics of crawling movement types, sexual-internal reproduction, and free-living habits. In addition to changes in hydrographic conditions, increased current speed through Bering Strait (Woodgate, 2018) could lead to changes in sediment grain size on the southern Chukchi Sea shelf (Abe et al., 2019). While these environmental changes may challenge the fitness of some traits currently abundant in this Arctic shelf system, they likely contribute to a northward shift of boreal benthic taxa into the Arctic (Mueter and Litzow, 2008; Grebmeier et al., 2015b; Renaud et al., 2015). This study suggests that these northward-moving benthic taxa will have a competitive advantage over current Chukchi Sea shelf inhabitants if they possess favorable behavioral and life history functional traits that can pass through the local environmental filters. It is unknown if expected environmental changes on the Beaufort Sea shelf may affect environmental filters in that system. It is expected that warmer temperatures will lead to less seasonal sea ice and, therefore, less ice-scour on the shallow shelf (Wadhams, 2012), along with increased wave action along the coast (Pickart et al., 2009). This will also lead to more disturbances from increased terrestrial input from coastal erosion (Rachold et al., 2000; Doxaran et al., 2015) and increased sedimentation from river outflow (Weingartner et al., 2017; Bonsell and Dunton, 2018). It remains to be seen if these changing conditions would strengthen or further weaken environmental filters, or if they would remain part of a changing disturbance regime in which biological interactions play a greater role in structuring epibenthic functional composition.

One caveat to consider in our study, which is typical for most polar field studies, is the fact that the environmental measurements used were all taken during a relatively short sampling period. In our case that was during summer when these Arctic shelf systems are ice-free and accessible. The local range for some dynamic variables, such as temperature and salinity, will be much larger than used here if year-round ranges would be considered (Danielson et al., 2017; Hauri et al., 2018). Hence, the mostly long-lived Arctic invertebrates are exposed to larger local environmental gradients of some variables than applied in this study. Applying full seasonal ranges of environmental gradients would likely even strengthen the relationship with certain functional traits or with trait convergence. Since those environmental data are often not available at the spatial resolution of a specific station distribution, modeling approaches will be needed to more fully predict future scenarios of functional changes in such benthic systems. Here, we provided a benchmark to predict which functional traits will have competitive advantages by evaluating community assembly through an environmental filtering lens. While we focused on two Arctic shelf regions, we postulate that our framework of examining functional trait-environment relationships is applicable to many other systems. We suggest that this environmental filter lens will be particularly critical in regions of rapid environmental change such as the Arctic.

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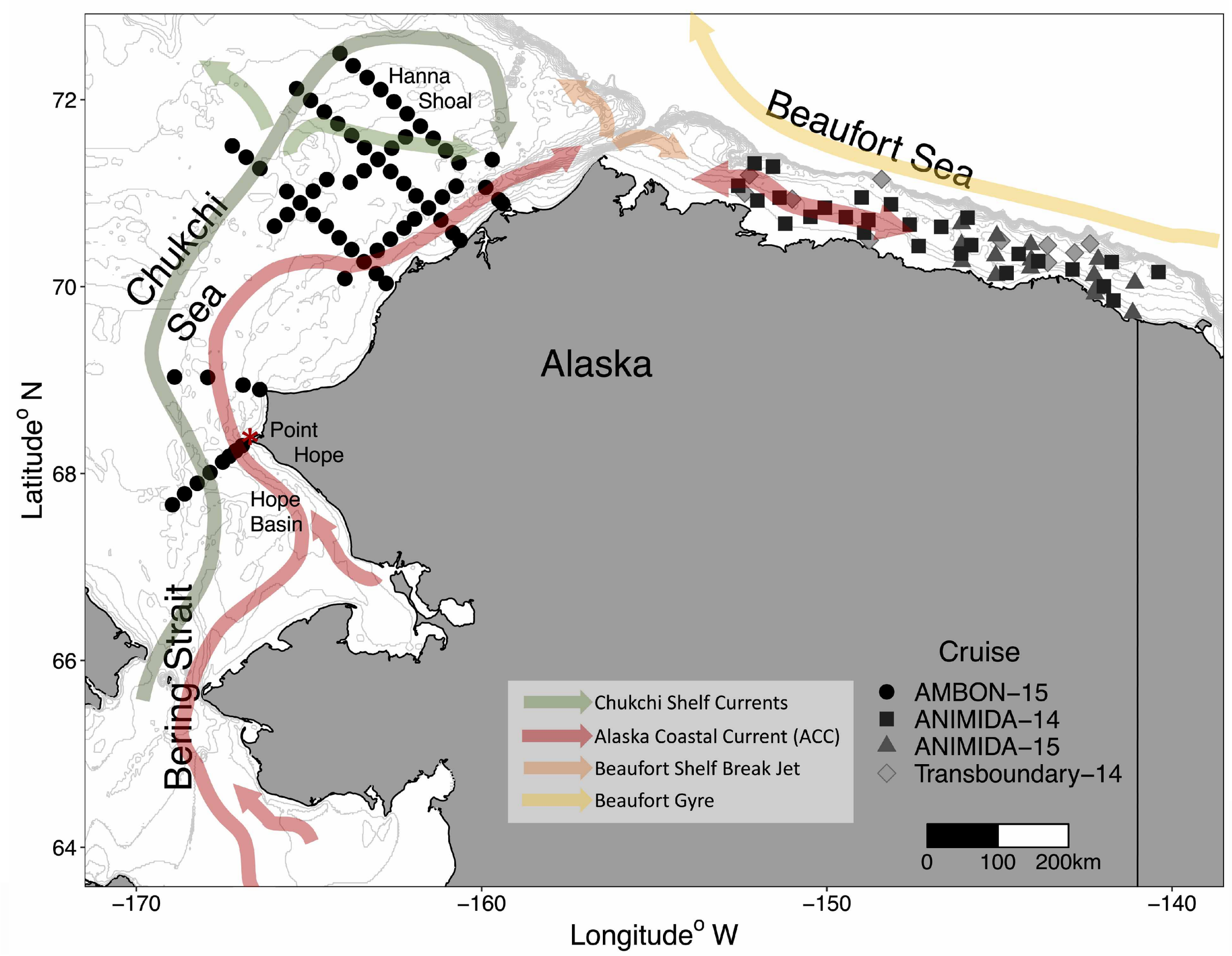


Figure 3.1. Stations sampled for epibenthic communities during four cruises in the Chukchi and Beaufort seas in 2014 and 2015. Depth contours in the study regions are shown in gray at 10 m intervals. Stations are designated by symbols for different cruises.

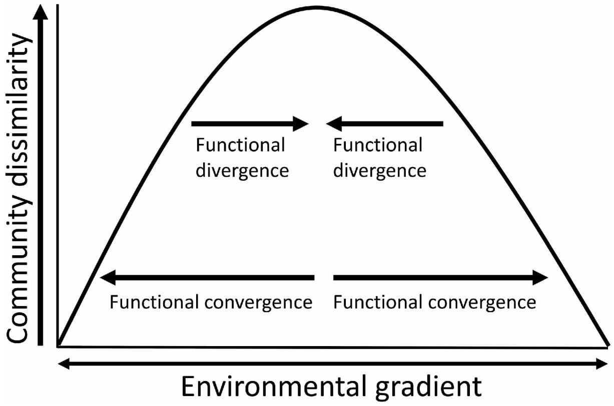


Figure 3.2. Environmental filtering can be expressed as the relationship between community dissimilarity and environmental gradients. The hypothesized relationship predicts that community dissimilarity decreases toward the more extreme values of an environmental gradient (i.e., strong environmental filtering). Adapted from Muscarella and Uriarte (2016).

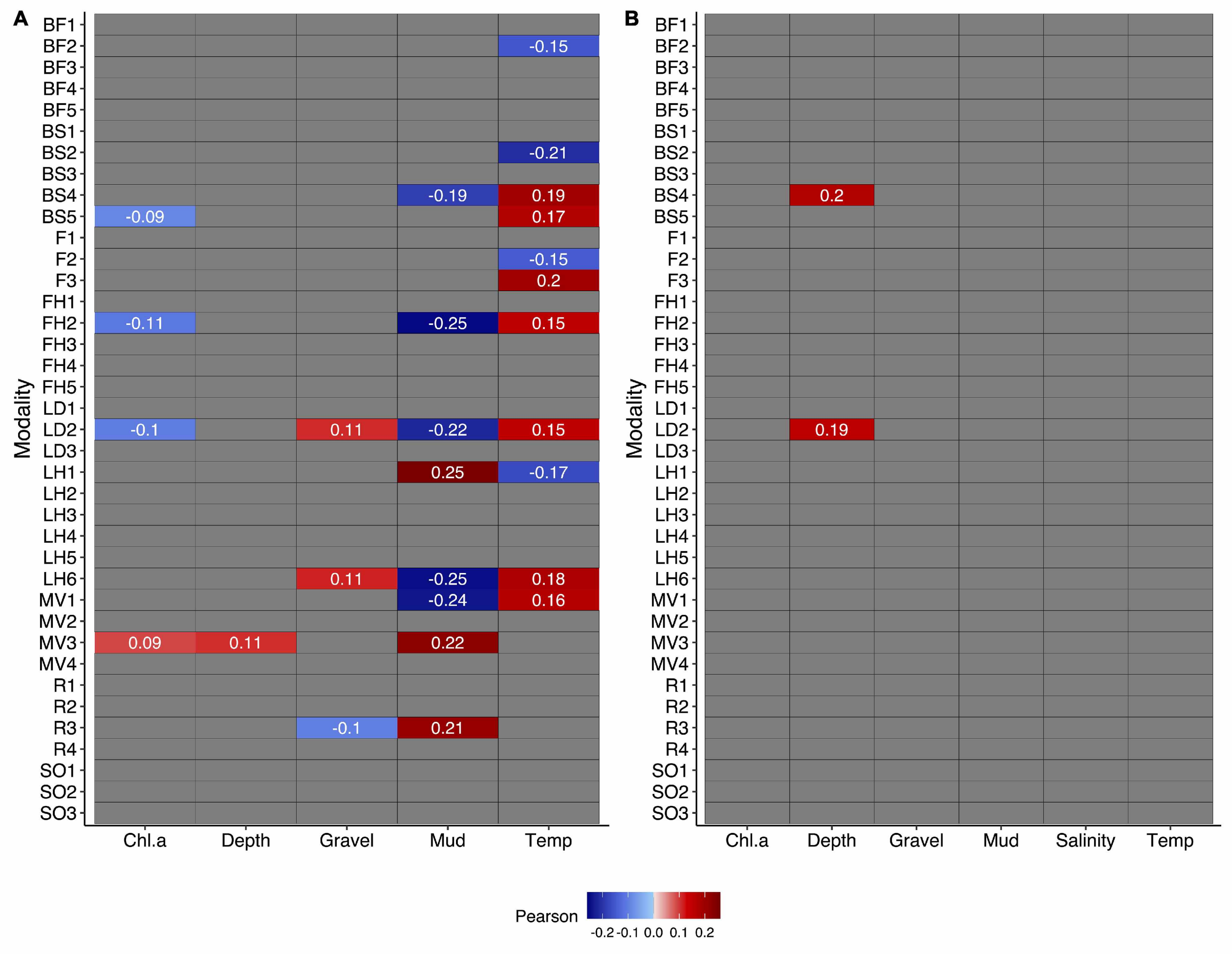


Figure 3.3. Fourth corner tests show significant bivariate relationships between modalities and environmental variables for the Chukchi Sea (A) and the Beaufort Sea (B). Significant positive relationships are represented by red colors and significant negative relationships are represented by blue colors. Gray colors indicate no significant relationships. Pearson correlation values are included for significant bivariate relationships with darker colors indicating stronger relationships.

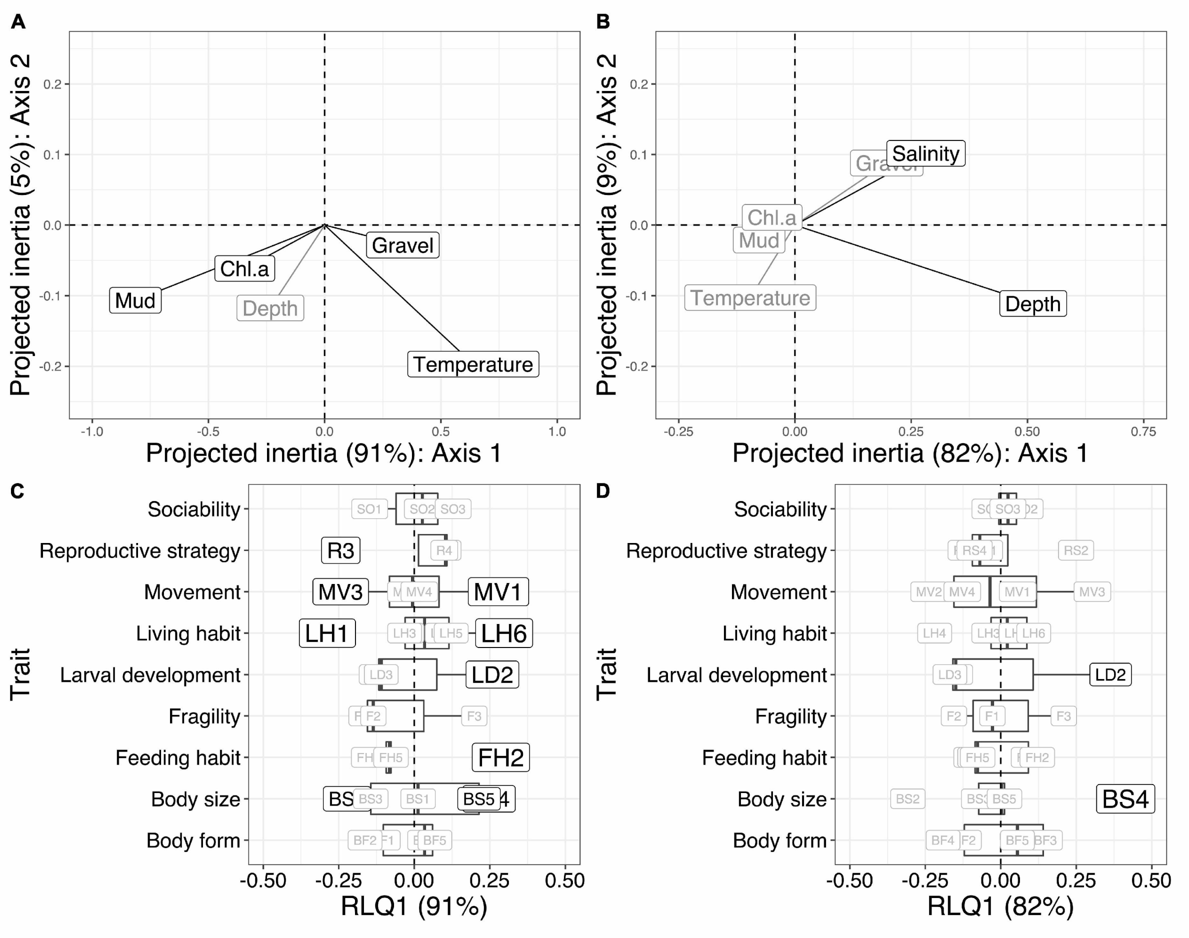


Figure 3.4. The covariation of the first two RLQ axes of the environmental variables are shown for the Chukchi Sea (A) and Beaufort Sea (B). Significant relationships of environmental variables to RLQ trait axes ($p < 0.05$) are shown in black while environmental variables with non-significant relationships to RLQ trait axes are shown in gray for the Chukchi Sea (A) and Beaufort Sea (B). Significant relationships of modalities ($p < 0.05$) to the first RLQ environmental axes are shown for the Chukchi and Beaufort Sea (C, D). Size of the modality boxes correspond to the strength of the Pearson correlation values. Modality abbreviations are shown in Table 3.1 and RLQ outputs are shown in Table 3.2.

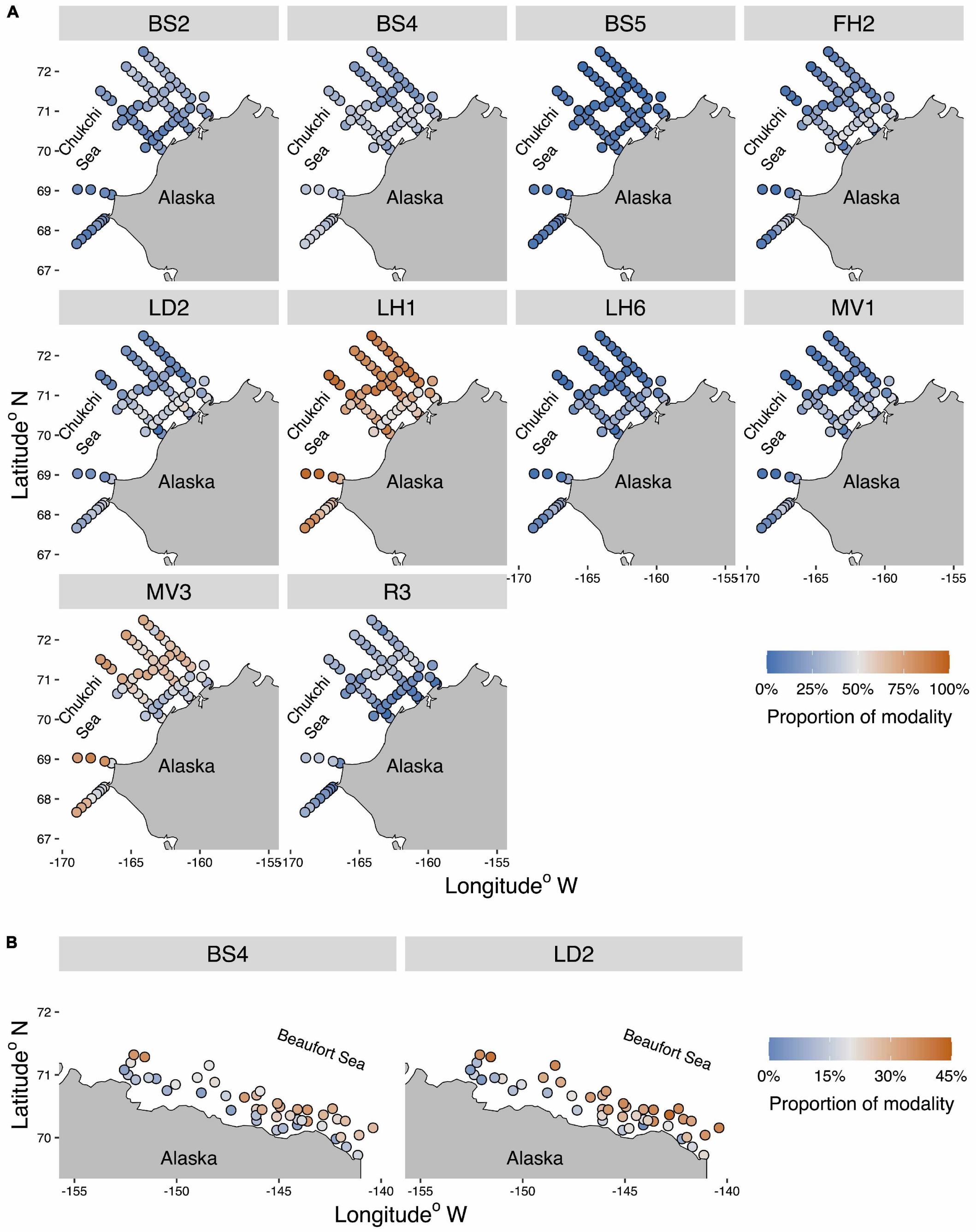


Figure 3.5. Spatial representation of the significant modalities with absolute Pearson correlations > 0.15 for the first axis of the RLQ plot in the Chukchi Sea (A) and modalities with absolute Pearson correlations > 0.1 for the first axis of the RLQ plot in the Beaufort Sea (B) (see Figure 3.4). Pearson correlation cutoff levels were chosen based on the highest relative correlations on the first axis for the RLQ among all traits for each shelf. The full suite of spatial representations for all modalities in both seas is shown in Supplementary Figure S3.3.

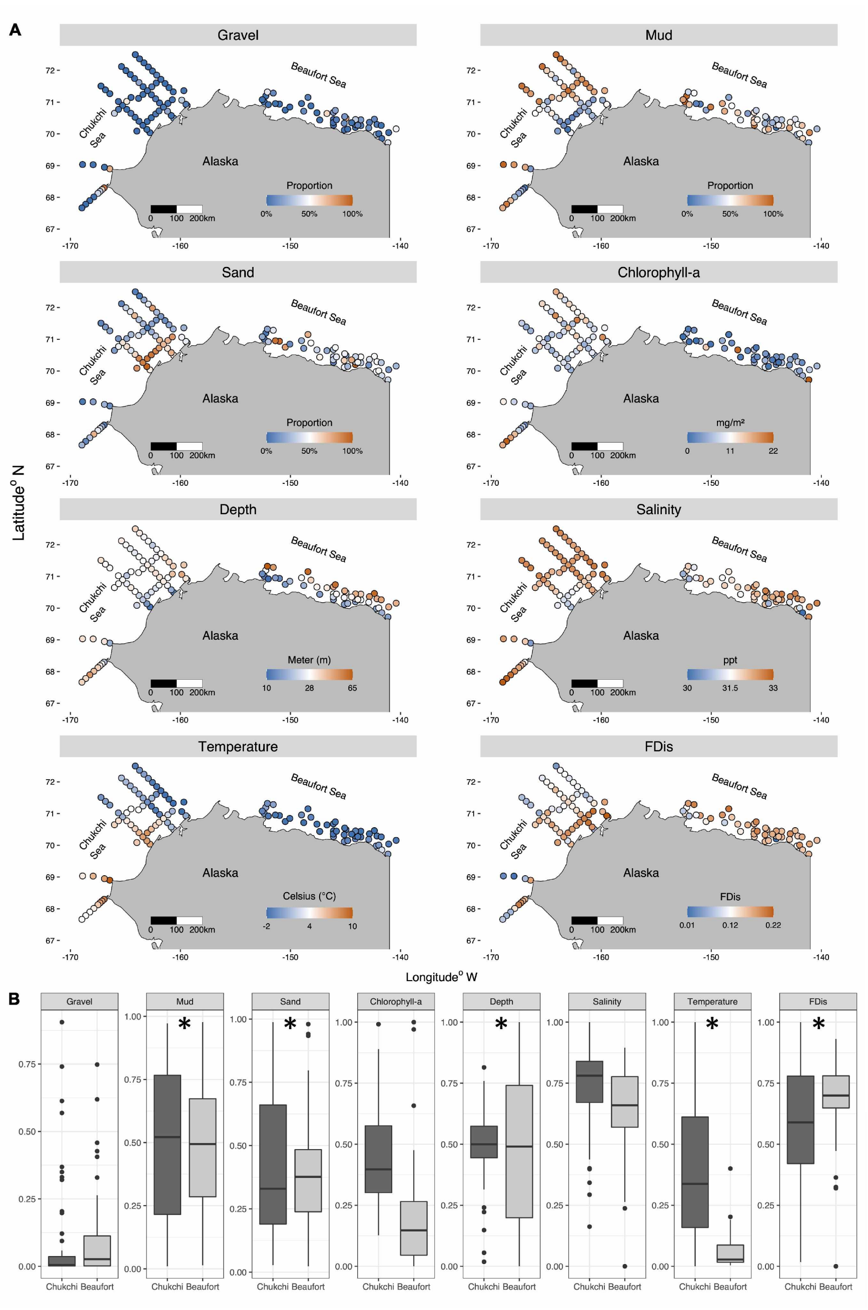


Figure 3.6. Spatial representation of the Chukchi and Beaufort Sea environmental variables and of functional dispersion (FDis) (A). Variance of environmental variables and FDis were compared between the Chukchi Sea (dark gray) and the Beaufort Sea (light gray) (B). Horizontal lines: median, boxes: inter-quartile range (IQR); whiskers: highest/lowest values ≤ 1.5x IQR above/below box; black points: outliers; *: significance ($p < 0.05$) of variance of environmental variables and FDis using Levene's Tests.

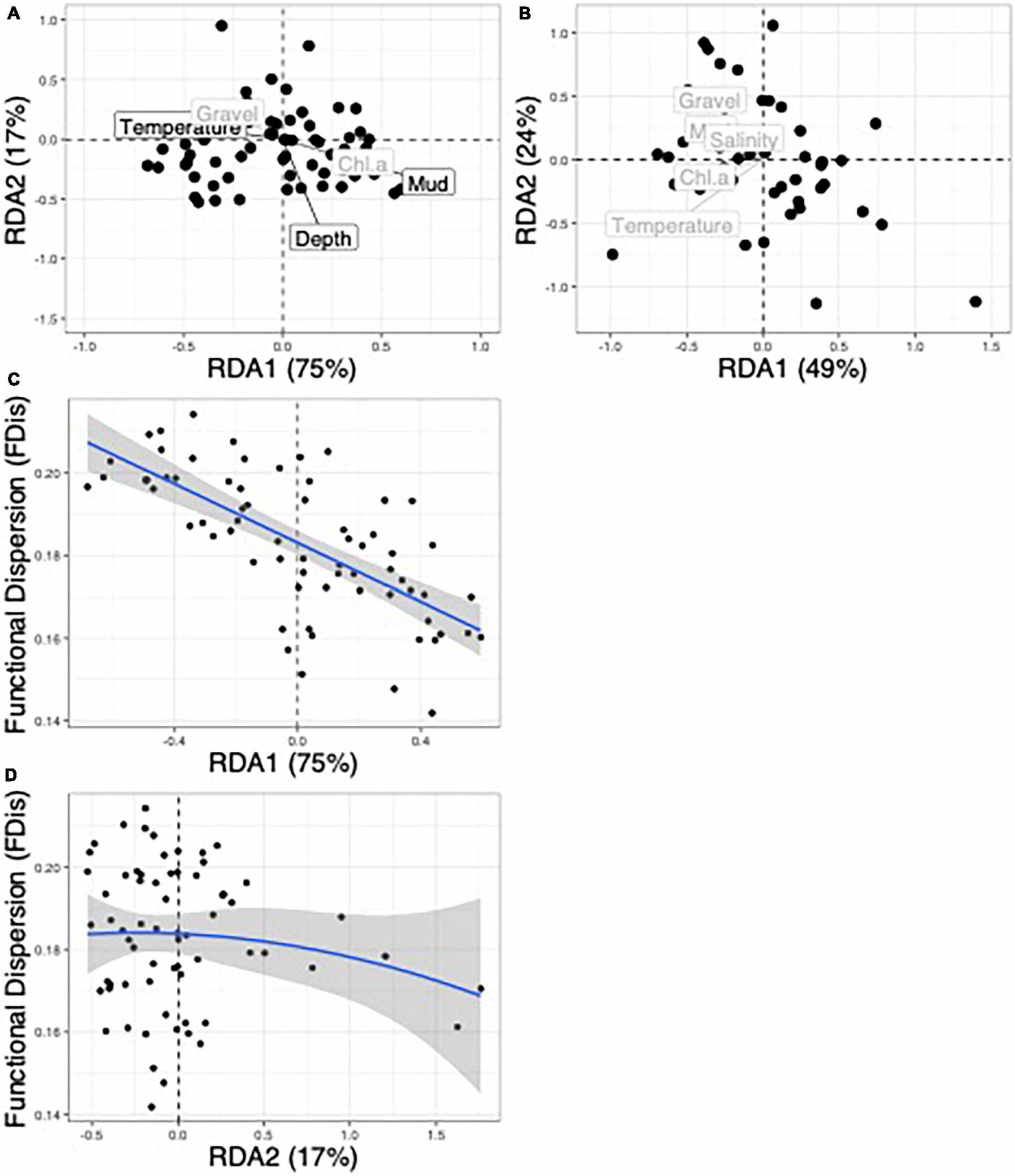


Figure 3.7. Community-weighted-mean redundancy analysis (CWM-RDA) of functional traits and environmental variables in the Chukchi Sea (A) and the Beaufort Sea (B). Length of vectors represent the loadings of environmental variables. The relationship of functional dispersion (FDis) with environmental gradients via a generalized-least-squares polynomial linear model is shown for the Chukchi Sea for the first CWM-RDA axis (from left to right along the RDA axis) representing high percent mud to high temperature (C) and for the second axis (from bottom to top) representing a decreasing depth gradient (D).

Table 3.1. Biological traits, modalities, descriptions, and ecological relevance are shown for epibenthic invertebrates collected in the Chukchi and Beaufort seas, following Degen and Faulwetter (2019).

Biological trait	**Modality**	**Abb.**	**Description**	**Ecological relevance**
Body form	Globulose	BF1	Round	Ecological role of species (e.g., habitat forming) and/or vulnerability to mechanical disturbances
	Vermiform	BF2	Wormlike	
	Dorso-ventrally compressed	BF3	Flattened/encrusting	
	Laterally compressed	BF4	Thin	
	Upright	BF5	Body forms upward from seafloor	
Size (wet weight in grams)	Small	BS1	0.01–0.1	Effect on productivity, energy flow, trophic, and food web structure
	Small-medium	BS2	0.1–1.0	
	Medium	BS3	1.0–10	
	Medium-large	BS4	10–100	
	Large	BS5	>100.0	
Feeding habit	Deposit feeder	FH1	Removal of detrital material from sediment	Indicative of hydrodynamic conditions and carbon transport
	Filter/suspension feeder	FH2	Filter food from the water column	
	Opportunist/scavenger	FH3	Scavenges food	
	Predator	FH4	Actively hunts live prey	
	Parasite	FH5	Feeds off other organisms	
Fragility	Fragile	F1	Easily damaged due to physical impacts	Sensitivity to physical and/or predatory disturbances
	Intermediate	F2	Moderately damaged due to physical impacts	
	Robust	F3	Unlikely damaged due to physical impacts	
Larval development	Planktotrophic	LD1	Larvae feed and grow in water column	Ability to disperse, become invasive, or recover from disturbance
	Lecithotrophic	LD2	Larvae with yolk sac, pelagic for short periods	
	Direct development	LD3	No larval stage (eggs develop into juveniles)	
Living habit	Free living	LH1	Not limited to any restrictive structure	Vulnerability to predation and perturbations, habitat facilitation, storage, and movement of energy
	Crevice dwelling	LH2	Inhabiting coarse/rock or algal holdfasts	
	Tube dwelling	LH3	Tube lined with sand, mucus or CaCO3	
	Burrow dwelling	LH4	Species inhabiting burrows in the sediment	
	Epi/endo zoic/phytic	LH5	Biogenic species or algal holdfasts	
	Attached	LH6	Adherent to a substratum	
Movement	Sessile/none	MV1	No movement as adult	Movement of energy through nutrient cycling, carbon deposition, and maintain habitat stability
	Burrower	MV2	Movement in the sediment	
	Crawler	MV3	On surface via movement of appendages	
	Swimmer	MV4	Movement above the sediment	
Reproductive strategy	Asexual	R1	Budding	Ability to withstand disturbances and carbon transportation
	Sexual—external	R2	Eggs/sperm released into water	
	Sexual—internal	R3	Eggs deposited on substrate/internal fertilization	
	Sexual—brooder	R4	Eggs are brooded, larvae/mini-adult hatches	
Sociability	Solitary	SO1	Single individual	Sensitivity to disturbance and/or habitat forming
	Gregarious	SO2	Single individuals found in groups	
	Colonial	SO3	Living in permanent colonies	

Abb: Modality abbreviations used in figures.

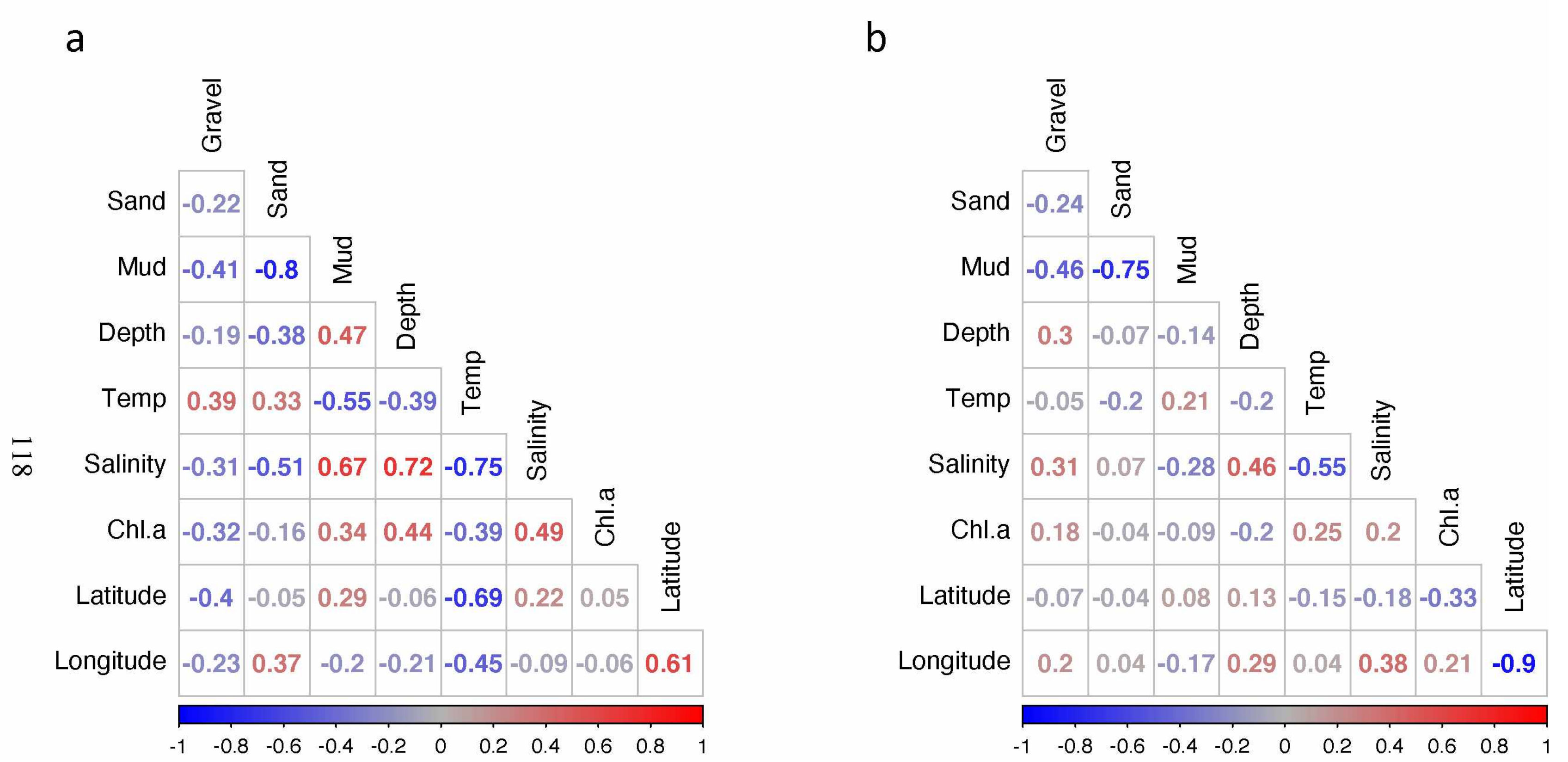
Table 3.2. Summary of the RLQ analysis for the Chukchi Sea (left) and Beaufort Sea (right).

	Chukchi					**Beaufort**				
Total inertia:	1.486					0.484				
Global Significance:	$p < 0.001$					$p = 0.007$				
Model 2:	$p < 0.001$					$p < 0.001$				
Model 4:	$p < 0.001$					$p < 0.001$				
Eigenvalues:										
	Axis 1	Axis 2				Axis 1	Axis 2			
	1.357	0.068				0.399	0.042			
Projected inertia (%)										
	Axis 1	Axis 2				Axis 1	Axis 2			
	91.37%	4.61%				82.43%	8.59%			
Cumulative projected inertia (%)										
	Axis 1	Axis 2				Axis 1	Axis 2			
	91.37%	95.98%				82.43%	91.02%			
Eigenvalues decomposition:										
	Eig	**Covariance**	**sdR**	**sdQ**	**Correlation**	**Eig**	**Covariance**	**sdR**	**sdQ**	**Correlation**
eig1	1.357	1.165	1.544	2.257	0.334	0.399	0.631	1.317	2.064	0.232
eig2	0.068	0.262	0.724	2.039	0.177	0.042	0.204	1.037	2.089	0.094
Inertia and coinertia R:										
	Inertia	**Max**	**Ratio**			**Inertia**	**Max**	**Ratio**		
eig1	2.384	2.660	0.895			1.735	2.166	0.801		
eig1 + 2	2.908	3.418	0.851			2.810	3.681	0.764		
Inertia and coinertia Q:										
	Inertia	**Max**	**Ratio**			**Inertia**	**Max**	**Ratio**		
eig1	5.092	7.211	0.706			4.260	6.171	0.690		
eig1 + 2	9.251	11.767	0.786			8.622	11.017	0.783		
Correlation L:										
	Correlation	**Max**	**Ratio**			**Correlation**	**Max**	**Ratio**		
eig1	0.334	0.691	0.484			0.232	0.658	0.353		
eig2	0.177	0.547	0.324			0.094	0.572	0.164		

Table 3.3. CWM-RDA outputs are shown as the loadings of environmental variables for the first two axes.

	Chukchi Sea			Beaufort Sea		
Environmental variable	**RDA1**	**RDA2**	**Term significance**	**RDA1**	**RDA2**	**Term significance**
% Gravel	–0.28	0.23	0.107	–0.35	0.47	0.129
% Mud	0.74	–0.36	0.001	–0.35	0.24	0.138
% Sand	–	–	–	–	–	–
Depth	0.21	–0.82	0.001	–	–	–
Temperature	–0.51	0.12	0.004	–0.6	–0.51	0.069
Chlorophyll-a	0.41	–0.19	0.694	–0.38	–0.14	0.952
Salinity	–	–	–	–0.12	0.17	0.200
Model significance:	0.001			0.179		
Axis sig:	0.001	0.01		0.300	0.740	
Adjusted R^2:	0.240			0.226		
Conditioned variance:	28.45%			34.94%		
Constrained variance:	26.24%			9.48%		
Unconstrained variance:	45.31%			55.58%		

3.6 Appendix



a

	Gravel	Sand	Mud	Depth	Temp	Salinity	Chl.a	Latitude
Sand	-0.22							
Mud	-0.41	-0.8						
Depth	-0.19	-0.38	0.47					
Temp	0.39	0.33	-0.55	-0.39				
Salinity	-0.31	-0.51	0.67	0.72	-0.75			
Chl.a	-0.32	-0.16	0.34	0.44	-0.39	0.49		
Latitude	-0.4	-0.05	0.29	-0.06	-0.69	0.22	0.05	
Longitude	-0.23	0.37	-0.2	-0.21	-0.45	-0.09	-0.06	0.61

b

	Gravel	Sand	Mud	Depth	Temp	Salinity	Chl.a	Latitude
Sand	-0.24							
Mud	-0.46	-0.75						
Depth	0.3	-0.07	-0.14					
Temp	-0.05	-0.2	0.21	-0.2				
Salinity	0.31	0.07	-0.28	0.46	-0.55			
Chl.a	0.18	-0.04	-0.09	-0.2	0.25	0.2		
Latitude	-0.07	-0.04	0.08	0.13	-0.15	-0.18	-0.33	
Longitude	0.2	0.04	-0.17	0.29	0.04	0.38	0.21	-0.9

Figure S3.1. Environmental variables were evaluated for collinearity via pair-wise comparisons of Pearson correlation coefficients for the Chukchi (a) and the Beaufort (b). If two variables were high collinear (|Pearson| > 0.70), only one variable was used in analyses. The exception was latitude and longitude in the Beaufort Sea where both variables were included in the conditioned matrix for the CWM-RDA.

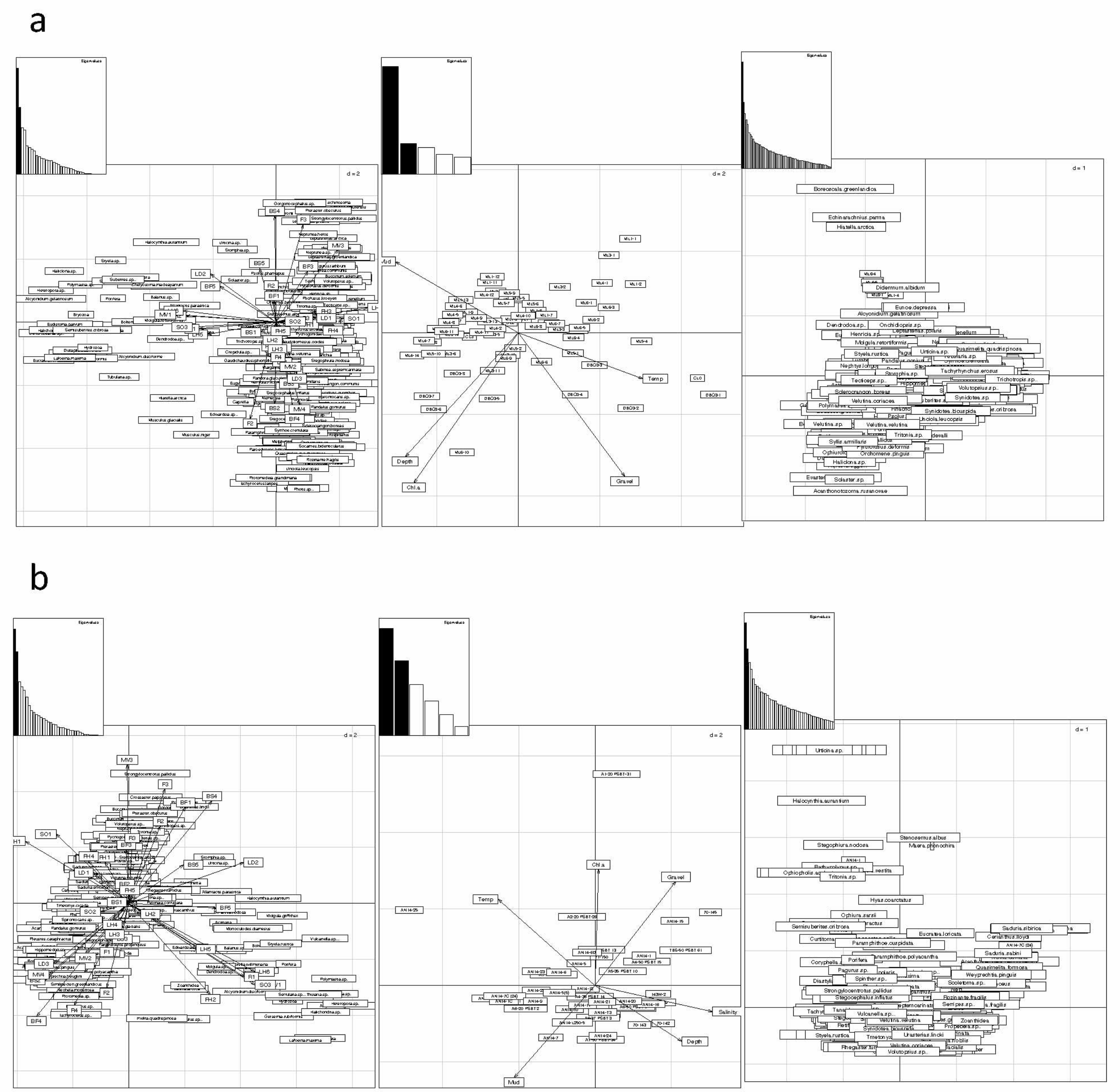


Figure S3.2. Results of the correspondence analysis (CA) on the L-matrices and principal components analysis (PCA) on the Q and R matrices are shown for the Chukchi (a) and Beaufort (b). Eigenvalues are shown in the top left of each ordination.

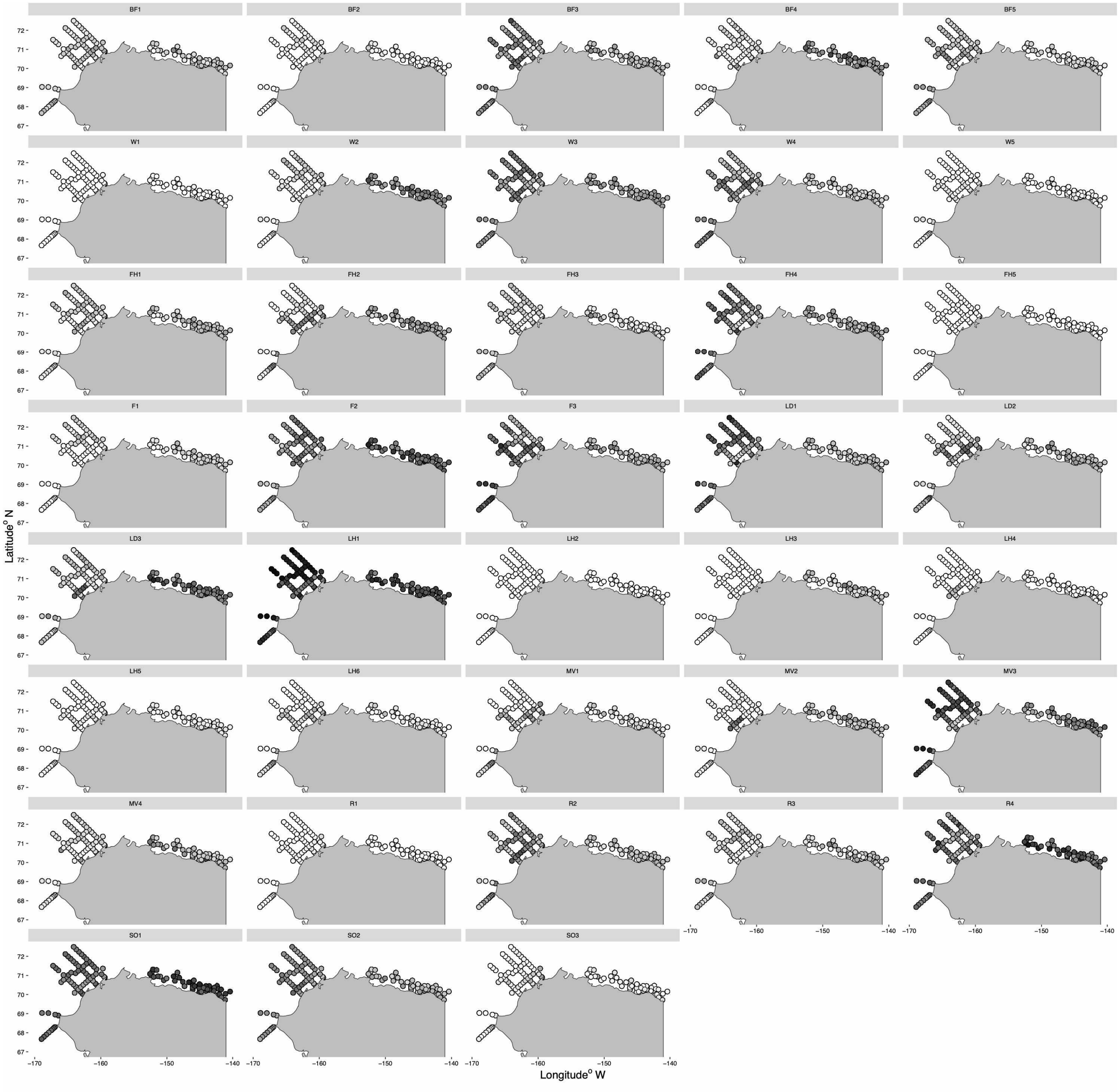


Figure S3.3. The full suite of spatial representations for all modalities in both seas. Darker shades indicate higher levels of a modality.

Environmental variable	F-statistic	Alpha
Gravel	0.43	0.51
Sand	3.98	**0.05**
Mud	5.14	**0.03**
Depth	25.23	**0.00**
Temperature	81.14	**0.00**
Salinity	0.78	0.38
Chlorophyll-a	0.04	0.84
Fdis	10.19	**0.01**

Table S3.1. Levene’s test output comparing the variability in environmental variables between the Chukchi Sea and Beaufort Sea. Significant differences are in bold.

CHAPTER 4: PREDICTING EPIBENTHIC FUNCTIONAL DISTRIBUTION ON CHANGING ARCTIC SHELVES

Abstract

Increasingly strong ocean changes influence all marine ecosystems, but especially so in the Pacific Arctic, where climate changes occur two to four times faster than elsewhere. These oceanographic changes will affect the suitability of Arctic marine habitats for current resident species. Understanding habitat suitability and its changes is an essential part of predicting and adapting to changes in ecosystem functioning. Here, we employed a functional traits approach for Arctic epibenthic communities to use trait-environment relationships from historical data to predict future habitat suitability. We used the Northern Bering Sea and Chukchi Sea shelves as an example system, where the historically cold, stable, and relatively undisturbed benthic habitats may be changing as a result of oceanographic changes, among others, resulting in an increasing poleward migration of benthic boreal taxa. We first investigated how benthic communities have changed in the past decade (2009-2019) using regional mean bottom salinities and temperatures for ice-free periods from the hindcast Pan-Arctic Regional Ocean Model System (PAROMS). To predict future changes in functional composition by the middle and end of the century, we used predicted regional mean bottom salinities and temperatures based on the high-carbon emission, low mitigation effort Shared Socioeconomic Pathways (SSP) 5 scenario (i.e., “worst case scenario”). Regions in the Northern Bering Sea exhibited functional changes longitudinally in a coastal to offshore direction, while the offshore Northern Chukchi Sea region had a clear south to north change in functional composition over time. These patterns followed past and predicted shifts in hydrographic conditions for these Arctic inflow shelves (i.e., generally increased temperatures and decreased salinities). Most prominent shifts in functional composition occurred between the beginning and end of the study period for the most northern region, mostly driven by the functional traits of movement and skeleton, with little change in the middle of the study period. In the most southern region, most prominent changes occurred during the end-of-century timeframes, mostly driven by a combination of body size, larval development, and movement. The relatively small changes in functional composition for all regions between the recent decade and the projected mid-century period suggest that the current Arctic epibenthos

may have already undergone a larger functional transformation in response to changes in the environment than those expected in the near future.

4.1 Introduction

Unprecedented climate changes are testing the boundaries as to what makes habitats suitable for biological communities worldwide. Habitat suitability is defined by a habitat's potential resources to support a particular species, related to specific habitat features (e.g., substrate, temperature, food resources) and the ability to support a species' carrying capacity (Cheung et al., 2009). Climatic changes, therefore, impact habitat suitability for much of the global flora and fauna, including from changes in temperature, ocean acidification, freshwater input, precipitation, global sea levels, sea ice duration and extent, and primary production, among others (Arenas-Castro & Sillero, 2021). Marine species are at particular risk of changes in habitat suitability as the world's oceans change. As places of typically smaller temperature ranges at daily, seasonal, and annual scales compared to terrestrial habitats, marine systems serve as sinks for excess heat; therefore, increasing global ocean temperatures from climate warming (Parry et al., 2007) can significantly affect marine biological communities that are adapted to narrow temperature ranges. As such, marine taxa have tracked changes in ocean warming and isotherms much more closely compared to terrestrial taxa experiencing warming of the land-air interface (Lenoir et al., 2020). Warming ocean temperatures have expanded some taxa's habitat, while contracting others, depending on their habitat preferences (Doney et al., 2012; Lenoir et al., 2020).

Due to the phenomenon known as Arctic amplification (Serreze & Francis, 2006; Serreze & Barry, 2011), the Arctic is warming at least two and up to four times as fast as the rest of the world (Stroeve et al., 2012; Rantanen et al., 2022; Shu et al., 2022). Changing habitat ranges due to increased temperature are acutely evident in Arctic marine systems, resulting in the movement of taxa poleward and follow the borealization of water masses (Fossheim et al., 2015; Renaud et al., 2015; Polyakov et al., 2020; Mueter et al., 2021a). The sweeping impact of borealization across the Arctic is evident across taxonomic groups, including seabirds (Vihtakari et al., 2018; Descamps & Strøm, 2021), fish (Mueter & Litzow, 2008; Alabia et al., 2020), zooplankton

(Møller & Nielsen, 2020), and infaunal invertebrates (Grebmeier et al., 2018). These shifts closely track changes in water masses and sea ice declines (Danielson et al., 2020; Polyakov et al., 2020) and are in line with changing habitat suitability. In the Pacific region, the shallow Chukchi Sea shelf is at a particularly high invasion risk from temperate species through the narrow and shallow Bering Strait connection (Carmack & Wassmann, 2006; Renaud et al., 2015). Until recently, a strong cold pool, created by brine ejection during winter sea ice formation, resided in bottom waters south of the Bering Strait (Thorson, 2019). The cold pool traditionally provided an effective block to many northward species migrations, especially benthic taxa (Mueter & Litzow, 2008; Hu & Wang, 2010). This cold pool is showing signs of dissipating with decreasing sea ice formation, thus increasingly opening the gate for North Pacific species to enter the Chukchi Sea (Mueter & Litzow, 2008; Thorson, 2019). Indeed, in recent years (e.g., in 2018) the cold pool was virtually absent from the northern Bering Sea (Stabeno & Bell, 2019). Therefore, a driving question is if climate change induced modifications in Chukchi Sea benthic habitat suitability will result in a shift in benthic communities, now that the cold pool barrier to more boreal species in the Northern Bering Sea is likely to become less restricting. In other words, will the "future north" become similar to the "current south"?

While previous studies in the Arctic region have focused on the patterns of many species following borealization, from phytoplankton to seabirds (Fossheim et al., 2015; Renaud et al., 2015; Polyakov et al., 2020; Mueter et al., 2021a), a focus of possible epibenthic borealization is underrepresented (but see Mueter, et al., 2021b; Logerwell et al., 2022). This is somewhat surprising given that benthic communities are extremely important in Arctic shelves via the prominent roles they play in many ecosystem functions. These functions include the movement of energy through the Arctic food web through trophic transfers (Iken et al., 2010) and energy turnover (Hall et al., 2009), benthic remineralization (Ambrose et al., 2001), and nutrient cycling (Kristensen & Kostka, 2013). Additionally, the tight pelagic-benthic coupling on the Chukchi Sea shelf (Dunton et al., 2005; Grebmeier et al., 2015; Moore et al., 2018) results in a high benthic biomass and, in turn, fuels upper trophic levels, such as diving sea birds (Lovvorn et al., 2003), bearded seals *Erignathus barbatus*, and walruses *Odobenus rosmarus divergens Illiger* (Fay, 1982; Dehn et al. 2007), demersal fish (Whitehouse et al., 2017), and gray whales *Eschrichtius robustus* (Kim & Oliver, 1989; Coyle et al., 2007). Additionally, high taxonomic

(Bluhm et al., 2009; Ravelo et al., 2014; Blanchard, 2015; Iken et al. 2019) and functional diversity (Rand et al., 2018; Liu et al., 2019; Alabia et al., 2020; Sutton et al., 2020) in the epibenthos fulfills and fuels many ecosystems functions in this region.

Functional diversity is increasingly viewed as a key driver of ecosystem resilience to environmental change and provider of ecosystem services (Laliberté et al., 2015; Biggs et al., 2020). Based on functional traits that describe species' life history, morphology, and behavior (Bremner et al., 2003, 2006), functional diversity differs from taxonomic diversity in that similar species can have different functions within a community (Hewitt et al., 2008; Krumhansl et al., 2016) and conversely, different taxa can play a similar functional role in a community based on their traits. For example, functional benthic diversity In the Chukchi and Beaufort seas are less distinct from each other compared to their taxonomic diversity, and functional composition has greater niche overlap between the epibenthic communities on the two shelves than taxonomic composition (Sutton et al., 2020). Functional traits inherently describe different ways in which species affect ecosystem functioning, such as how species move (e.g., burrowing movement increases bioturbation) or how they feed (e.g., filter feeding takes in particulate organic matter, efficiently moving carbon from the pelagic to the benthic system) (Degen & Faulwetter, 2019). Some traits have shown strong relationships with environmental drivers in these Arctic regions; for example, the traits that describe body size, feeding habit, larval development, and movement relate strongly to temperature, salinity, and sediment grain size (Sutton et al., 2021). Other traits, such as skeletal type, are assumed to be an important proxy for the effects of ocean acidification (Costello et al., 2015). Therefore, as the oceans change, we can predict benthic habitat suitability for functional traits based on past and current trait-environment relationships, essentially creating functional habitat suitability models (Moritz et al., 2013).

The strong relationships between epibenthic functional traits and environmental filters in the Chukchi Sea (Sutton et al., 2021), and the severe climate impacts in the Pacific Arctic (Danielson et al., 2020), set the stage for employing environmental models to predict future functional composition. The Pan-Arctic Regional Ocean Model System (PAROMS) is a three-dimensional, temporally explicit framework for modeling ocean circulation (Danielson et al., 2011), where many environmental variables, including bottom temperature and bottom salinity, have been modelled dating back to the 1980s. Hindcasts of spatial and temporal information from these models are helpful in regions that have missing annual data coverage, such as the seasonally sea ice-covered Arctic shelves in the Northern Bering and Chukchi seas. Being able to account for interannual fluctuations and changes in past environmental conditions then sets the stage for expanded predictions of borealization and habitat suitability of ecosystem function using functional traits based on forecasted future environmental changes.

Modern community ecology seeks to understand what processes shape communities, specifically assuming that environmental filtering plays a major role in which species exist on regional and local scales (Götzenberger et al., 2012; Kraft et al., 2015). Building on our previous work identifying the functional traits that are most important to characterize Arctic epibenthic shelf communities (Sutton et al., 2020) and the environmental drivers shaping them (Sutton et al., 2021), we propose that we are accounting for the most important combinations of functional traits by selecting those that have shown strong relationships with environmental drivers. Furthermore, we assume we are selecting these traits from a discrete functional trait pool for current and future Arctic epibenthic communities. We use this approach as an opportunity to include functional traits in community modelling for future predictions of community structure, an opportunity that is not possible when only considering taxonomy (Bosch-Belmar et al., 2021). One clear limit of using taxonomic identity as the basis of distribution models is that predictions of which species will immigrate or emigrate to and from a region are impossible to make, if those species are not present in the current datasets used to create distribution models (Gross et al., 2017). Using a specific trait pool, this is no longer a limitation of the models. Our study is set along a south to north gradient that reflects both the anticipated direction of change in the environment (inflow of heat and freshwater from the Bering Sea into the Chukchi Sea through the Bering Strait; Danielson et al., 2020), as well as the major conduit of species migrations during borealization (Mueter et al., 2021a). This setting provides a powerful background for functional trait-environment models to predict which functional traits are likely to increase or decrease across the Bering and Chukchi Sea regions; potential migration candidate species can then be identified based on their functional trait profile (Hewitt et al., 2008).

At the foundation of this work is the concept that the functional structure of Arctic marine communities is influenced by the prevailing environmental conditions via environmental filtering (Sutton et al., 2021; Jørgensen et al., 2022). Here, we used joint species distribution models (JSDMs) that incorporate the effect of functional traits on species' communities (Ovaskainen et al., 2017a; Tikhonov et al., 2020) to investigate how changes in the environment structure Arctic communities, from the past to the future. Building on our current understanding of functional composition and environmental linkages based on two recent years of data (Sutton et al., 2021), we used benthic invertebrate information and hindcasted environmental data from the Bering and Chukchi seas dating back to 2009 to establish longer-term functional – environmental relationships. Based on these relationships, we developed predictive distribution models for epibenthic invertebrate functional groups on the northern Bering Sea and Chukchi Sea shelves and hypothesized that functional composition in these regions will change by the end of the century in response to predicted changes in environmental conditions.

4.2 Methods

4.2.1 Study Site and Sample Collection

The Northern Bering and Chukchi seas are Pacific-influenced Arctic inflow shelves separated by the narrow Bering Strait (Danielson et al., 2020). The Bering Sea is upstream of the Chukchi Sea, and differences in sea surface height create a mostly net northward transport, including the nutrient-rich, cold Anadyr/Bering shelf waters through the western part of the Strait and the nutrient-poor, warmer waters from the freshwater-influenced Alaska Coastal Current through the eastern part of the Strait (Williams & Carmack, 2015). Despite their proximity and connectivity, these two shelves vary in many environmental influences, including differences in temperature, salinity, and sediment grain sizes (Grebmeier et al., 1989). These overall flow conditions make the Northern Bering Sea make it a conduit for environmental changes and the transport of boreal/North Pacific taxa into the Chukchi Sea, both part of borealization (Polyakov et al., 2020; Mueter et al., 2021a). To assess epibenthic community changes over time in a spatial fashion that reflects this south to north gradient, the overall study domain was split into three regions: the region south of St. Lawrence Island (SSLI), the Chirikov Basin (CB), both in the northern Bering

Sea, and the offshore Chukchi Sea region (OCS; Figure 4.1). Insufficient biological data were available to include the southern Chukchi Sea region in this study.

All stations (n=686) within these three study regions were between 10 and 90 m deep. Stations in the SSLI (n=221) and CB (n=201) regions were sampled in 2010, 2017, 2018, and 2019 during the Bering Arctic and Subarctic Integrated Survey (BASIS; https://www.fisheries.noaa.gov/resource/data/bering-arctic-subarctic-integrated-survey-basis-oceanography-data), while stations in the OCS region (n=264) were sampled in 2009, 2010, 2012, 2015, 2017, and 2019 during five research programs (some programs spanned multiple years; Figure 4.1). The data from these years were used to create the model described below. Epibenthic invertebrates were collected with an otter trawl (SSLI and CB), or plumb staff beam trawl (OCS), with the same trawl type used within a region across study years. Otter trawl mouth openings ranged from 1.2 – 2.0 m high and 2.6 – 25.3 m wide, with 0.7 – 10.0 cm mesh, and codend mesh that ranged from 0.4 – 8.9 cm. The beam trawl had a mouth opening of 2.6 m wide and 1.2 m high, as well as a 0.7 cm mesh and 0.4 cm codend liner. The use of epibenthic community data from different collection gears was possible, because hind- and forecast models were applied to each region separately, so only one gear type was used for each model. The catch from either trawl was typically sorted on deck of the research vessel to the lowest feasible taxonomic level. Taxonomic resolution was standardized across all collections for this study. This provided 53, 68, and 121 invertebrate taxa for SSLI, CB, and OCS regions, respectively. The environmental variables salinity and temperature for all study years were inferred from model output (i.e., mean salinity and mean temperature via the PAROMS model; see below; Figure S4.1a,b, S4.2a,b). This model reproduces subsurface water temperature and sea ice concentration reasonably well (Danielson et al., 2011). While it is known that sediment grain size is changing in some parts of the study region (Grebmeier & Cooper, 2016), there are no model data available to predict these changes and sediment grain size was not included in our models, although we acknowledge the strong association between sediment grain size and the epibenthos (e.g., Snelgrove et al., 2001; Thrush et al., 2004; Bluhm et al., 2009). We used the taxon composition of the most abundant epibenthic invertebrates that comprise 90% of the biomass found at each station to produce each station’s functional trait profile (see below).

4.2.2 Epibenthic Functional Composition

Epibenthic invertebrate functional composition was expressed through five biological traits (i.e., body size, feeding habit, larval development, movement, skeleton) that have previously been used to characterize these communities and that have strong relationships with environmental drivers (Sutton et al., 2020, 2021; Bednaršek et al., 2021). A description of the biological traits and categories that describe each trait, as well as the ecological relevance of each trait, can be found in Table 4.1 (also see Degen & Faulwetter, 2019). Each trait was subdivided into multiple modalities that can be expressed within a trait. We used a fuzzy coding approach that allowed taxa to express more than one modality within a trait by assigning a score ranging from 0, to express no affinity to a modality, to a score of 3, indicating a strong affinity for a modality (Chevenet et al., 1994; Degen & Faulwetter, 2019; Sutton et al., 2020, 2021). This created unique biological trait profiles for all taxa.

4.2.3 Joint Species Distribution Models Using Hierarchical Modeling of Species Communities

We used JSDMs to make inferences about relationships between taxa and their environment on the community level. JSDMs assume that taxa within a community respond to environmental pressures jointly with other taxa within that community, meaning that instead of one response variable (e.g., a specific species), the response is an biomass-weighted occurrence matrix of multiple species (Ovaskainen et al., 2017a,b). Within the JSDM framework, we used a hierarchical modeling of species communities (HMSC) approach to incorporate species traits into the modeled community assembly processes (Tikhonov et al., 2020). JSDMs using HMSC are hierarchical generalized linear mixed models that use a Bayesian framework that enable predictions of species' responses to environmental pressure based on their functional traits. Regionally-specific JSDM using the HMSC approach included five steps: 1. Setting and fitting the model, 2. Examining the Markov chain Monte Carlo (MCMC) convergence, 3. Evaluating model fit via explanatory model power and predictive model power via cross-validation, 4. Exploring parameter estimates, and 5. Making predictions (Tikhonov et al., 2020). To fit the model, we used biomass of the taxa that represented the top 90% of the biomass at each station to create a community-level biomass matrix, a traits matrix with unique biological trait profiles based on these species, and an environmental matrix from PAROMS model output (see below). We assigned environmental covariates as fixed effects that represented either a "climate" variable (temperature, salinity), or a "habitat" variable (depth) to account for covariances that may exist between environmental covariates. Additionally, we included two random effects for year and station (latitude and longitude) to account for spatial and temporal auto-correlation. Three models were compared via Tjur's R^2 (Tjur et al. 2009): 1. The full model including depth, temperature, salinity, and two random effects (year and spatial coordinates), 2. the spatial model including spatial coordinates as the sole random effect, and 3. The temporal model including year as the sole random effect. The model with the highest Tjur's R^2 was chosen for each region. The HMSC models sampled the posterior distribution with five MCMCs , each of which were run for 5,000 iterations, with 1,000 of these iterations as burn-in that were then removed. These sampled iterations were further thinned by a factor of 10 to yield 400 samples per MCMC or 2,000 posterior samples in total (Tikhonov et al., 2020). Biomass data were fourth-root transformed prior to the JSDM to obtain biomass that were normally distributed, and we used a normal distribution in the model. This was deemed appropriate due to the consistent occurrence of the selected taxa across each region. Model parameters were investigated via variance partitioning for taxa, traits, and environmental covariates.

The relationships of traits and environmental covariates in the regional JSDM models were used to create functional clusters (FCs), based on functional traits. We included a "dummy" environmental dataset derived from a combination of the hindcast PAROMS model (Danielson et al., 2017) and regionally forecasted temperature and salinity data for time intervals 2040-2050 and 2090-2100 obtained from the Shared Socioeconomic Pathways (SSP) 5 scenario, also known as the "fossil-fueled development" or "worst case scenario" (IPCC, 2014). The PAROMS model provided estimated mean bottom temperature and bottom salinity for each of the Bering and Chukchi seas regions for each year between 2009 and 2019 during the ice-free season (June-October; Figures S4.1 and S4.2 for temperature and salinity, respectively). Using the PAROMS model output is advantageous over using in situ point-in-time measurements, as model values capture seasonal variability and allow predictions for an entire region for all years regardless of specific stations sampled in each year. Regionally-specific environmental future predictions were made for two future timeframes, the mid-century period (2040-2050) and the end-of-century period (2090-2100), using the CNRM-ESM2-1 SSP-5 simulation (Séférian et al., 2019) from the Coupled Model Intercomparison Project Phase 6 (Eyring et al., 2016). Here, average salinity and temperature were first computed for a reference period from 2015-2025 for each region. Then, to calculate salinity and temperature changes between the reference period and the mid-century period and end-of-century period, respectively, the differences between the reference period, the mid-century period, and the end-of-century period were computed for each study region and added to the PAROMS output. In general, salinity is projected to decrease over time and temperature is projected to increase over time.

Functional clusters (FCs) of functional traits were based on each regional JSDM and the "dummy" environmental datasets that comprised the modeled (hindcast and forecast) salinity and temperature for each grid point from the PAROMS. These FCs were created by first calculating the biological community-weighted means (CWMs) for all PAROMS grid points within each region. CWMs were calculated by multiplying the traits by taxa matrix with a taxon by biomass matrix, accounting for fuzzy coding of the trait profiles through standardizing the functional trait modalities, so that they sum to 1 for each trait (Chevenet et al., 1994; Sutton et al., 2020). Within each region, FCs were clustered across all timeframes based on similar predicted functional composition of PAROMS grid points. The optimum number of clusters, "k" was based on the inflection point of the total weighted sum of squares for predicted functional composition. The resulting FCs were similar in functional traits composition and, thus, similar in their responses to environmental covariates. We categorized years into the timeframes 2009-2014, 2015-2019, 2040-2050 (mid-century), and 2090-2100 (end-of-century). These timeframes were chosen based on common oceanographic conditions, such that years before 2015 were typically cooler than years after 2015 (Danielson et al., 2020) and to visualize changes in FC distribution within each region over time. Rate of FC change was calculated for each region over time by comparing the change in FC of PAROMS grid points across consecutive timeframes. For example, we compared the SSLI region 2009-2014 PAROMS grid points to the same SSLI region PAROMS grid points in the 2015-2019 timeframe to determine if they changed in their FCs. Thus, the total rate of change was determined for each region between each consecutive timeframe (four time frames total), resulting in three rates of change calculated for each region. Additionally, we evaluated the predicted relationship of the proportion of trait modalities to temperature and salinity via generalized least squares models for each region. All JSDMs were performed using the hmsc package in R (Version 2022.2.2.485; Ovaskainen et al., 2017a,b; Tikhonov et al., 2020). K-means clustering was done using the cluster (Maechler et al., 2016) and factoextra (Kassambara & Mundt, 2020) packages in R, while fuzzy coding was performed using the ade4 package in R (Version 2022.2.2.485; Chevenet et al., 1994; Dray & Dufour, 2007; Thioulouse et al., 2018).

4.3 Results

4.3.1 Epibenthic functional composition changes over time

The predicted proportions of modalities varied over time with the most prominent changes occurring in the SSLI and OCS regions and less change over time in the CB region (Figure 4.2). Modality composition changed most within the traits body size and larval development for the SSLI region (Figure 4.2a), in contrast to slight changes in larval development and movement for the CB region (Figure 4.2b), and prominent changes over time in modalities within movement and skeleton in the OCS region (Figure 4.2c). Within body size, epibenthos of the SSLI region was projected to increase in both the proportion of smaller-sized (BS2) and larger-sized taxa (BS5) and decrease in proportion of medium body size (BS3) by the end of the century (Figure 4.2a). In the SSLI and CB regions, the proportion of planktotrophic larval development (LD1) increased over time, while the proportion of swimming movement (MV4) and chitinous skeleton (SK3) increased in the OCS region (Figure 4.2). Modality relationships to temperature and salinity tended to be strongest in the most southern (SSLI) region and most northern (OCS) region (Figure S4.3, S4.4), with many modalities having similar relationships to these climate variables among regions. For example, large body size (BS5) and direct larval development (LD3) were positively and negatively correlated, respectively, with temperature in all regions. Similarly, calcareous skeleton (SK3) was negatively correlated with increased temperature and positively correlated with increased salinity in all regions.

The three regional JSDMs performed moderately well for all regions, with acceptable MCMC convergences in all three regions (ESS > 90; Table S4.1). All JSDMs had higher explanatory power compared to predictive power in all regions (Table 4.2). Explanatory model power was highest in the most southern region (SSLI; 32%) and most northern region (OCS; 32%), while it was lowest in the mid-latitude region (CB; 28%). Predictive model power was similar across regions with the highest in the SSLI region (14%), followed by the OCS region (13%), and CB region (12%; Table 4.2). The proportion of variation that traits accounted for in taxon biomass was highest in the OCS region (15%), closely followed by the SSLI region (14%), and lowest in the CB region (13%, Table 4.2). Functional traits explained the highest amount of variation in species responses to the environmental variables, specifically depth in the SSLI and CB regions and temperature in the OCS region. Functional traits explained a lower amount of the variation in the CB region compared to the other two regions (Table 4.2). The model for the SSLI region suggests that the largest portion of total variance in species' biomass was associated with the fixed climate effects (i.e., salinity and temperature), while the models for the CB and OCS regions suggest that the largest portion of total variance in species biomass was associated with random effects (i.e., year and station location, respectively; Table 4.2). These results indicate that climatic environmental drivers play a major role in structuring functional composition in the SSLI region, while other random effects played a major role in the CB and OCS region. Additionally, predicted species' biomass differed between regions with marked differences in many taxa, including predicted snow crab biomass (*Chionoecetes opilio*) that decreased in the Northern Bering Sea and increased in the Chukchi Sea (Figure S4.5).

4.3.2 Functional composition

Changes in functional composition among regional functional clusters (FCs) were predominantly related to changes in modality proportions within body size (BS) in the SSLI region, and larval development (LD) in both the SSLI and CB regions (Figure 4.3a, 4.4a). For example, medium body size (BS3) and an even distribution of planktotrophic (LD1) and direct larval development (LD3) dominated the offshore SSLI and CB regions in the early part of the study period (e.g., FC1, FC5) and shifted to more medium-large (BS4) and large body sizes (BS5) and an increase in planktotrophic development (LD1) by the end of the century (FC3, FC7; Figure 4.3a, 4.4a). The greatest shift in the OCS region was from calcareous skeleton, dominant across the OCS early in the study period in FC9, to chitinous skeleton, dominant by the end of the century in

FC12 (Figure 4.5a). Spatially adjacent FCs within each region exhibited incremental changes in modality composition (Figures 4.3, 4.4, 4.5). FCs were most distinct in functional composition among the most offshore and most coastal FCs in the SSLI (FC1 and FC4, respectively) and CB (FC5 and FC8, respectively) regions (Figure 4.3, 4.4). In the OCS region, the most dominant FC in the 2009-2014 timeframe (FC9) and the most dominant FC in the 2090-2100 timeframe (FC12) differed the most in composition (Figure 4.5).

The predicted functional composition changed over time in all regions as indicated through clear changes in the distribution of FCs in each region (Figure 4.3b, 4.4b, 4.5b, Table 4.3). The rate of change in FCs in the SSLI region increased over time with the smallest rate of change occurring in the earlier parts of the study period and to the mid-century projection, and dramatic changes at the end-of-century projection (Table 4.3). Shifts in FC distribution in the CB region were most distinct in the most recent study period, with fewer changes by the mid and end of the century. In the OCS region, FC distribution experienced strong changes both during the transition from the historical decades' cold to recent warmer period, and then most strongly again towards the end-of-century projections, with the least change in FC distribution between the present (2015-2019) and the mid-century (Table 4.2).

Distributions of FCs over time followed longitudinal changes in the Northern Bering Sea regions along an east-west pattern (Figure 4.3b, 4.4b) and latitudinal changes in the Chukchi Sea in a south to north fashion (Figure 4.5b). The dominant FCs in both Bering Sea regions in the past decades (i.e., FC1 and FC2 in the SSLI and FC5 and FC6 in the CB region) contracted towards the more central locations in each of the regions, mirroring similar changes in temperature and salinity gradients (Figure S4.1a,b, S4.2a,b). Likewise, FCs occurring only in the easternmost areas of both of these regions (FC4 in SSLI and FC7 and FC8 in CB), as well as westernmost (FC 3) in the SSLI region, expanded during the end-of-century (Figure 4.3b, 4.4b). In the OCS region, FC11 was previously limited to the southern edge of the region but expanded to cover much of the study region by the middle of the century (Figure 4.3b). Likewise, FC12 only started to occur during the mid-century projection at the southern edge of the study area but was dominant across the OCS region by the end-of-century projection. Of note is the almost entire loss of the most prevalent FC in the SSLI region (FC1), the CB region (FC5), and OCS region

(FC9) from the most recent years compared to the end-of-century projection (Figure 4.3b, 4.4b, 4.5b). Generally, domains within regions that had the coldest temperatures at the beginning of the study period (2009-2014) changed least in functional composition throughout the study period, while domains with the warmest temperatures at the beginning of the study period had the most obvious changes in FC (Figures 4.3b, 4.4b, 4.5b, S4.1, S4.2).

4.4 Discussion

We used functional traits of epibenthic communities on the Northern Bering and Chukchi Sea shelves to model how functional composition may change by the end of this century based on predicted environmental changes in this Arctic inflow region. Our results suggest that functional composition is at least in part structured by environmental drivers and will change over time most where climate projections suggest the largest environmental changes. These functional changes were especially prominent in the southern SSLI region at the end of the century. The magnitude of functional composition changes decreased over timeframes in the CB region, while it was especially large in both the early and the late (end-of-century) timeframes in the OCS region. The dominant functional composition in the past decades for the SSLI and CB regions was predicted to be replaced by functional trait compositions that are currently restricted to the coastal or more western domains within those regions. Similarly, modalities within functional traits that are currently more prominently expressed at the southern portion of the OCS study region (e.g., chitinous skeleton) were predicted to increase in spatial coverage and replace the functional composition currently present in the northern domain of the OCS by the end of the century. These shifts in function, driven by shifts in the proportions of select modalities within functional traits (e.g., modalities within body size in the SSLI region, larval development in the SSLI and CB regions, and skeleton in the OCS region), followed changes in temperature and salinity in all regions and are in line with patterns of species distributions based on physiological temperature ranges (Logerwell et al., 2022) and borealization trends of taxonomic composition (e.g., Mueter et al., 2021b). We propose that the functional approach of the present study offers a complementary view to a taxonomic approach that emphasizes the functional traits that taxa must possess to contribute to patterns following environmental borealization of these shelves in the future. Our model predictions also suggest that major functional composition changes in some of the Alaskan Arctic shelf regions may have already occurred based on high rates of functional change between the early part of our study (2009-2014) and the most recent part of our study (2015-2019).

Prominent changes in functional composition over time and space, as shown in this study via the changing spatial distribution of FCs, are consistent with the dominant oceanographic and environmental changes in all regions. The current distribution of FCs in the SSLI and CB regions reflect the east-to-west arrangement of major water masses that currently influence the Northern Bering Sea: the cold, nutrient-rich Anadyr Current to the west, Bering Shelf water with intermediate temperature and nutrient input on the mid shelf, and warm and nutrient poor Coastal Water to the east (Danielson et al., 2020). Temporal change in functional composition in the SSLI generally aligns with the recent expansion of the freshwater-influenced, warmer Alaska Coastal Current and, to a lesser extent, the contraction of the area influenced by Bering Shelf water in the Bering Sea SSLI region (Danielson et al., 2020). Additionally, the area to the southwest of St. Lawrence Island is influenced by the St. Lawrence Island polynya (SLIP), known for its high infaunal benthic biomass (Grebmeier et al., 2015; Feng et al., 2020). We observed an almost complete replacement of the currently dominant functional composition (FC1) in the SSLI region, including the SLIP region, by the end of the century (replaced by FC3). This mirrors noticeable taxonomic changes already documented for the macrofaunal invertebrate community (Grebmeier et al., 2018) and may be related to changes in the timing of polynya formation, driven by changes in atmospheric circulation and also ocean surface currents (Lynch et al., 1997). Likewise, prominent east to mid-shelf FC changes in the CB region align with the expansion of warmer coastal water, encroaching on regions of higher benthic infaunal biomass on the western side of the basin (Grebmeier et al., 2006; Danielson et al., 2020). Similarly, the environmental changes in the OCS region with increasingly warmer and fresher conditions expanding from south to north corresponded with the direction of FC expansions in that region. Changes in both the Arctic environment and in benthic composition have been suggested as evidence of the Bering and Chukchi seas study region as reaching a “tipping point”, heading for a new normal (Grebmeier et al., 2018; Huntington et al., 2020). Accordingly, we saw across all three regions that relatively small changes in epibenthic functional composition were predicted to occur between the most recent time frame of the hindcast model (2015-2019) and the mid-century projected years (2040-2050), as well as relatively large changes between the earliest part of the study (2009-2014) and most recent years (2015-2019) for the CB and OCS regions. This suggests that the current Arctic epibenthos may have already functionally transformed to a new state during the past study years of this work that is similar to mid-century epibenthic functional composition.

FCs represent areas within a region that have similar proportions of modalities, or similar functional trait profiles. Based on projected FCs, and thus the projected increases in the proportions of modalities over time, we can infer which trait modalities will likely be advantageous in each region under future environmental conditions. For example, planktotrophic larval development increased in both the SSLI and CB regions over time, together with larger body sizes, while chitinous skeletons became most prominent in the OCS region. Therefore, taxa that have these suites of biological traits will likely be able to be competitive in these regions. In the OCS region, for example, projected increase in chitinous skeletons, along with other dominant modalities, such as crawling movement and scavenging and predatory feeding habits, describe decapods, such as hermit crabs (e.g., *Pagurus* spp. or *Labidochirus* sp.) or the economically important snow crab *Chionoecetes opilio* (which has mostly a chitinous skeleton). The Alaskan Arctic is currently closed to commercial fishing (NPFMC, 2009), but snow crab have been identified as a potential target fishery in the Arctic in the future. Snow crab are abundant in the Chukchi Sea, but their body size is too small to make commercial harvest economically viable, possibly due to stunted growth based on the low bottom water temperatures (Divine et al., 2019). If the expected temperature increases in the Chukchi Sea result in snow crab reaching harvestable sizes, and other economically important species continue to move poleward, such as Pacific cod (*Gadus macrocephalus*) or Walleye pollock (*Gadus chalcogrammus*), a fishery in the Chukchi Sea could be considered in the future. Snow crab biomass has recently declined dramatically in the Eastern Bering Sea region, one of the most important commercial snow crab fishing regions, with the lowest catch biomass on record in 2021 (Zacher et al., 2021) and a complete closure of the commercial snow crab fishery for the 2022/23 season, because of below-sustainability biomass (Alaska Department of Fish and Game Advisory Announcement, release 10/10/2022, http://www.adfg.alaska.gov/static/applications/dcfnewsrelease/1441272349.pdf). While reasons for this decline are currently being investigated, snow crab have the potential to increase in biomass in more northern regions, such as the Chukchi Sea shelf. Similarly, larvae of the boreal sister species, Tanner crab (*C. bairdi*), have recently been observed in the Chukchi Sea (Landeira et al., 2018). Planktotrophic larval development and projected increases in northward flow from the Northern Bering Sea into the Chukchi Sea provide taxa with this life history trait the ability to spread and increase their numbers in more northern latitudes (Ershova et al., 2019).

An increase in taxa with chitinous and decrease in those with calcareous skeleton may be advantageous in a freshening Arctic. Due to naturally occurring low carbonate concentrations resulting from low water temperatures, oceans in high latitudes, such as the Alaskan Arctic are at great risk of ocean acidification (Feely & Chen, 1982; Feely et al., 1988; Byrne et al., 2010). Increases in sea-ice melt and riverine freshwater input, along with other drivers, such as increased wind-driven upwelling from a decline in seasonal sea ice, exacerbate CO_2-driven ocean acidification (Yamamoto-Kawai et al., 2009; Mathis et al., 2015; Carmack et al., 2016). While we did not evaluate carbon chemistry as a specific driver, calcareous skeletal type had strong positive relationships with salinity (see Figure S4.4) in the OCS and SSLI regions. This skeleton type consequently decreased in proportional abundance over time, particularly in the OCS region, aligned with the predicted freshening of the Arctic seas. Freshening of the Arctic contributes to increased ocean acidification (Yamamoto-Kawai et al., 2009; Terhaar et al., 2021), which would be detrimental to taxa with calcareous skeletons (Fabry et al., 2009). Not only do our results highlight regions of vulnerability to ocean acidification via changes in calcareous taxa (e.g., sand dollars, gastropods), a decline in calcareous skeleton can also affect ecosystem functioning, such as inorganic carbon sequestration.

Our model captured the relationships among many functional traits that are correlated to water mass characteristics of temperature and salinity, but lacked information on projected increases in primary production, a key driver of Arctic benthic food webs (Lewis et al., 2020). The Alaskan Arctic has strong pelagic-benthic coupling due to the timing of sea-ice retreat, leading to known benthic hotspots (Grebmeier et al., 2015; Feng et al., 2020). As the timing of sea-ice retreat becomes earlier in a warmer Arctic, the quality and quantity of production that is directly exported to the benthos is also likely to shift (Tremblay et al., 2012; Belanger et al., 2013), presumably affecting trophic transfers. Previously, pelagic-benthic coupling was forecasted to weaken with the reduction in sea ice that would, in turn, contribute to the loss of sea ice algae and increase pelagic grazers on phytoplankton blooms (Carmack & Wassmann, 2006; Grebmeier, 2012). However, recent studies have shown that even in years with minimal sea ice, such as in 2018, unprecedented amounts of production were transported to the benthos on Pacific Arctic shelves, which would continue to support a diverse and robust benthic community (Lalande et al., 2020; O'Daly et al., 2020). Maintenance of the current state of pelagic-benthic coupling, or even increases in export, are important drivers of benthic communities and should be further considered in future models.

4.5 Conclusion

The analyses conducted here represented the relationships of epibenthic functional trait modalities to environmental variables, as well as the spatial changes in functional composition over time, including projections into the future. We acknowledge that our projections of functional composition for the mid- and end-of-century predictions were based on only one SSP-5 simulation and one global model for increases in temperature and decreases in salinity. However, we believe that these regional projections provide a reasonable basis for exploring the responses of benthic communities to possible future conditions, although changes in temperature and salinity are unlikely to be uniform across space within each region as assumed here. We conducted these analyses for separate study regions, as they are known to differ in epibenthic community structure (Iken et al., 2019), are distinct in their environmental conditions (Danielson et al., 2020), and here we also found them to be different in their epibenthic functional composition. This regional approach follows a concept used in management known as bioregionalization, where communities are classified into distinct biogeographical units (Ovaskainen & Abrego, 2020). The FCs we identified for the three study regions can be used for many conservation purposes, including reserve selection for regions of high functional diversity, or defining management units for species of interest based on their functional trait profile (Hill et al., 2017; Miatta et al., 2021). Similarly, managers could select regions for protection of specific ecosystem functions, such as conservation of energy flow (Cheng et al., 2019) or maintaining larval transport corridors (Treml et al., 2012; D'Aloia et al., 2017), if the relationships between critical modalities and the environment are well understood. Indeed, in other marine ecosystems in the world, such as coral reefs, using biological traits to assess the stability and resilience of communities is leading the field of conservation science and creating roadmaps for protected areas and conservation efforts (Madin et al., 2016; Hill et al., 2017; van Oppen et al., 2017; Zawada et al., 2019). The modeling work produced here, together with previous foundational work on the current distribution of functional traits and their environmental relationships in the Bering and Chukchi seas (Rand et al., 2018; Liu et al., 2019; Sutton et al., 2020, 2021; Zhulay et al., 2021) may build the basis for the application of such a conservation and management approach for the Arctic benthos as well. Future work could include additional environmental drivers, such as ocean acidification, as well as changing biotic interactions, e.g., from the influx of new top predators, such as Pacific cod or Walleye pollock, to provide a more refined picture of future functional changes on these Arctic shelf systems. A holistic approach to management is becoming increasingly important as environmental changes (e.g., warming and freshening) and human interest in Arctic resource use (e.g., oil and gas extraction, fishing, shipping routes, tourism) are ever increasing.

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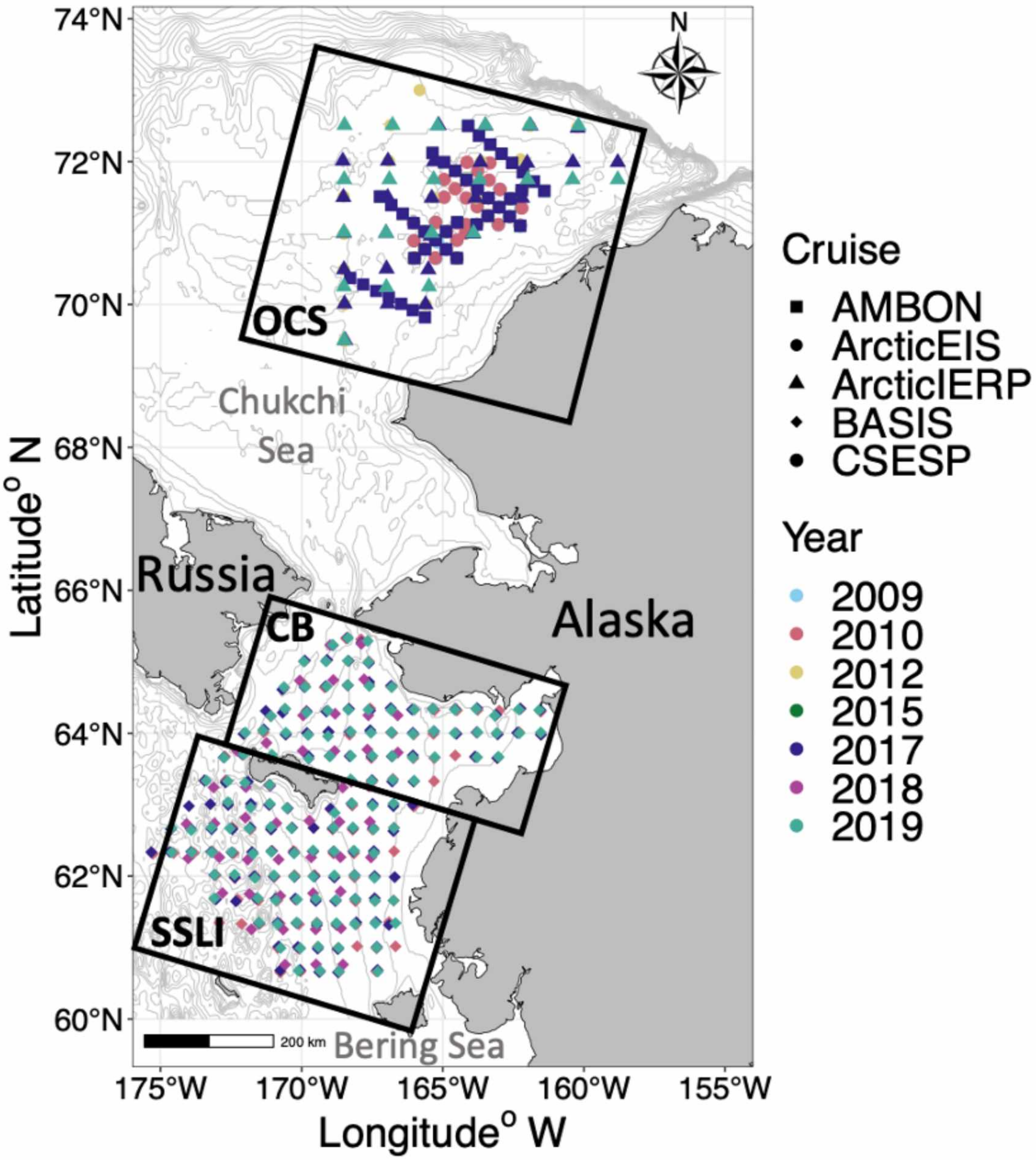


4. 1. Map of study area, divided into three subregions. Each point represents a station sample d, lor indicating sampling year and shape indicating the research program under which sampling nducted. SSLI = South of St. Lawrence Island, CB = Chirikov Basin, OCS = Offshore Chukchi

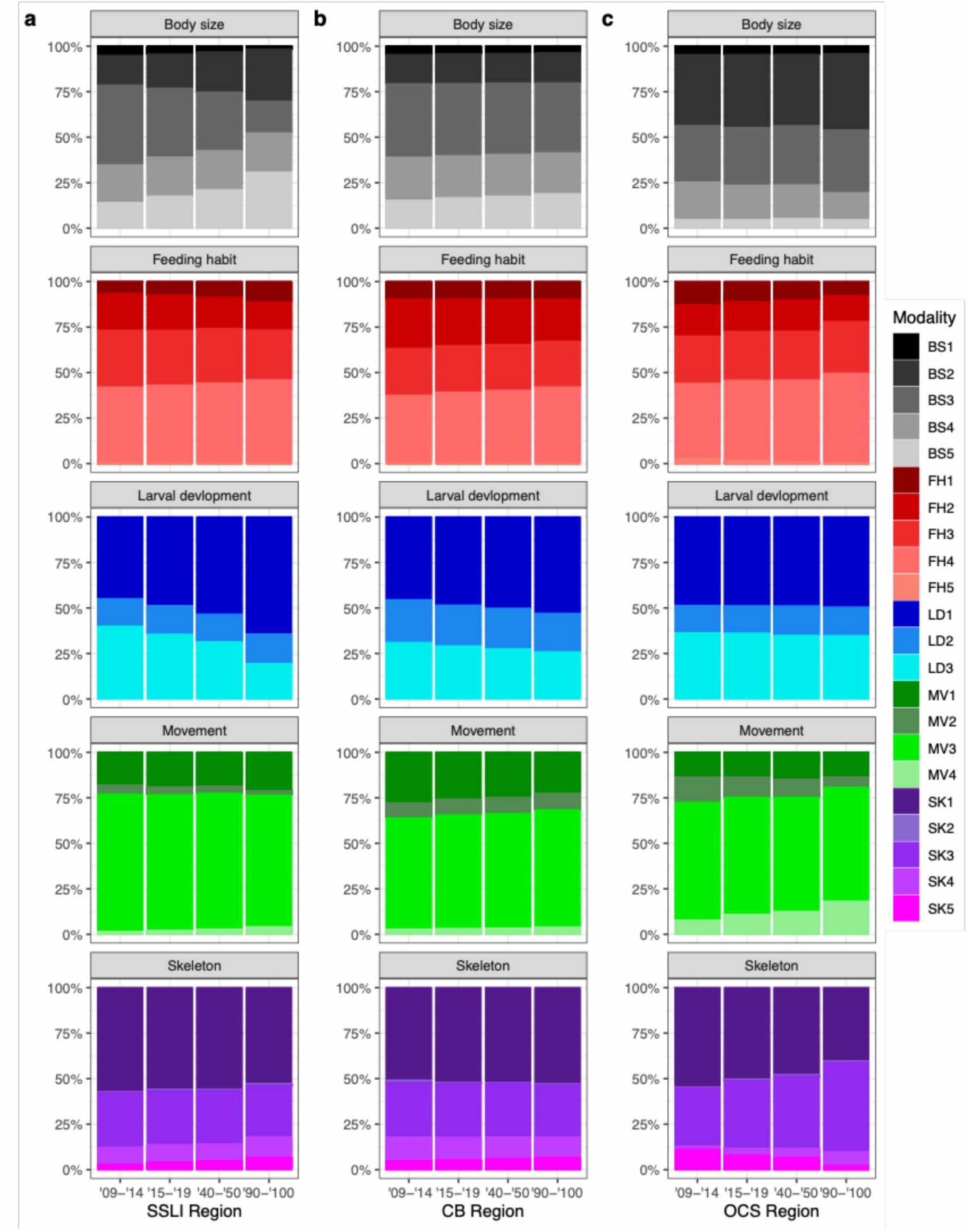


Figure 4.2. Changes in the proportion of modalities within each trait over time for a: the South of St. Lawrence Island (SSLI) region, b: the Chirikov Basin (CB) region, and c: the Offshore Chukchi Sea (OCS) region. Colors represent modalities and abbreviations can be found in Table 3.1.

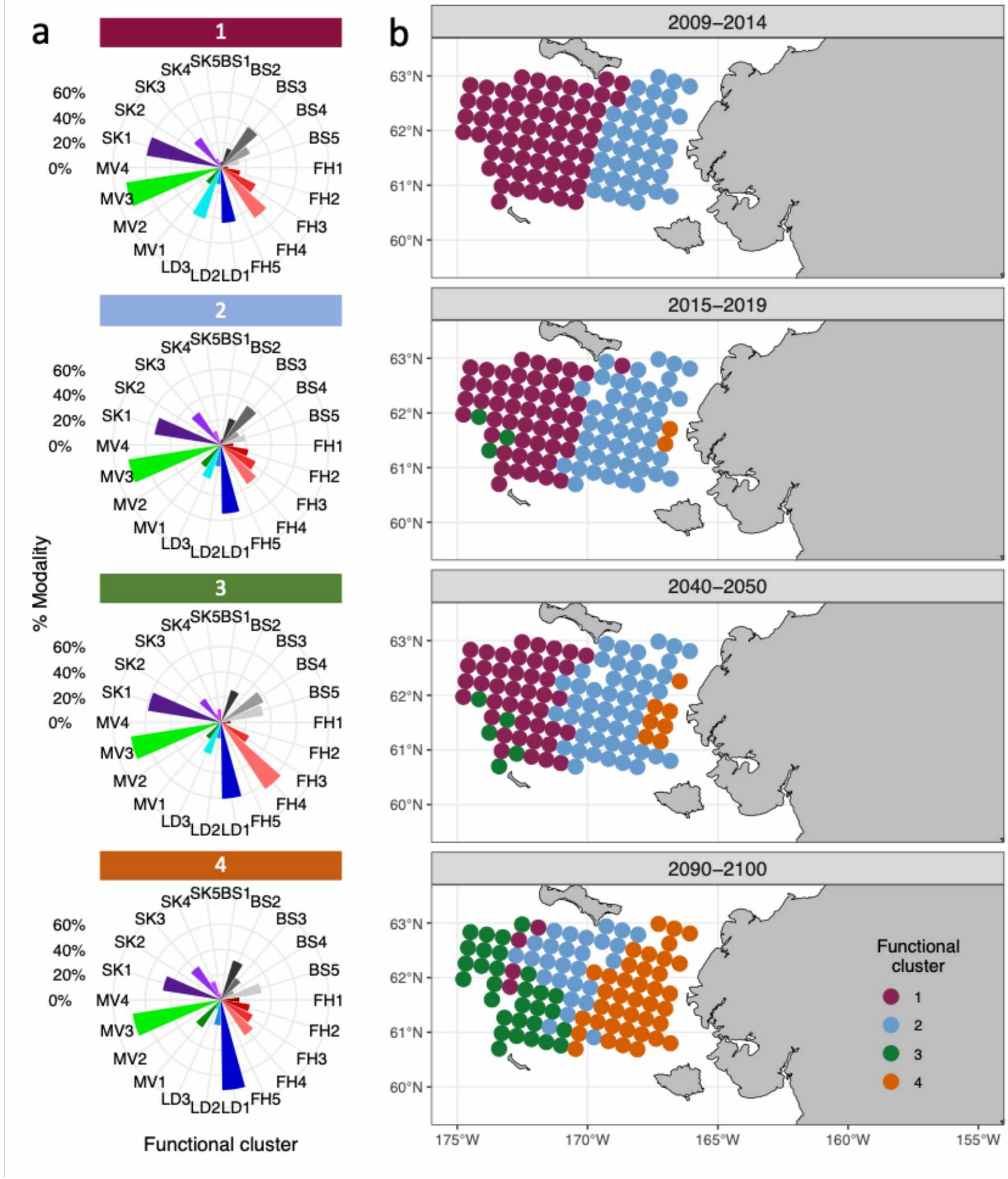


Figure 4.3. The distribution of (a) modalities of the five functional traits within the different functional clusters (FCs) are represented as circular bar plots for the region South of St. Lawrence Island (SSLI), west of Alaska. Modality abbreviations are as in Table 4.1. Spatial distributions (b) of functional clusters (FC) that describe functional composition clusters in the SSLI region for four timeframes: 2009-2014 and 2015-2019 are based on hindcast models, and 2040-2050 and 2090-2100 are based on projected increases in temperature and decreases in salinity via the CMIP6 CNRM-ESM2-1 SSP-5 “worst case” scenario.

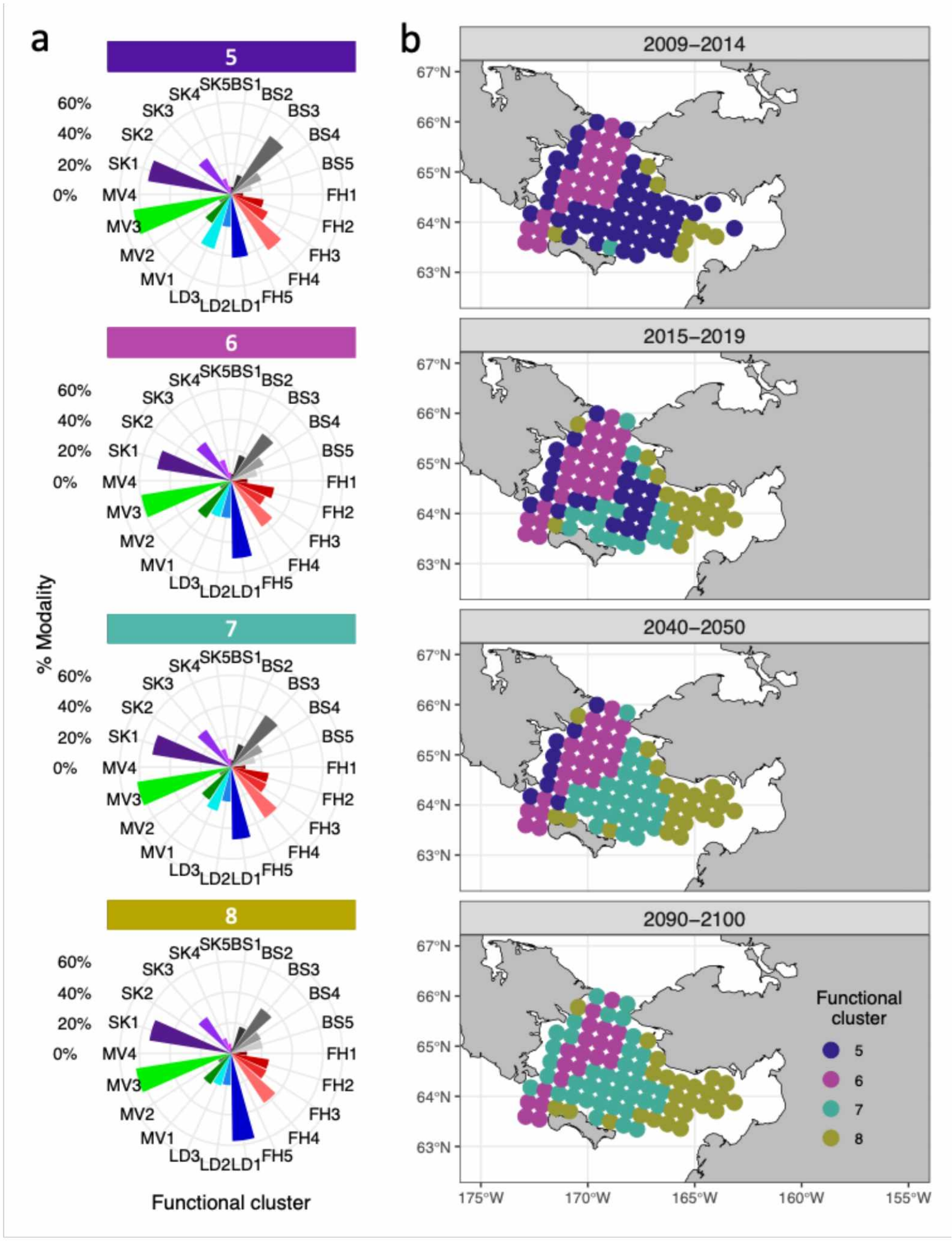


Figure 4.4. The distribution of (a) modalities of the five functional traits within the different functional clusters (FCs) are represented as circular bar plots for the region Chirikov Basin (CB), west of Alaska. Modality abbreviations are as in Table 4.1. Spatial distributions (b) of functional clusters (FC) that describe functional composition clusters in the CB region for four timeframes: 2009-2014 and 2015-2019 are based on hindcast models, and 2040-2050 and 2090-2100 are based on projected increases in temperature and decreases in salinity via the CMIP6 CNRM-ESM2-1 SSP-5 "worst case" scenario.

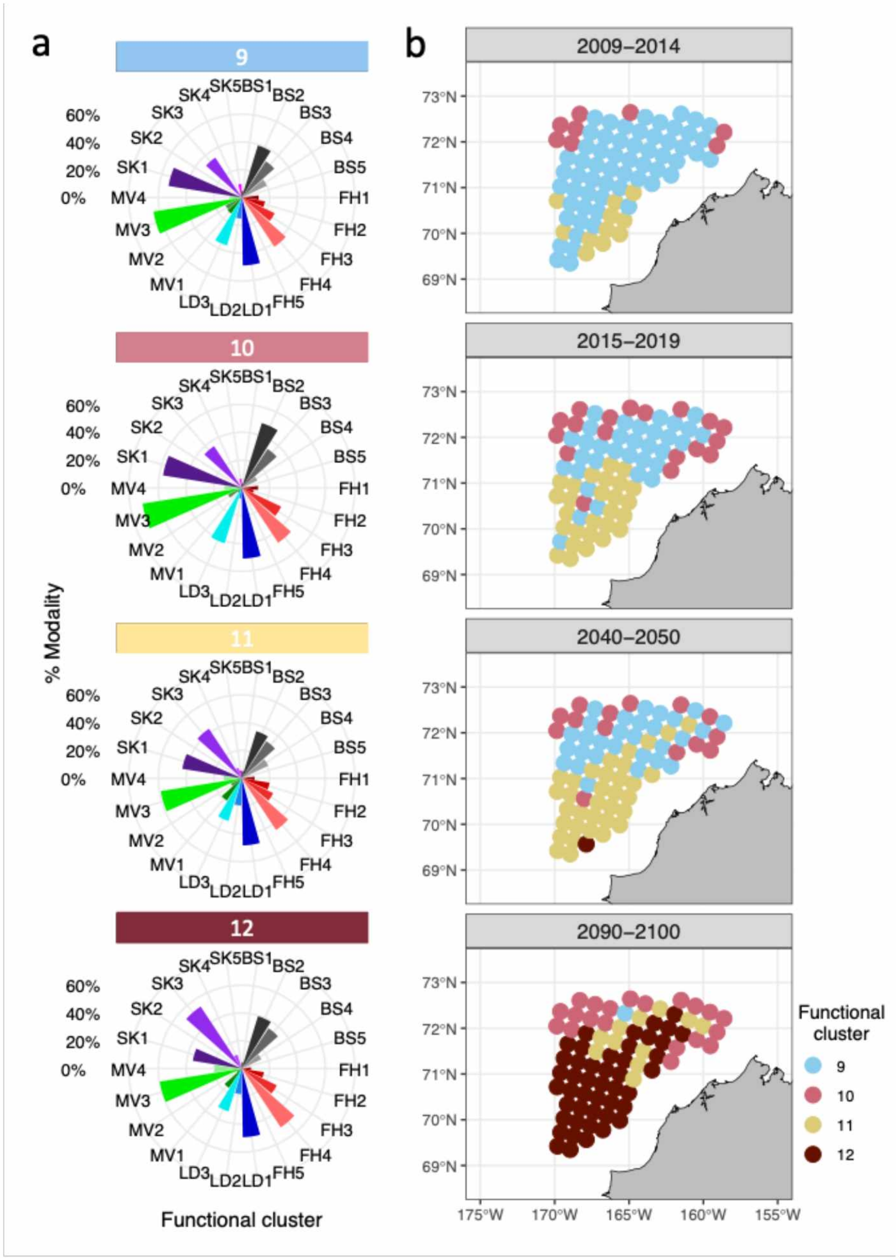


Figure 4.5. The distribution of (a) modalities of the five functional traits within the different functional clusters (FCs) are represented as circular bar plots for the region Offshore Chukchi Sea (OCS), west of Alaska. Modality abbreviations are as in Table 4.1. Spatial distributions (b) of functional clusters (FC) that describe functional composition clusters in the OCS region for four timeframes: 2009-2014 and 2015-2019 are based on hindcast models, and 2040-2050 and 2090-2100 are based on projected increases in temperature and decreases in salinity via the CMIP6 CNRM-ESM2-1 SSP-5 “worst case” scenario.

Table 4.1. Biological traits, modalities, descriptions, and ecological relevance are shown for epibenthic invertebrates collected in the Chukchi and Bering seas, following Degen & Faulwetter (2019). Abb: Modality abbreviations used in figures.

Biological trait	Modality	Abb.	Description	Ecological relevance
Size (length in mm)	Small	BS1	<10 mm	Effect on productivity, energy flow, trophic and food web structure
	Small-medium	BS2	10 - 50 mm	
	Medium	BS3	50 - 100 mm	
	Medium-large	BS4	100 - 300 mm	
	Large	BS5	> 300 m	
Feeding Habit	Deposit feeder	FH1	Removal of detrital material from sediment	Indicative of hydrodynamic conditions and carbon transport
	Filter/suspension feeder	FH2	Filter food from the water column	
	Opportunist/scavenger	FH3	Scavenges food	
	Predator	FH4	Actively hunts live prey	
	Parasite	FH5	Feeds off other organisms	
Larval Development	Planktotrophic	LD1	Larvae feed and grow in water column	Ability to disperse, become invasive, or recover from disturbance
	Lecithotrophic	LD2	Larvae with yolk sac, pelagic for short periods	
	Direct development	LD3	No larval stage (eggs develop into juveniles)	
Movement	Sessile/none	MV1	No movement as adult	Movement of energy through nutrient cycling, carbon deposition, and maintain habitat stability
	Burrower	MV2	Movement in the sediment	
	Crawler	MV3	On surface via movement of appendages	
	Swimmer	MV4	Movement above the sediment	
Skeleton	Calcareous	SK1	Skeleton material aragonite or calcite	Indicative of vulnerability, resistance to predation, and ecosystem engineering
	Siliceous	SK2	Skeleton material silicate	
	Chitinous	SK3	Skeleton material chitin	
	Cuticle	SK4	No skeleton but a protective structure like a cuticle	
	No protection	SK5	No form of protective structure	

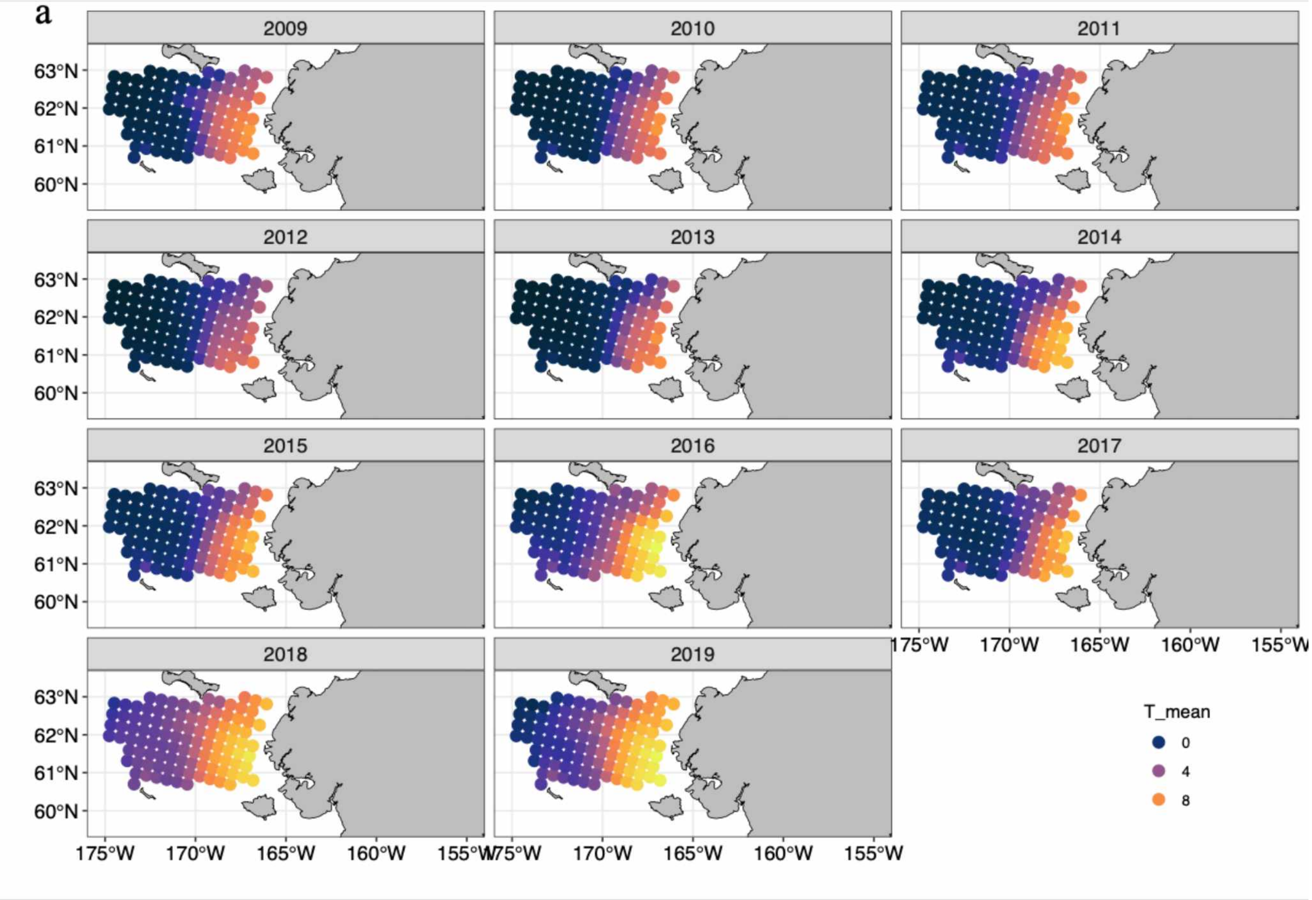
Table 4.2. Joint species distribution model fit was evaluated for explanatory and predictive power for species distributions via Tjur's R^2 with root mean squares error (RMSE), and trait explanatory power (β) for the three study regions: South of St. Lawrence Island (SSLI), Chirikov Basin (CB), Offshore Chukchi Sea (OCS). Trait-environment, trait-taxa, and taxa-environment relationships are represented by percent variation explained per relationship.

Model parameter		**SSLI**	**CB region**	**OCS Region**
Model explanatory power for species Tjur's R^2		32.18%	27.52%	31.70%
Explanatory RMSE for species		1.22	0.26	0.73
Predictive power for species Tjur's R^2		13.62%	11.71%	12.56%
Predictive RMSE for species		1.44	0.29	0.85
Variation in taxon biomass explained by traits (ß)		14.33%	12.40%	14.91%
Variation explained by traits in response to environment	Temperature	10.64%	6.42%	22.00%
	Salinity	22.56%	3.18%	12.84%
	Depth	26.51%	10.14%	10.38%
	Intercept	23.41%	3.81%	12.59%
Mean variance partition for species biomass	Habitat (fixed; depth)	19.07%	13.40%	9.20%
	Climate (fixed; temperature, salinity)	39.33%	15.97%	27.23%
	Year (random)	22.21%	49.41%	28.95%
	Station (random)	19.38%	21.22%	34.63%

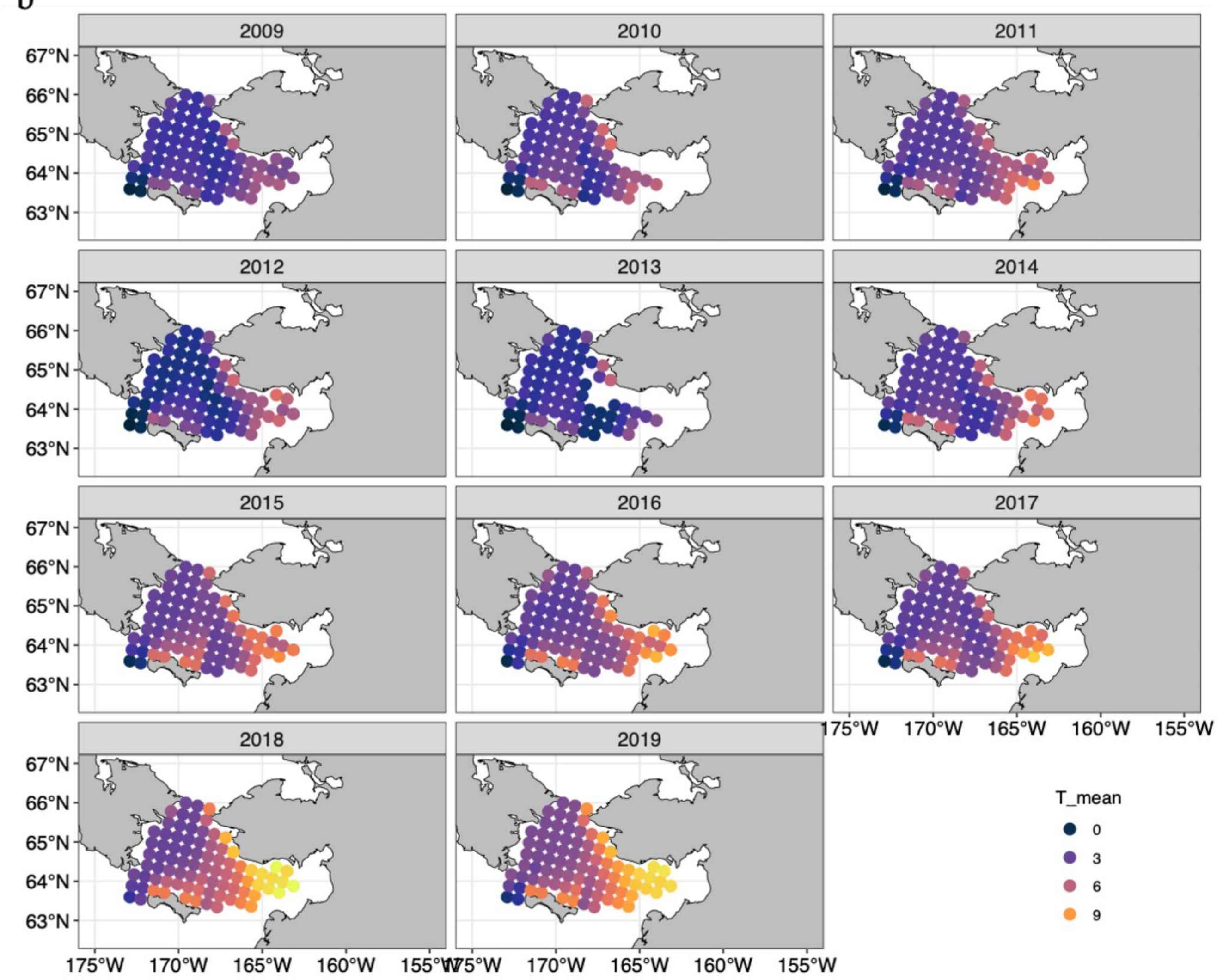
Table 4.3. The rate of change between consecutive time periods was calculated as the proportion of grid cells changing functional cluster (FC) membership for all regions: South of St. Lawrence Island (SSLI), Chirikov Basin (CB), Offshore Chukchi Sea (OCS).

Time period comparison	**SSLI region**	**CB region**	**OCS region**
09'/14' vs. 15/'19	13.00%	31.25%	35.90%
15'/'19 vs. 40'/50'	13.00%	23.75%	16.67%
40/50 vs. 90/100	73.00%	18.75%	78.21%

4.6 Appendix


a
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
2019
63°N
62°N
61°N
60°N
175°W
170°W
165°W
160°W
155°W
T_mean
0
4
8

b


2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
2019
67°N
66°N
65°N
64°N
63°N
175°W
170°W
165°W
160°W
155°W
T_mean
0
3
6
9

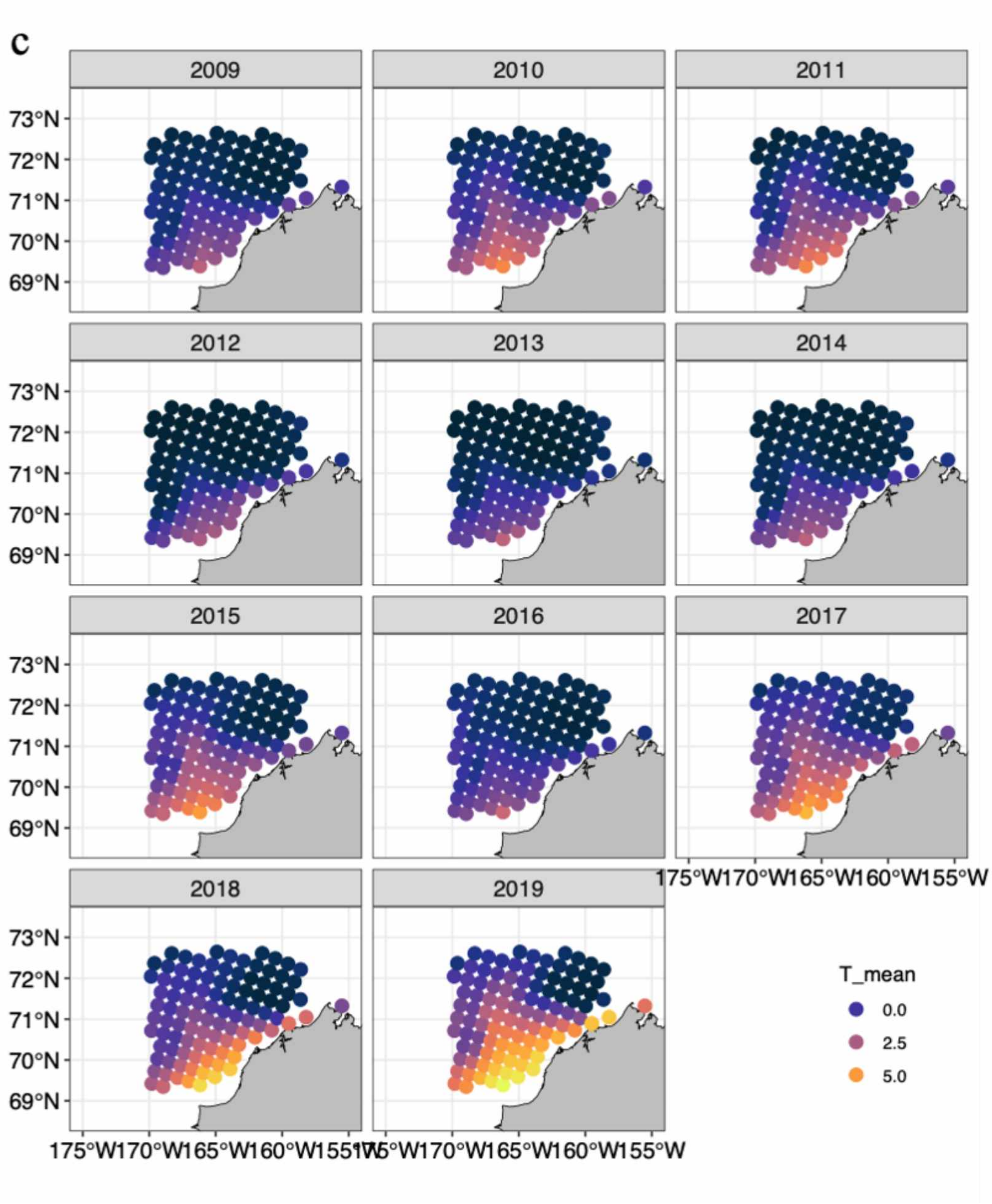
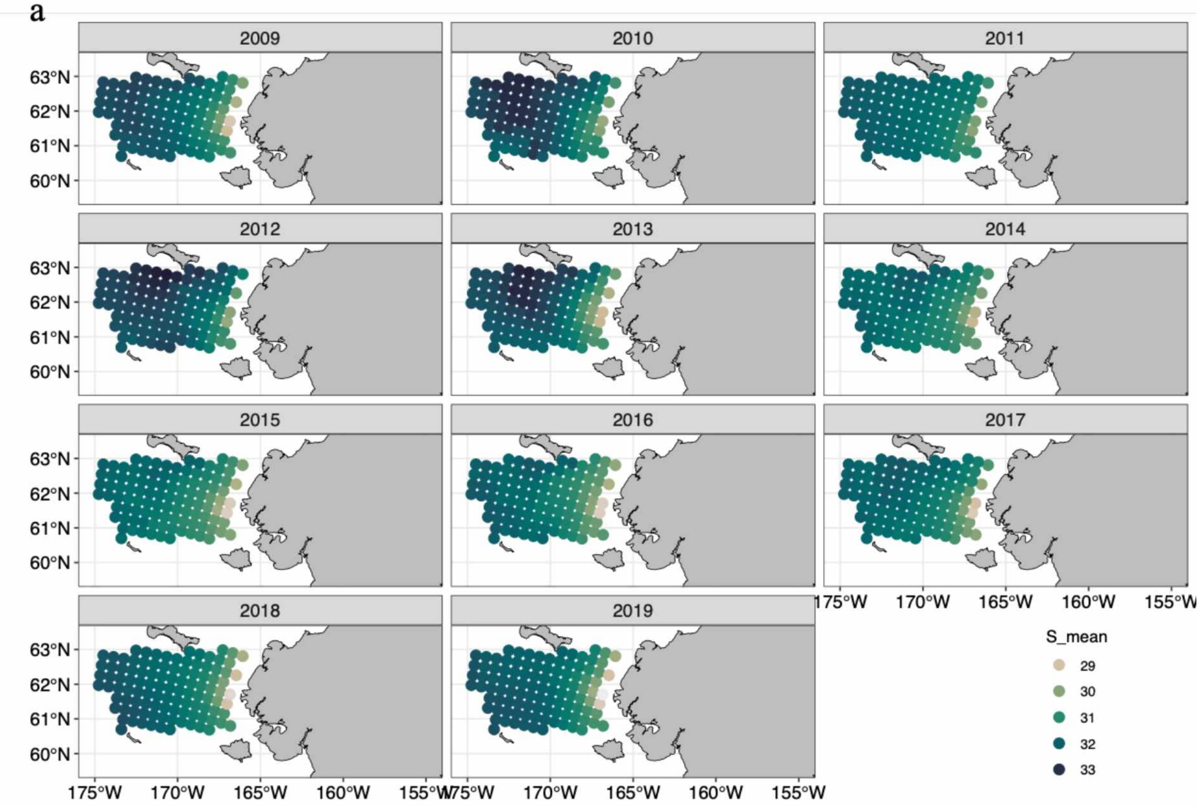


Figure S4.1. Annual temperature from the PAROMS model output for the 2009-2019 period for the (a) South of St. Lawrence Island (SSLI) region, (b) Chirikov Basin (CB) region, and (c) Offshore Chukchi Sea (OCS) region.

a


2009
2010
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2015
2016
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2019
63°N
62°N
61°N
60°N
175°W
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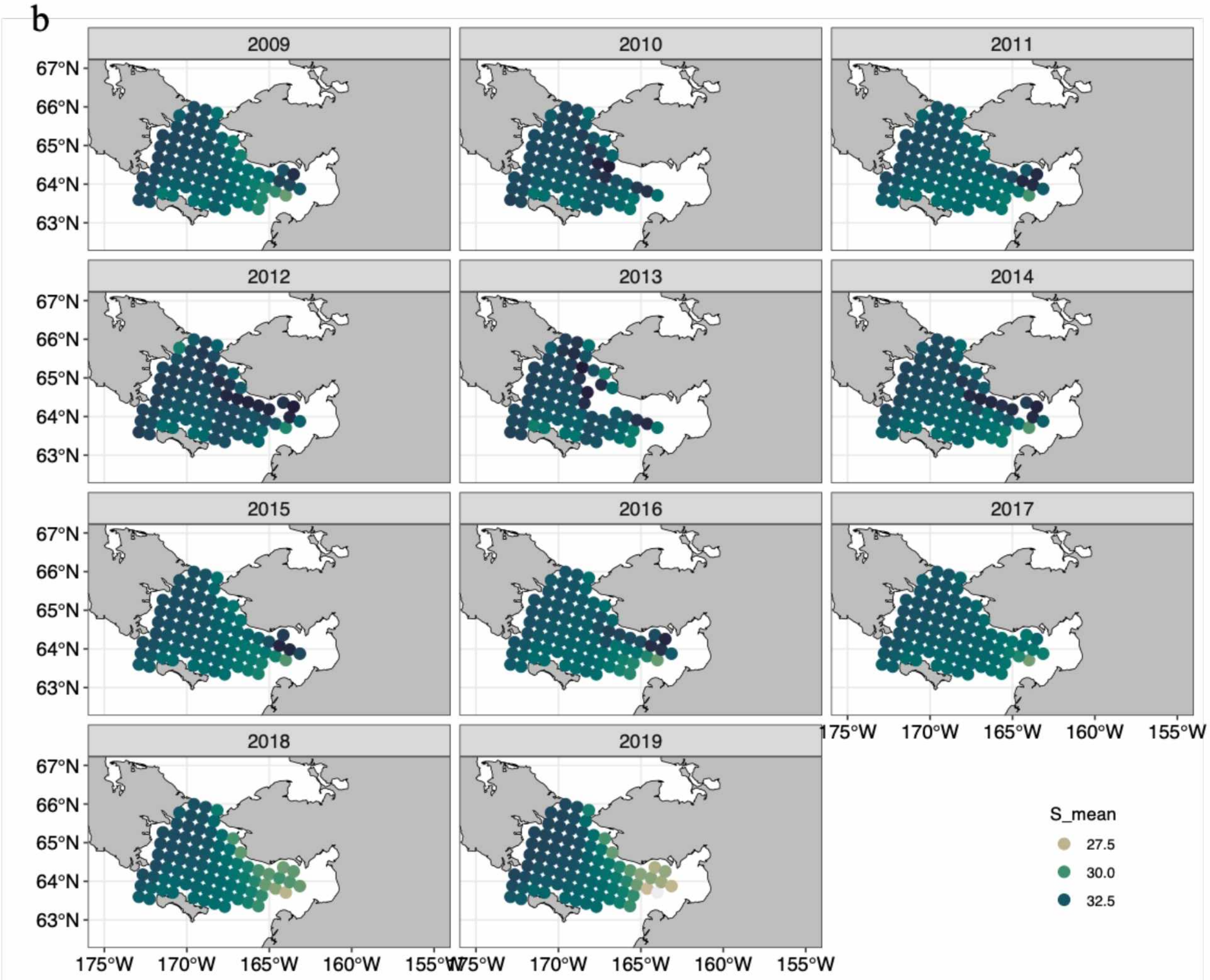
165°W
160°W
155°W
S_mean
29
30
31
32
33

b


2009
2010
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2017
2018
2019
67°N
66°N
65°N
64°N
63°N
175°W
170°W
165°W
160°W
155°W
S_mean
27.5
30.0
32.5

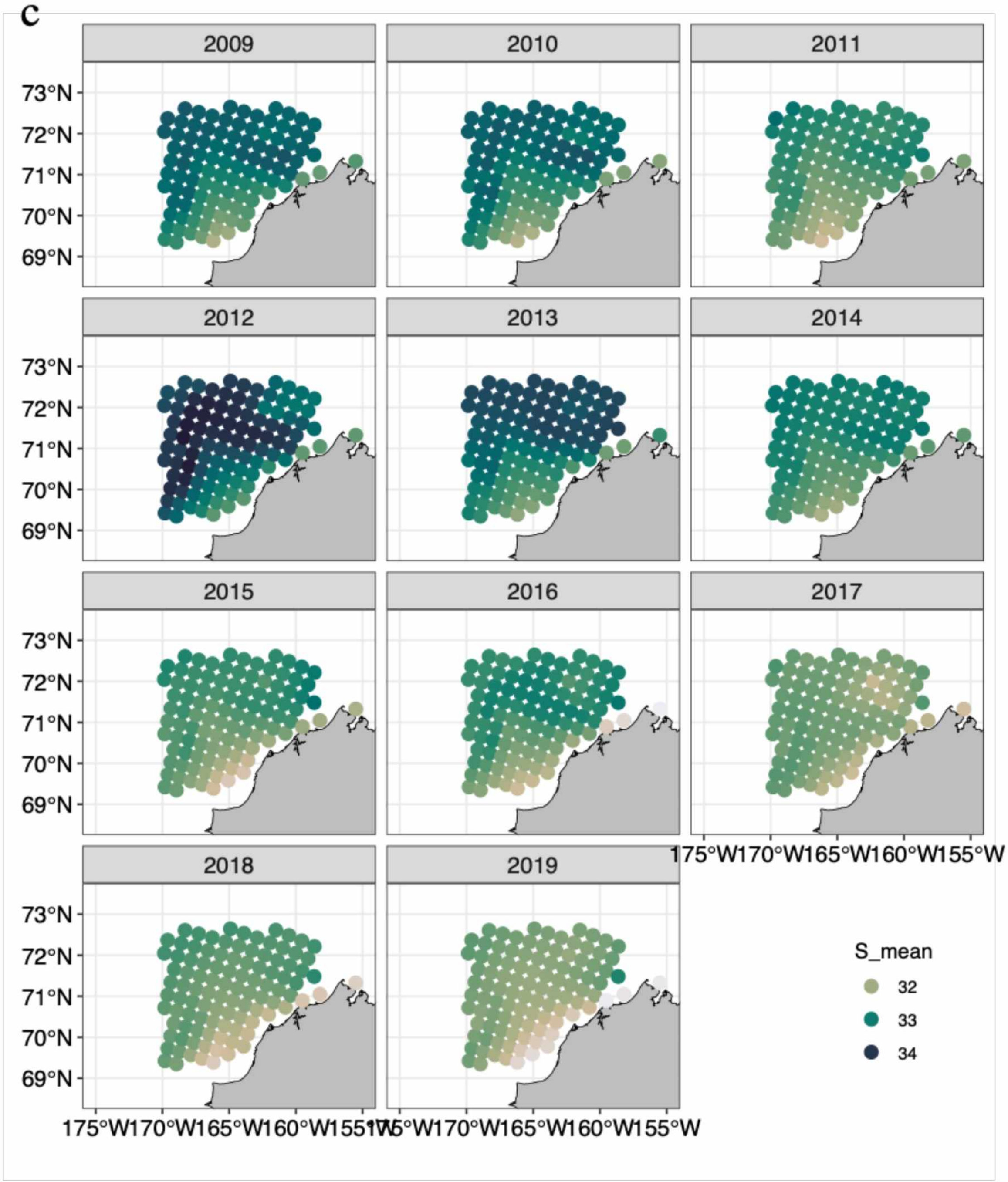

Figure S4.2. Annual salinity from the PAROMS model output for the 2009-2019 period for the (a) South of St. Lawrence Island (SSLI) region, (b) Chirikov Basin (CB) region, and (c) Offshore Chukchi Sea (OCS) region.

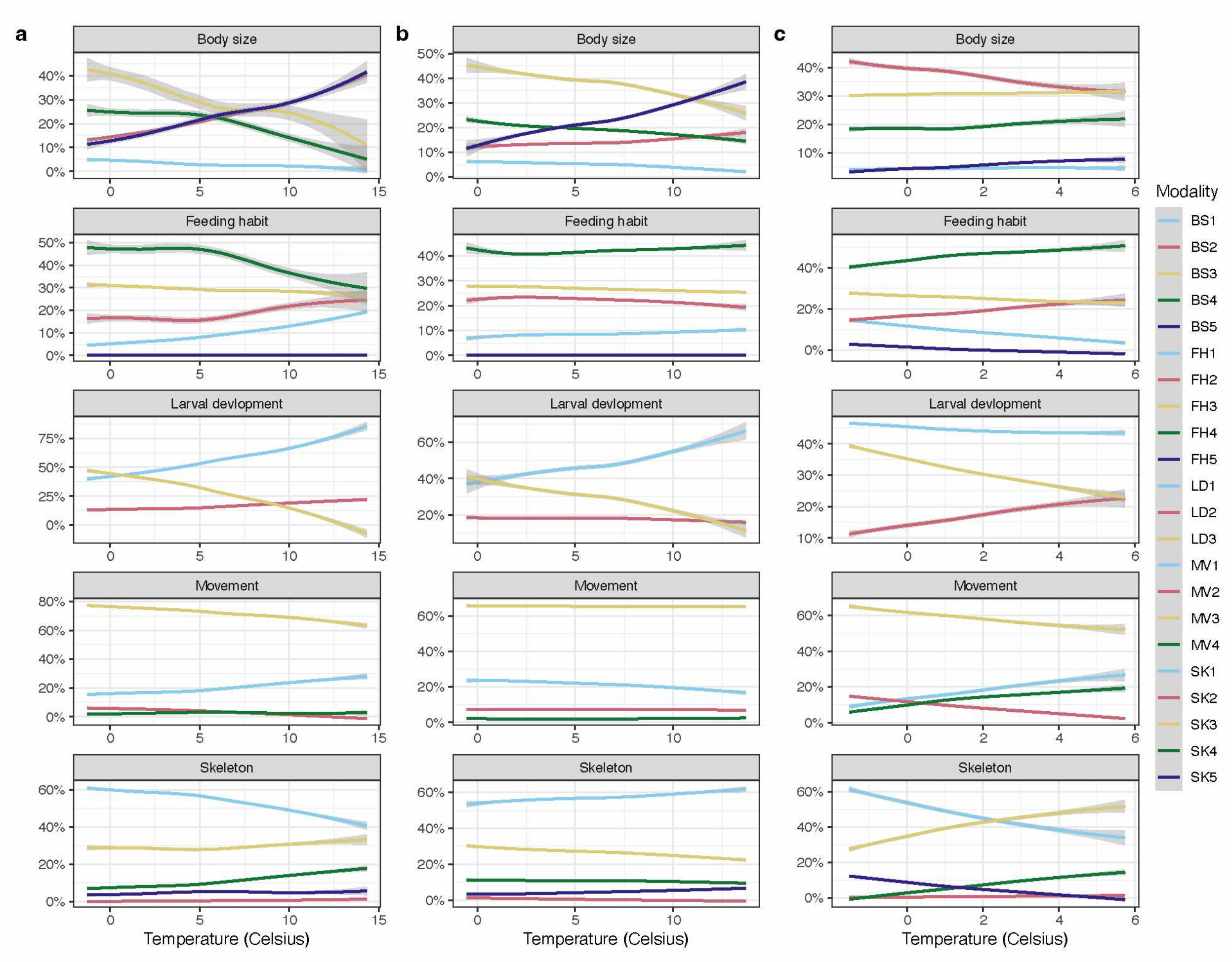

Figure S4.3. Relationships between modalities and temperature for each region using a generalized least squares approach, faceted by traits. Colors correspond to different modalities within each trait for the (a) South of St. Lawrence Island (SSLI) region, (b) Chirikov Basin (CB) region, and (c) Offshore Chukchi Sea (OCS) region.

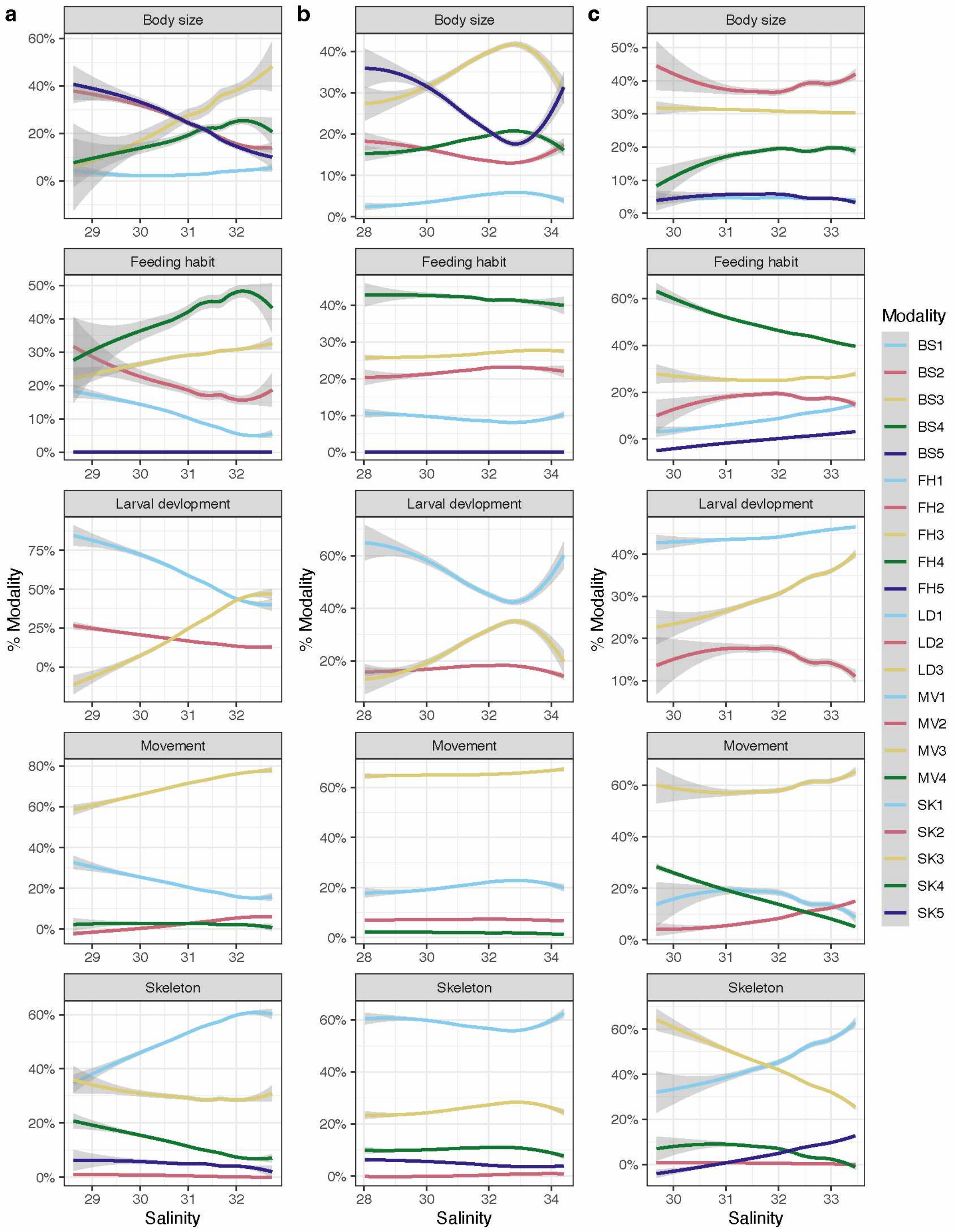

Figure S4.4. Relationships between modalities and salinity for each region using a generalized least squares approach for each region, faceted by traits. Colors correspond to different modalities within each trait for the (a) South of St. Lawrence Island (SSLI) region, (b) Chirikov Basin (CB) region, and (c) Offshore Chukchi Sea (OCS) region.

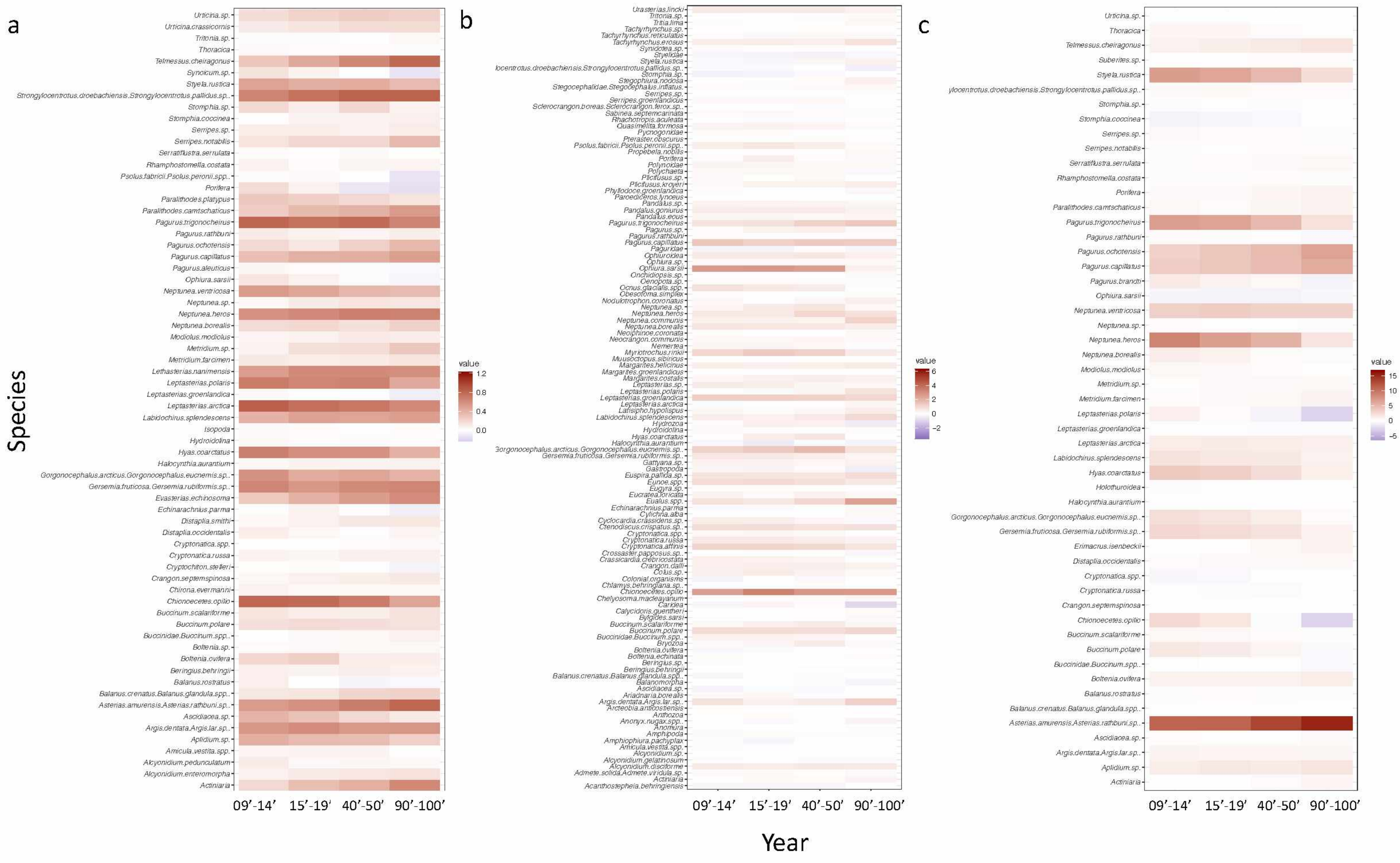

Figure S4.5. Joint species distribution model output for predicted species changes for the (a) South of St. Lawrence Island (SSLI) region, (b) Chirikov Basin (CB) region, and (c) Offshore Chukchi Sea (OCS) region over the early time period (2009-2014), recent time period (2015-2019), mid-century time period (2040-2050), and end-of-century time period (2090-2100). Red colors indicate predicted increase in species distributions, while blue colors indicate decreases in species biomass.

Table S4.1. Markov Chain Monte-Carlo (MCMC) convergence parameters were investigated via Gelman and Rubin’s convergence diagnostics to derive potential scale reduction factors (beta, sigma), and mean estimated effective sample size (mean ESS) for all regions: South of St. Lawrence Island (SSLI), Chirikov Basin (CB), Offshore Chukchi Sea (OCS).

Model metrics	**SSLI**	**CB**	**OCS**
Mean ESS	94.05	109.21	92.73
Beta	1.37	1.05	1.18
Sigma	2.41	1.07	1.33

CHAPTER 5: GENERAL CONCLUSION

Functional traits allow the investigation of diversity from a more mechanistic perspective compared to using taxonomic diversity alone. Additionally, functional traits present opportunities to answer foundational ecological questions that explore if ecosystem function increases with increasing biodiversity (Loreau et al., 2001; Cardinale et al., 2009, 2012) and how strong environmental filters structure communities and ecosystem function (Keddy, 1992; Kraft et al., 2015; Menegotto et al., 2019). Functional trait analyses build on taxonomic analyses, but are based on a large set of biological traits, and various modalities within each trait. These modalities are assumed to encompass all possible trait expression combinations used for these analyses. Different species would not change the actual traits included in the analysis but could change the trait profiles expressed in a particular region. This is an advantage over the use of taxonomic diversity alone, which can be acutely limiting, especially for predictive models of changes in diversity, as the set of potentially new species is unknown. The use of traits in modelling is beneficial in a region, such as the Alaskan Arctic, where information from systematic community analyses is sporadic over only one to two decades.

Epibenthic communities on the Alaskan Arctic Chukchi and Beaufort Sea shelves followed the Biodiversity-Ecosystem-Functioning (BEF) hypothesis prediction that increased taxonomic diversity would lead to increased ecosystem function (Loreau et al., 2001). In support of this, I found higher functional and taxonomic diversity in the Beaufort Sea compared to the Chukchi Sea to be associated with a more even distribution of functional traits; this is an indicator of higher resource partitioning and a more effective use of resources in a system. Higher resource partitioning in the Beaufort Sea epibenthos was driven both by taxa with highly specialized functions, as well as taxa that were more functionally diverse from each other. These functionally diverse and specialized taxa provided more opportunities to exploit a wider resource availability, reflecting greater niche complementarity (Hewitt et al., 2008). Greater niche complementarity also reflects higher stability of ecosystems and makes a region less vulnerable to the invasion of non-indigenous taxa (Mason et al., 2005). Conversely, less niche complementarity, such as in the Chukchi Sea, may promote more species' invasions from more southern regions, such as those migrating northward from the Bering Sea. Differences in sediment grain size (Naidu, 1974; Grebmeier et al. 2015), or in carbon sources (Bell et al. 2016; Harris et al. 2018) are two examples of various habitat niches that may drive the unique functional composition between shelves. Key differences in functional trait composition, such as the distinct expression of larval development and body size, and the evenness of trait modalities within these functional traits, likely contributed to disparities in energy flow and stability of ecosystems between the Beaufort and Chukchi seas shelf communities. Differences in ecosystem function and niche complementarity, based on the investigation of functional traits of these Arctic shelf communities, fueled questions about the relationships between dominant environmental influences and functional structure.

Assuming the Chukchi Sea shelf is more prone to species invasions compared to the Beaufort Sea shelf, based on lower functional diversity and less niche complementarity, then the Chukchi Sea shelf could be more affected by environmental influences compared to the Beaufort Sea shelf. Questions spanning from how trait-environment relationships differed between the two seas to the relative strength of an environmental filter on functional diversity within each shelf community drove my investigation of environmental filtering and functional diversity. I found environmental filtering was much more evident on the Chukchi Sea shelf, driven by a habitat niche structured by temperature, depth, and mud compared to a weaker environmental filter on the Beaufort Sea shelf, driven by depth and salinity. In the Chukchi Sea, warmer temperatures in the Alaska Coastal Current region were linked to larger, sessile, filter feeding taxa and lecithotrophic larval development, indicating a relationship of these traits with warmer temperatures. While physiological tolerances of taxa were not explicitly included in the suite of the applied traits (but see Logerwell et al. (2022), where thermal tolerance was the primary functional trait used in analyses), temperature was used as a proxy for water mass influences as opposed to direct metabolic-temperature relationships. As such, these temperature-trait relationships exhibited a spatial pattern, where sessile filter feeders on the coastal Chukchi Sea shelf were positively associated with warm temperatures, strong water velocity, and abundant coarser substrate. Similarly, sediment grain size has been used as a proxy for current velocities and deposition (Snelgrove & Butman, 1994; Pisareva et al., 2015). In the Chukchi Sea, finer sediment grain size in slower current regimes was linked to free-living, crawling movement and smaller body size, relationships also found elsewhere on Arctic shelves (Krumhansl et al., 2016).

Additionally, areas of highly mobile, free-living epibenthic invertebrates found on the offshore Northeast Chukchi Sea shelf can support taxa with tight pelagic-benthic coupling as indicated by consistent macrobenthic hotspots (Grebmeier et al., 2015). Depth was an environmental filter of functional composition in the Beaufort Sea, although somewhat weak, which has been seen in many other taxonomic studies of Arctic benthic systems as a driving force in compositional structure (Cochrane et al., 2012; Włodarska-Kowalczuk et al., 2012; Liu et al., 2019). I postulated that depth likely represented a combination of other environmental influences due to the depth profile of the Beaufort Sea shelf that increases unidirectionally from shore (Jakobsson et al., 2012). These linked influences could include impact of terrestrial input from coastal erosion (Doxaran et al., 2015), riverine influence from major Arctic rivers (Rachold et al., 2005), changes in food supply (Stasko et al. 2018), and nearshore ice-scouring (Mahoney et al., 2014). Consequently, the Beaufort Sea shelf likely reflected an area of disturbance-induced niche complementarity, where communities with more diverse functional traits exploit diverse resources (Roxburgh et al., 2004), compared to the Chukchi Sea, where low niche complementarity was previously found (Sutton et al., 2020). In both these regions, I expected to see low functional diversity resulting from strong environmental pressures (e.g., very high or very low temperatures) and higher diversity, where environmental pressures were more moderate (e.g., intermediate temperatures). However, only the relationships in the Chukchi Sea had a resemblance to this expected association, and seemingly only supported one end (e.g., high percent mud of the gradient) of the functional diversity – environment relationship. This could be the result of small ranges of environmental conditions in these regions during our study period, and perhaps a shift to lower diversity will occur with a widening of environmental ranges, for example, from ocean warming, as has been seen in many marine taxa globally (Lenoir et al., 2020). For this, modelling studies represent a way forward to investigate patterns in future functional composition under projected climate scenarios.

Lower niche complementarity, which points to underutilized resources, of epibenthic communities on the Chukchi Sea shelf, along with vulnerability to increasing temperate or newly arriving boreal taxa from northward migrations, made the Chukchi Sea shelf, together with the upstream Northern Bering Sea, a prime system to study the effects of functional change over time. Important functional trait-environment relationships were used from the previous environmental filtering analyses (Sutton et al. 2021) as the basis for predictive functional models. I used joint species distribution models that incorporated functional trait composition to predict which functional traits are likely to increase in different regions of the Northern Bering Sea and the Chukchi Sea. These regions are aligned along a south to north gradient that reflects increasingly Arctic environmental conditions towards the north (Chukchi Sea). Also, climate change-related shifts are likely to develop in a south to north fashion, until environmental conditions in the Chukchi Sea become more similar to those currently existing in the Bering Sea (Polyakov et al., 2020). These environmental patterns also apply to biota, and the Chukchi shelf biological communities have been shown to exhibit patterns similar to borealization (Ershova et al., 2015; Mueter et al., 2021), where the Northern Bering Sea may "seed" the communities of a future Chukchi Sea. Functional distribution models showed that trait-environment relationships were regionally specific, leading to functional trait changes by the end of the century under a "worst case" climate scenario (IPCC, 2019). Furthermore, functional composition changed more between the early and later part of the past decade (2009-2019) than towards the mid-century projection in the Chirikov Basin and Chukchi Sea shelf, suggesting a significant community regime shift may already have occurred, similar to what Huntington et al. (2020) described for taxonomic shifts in the Alaskan Arctic during this time period. Changes in functional composition over the entire study period (2009-2100) included an increase in planktotrophic larval development in the Northern Bering Sea regions and a shift from calcareous to chitinous skeletons in the Chukchi Sea.

In this dissertation, I employed new functional ecology tools to investigate changes in benthic community composition and provided a benchmark for future Arctic research to study many additional facets of functional diversity. These facets could include tracking trophic diversity in comparison with overall functional diversity to determine if Arctic food webs have changed over time. Also, changes in taxonomic-functional diversity associations could be further investigated to understand which environmental drivers highlight ecosystem stability or vulnerability measured via functional redundancy. As the Arctic continues to change, having multiple approaches available to study changes in community ecology is crucial. Arctic benthic communities will likely increase in interest, as many upper trophic level animals that depend on this community as a food source are affected by Arctic climate changes in their migration timing and distribution (Huntington et al., 2016), especially considering that species' will consume what is available and easily accessible (MacArthur and Pianka 1966). Supposing species are the building blocks of ecosystem function (Bellwood et al., 2019), diversity in their functional traits can illuminate which attributes of species influence ecosystem function (Loreau et al., 2001; Tilman, 2001). Knowing the functional attributes that will be selected for in the future through new environmental filters from a changing climate provides researchers and other stakeholders valuable information of the types of species that may be most susceptible to disturbance and climatic perturbation. Conversely, traits that increase or remain dominant in model predictions can assist in isolating potential boreal species that will likely do well in a warmer Arctic. This information is also helpful to ascertain which regions are most susceptible to changes based on established functional-environment relationships. For example, epibenthic taxa with pelagic larval development are predicted to remain dominant in the Chukchi Sea, which may maintain ecosystem function after disturbances across Arctic shelves via the ability to spread fast and far and occupy recently vacant niches (Weslawski et al., 2011). This could also rapidly increase the rate of species' movement poleward through larval dispersal rather than adult migration (Ershova et al., 2015; Renaud et al., 2015). The predicted decrease in calcareous skeletons in the Chukchi Sea may be a consequence of community vulnerability to ocean acidification (Byrne et al., 2010), and conversely, the predicted increase in chitinous skeletons reflect increased habitat suitability for crustaceans. Additionally, changes in skeleton type affect the ecosystem function to sequester inorganic carbon, where decreasing calcareous skeletons would decrease a communities' ability to moderate increased carbon input (McConnaughey & Whelan, 1997). Likewise, different movement types affect nutrient cycling, where crawling and burrowing movements generally increase nutrient cycling through bioturbation, while sessile, filter feeding taxa contribute more to the cycling of carbon from the water column down to the benthos (Degen & Faulwetter, 2019; Austen et al., 2002;). Hence, instead of predicting the increase or decrease of specific taxa, from an often imperfectly known regional species pool, this approach can predict the functional traits that are likely to increase or decrease, and with that, which ecosystem functions may change in the future.

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