UiT The Arctic University of Norway

Faculty of Biosciences, Fisheries and Economics Department of Arctic and Marine Biology

Arctic deep-sea benthos: biodiversity, biological traits, and food webs

Irina Zhulay

A dissertation for the degree of Philosophiae Doctor, May 2022

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Summary

Understanding Arctic deep-sea ecosystem structure and functioning is an urgent task considering that ongoing sea-ice reduction modifies and opens up these understudied regions for resource exploitation. Therefore, the present thesis aims to increase knowledge on epibenthic communities in a heterogeneous area of the Amerasian deep Arctic Ocean, the Chukchi Borderland. **Paper I** studies epifaunal taxonomic and biogeographic composition in three habitat types in the region (ridge, plateau with pockmarks, and basins), based on samples collected in the summer of 2016 with a beam trawl and Remotely Operated Vehicle (ROV) from 486 to 2610 m depth. **Paper II** performs Biological Trait Analysis on epifauna collected in 2016 to assess dominant faunal behavioral, life-history, and morphological characteristics and potential differences in their distribution between mid-depth (plateau and pockmarks locations, 486–1059 m) and deep layers (basin locations, 1882–2610 m). **Papers I and II** identify the most important environmental parameters in structuring epifaunal community composition and function. **Paper III** compares the strength of pelagic-benthic coupling between years of higher (2005) and lower (2016) sea-ice extent, based on δ^{13}C and δ^{15}N bulk stable isotope values of end members and pelagic and benthic consumers.

Results of **Paper I** indicate overall low epifaunal abundances and biomass across the Chukchi Borderland. In total, 152 taxa and morphotypes were identified from the ROV images and trawl samples, with Echinodermata and Arthropoda dominating taxon richness. Cnidaria, Echinodermata, and Arthropoda dominated epifaunal abundance and biomass. Taxonomic community composition of Chukchi Borderland epifauna was similar to that observed in other Arctic deep-sea areas, including the Eurasian Basin and Eastern Fram Strait. In fact, the majority of epifauna in the study area had Atlantic biogeographic affinity, presumably mediated by Atlantic water dominance in the deep-water layers of the Amerasian Basin. Results of **Paper II** generally support the current view of the most common trait modalities in deep-sea epifauna being of “small-medium” size and “mobile”, and having “benthic direct” and “lecithotrophic” larval development, and “predatory” and “suspension” feeding modes.

There was no significant difference between mid-depth ridge and plateau stations in abundance, biomass, and species number. However, taxonomic and functional composition differed between western and eastern parts of the Chukchi Borderland. Higher food input on the western side of the Chukchi Borderland was positively correlated with “sessile”, “tube-dwelling”, and “deposit-feeding” modalities, in part represented by highly abundant annelids

of Ampharetidae and Sabellidae families, and ophiuroids (**Papers I, II**). Higher drop-stone availability on the eastern side of the study area was, in turn, positively correlated with higher proportional abundance of the modalities “attached”, “upright”, and “predators”, mostly represented by cnidarian polyps. Mid-depth stations showed higher functional diversity than deep stations, indicating more variable resource use in the more heterogeneous mid-depth habitats.

Water depth significantly influenced epifaunal community structure and function (**Papers I**, **II**). Deep basins had lower species richness, abundances, and biomass than the mid-depth plateau and ridges (**Paper I**). Here, proportional abundances of the modalities “free-living”, “swimming”, “suspension feeders”, and “opportunists/scavengers” were higher than at the mid-depth layer (**Paper II**). The most abundant fauna possessing one or several of those modalities were annelids of the Macellicephalinae sub-family, the holothuroid *Elpidia* sp., and poriferans of the Polymastiidae family (**Papers I**). Functional redundancy was higher in basin communities than at mid-depth stations, suggesting adaptation of fauna to the more homogeneous deep environment by fewer and shared traits.

Results of **Paper III** suggest potentially tighter pelagic-benthic coupling in a high sea-ice cover year (2005) compared to 2016 when the region experienced low sea-ice cover. Higher isotopic niche overlap and shorter isotopic distances between pelagic and benthic food web components in 2005 illustrate this tighter connection between the two compartments. Potentially higher ice algal contribution to the food web in 2005 than in 2016 was indicated by higher $\delta^{13}C$ values of pelagic particulate organic matter and zooplankton that year. In addition, $\delta^{15}N$ values suggest more refractory food was consumed by benthos in 2016 under the low ice cover scenario.

This study adds much-needed epifaunal abundance and biomass data and extends the species inventory, including new geographic and depth extension ranges for some Mollusca and Porifera species and two bivalve species potentially new to science. Also, ROV records extend knowledge on behavioral characteristics of deep-sea fauna. The results indicate that Chukchi Borderland epifauna at mid-depth is characterized by low functional redundancy, and, thus, might be vulnerable to disturbance through the risk of function loss. Across the study area, the high occurrence of taxa with low dispersal ability among adult and larval life stages may also render these communities unable to adapt to changes in the environment given their reduced ability to escape perturbation or recolonize following disturbance. The inferred change in pelagic-benthic coupling under low sea-ice conditions raises questions about the future development of Arctic deep-sea benthic communities and highlights the need for establishing a deep-sea benthic monitoring program that can build on the present data to assess the effects of climate change on the system.

List of papers

The following papers are included in the thesis:

I. Zhulay, I., Iken, K., Renaud, P. E., & Bluhm, B. A. (2019). Epifaunal communities across marine landscapes of the deep Chukchi Borderland (Pacific Arctic). Deep Sea Research Part I: Oceanographic Research Papers, 151, 103065, doi: 10.1016/j.dsr.2019.06.011

II. Zhulay, I., Bluhm, B. A., Renaud, P. E., Degen, R., & Iken, K. (2021). Functional pattern of benthic epifauna in the Chukchi Borderland, Arctic deep sea. Frontiers in Marine Science, 8, 520, doi: 10.3389/fmars.2021.609956

III. Zhulay, I., Iken, K., Renaud, P. E., Kosobokova, K., & Bluhm, B. A. Reduced efficiency of pelagic-benthic coupling in the Arctic deep sea during lower ice cover (Manuscript)

Data repositories

Papers I and III: https://mbon.ioos.us/#metadata/edc232ee-8582-4059-9c4c-7018b5af66a0/project/files

Paper II: https://dataverse.no/dataset.xhtml?persistentId=doi:10.18710/OGOAWN and https://www.univie.ac.at/arctictraits/

Images

Images of seafloor and benthic organisms are taken during the Hidden Ocean 2016: Chukchi Borderland expedition, UAF/NOAA-OER/Global Explorer-Oceaneering.

Author contributions

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Abbreviations

CBL – Chukchi Borderland

ROV – Remotely Operated Vehicle

FD – Functional Diversity

FR – Functional Redundancy

TL – Trophic Level

1 Introduction

1.1 Motivation

1.1.1 Why study Arctic deep-sea benthos?

The deep sea, often defined as the region below 200 m depth, occupies around 90% of the marine environment and covers over 50% of Earth's surface (Thistle, 2003; Ramirez-Llodra et al., 2010). It takes part in regulating the entire biosphere by providing important ecosystem functions, i.e., processes operating in ecosystems such as nutrient regeneration or buffering biogeochemical circulation (Loreau, 2008; Thurber et al., 2014). These processes, in turn, help to sustain primary and secondary production (Danovaro et al., 2008) that along with high diversity of habitats and species, supported by the deep sea (Ramirez-Llodra et al., 2010), provide ecosystem services beneficial for humans (e.g., available fish stock, oil and gas, minerals, bioprospecting potential) (Thurber et al., 2014; Sweetman et al., 2017). Therefore, healthy functioning of the deep-sea is vital for well-being of our planet and availability of resources for humans. The deep-sea environment is, however, experiencing increased human pressures with anthropogenic activities evolving from largely disposal of waste (earlier) to resource exploitation (nowadays) that affect deep-sea habitats and fauna in various ways (Ramirez-Llodra et al., 2011). At the same time, knowledge about deep-sea habitats is limited and not as advanced as for coastal habitats, mainly due to remoteness of the deep sea and challenges associated with sampling these environments (Thistle, 2003). In fact, less than 0.0001% of the deep-sea regions have been investigated up to now (Danovaro et al., 2017). This knowledge gap particularly applies to the Arctic deep sea, where multiyear ice-cover adds to challenges related to sampling at great depth and far offshore. Studies over the Arctic Ocean deep areas, therefore, have been sporadic (Kosobokova et al., 2011), leading to multiple knowledge gaps in Arctic deep-sea ecology (Clarke, 2003). In recent years, technical progress and increased interest in the Arctic have helped improve current knowledge of Arctic deep-sea ecosystems (Bluhm et al., 2015). Specifically, we gained more knowledge through programs such as the International Polar Year 2007–2009, Census of Marine Life (e.g., Bluhm et al., 2011), long-term studies at the deep-sea observatory located in Fram Strait (HAUSGARTEN; Soltwedel et al., 2009; Meyer et al., 2013; Taylor et al., 2017), and individual studies on Arctic deep-sea areas (e.g., Roy et al., 2014; Yunda-Guarin et al., 2020). Despite these efforts, sampling logistics remain difficult and expensive, leading some components of the Arctic deep-sea ecosystems remaining poorly known (Bluhm et al., 2015).

The lack of understanding of deep-sea ecology on regional scales prevents the pan-Arctic picture from being complete.

One of the most poorly studied components of the Arctic deep-sea ecosystem is benthic epifauna (except at HAUSGARTEN; Bergmann et al., 2011; Meyer et al., 2013), while studies on macro- and meiobenthos are more common (Soltwedel et al., 1996; Renaud et al., 2006; Bluhm et al., 2011; Vedenin et al., 2021). Moreover, studies on epifaunal megafauna are scattered over different Arctic deep-sea areas (Piepenburg et al., 1996; Bluhm et al., 2005; Schulz et al., 2010; Rybakova et al., 2019) with the majority of studies being a snapshot in time (e.g., discussed in Schoening et al., 2012). In addition, we have very limited quantitative data on epifaunal taxonomic community composition, diversity, abundance and biomass in the Arctic deep-sea areas (Soltwedel et al., 2009; MacDonald et al., 2010; Rybakova et al., 2019). Therefore, the question **"who is there and how many?"** is arising.

It is known from Arctic shelf studies that epifauna contribute considerably to total benthic biomass and play important roles in ecosystem processes such as organic matter transfer to higher trophic levels, bioturbation, and remineralization (Feder et al., 2005; Piepenburg, 2005). However, different species contribute to ecosystem functioning in different ways. The ecological role of species can be indicated by a set of biological characteristics/traits describing life history, morphology and behavior of species present in a community since organismal traits are important properties by which species directly or indirectly affect ecosystem processes (Bremner et al., 2003; van der Linden et al., 2012). Therefore, an assessment of these traits can provide a deeper insight into a community's functional structure and its spatial and temporal variability than is possible with a taxonomic description alone (Bremner, 2005; Petchey and Gaston, 2006). Thus, not only taxonomic composition of epifaunal communities is important but also what traits these species possess or in other words, **"what do they do?"** in terms of ecosystem processes. Studies describing biological traits of benthos have been conducted on Arctic shelves and were done primarily for macrofauna (Cochrane et al., 2012; Krumhansl et al., 2016; Kokarev et al., 2017; Rand et al., 2018; Sutton et al., 2020). Very few studies have focused on traits of macrobenthos in the Arctic deep sea (Degen, 2015; Liu et al., 2019; Käß et al., 2021) and none, to our knowledge, comprehensively described traits of Arctic deep-sea *epifauna*.

Epifaunal community characteristics (diversity, abundance, biomass, community composition) and function (here, traits of organisms) can be affected by a range of factors, including anthropogenic (e.g., trawling, mining), biological (e.g., competition, predation), and environmental factors (Levin et al., 2001; Bremner et al., 2006; Meyer et al., 2015; Liu et al., 2019). Among environmental factors, sediment characteristics, sea floor morphology, current flow regimes, chemical conditions, depth, and food availability have been previously described as important in structuring deep-sea benthic communities (Levin et al., 2010; Bluhm et al., 2011; Pierdomenico et al., 2015; Simon-Lledó et al., 2019). Given the limited number of studies on Arctic deep-sea epifauna, the question **"what environmental factors affect epifauna community structure and function?"** is of interest.

Food availability has often been described as a major factor affecting benthic community properties in the energy-limited deep-sea habitats (Iken et al., 2005; Soltwedel et al., 2009; Kröncke et al., 2013). The food supply to benthos, in turn, depends on strength of pelagic-benthic coupling, i.e. exchange of energy, mass or nutrients between benthic and pelagic realms (Griffiths et al., 2017). The strength of pelagic-benthic coupling varies among Arctic regions and is determined by water depth, distance from shore, presence and timing of sea-ice coverage, and amount of primary production and consumers of this production (Grebmeier and Barry, 1991; Piepenburg, 2005; Iken et al., 2010). Trophic structure and pelagic-benthic coupling are comparatively well studied for some Arctic shelf regions (e.g. the Barents, Bering and Chukchi Seas) (Carmack and Wassmann, 2006; Renaud et al., 2008; Iken et al., 2010). In contrast, knowledge on food webs and pelagic-benthic coupling in the less accessible regions of the Arctic slopes and deep-sea basins is very scarce (but see Iken et al., 2005; Bergmann et al., 2009; Kędra and Grebmeier, 2021). Sea-ice extent has decreased in recent years in Arctic regions (Kwok, 2018; Perovich et al., 2020). As sea-ice is a main structuring factor of the Arctic marine ecosystem, its changes could have affected pelagic-benthic coupling. However, it has not yet been evaluated whether the strength of the coupling has been modified by climate change, which is difficult or impossible to determine for some Arctic regions because few or no baseline data are available from former years (Wassmann et al., 2011). Therefore, the question **"Does pelagic-benthic coupling in the present-day Arctic deep sea differ from that in former years with higher sea-ice cover?"** is important to answer. Additional knowledge on deep-sea epifaunal food webs is also highly desirable.

The Arctic ecosystem continues to be in a state of transition due to warming and the decline in ice coverage and decrease in sea-ice thickness (Richter-Menge et al., 2016; Kwok, 2018). Sea-ice loss is expected to continue and an ice-free Arctic Ocean in summer is predicted before the middle of this century (Stocker et al., 2013). These changes might lead to manifold dramatic alterations in the Arctic marine ecosystems (Grebmeier et al., 2006). This makes the description of Arctic ecosystem functioning in terms of both energy flow in the system and biological trait composition, as well as more comprehensive documentation of current species composition and community structure, an urgent need. Limited knowledge on the ecology of organisms inhabiting deep-sea areas constrain our capacity to predict future responses not only to climate change but also to potentially increasing anthropogenic pressure (Danovaro et al., 2017). The ice free summer opens up opportunities for exploitation of Arctic deep-sea resources, which are now widely discussed (Cuyvers et al., 2018; Jørgensen et al., 2020). Human activities might negatively affect or destroy Arctic deep-sea habitats and fauna before we even know what is there. Therefore, baseline data and assessment of habitat sensitivity to human disturbances in the Arctic deep-sea are highly important and urgent.

1.1.2 Why study Arctic deep-sea benthos in the Chukchi Borderland?

Data for the present thesis has been collected in the deep-sea Chukchi Borderland (**CBL**) within the Pacific Arctic. This region has received little attention in terms of benthic ecology studies. To our knowledge, only a few studies have been conducted from drifting stations in the 1960s-70s (Cromie, 1961; Mohr and Geiger, 1968; Hunkins et al., 1970), and two relatively recent studies were conducted in this region under the Hidden Ocean initiative (https://oceanexplorer.noaa.gov/explorations/05arctic/welcome.html; Bluhm et al., 2005; MacDonald et al., 2010). However, the region's varied bathymetric and hydrographic features and location make it interesting for biological investigations.

The region is hydrographically complex, with Arctic, Pacific and Atlantic water masses meeting and mixing here (McLaughlin et al., 2004; Woodgate, 2013). The presence of different water masses might lead to presence of fauna of various biogeographic affinities. The adjacent Chukchi shelf is under strong influence of Pacific water inflow via Bering Strait, which results in high proportion of Pacific-boreal benthic species (Dunton, 1992). At the same time, the adjacent deep Canada Basin hosts a high proportion of Atlantic affinity species (Bluhm et al., 2005) due to deep-water layers being of Atlantic origin (Bluhm et al., 2015). In turn, the CBL is located at the transition where the Chukchi Sea shelf drops off into the central Arctic Basin. Therefore, and in light of ongoing shifts in sub-Arctic and Arctic faunas (Fossheim et al., 2015; Huntington et al., 2020), present biogeographic composition of benthos in the CBL is of interest, in particular proportions of Atlantic and Pacific affinities species.

In addition, the CBL has enormously complex bottom topography with canyons, shallow ridges and plateaus, abyssal trenches, and isolated basins (Jakobsson et al., 2008). This complex topography might host intricate faunal communities different from those observed in more homogeneous abyssal environments. Another intriguing topographic feature of the CBL is the presence of pockmarks, rounded or elliptical depressions of <1 to >100 m in diameter and depth that were formed by explosion of gas or fluids in underlying sediment layers (Hovland and Judd, 1988; Astakhov et al., 2014). The presence of pockmarks holds potential for discoveries of chemosynthetic fauna or signs of enhanced biological activities.

Finally, the CBL is located in a region of dramatic sea ice melting (Perovich, 2011; Watanabe et al., 2015), warming Atlantic water below the surface and halocline waters (Shimada et al., 2004), and increased Pacific water inflow through Bering Strait in surface waters (Woodgate et al., 2007). Therefore, the region is likely undergoing significant biological transformations. The changes are expected to happen in both pelagic and benthic realms with consequences for primary and secondary production, and the coupling between the two realms. This, in turn, might lead to changes in benthic community composition, while the changes in water mass distribution and properties might, at the same time, have an effect on biogeography of benthos. Therefore, (1) a taxonomic and biogeographic inventory, (2) documentation of benthic biological traits, and (3) influences by environmental conditions they experience, as well as (4) connection of benthic and pelagic realms in the CBL region can contribute to a pan-Arctic data synthesis. In addition, by documenting this information, we provide urgently needed baseline data for further evaluation of the ecosystem state under climate change and/or human pressure effects.

1.2 The Arctic deep-sea environment

Numerous environmental factors have been shown to be important in structuring deep-sea benthic communities. Food availability is usually considered the most important factor shaping benthic community composition (Iken et al., 2001; Piepenburg, 2005; Ramirez-Llodra et al., 2010) and function (Degen, 2015; Käß et al., 2021) in the deep sea. In general, most deep-sea ecosystems are heterotrophic, i.e. largely sustained by organic matter produced in the overlying waters by photosynthesis (Iken et al., 2001; Ramirez-Llodra et al., 2010), except hydrothermal vents (Sweetman et al., 2013; Ramirez-Llodra et al., 2020) and cold seeps (Åström et al., 2018; Sen et al., 2018). The great distance between primary production in the euphotic zone and the deep-sea floor results in only a small amount (~0.5–2%) of largely reworked detrital organic material reaching the seafloor, making the deep-sea benthic environment among the most food-limited on Earth (Gage and Tyler, 1991; Fischer et al., 2000; Ramirez-Llodra et al., 2010). Food limitation is even higher in the Arctic deep sea (Iken et al., 2005; Kędra and Grebmeier, 2021). This is due to primary production being highly seasonal and mainly restricted to the few months when solar radiation is available for photosynthesis (Leu et al., 2015; Aune et al., 2018). In general, the higher the latitude, the shorter the time window when primary production occurs (Daase et al., 2021). For example, phytoplankton production on Arctic shelves starts approximately in April – May, while this production occurs no earlier than July in the central Arctic (Wassmann et al., 2020; Daase et al., 2021). Even when light becomes available, the sea-ice and snow cover its limit the penetration into the water column (Nicolaus et al., 2012). In addition, sea-ice cover affects water mass stratification, with especially strong stratification in the Canada Basin, and mixing processes that are essential in terms of nutrient replenishment to the euphotic zone (Leu et al., 2015). Therefore, the primary production period is generally longer in regions covered by seasonal ice, where it can last up to 180 – 200 days, compared to regions where multiyear ice is still in part present with up to 70 – 100 days of production (Strass and Nöthig, 1996; Niebauer, 1999). Consequently, Arctic deep-sea ecosystems are usually described as oligotrophic with low and highly seasonal food supply to the benthos (Iken et al., 2005).

Besides processes in surface waters that determine food availability, benthic communities are also structured by physical conditions at the seafloor. Among those, sediment grain size composition, hydrodynamics, temperature and oxygen concentrations were identified as important for deep-sea benthic communities (Levin et al., 2001; Durden et al., 2015; Rand et al., 2018). All these parameters generally change with increasing water depth, where they interact with each other and create patterns in benthic communities (Soltwedel et al., 2009; Grzelak et al., 2017). In general, the environment becomes more stable with depth compared to shallower and pelagic environments (Ramirez-Llodra et al., 2010). Deep-sea benthic organisms live in total darkness, constantly high pressure, low bottom water temperature (typically, 0.01–4°C, but down to sub-zero values in the Arctic), low current velocity and resuspension, and are surrounded by mostly fine sediments (Gage and Tyler, 1991; Thistle, 2003; Sweetman et al., 2017). These environmental settings are often observed at the visually homogeneous abyssal plains that cover much of the deep seafloor (Ramirez-Llodra et al., 2010; Levin and Le Bris, 2015).

The seafloor of the Arctic Ocean is not uniform and contains a series of basins separated by geological structures (Jakobsson, 2002). The enormous submarine mountain range of the Lomonosov Ridge separates the Arctic Ocean into the two major basins - Eurasian and Amerasian Basins (Jakobsson et al., 2004). The ultraslow-spreading Gakkel Ridge divides the Eurasian Basin into the Amundsen and Nansen basins (Jakobsson et al., 2004; Cochran, 2008). On the Amerasian side, the seismically-inactive Alpha–Mendeleyev Ridge separates the large Canada Basin from the smaller Makarov Basin (Clarke, 2003; Jakobsson et al., 2004). On a smaller scale, complexity of the seafloor is further provided by such formations as plateaus, rises (e.g., Chukchi Plateau, Yermak Plateau, and Morris Jesup Rise, (Jakobsson et al., 2008; Dowdeswell et al., 2010; Kristoffersen et al., 2021)), mud volcanoes (Håkan Mosby mud volcano, (Jerosch et al., 2007; Galkin et al., 2013)), methane seeps (Åström et al., 2020), hydrothermal vents (Edmonds et al., 2003), seamounts (e.g., Karasik seamount with a giant sponge ground; Morganti et al., 2022) and inactive pockmarks (Vogt et al., 1994; MacDonald et al., 2010). This heterogeneity of the seafloor modifies local environmental settings and creates a variety of habitats, making home for various benthic organisms that perform different ecosystem functions. The Arctic deep seafloor morphology and depth have been extensively studied in recent decades, and summarized through the International Bathymetric Chart of the Arctic Ocean (IBCAO) (Jakobsson et al., 2020). However, our view of the seafloor morphology is still incomplete with new features being discovered and studied (Gardner et al., 2007; Bünz et al., 2020; Jakobsson et al., 2020). In this sense, the topographically and hydrographically-complex Chukchi Borderland area is an exciting geological formation for potential discoveries. In addition, it is still not completely understood which environmental factors are the most important in structuring *epifaunal* benthic communities and function in this region. Therefore, the present thesis partly covers this knowledge gap and investigates environmental factors that explain variation in epifaunal community composition (**Paper I**) and distribution of biological traits within the communities **(Paper II**) in the CBL.

1.3 Arctic deep-sea fauna

Currently, the Arctic Basins are portrayed as oligotrophic systems with extreme seasonal gradients of light, low water temperature, short ice-free period, and generally a short food pulse (Piepenburg et al., 2011). It was previously suggested that these conditions shape a desert-like ecosystem with poor benthic biodiversity and low abundance. This statement was mainly based on limited data (Zenkevitch, 1963; Curtis, 1975). In recent years, however, research efforts showed higher biodiversity than expected (Piepenburg, 2005; Bluhm et al., 2015). Sirenko (2001) documented around 700 benthic species in the central Arctic basins, though a more recent inventory showed that at least 1,125 taxa inhabit the central Arctic area deeper than 500 m and a higher species diversity than currently documented is likely (Bluhm et al., 2011). Indeed, new species are being described in the Arctic deep sea (Gagaev, 2009; Rodríguez et al., 2009; Åström et al., 2017), and greater depth and geographical range extension of previously described species are reported (Vedenin et al., 2018; Rybakova et al., 2019).

Generally, benthic communities are composed of different size fractions, which, to a large extent, occupy different regions the habitat (either inside the sediments, on top of sediments or just above the sediments). Among them, epifaunal megafauna is the least studied (Bluhm et al., 2011). Epifauna is defined as invertebrates and demersal fish living on top of the sediment and typically ≥ ca. 5 mm (Nichols and Williams, 2009). The few previous studies of the Arctic deep sea showed that epifauna is dominated by echinoderms (mainly holothurians), cnidarians, and polychaetes in terms of abundance (Soltwedel et al., 2009; MacDonald et al., 2010; Rybakova et al., 2019). The most speciose epifauna taxa are arthropods, mainly amphipods (Bluhm et al., 2011).

Global bathymetric trends in abundance and biomass (Rex et al., 2006; Wei et al., 2010) are also generally observed for the Arctic benthic fauna, where food limitation leads to steep gradients in faunal abundance and biomass from slopes to the basins (Piepenburg, 2005; Bluhm et al., 2011; Vedenin et al., 2022). The decrease in benthic abundance and biomass with depth was, however, reported to be more rapid in the Arctic than in temperate and tropical areas of the Atlantic and Pacific oceans (Soltwedel et al., 2009; Bluhm et al., 2011; Degen, 2015; Vedenin et al., 2018). Diversity of the Arctic deep-sea benthos also decreases with depth (Bluhm et al., 2011; Vedenin et al., 2018). This decrease is continuous with no pronounced peaks in diversity (Wlodarska-Kowalczuk et al., 2004; Renaud et al., 2006) in contrast to the mid-depth (1500–3000 m) diversity peak in temperate oceans, known mostly from the Atlantic Ocean (discussed in Bluhm et al., 2011). Recent studies, however, indicated a peak in Arctic benthic diversity at 100–600 m for macrofaunal species (Vedenin et al., 2018). Given that the majority of the Arctic deep seafloor is relatively poorly sampled, new sampling efforts for different benthic size fractions might still reveal peaks in diversity or confirm their absence.

Biodiversity and abundance of epifauna can be enhanced on a local scale where small, isolated hard substrate is present in otherwise soft-bottom dominated environment. Examples include drop-stones from ice-transport processes (Schulz et al., 2010; Meyer et al., 2016) and carbonate crusts at methane seeps (Åström et al., 2018); in other deep-sea areas enhanced biodiversity and abundance was reported in association with whalebones (Baco and Smith, 2003) and manganese nodules (Kuhn et al., 2020). In addition, increased complexity of seafloor morphology such as ridges, plateaus, and canyons may also increase biodiversity and biomass of benthos compared to abyssal plain environments (McClain and Barry, 2010; Pierdomenico et al., 2015). Such seafloor morphological features interact with local and regional hydrodynamics and can enhance currents and turbulence, which in turn influences food supply and increases delivery of suspended particles (Hanz et al., 2021). Pockmarks with active gas venting can, for example, contain seep-associated communities of high abundance including characteristic organisms such as bacterial mats, siboglinid tubeworms and, outside the Arctic, seep mussels, vesicomyid clams and others that rely on chemosynthetic energy (Hovland and Svensen, 2006; Olu-Le Roy et al., 2007; Åström et al., 2018). Many pockmarks are relicts and do not have active seepage (Webb, 2009a; Buhl-Mortensen et al., 2015). These pockmarks have also been reported to hold increased benthic faunal abundance, biomass and diversity because pockmarks can increase collection and retention of food particles, increasing food availability for organisms (Webb, 2009a; MacDonald et al., 2010). The pockmarks of the Arctic deep seafloor and epifauna present there have, however, been poorly studied (MacDonald et al., 2010; Åström et al., 2018). In **Paper I** of the present thesis, we focus on the investigation of epifaunal community composition and characteristics such as abundance, biomass and diversity in the topographically-heterogeneous CBL. Specifically, we investigate how epifauna differs among plateaus with pockmarks, ridges and basin habitats based on samples collected with a trawl and ROV.

It has also been shown that Arctic deep-sea benthos has a relatively high number of eurybathic animals that also occur on Arctic shelves; over 60% taxa are shared with the shelves (Bluhm et al., 2011; Piepenburg et al., 2011). The previous estimate of endemism in the Arctic deep-sea water was high (50–80%; Vinogradova, 1997). However, the level of endemism may be overestimated owing to generally low sampling intensity in the Arctic deep sea (Bluhm et al., 2011). For example, the previously considered Arctic endemic sea cucumbers *Elpidia glacialis* and *Kolga hyalina* (Rogacheva, 2007) were also collected at 2,700 m in the sub-Arctic Norwegian Sea (Buhl-Mortensen and Buhl-Mortensen, 2009). Despite the boundary character of the ridges intersecting the deep Arctic, similarity in faunal assemblages between the Eurasian and Amerasian Basins suggests these ridges do not form strong biogeographic barriers (Bluhm et al., 2011). Today's Arctic deep-sea benthos is most closely related to the present North Atlantic fauna (Bluhm et al., 2011; Ravelo et al., 2020), which is likely due to a high connectivity of the central Arctic to the North Atlantic and Arctic shelf faunas, and very limited connectivity to the current Pacific fauna (Bluhm et al., 2011). The proportion of Pacific fauna might potentially be higher in the Amerasian than Eurasian basin due to the vicinity to the North Pacific and Pacific-origin water prevalence. Yet, a previous study in the Canada Basin showed cosmopolitan Arctic boreal and Atlantic boreal species dominating over Pacific biogeographic affinities in the infaunal communities (Bluhm et al., 2005). Biogeographic patterns and transitions in epifaunal communities of the Amerasian Basin and slope have not been studied extensively. Thus, **Paper I** of the thesis describes biogeographic affinities of epifauna across the CBL and identifies if the proportion of Pacific affinities declines with depth in the study area.

1.4 Arctic deep-sea traits: Current paradigms

Seafloor fauna, including epibenthos, play significant roles in ecosystem processes due to their trophic interaction with other organisms, bioturbation activity, nutrient renewal, habitat provisioning, as well as contribution to total benthic energy turnover (Feder et al., 2005; Piepenburg, 2005; Kędra and Grebmeier, 2021). In addition, benthic communities can be used as indicators of ecosystem status because they integrate naturally or anthropogenically-induced effects of physical, chemical and biological factors (Ramirez-Llodra et al., 2011). The role of benthos in ecosystem processes is tightly related to morphological, behavioral and life history characteristics or **traits** that species exhibit in a community (Usseglio-Polatera et al., 2000; Bremner, 2005; Oug et al., 2012). For example, mobility of organisms partly defines their ability to disperse, escape disturbance, and contribution to energy and nutrient cycling (Beauchard et al., 2017; Degen et al., 2018). Reproduction and body size can define a species' contribution to secondary production (Bremner, 2005; Degen et al., 2018). Feeding habit can be used as an indication of nutrient fluxes and trophic interaction (Törnroos, 2014; Degen et al., 2018).

Biological traits can also indicate adaptations that organisms developed to environmental conditions they inhabit (Bremner, 2005). The Arctic deep sea is characterized by unique environmental settings outlined above including the seasonal and limited food supply, and otherwise relatively constant physical condition (cold, dark, high pressure) as generally observed in other deep-sea environments (Gage & Tyler 1991). It has not, however, been summarized if such conditions have led to a unique set of biological traits in Arctic deep-sea benthos, with only sporadic studies describing biology of benthic organisms in this environment. The size of deep-sea species has previously been suggested to be generally small mainly due to the food limitation (size-structure hypothesis, Thiel, 1975), which was confirmed by later studies describing bathymetric trends (Rex et al., 2006; Wei et al., 2010). Benthic species, however, span a broad range of size classes in the deep sea (Billett et al., 2001; Bluhm et al., 2011; Rybakova et al., 2019). Feeding modes of benthos are also diverse with deposit feeders, suspension feeders, predators and scavengers present in communities (Iken et al., 2001; Premke et al., 2006; Bergmann et al., 2009). The low primary production and export flux are reflected in a dominance of deposit feeders (Iken et al., 2005; van Oevelen et al., 2011). Suspension-feeding is less frequent and likely less advantageous due to low ambient current velocity in the deep-sea (Kröncke, 1998; Bergmann et al., 2009). Abundance of predators is also low potentially due to low densities of prey (Thistle, 2003; Bluhm et al., 2011). Scavengers might be less abundant due to food falls such as whale or fish falls being rare in the Arctic deep sea (Bluhm et al., 2011). Among behavioral traits, mobility has been previously suggested to be more efficient for finding food in food-limited deep-sea environments (Thistle, 2003; Boetius et al., 2013), as opposed to sessile taxa that might only survive in regions with enough organic matter flux or stronger bottom currents (Degen, 2015). Life-history traits of deep-sea benthos are also variable and include direct development and indirect development (with lecithotrophic or planktotrophic larvae) (Pearse and Lockhart, 2004; Berecoechea et al., 2017; Lauretta et al., 2020). The traditional view of benthic reproduction describes increased importance of lecithotrophy and direct development with latitude and in the deep sea (Thorson, 1950; Mileikovsky, 1971), though recent studies for Arctic shelves indicated higher abundance and diversity of meroplankton for long periods of the year than previously known (Fetzer and Arntz, 2008; Kuklinski et al., 2013; Ershova et al., 2019). The patterns of life history trait dominance have not been resolved for Arctic deep-sea benthos. To summarize, the current literature describes deep-sea benthos as primarily small-sized, mobile, deposit feeding and developing either directly or indirectly.

In **Paper II**, we test if these current deep-sea paradigms hold true for epifauna sampled with an ROV and trawl in the CBL. In addition, we assess variability in epifaunal traits distribution between mid-depth (plateau and ridge) and deep stations (basins). We use biological trait analysis (BTA) that incorporates information on species distribution and their biological characteristics to generate a summary of traits distribution in a given community (following Bremner, 2005). This approach allows for assessment of current ecosystem functioning in terms of trait distribution and functional diversity, future response to environmental perturbation, and potential vulnerability to environmental changes (Bremner, 2005; van der Linden et al., 2012; Degen, 2015). BTA is relatively new to marine science, particularly to the Arctic Ocean (e.g., Degen, 2015; Kokarev et al., 2017; Liu et al., 2019; Sutton et al., 2020). To our knowledge, BTA has not been applied to the Arctic deep-sea epifauna before.

1.5 Pelagic-benthic coupling in the Arctic deep sea

As summarized above, the pronounced seasonality and restricted food availability play a significant role in food web structure and, consequently, in growth and survival of Arctic fauna (Iken et al., 2005). Primary production in the offshore Arctic marine ecosystem is mainly based on sea-ice algae and pelagic phytoplankton (Leu et al., 2015), with a larger contribution of ice algae in the basins (>50%; Gosselin et al., 1997) than on Arctic shelves (4 – 25%; Legendre et al., 1992). The sea-ice algal production starts earlier than the open water production; pelagic phytoplankton production is then initiated by the sea-ice retreat (Leu et al., 2015; Kędra and Grebmeier, 2021). As outlined above, annual primary production in the deep Arctic Ocean is the lowest documented in the world ocean and is one or two orders of magnitude less than on Arctic continental shelves (Arrigo et al., 2008; Gradinger, 2009; Arrigo and van Dijken, 2015; Kędra and Grebmeier, 2021). Measurements of primary production in deep basins vary from 0.6 to 25 g C m^{-2} y^{-1} (Clarke, 2003; Wassmann et al., 2010), while on the Arctic shelves the mean production values can reach 100 - 160 g C m^{-2} y^{-1} (for Barents and Chukchi Sea, respectively; Sakshaug, 2004). This primary production serves as a direct food source for ice-associated and pelagic organisms, and, indirectly, for benthos (Iken et al., 2005).

The basin zooplankton fauna in the surface layers (primarily ice-associated and upper water column pelagic crustaceans) has adapted to the food limitation by close coupling to fresh algal production, in other words, by occupying low trophic levels in the food web (Iken et al., 2005). In contrast, the deeper plankters use different food sources, since a considerable part of the fresh organic matter is already converted into fecal material and marine snow (Olli et al., 2007). Consequently, carnivory and omnivory/detritivory are dominant feeding modes in meso- and bathypelagic zooplankton fauna (Laakmann et al., 2009; Kosobokova et al., 2011). Based on studies from shelves with seasonal ice cover, we know that grazing intensity is generally low at the time when early ice-algal production starts (Grebmeier and Barry, 1991; McTigue and Dunton, 2014; Divine et al., 2015). Therefore, a large portion of usually fast sinking and fresh primary production reaches the benthos (Iken et al., 2005; Divine et al., 2015; Kędra and Grebmeier, 2021). After the sea-ice retreat, the fast-growing (until nutrients are depleted) open water phytoplankton production is extensively grazed by already established zooplankton populations. This leads to a lower proportional flux of this fresh material to the seafloor (summarized in Kędra and Grebmeier, 2021).

The benthic fauna is the ultimate recipient of pelagic production (Grebmeier and Barry, 1991; Iken et al., 2005), which arrives at the seafloor not only in the form of direct sedimentation of phytoplankton, but also through fecal pellets, zooplankton carcasses, molts and marine snow (Grebmeier and Barry, 1991; Iken et al., 2005). The low vertical carbon flux to the Arctic deep seafloor (summarized in Kędra and Grebmeier, 2021) yields little and generally reworked food with low nutritional value for benthic fauna (Iken et al., 2005; Bergmann et al., 2009). However, aggregates of the fast-sinking sea-ice algae *Melosira* have been documented on the seabed of the central Arctic Ocean, showing that relatively fresh carbon can reach deep benthic fauna (Boetius et al., 2013).

Pelagic-benthic coupling is tight in some Arctic shelf regions (e.g. the Barents, Bering and Chukchi Seas), albeit with variations among and within regions (Carmack and Wassmann, 2006; Renaud et al., 2008; Iken et al., 2010). Specifically, the inflow areas have high primary production and vertical flux, partly fueled by sub-Arctic advective inputs of nutrients and organic matter (Bluhm et al., 2015). In contrast, interior Arctic shelves have generally lower primary production but additional carbon inputs from terrestrial sources, which can also be used as food supply (Dunton et al., 2012; Bell et al., 2016). In contrast to Arctic shelf-regions, knowledge on food webs in the Arctic deep-sea basins is very scarce (Iken et al., 2005). Additional supply of carbon through particles advected from productive shelves and from terrestrial carbon brought in by rivers was also described to be low in the basins (Clarke, 2003; Bluhm et al., 2015). Hence, previous studies in the Arctic deep sea showed longer food webs than on Arctic shelves with up to five trophic levels as a result of continuous reworking of food particles (Iken et al., 2005; Bergmann et al., 2009).

Food web structure and pelagic-benthic coupling is likely to change with the ongoing changes of sea-ice extent and thickness. Specifically, the shortened sea-ice season leads to increased availability of photosynthetically-active light but water stratification has increased due to ice melt and increased freshwater input in the Amerasian Basin (Wassmann and Reigstad, 2011; Polyakov et al., 2020). Climate change will affect phenology and composition of phytoplankton and zooplankton with consequent changes in carbon export to the benthic environment. In particular, ice retreat and loss of multi-year ice is expected to lead to a shift in dominance from fast-sinking sympagic algae to pelagic phytoplankton, which may be retained more efficiently in the upper water column (Moran et al., 2012). These changes could shift an ecosystem characterized by strong benthic–pelagic coupling to one characterized by a water column-dominated food web and reduced carbon flux to the seafloor (Grebmeier et al., 2006; Moran et al., 2012). This scenario has mainly been discussed for the Arctic shelves and can potentially be applied to the Arctic deep sea, meaning even more decreased carbon deposition to the already food-limited deep-sea environment. However, limited knowledge on Arctic deep-sea food webs and linkages of pelagic production with benthic communities constrain our understanding of carbon flow transformation in response to climate change (Kędra et al., 2015).

Therefore, **Paper III** focuses on pelagic-benthic coupling in the CBL and compares the pelagic-benthic coupling between two years with different sea-ice settings (2005 and 2016). In 2005, the Arctic system was already under the influence of lowered sea ice cover (Richter-Menge et al., 2006), though signs of warming were not as pronounced as in most of the following years (Perovich et al., 2020). By 2016, the Arctic system had experienced a series of very low sea ice years and undergone more substantial transformations due to climate change (Perovich et al., 2020). Therefore, we expected to observe tighter coupling in the earlier ice-dominated year compared to 2016 when the CBL was covered by less ice. We used stable carbon and nitrogen isotope analysis following earlier studies on trophic ecology in the Arctic Ocean (Hobson et al., 1995; Iken et al., 2005; Bergmann et al., 2009; Iken et al., 2010) and compared food source use and trophic niche space between the two years. Based on this approach, we expected to find higher $\delta^{15}N$ values of benthic taxa in a food web where pelagic-benthic coupling is weak due to the progressive enrichment in the heavier isotope with increasing trophic level (Post, 2002). The tissues of pelagic and benthic consumers are expected to be more enriched in the ^{13}C in 2005, where sea-ice algae were assumed to be more abundant and assumed to serve as a main food source. This assumption is based on the facts that 1) carbon stable isotope ratios can indicate food source (Zanden and Rasmussen, 2001; Post, 2002) and that 2) previous studies showed more enriched ^{13}C in sea-ice algae compared to phytoplankton (on average by 4–5‰, though variable; Hobson et al., 2002; Tamelander et al., 2006). Both trophic markers ($\delta^{15}N$ and $\delta^{13}C$) combined describe trophic niches in isotope biplot space (Jackson et al., 2005). The high overlap of isotopic niches of pelagic and benthic members in a given food web can indicate tighter coupling between these two realms. In addition to the findings presented in Paper **III**, I briefly describe benthic food web structure for 2016 to add to the poor knowledge on trophic benthic ecology in the Arctic deep sea, in particular for *epifaunal* taxa. Here, I expect to observe high $\delta^{15}N$ values for most of the benthos and, possibly, an increase in $\delta^{15}N$ values with depth.

2 Objectives

The overall aim of the thesis was to characterize Arctic deep-sea benthic community composition, functional structure and the connection of benthic to pelagic realms in the poorly-studied CBL. The specific objectives of the thesis were:

1. to assess differences in epifaunal community characteristics (abundance, biomass, taxonomic diversity, and species distributional patterns) among three habitat types of the study area (ridge, plateau and basins) **(Paper I)**;
2. to determine dominant biogeographic affinities in the study area **(Paper I)**;
3. to evaluate dominant biological characteristics/traits of CBL epifauna and variation of their distribution between different depth strata **(Paper II)**;
4. to identify environmental characteristics that affect epifaunal community structure **(Paper I)** and traits distribution **(Paper II)**;
5. to assess pelagic-benthic coupling in the study area and its potential difference between two years varying in sea-ice settings - 2016 (year of low sea-ice extent) and 2005 (year of higher sea-ice extent) **(Paper III)**;
6. to explore stable isotope composition of taxa present in the area and its variability between depth strata **(Supplementary results)**.

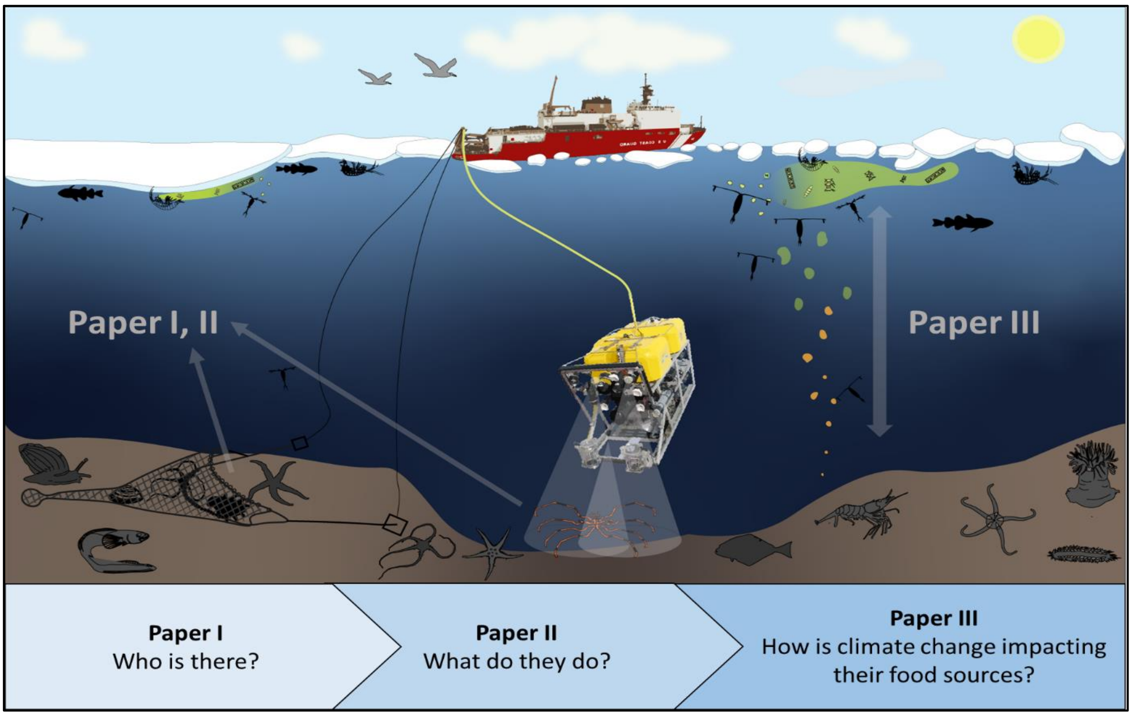


Figure 1. Conceptual figure illustrating questions covered and setting in the thesis.

3 Hypotheses

1. Considering the large difference in depth between the stations sampled in the CBL and the heterogeneous topography of the area, we expect epifaunal community structure to differ among plateau, basin and ridge locations, with the highest diversity and abundance at the shallower pockmark and plateau locations and the lowest at deep basin locations **(Paper I)**.
2. The epifaunal species inventory represents a gradient of declining Pacific-affinity proportion with increasing depth owing to the increasing importance of Atlantic origin water with increasing depth in the CBL **(Paper I)**.
3. The current deep-sea paradigms suggesting that deep-sea benthic communities are dominated by small-sized, mobile deposit-feeders, with equal representation of direct and indirect development, hold true for the epifauna in the CBL **(Paper II)**.
4. Given that environmental conditions change with depth, we hypothesize functional structure will differ between mid-depth and deep stations as follows:

    a. Trait modality composition differs between depth strata,
    b. Functional diversity is higher at more environmentally heterogeneous mid-depth stations, while functional redundancy is higher at deep and more homogeneous basin stations **(Paper II)**.

5. Food availability and depth are the main environmental factors influencing epifaunal communities in terms of abundance, diversity, taxonomic composition, and biological traits distribution **(Papers I and III)**.
6. Considering sea-ice cover was generally higher in the early 2000s compared to later years, we hypothesize that pelagic-benthic coupling was tighter in 2005 compared to 2016, which would be reflected in 1) a lower overlap of pelagic and benthic isotopic niches, 2) higher δ^{15}N values of benthic organisms, 3) lower δ ^{13}C values from reduced ice algal uptake associated with lower ice extent in 2016 **(Paper III)**.
    6.1. In addition, we tested the hypothesis that the majority of benthic taxa inhabiting the CBL occupy high trophic levels, and isotopic composition differs between mid-depth and deep stations, owing to changes in environmental conditions with depth **(Supplementary results, exploratory)**.

4 Material and Methods

4.1 Study area

4.1.1 Sea floor topography

The Chukchi Borderland (CBL) is an area that juts into the Canada Basin north of Alaska's Beaufort and Chukchi shelves (Fig.2) (Hall, 1990). The origin of the CBL formation is controversial (Edwards and Coakley, 2003; Arrigoni, 2010). However, the most widely accepted model suggests the CBL, together with Arctic Alaska and Chukotka, rifted from the Canadian Arctic shelf between *ca*. 195 and 160 million years ago and later separated from the East Siberian shelf and was brought to its present position by clockwise rotation toward the Canada Basin (Grantz et al., 1998; Arrigoni, 2010; Pease et al., 2014). The CBL was stretched and dissected into graben and half-graben structures through extension during the last phase of tectonic deformation (Arrigoni, 2010). Therefore, the region has complex seafloor morphology and consists of a group of north-trending topographic highs that surround the small Northwind Basin (Hall, 1990). The two largest topographic highs are the Northwind Ridge and Chukchi Plateau (other names found in the literature are Chukchi Rise or Chukchi Cap), located on eastern and western sides of the Northwind Basin, respectively (Jakobsson et al., 2008). The Northwind Ridge is deeper than the Chukchi

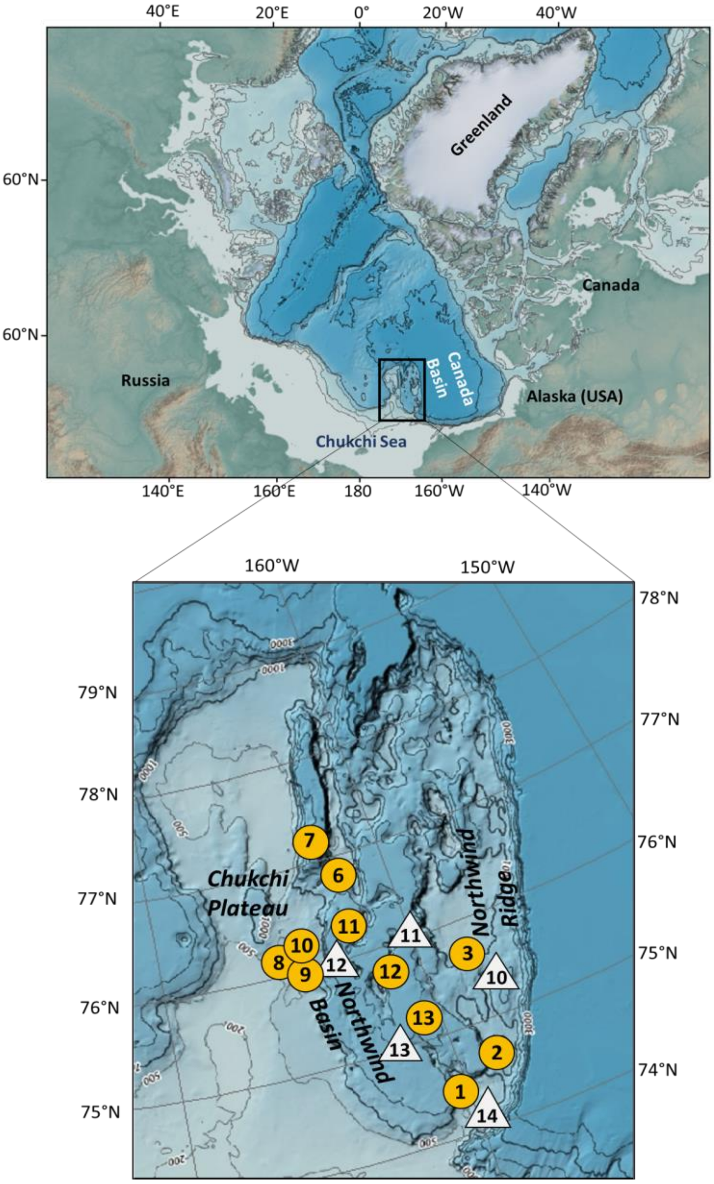


Figure 2. Station map. Yellow circles are stations sampled in 2016; white triangles are stations sampled in 2005.

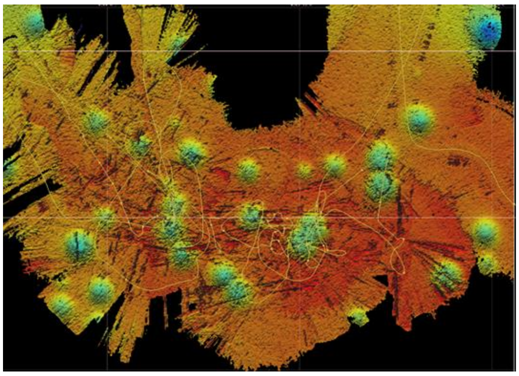


Figure 3. Bottom topography of pockmark field on the Chukchi Borderland plateau, mapped by US Coast Guard Healy during the Hidden Ocean 2016: Chukchi Borderland expedition. Green-blue color indicates pockmarks as roundish depressions of approximately 30-50 m depth and 300-400 m in diameter, while orange-red colors show the slightly shallower background seafloor.

Plateau, and has a very steep slope towards the Canada Basin. In addition, several much smaller ridges rise above the floor of the Northwind Basin (Jakobsson et al., 2008). The Chukchi Plateau is characterized by the presence of pockmarks, seabed craters of <1 to >100 m in diameter, which usually indicate the escape of fluid and/or gas, such as sulphur or carbon compounds, from soft bottom sediments (Fig. 3) (Hovland and Judd, 1988). Pockmarks were first discovered on the Plateau in 2003 at approximately 76.6°N, 163.9°W (Gardner et al., 2007). Extended survey found numerous sub-circular pockmarks, typically 300-400 m in diameter and 30 to 50 m deep (Mayer et al., 2010). The Chukchi Plateau is thought to be a fragment of continental margin (Butsenko et al., 2019), thus, the pockmarks were likely formed by methane seepage (Armstrong et al., 2015), with the last modification about 30 000 – 15 000 years ago (Astakhov et al., 2014).

For the present study, we were able to collect samples from three types of seafloor formations in 2016: basin, ridge, and plateau with pockmarks (Fig.2):

- Four basin stations were sampled. Three (stations 11, 12, 13) were located within the Northwind Basin, and one (station 7) was in a narrower basin isolated by a ridge from the Northwind Basin.
- Four ridge stations were sampled. Three (stations 1, 2, 3) were located on the Northwind Ridge, and one (station 6) on the narrow ridge arising from the Northwind Abyssal Plain and isolating the basin station 7.

Three plateau stations were sampled, located on the Chukchi Plateau (stations 8, 9, and 10). For stations 9 and 10, it was possible to investigate epifauna within pockmarks and on the plateau surrounding pockmarks. Station 8 was in a large groove linked to a pockmark.

4.1.2 Hydrology

The hydrological structure of the area is also complex, though water mass distribution and pathways through the Chukchi Borderland yet are far from being fully understood, with some features mapped only in very recent years (Corlett and Pickart, 2017; Boury et al., 2020; Li et al., 2020). We do know that Pacific, Atlantic, and Arctic water masses meet and mix here. The water masses layering in the region can be described as follows: 1) Polar surface layer (~ 0 – 50 m); 2) Pacific (summer and winter) water layer (~ 50 – 200 m); 3) Atlantic water layer (~ 200 – 2000 m); 4) Arctic Bottom water (~ over 2000 m) (McLaughlin et al., 2005; Woodgate et al., 2007), (Fig 4).

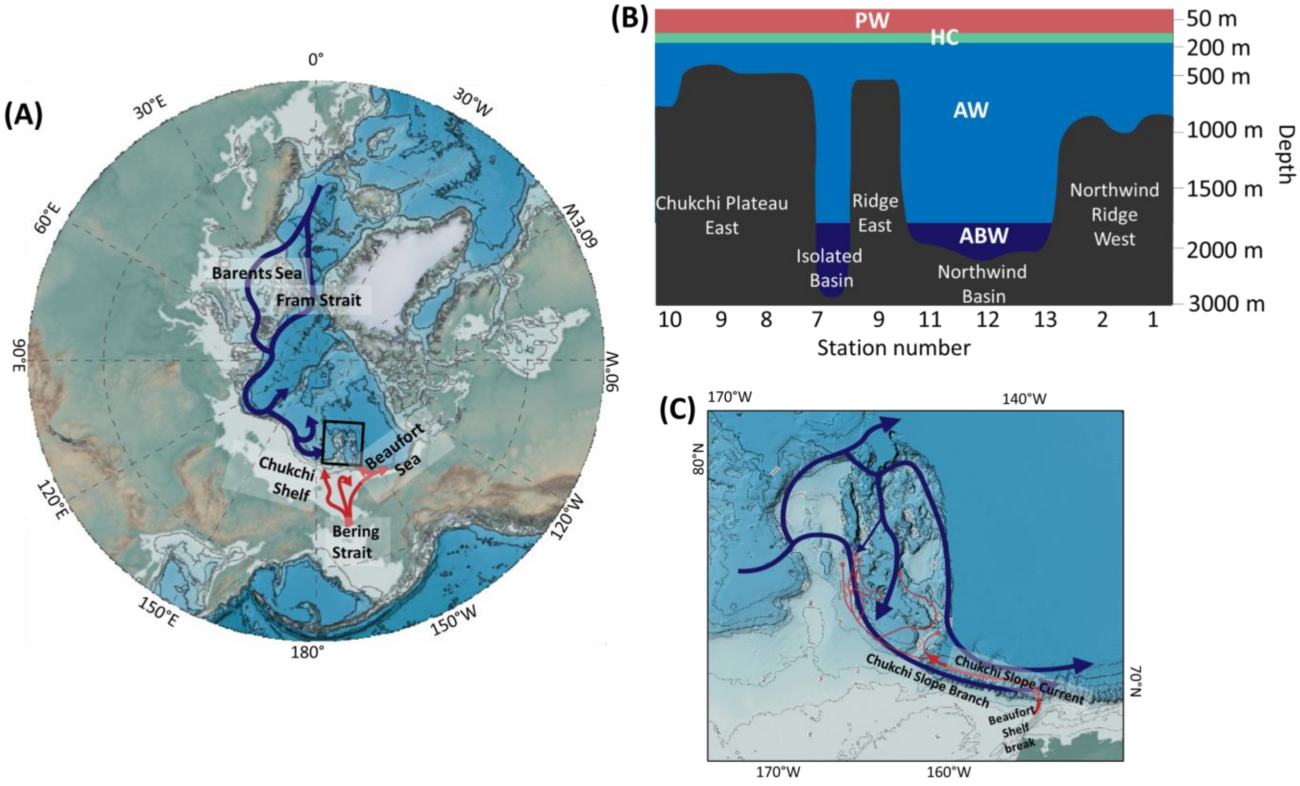


Figure 4. Schematic representation of Atlantic (blue) and Pacific (red) water circulation and water mass distribution adapted from Watanabe et al. (2017); Boury et al. (2020); Li et al. (2020). (B) Schematic water mass distribution is based on literature (e.g., McLaughlin et al., 2005; Woodgate et al., 2007) and CTD data acquired in our study. PW – Pacific water, HC – halocline, AW – Atlantic water, ABW – Arctic bottom water. (C) Thinner red lines indicate evidence of the Chukchi Slope Current in the CBL based on Boury et al. (2020) and Watanabe et al. (2017).

The Polar surface layer lies atop Pacific water and is, in general, Pacific water diluted by river inputs, ice melt, and net precipitation (summarized inBluhm et al., 2015). The Pacific water layer originates from North Pacific water entering the Arctic Ocean via the Bering Strait and the Chukchi shelf (Woodgate et al., 2005). These waters are a significant source of nutrients, freshwater and heat in the Pacific Arctic (Corlett and Pickart, 2017; Watanabe et al., 2017; Spall et al., 2018). The Pacific water progresses across the Chukchi shelf by three main flow branches: western, central, and eastern. (1) The Western branch flows into Herald Canyon, part of this branch progresses eastward and joins the central branch. (2) The Central branch flows between Herald and Hanna shoals and, together with the western branch, flows into Barrow Canyon. (3) The Eastern branch is adjacent to the Alaskan coast and mainly feeds Barrow Canyon (e.g., described in Corlett and Pickart, 2017). It was previously known that part of the water leaves the Chukchi shelf eastward through the Beaufort Shelf break Jet (e.g., Nikolopoulos et al., 2009). However, a stronger current flowing westward and emanating from the Barrow Canyon was recently documented by Corlett and Pickart (2017). This current was named the Chukchi Slope Current; it flows along the continual slope of the Chukchi Sea shelf, seaward from the Chukchi Shelf break Jet (Corlett and Pickart, 2017). The fate of this current and the way of how it reaches our study area are still not well described (Boury et al., 2020). Recent publications, however, show some evidence of the Chukchi Slope Current reaching Northwind Ridge (Watanabe et al., 2015) and, further north, the Chukchi Plateau (Watanabe et al., 2015; Boury et al., 2020), and Northwind abyssal plain (Boury et al., 2020), (Fig. 4).

The Atlantic water layer originates from the North Atlantic, entering the Arctic Ocean through the Fram Strait and the Barents Sea (referred to as Fram Strait Branch and Barents Sea Branch). Atlantic water transports high amounts of heat into the Arctic that gets distributed all the way to the Pacific Arctic, including the CBL (Woodgate et al., 2007; Woodgate, 2013). The inflowing Atlantic water is topographically steered along the continental slopes and trans-Arctic ridges and circulates cyclonically (anticlockwise) until it eventually reaches the Pacific side of the Arctic. When the current encounters the CBL, it bifurcates. One part flows southward and along the Chukchi Sea continental slope (= Chukchi slope branch). Another part flows northward and then eastward along the edge of the Chukchi Plateau, where it divides again (Shimada et al., 2004; Woodgate et al., 2007; McLaughlin et al., 2009). Some portion continues around the top of the Northwind Ridge. Another fraction of the current is diverted into the Canada Basin, while the rest of the current turns southward (Woodgate et al., 2007; McLaughlin et al., 2009). Recently, it was shown that this southward branch progresses along the western side of the Northwind Ridge (east of Northwind Abyssal Plain) and joins the Chukchi slope branch (Li et al., 2020). In addition, a minor flow branch was documented to the west of the Northwind Abyssal Plain; this branch also merges with the slope branch that, in turn, flows into the Beaufort Sea (Li et al., 2020), (Fig. 4).

Arctic bottom-water pathways in the Arctic Ocean are poorly known in general, and their distribution in the Chukchi Borderland is not described. The deep water is brought to the Amerasian Arctic by means of very slow water exchange from basin to basin; it is thought to be initially formed in the Greenland Sea and enter the Arctic basins through the Fram Strait (summarized in Bluhm et al., 2015).

Plateau and ridge stations sampled in our study (486–1059 m, salinity = 33.5 – 34.9 PSU) lie within the Atlantic water layer, while basin stations (1882–2610 m, salinity ≥ 34.9 PSU) are located within the Arctic bottom- water layer, (Fig. 4).

4.1.3 Changes in sea ice cover

Sea ice extent in the Arctic Ocean has declined significantly during recent years and between the two sampling years considered for **Paper III** – 2005 and 2016. For example, average Arctic sea-ice extent for September was 5.6 million km^2 in 2005, while September sea-ice extent was 4.1 million km^2 in 2016 (Richter-Menge et al., 2006; Richter-Menge et al., 2016; Perovich et al., 2020). The study area is located in the region of the most extreme sea ice melt in the Arctic with more intensive melt since 2007 (Hutchings and Faber, 2018). In addition, the Chukchi Borderland has shifted from a multiyear ice-covered area to an annual ice region in recent years (Watanabe et al., 2015). The changes in sea-ice are attributed to increased influxes of warming Atlantic water to the area (Woodgate et al., 2010; McLaughlin et al., 2011). In addition, heat (and freshwater) is brought to the area by Pacific water (Timmermans et al., 2014), the transport of which has also increased (Corlett and Pickart, 2017).

4.1.4 Sampling stations

For **Paper I**, sampling stations were chosen to represent the three main habitat types: basins (1882 to 2610 m depth), ridges (486 to 1059 m depth), and plateau with pockmarks (508 to 873 m depth, Fig. 2). Data for this paper were collected in 2016 and were used to investigate the epifaunal community composition and environmental settings.

For **Paper II**, the same set of stations, sampled in 2016, was used to describe epifaunal functioning in the study area. The stations were grouped into two depth strata: mid-depth stations (486–1059 m) that comprised ridge and plateau locations, and deep stations (1882–2610 m) that included basin stations.

For **Paper III**, samples collected in 2005 and 2016 were used to compare pelagic-benthic coupling between these years. For this comparison, station pairs that were geographically close to each other and located in similar bathymetric features (i.e., basin, ridge, and plateau) were selected. The selection resulted in five stations at depths from 621 to 2090 m sampled in 2005 and eight stations at depth between 486 and 2107 m sampled in 2016 to be included (Fig. 2). Supplementary exploratory results on the more extensive benthic food web are provided in the synthesis, and are based on samples collected in 2016 across all stations sampled that year.

4.2 Field sample collection

4.2.1 Biological sample collection

Epifaunal samples, including invertebrates and demersal fish, were collected with two main tools - a plumb-staff beam trawl and a Remotely Operated Vehicle, the ROV Global Explorer (**Paper I, II, and III**). Both trawls and ROVs are widely used in deep-sea research (MacDonald et al., 2010; Ayma et al., 2016; de Mendonça and Metaxas, 2021). The trawl is a more traditional tool for sampling distributional pattern, abundance and biomass of epifauna (summarized in de Mendonça and Metaxas, 2021). The main advantage of this tool is its capacity to collect more than a few species per sample for further detailed taxonomic identification. The tool, however, was adapted from coastal fisheries and is invasive to the habitat and damaging to fragile animals (de Mendonça and Metaxas, 2021). In addition, it is rather semi-quantitative than quantitative, due to difficulties related to identifying the area trawled and unequal performance on different seafloor types (Eleftheriou and Mcintyre, 2005). In contrast, an ROV has less contact with the seafloor and, thus, does not alter habitat structures (Soltwedel et al., 2009; Teixidó et al., 2011). Collection of animals with an ROV is also gentler compared to trawl collections. The ROV is more suitable for complex relief habitats due to it has high manoeuvrability (Sward et al., 2019). The tool is used to collect imagery of epifaunal organisms and observe species distribution and abundance (de Mendonça and Metaxas, 2021). This visual sampling technique enables us to observe some of what is usually missed by other sampling tools, e.g., intact benthic organisms in their natural environment and their behavior (e.g., interaction with other organisms, way of movement, feeding behavior) (Hewitt et al., 2004; de Juan et al., 2015). Therefore, imagery can be used to identify certain biological traits that trawl collections cannot provide (Hewitt et al., 2004). It can also provide information on habitat features including bottom-current strength and direction, sediment properties, geological and biogenic structures (“Lebensspuren”), and aggregations of detritus (Soltwedel et al., 2009). In addition, the ROV was proven to be more accurate in estimates of epifaunal abundance (McIntyre et al., 2015; Ayma et al., 2016), though taxonomic resolution and capacity for physical sample collection are low compared to trawl samples.

In the present thesis, an ROV was used to perform a photographic and video survey of the seafloor and its fauna in 2016 (**Papers I** and **II**), and for collection of epifauna in 2016 (**Papers I**, **II**) and 2005 (**Paper III**). The sample collection in 2005 was performed at three stations (**Paper III**). The photographic survey and sample collection was conducted at 11 stations in 2016 (**Paper I**, **II**). Collection of the epifaunal organisms was performed with the suction sampler and manipulator arm. 24-megapixel still images were collected with a downward-looking DSSI DPC-8800 digital camera along ca. 3.8 km long linear (where possible) transects every 5–8 s at each of ten stations over on average 3.5 h. Four digital laser pointers, one located at each corner of a fixed distance of a 10 - cm square, were used to estimate the photographed area at four stations, after which they stopped functioning. In addition to the still images, video samples were collected with the forward-looking 10x and 3.8x zoom 4K video cameras. Ca. 30 min trawl hauls along ca. 1.5 km were performed to collect epifauna (**Paper I, II**, and **III**) at six stations in 2016 with a modified plumb-staff beam trawl (4 mm in the cod end).

For **Paper III**, the epifaunal samples were complemented by macrobenthic (infaunal) samples collected with a 0.25 m^2 box core at station 12 in 2005 and at four stations (stations 2, 9, 10, and 13) in 2016. All benthic samples were washed to remove sediments (2 mm mesh size for beam trawl, 0.3 mm for box core samples) and fauna were identified to the lowest taxonomic level possible. All organisms from trawl samples were counted (**Paper I, II**) and weighed by taxon (**Paper I**). Vouchers were collected when identification was uncertain and identified later by experts (see acknowledgements). Taxon names were verified with WoRMS (www.marinespecies.org).

Benthic fauna collected for stable isotopes were subsampled for muscle tissue, where possible or else from body wall or tube feet and entire organisms were collected when body mass was small (**Paper III**). A total of 29 benthic organisms were collected in 2005. In 2016, 273 benthic samples were collected for isotope analysis (**Supplementary results**), from which 85 which were either the same or closely related taxa to those collected in 2005 were selected for comparison between years (**Paper III**). Replication varied from 1 to 3 individuals per species per station.

Zooplankton consumers were collected at 5 stations with a multi-net (Midi, Hydrobios, 150 μm) in 2005 and at 6 stations with the same Multinet in 2016. Five zooplankton species common to the upper water column in the Arctic Basin and representing different taxonomic groups and feeding types were chosen for the analysis: the copepods *Calanus glacialis* (grazer), *C. hyperboreus* (grazer), *Paraeuchaeta glacialis* (predator), the amphipod *Themisto abyssorum* (predator), and the chaetognath *Eukrohnia hamata* (predator, but see Grigor et al. (2020)). Often, several individuals of the same species were pooled by station for sufficient mass. A total of 71 zooplankton samples were collected in 2005 and 66 in 2016. Replication varied from 1 to 3 samples per species per station. All samples collected for isotope analysis were frozen at – 20°C immediately after collection until laboratory analyses.

4.2.2 Environmental sample collection

To identify environmental characteristics influencing epifaunal community composition (**Paper I**) and function (**Paper II**), a range of environmental variables was collected with a SBE9/11 + CTD and an Ocean Instruments BX 650 0.25 m^2 box corer at each station in 2016. Bottom water temperature and salinity were measured at around 20 m from the bottom. The upper surface (0–1 cm) of the sediments was sampled from the box core and frozen at −20 °C for later determination of grain size composition, organic carbon content, and concentration of sediment chlorophyll *a* and phaeopigments.

For **Paper III**, pelagic particulate organic matter (pPOM) and sediment organic matter (sPOM) were collected in 2005 and 2016. pPOM was collected from Niskin bottles attached to the CTD rosette at the chlorophyll maximum at each station in both years. Two-three water samples per station were collected from different bottles of the CTD rosette (n= 13 in 2005, n = 21 in 2016). The water samples were filtered onto pre-combusted, 25 mm diameter GF/F filters. sPOM was collected into a sterile plastic bag from the top ~1 cm of intact sediments from box cores (n = 3 in 2005, n = 7 in 2016). Samples were frozen at -20°C immediately after collection until laboratory analyses.

4.3 Sample and image processing

4.3.1 Image analysis

A subset of the useable images of the sea floor was chosen from each station for the image analysis (**Papers I** and **II**). In total, 940 images were manually analyzed for faunal abundance (stations with functional lasers), proportional abundance (**Papers I** and **II**) and organismal traits (**Paper II**), with typically 70 – 100 images per station. In addition, certain biological traits were identified from the images (**Paper III**). Faunal abundances and size of benthos were determined at the four stations (stations 1a, 6, 7, 8) where the laser pointers served as a size reference, otherwise taxa were counted per image (**Paper I, II**). The mean area per image varied from 0.2 to 0.8 m^2. Image processing and analyses were performed with ImageJ (https://imagej.nih.gov/ij/,Rasband, 2009). All putative taxa present in the study area were used to create a taxonomic image library that enabled consistent identification. Taxa were identified to the lowest possible level based on a combination of the ROV imagery, the voucher collection, and additional identifications by experts. Where identification was difficult, taxa were named morphotypes (taxa that are distinguishable on the basis of their gross morphology (Oliver and Beattie, 1996) (**Paper I, excluded in Paper II**). For **Paper II**, all morphotypes but morphotype 10 were excluded from the analysis due to difficulties related to assigning trait modalities to these organisms. In addition, lebensspuren, burrows, colour of the sediments, and frequency and size of larger stones and associated fauna were recorded (**Paper I**). The average number of stones per picture was calculated and included in the statistical analyses (**Paper I** and **II**).

4.3.2 Biogeographic affinities (Paper I)

In total 44 invertebrate and fish taxa sampled by trawl and identified to species level were assigned to one of the following biogeographic groups:

(1) Arctic – occurring only in the Arctic,
(2) Arcto-boreal-Pacific – found in Arctic and boreal Pacific waters,
(3) Arcto-boreal-Atlantic – found in Arctic and boreal Atlantic waters,
(4) Arcto-boreal – found in Arctic and in both Atlantic and Pacific boreal waters,
(5) other – occurring also outside of boreal and Arctic zones.

Biogeographic affinities were assigned based on the best current distribution information available in the published literature and internet sources (cited in **Paper I**), and expert knowledge by collaborating taxonomists.

4.3.3 Biological trait analysis (Paper II)

Paper II uses Biological Trait Analysis (BTA) and focuses on the distribution of biological traits of CBL epifauna to complement their taxonomic identity (**Paper I**). A total of 106 invertebrate and fish taxa were used for BTA, of which 53 taxa occurred in the ROV images and 77 taxa in trawls with 26 taxa common to both sampling gears.

Biological traits

In total, nine traits reflecting morphology (adult size, body form), behaviour (living habitat, mobility, adult movement, feeding habit, substrate affinity) and life-cycle characteristics (larval development and reproduction) were used for BTA. The traits were divided into 39 trait subcategories or modalities that represent various trait expressions/modalities (Table 2 in **Paper II**).

Trait information was obtained from:

(1) Our own observations made from trawl-collected material during the cruise and/or from ROV images (e.g., size, body form, adult movement, living habit, substrate affinity);
(2) other sources, including published literature, online traits databases (e.g., polytraits, (Faulwetter et al., 2014); the Arctic Traits Database (Degen and Faulwetter, 2019)) and relevant web pages (e.g., FishBase: www.fishbase.org, Sea Life Base: www.sealifebase.org).

Often information on epifaunal traits in the Arctic deep sea is limited or at times non-existent at the species level. When information for certain taxa was missing, trait modalities were described based on closely related species (following, e.g., Faulwetter et al., 2015; Rand et al., 2018; Sutton et al., 2020). In some cases, modalities at even higher taxonomic rank were applied.

Traits coding

For the coding of traits, a "fuzzy coding" procedure (Chevenet et al., 1994) was used. The "fuzzy coding" procedure allows taxa to be coded with multiple modalities to different degrees using a 0–3 code, where 0 indicates no affinity, 1 and 2 indicate partial affinity, and 3 indicates the exclusive affinity for a given modality. With this coding, it is possible to account for variation in trait expression within a species (Chevenet et al., 1994) and to incorporate information from species in the same genus or family (Charvet et al., 2000). For example, one species can use various feeding techniques or be affiliated with various substrates. For example, *Sclerocrangon ferox* mainly uses a predatory feeding strategy, but it has also been reported to feed on dead organic material, so this species was coded as "2" for predator and "1" for scavenger/opportunist feeder. To give the same weight to each taxon and trait, the fuzzy codes (0–3) were converted to proportions for each trait modality, totaling to 1 (e.g., Bolam et al., 2017).

Matrixes

BTA uses three matrixes (Degen, 2015; Beauchard et al., 2017):

1) a "traits by taxon" matrix summarizing all fuzzy coded biological traits of taxa present in a community.
2) a "taxa by stations" matrix indicating presence or (proportional) abundance of species in a community. In **Paper III**, we used three "taxa by stations" matrixes:

- presence/absence of taxa based on ROV and trawl samples combined;
- proportional abundances acquired from ROV samples;
- proportional abundances acquired from trawl samples.

In the paper, we used proportional abundance for ROV samples due to the above-mentioned failure of the laser pointers that made it impossible to calculate absolute abundances for all ROV stations. We used proportional abundance for trawl samples to be consistent with the ROV samples.

3) a "traits by stations" matrix generated by multiplication of matrixes 1) and 2), also described as Community Weighted Means (CWM) (Van der Linden et al., 2016). This matrix represents mean trait values in a community weighted by a

measure of species importance. As we used three “taxa by stations” matrixes, we acquired three “traits by stations” matrixes.

4.3.4 Stable isotope laboratory analysis

Prior to the analysis, samples were dried at 60 °C for 24 h and tissue samples were ground. Then, lipids and inorganic carbonates were removed, where needed. Samples were weighed, packed in tin capsules, and analyzed at the Alaska Stable Isotope Facility at the University of Alaska, Fairbanks.

In general, different tissues of organisms are characterized by different turnover times, and thus mirror assimilation of food from different time frames (Middelburg, 2014). To characterize a species' diet over a longer period of time, it is advised to collect tissue with slow turnover rate such as protein-rich muscle tissue (Fry, 2006). In turn, lipid tissue has a high turnover time relative to protein tissue (Graeve et al., 2005). In addition, lipids are depleted in ^{13}C (Griffiths, 1991; Sotiropoulos et al., 2004). However, collection of muscle tissue is not always possible, especially for small and lipid-rich Arctic zooplankton species. For these species, lipids were therefore removed prior to analysis to reduce variability in δ^{13}C, which is caused by seasonal fluctuations and high variability in lipid concentration within and among Arctic zooplankton species (Hobson et al., 1995). Inorganic carbon is more enriched in ^{13}C than organic carbon and may confound isotopic analyses of food webs (Boutton, 1991). Therefore, carbonates were removed from pPOM filters, sediments, and animals containing calcium carbonate.

All carbon and nitrogen stable isotope analyses were performed on a Thermo Finnigan Delta Isotope Ratio Mass-Spectrometer with Vienna PDB as standard for carbon and atmospheric N_2 as standard for nitrogen. Instrument error was < 0.2‰ for $\delta\,^{13}$C and <0.4‰ for $\delta\,^{15}$N in 2005, and < 0.2‰ for both $\delta\,^{13}$C and $\delta\,^{15}$N in 2016. Sample isotopic ratios were expressed in the conventional δ notation as parts per thousand (‰) according to the following equation:

$$\delta X = [(Rsample/Rstandard) - 1] \times 1000 \qquad (1)$$

where X is ^{13}C or ^{15}N of the sample, and *R* is the corresponding ratio of ^{13}C/^{12}C or ^{15}N/^{14}N.

4.3.5 Environmental sample processing

Sediment grain size was analysed on a Beckman Coulter Particle Size Analyser LS 13320 at the Geology Laboratory of UiT - The Arctic University of Norway in Tromsø. The samples were pre-treated with HCl and H_2O_2 to remove calcium carbonate and organic material, respectively.

The concentration of sediment chlorophyll *a* and phaeopigments (µg pigment/g dry sediment) was measured at the University of Alaska Fairbanks. Pigments were extracted with 5 ml of 100% acetone for 24 h in the dark at −20 °C. A Turner Designs TD-700 fluorometer was used to measure pigment concentration before and after acidification with HCl for determination of phaeopigments (Arar and Collins, 1997; Jeffrey and Welschmeyer, 1997).

4.4 Statistical analysis

4.4.1 Epifaunal community characteristics (Paper I)

Epifaunal attributes

Abundance, biomass, proportional abundance, number of taxa, and Simpson index (D) were used as univariate attributes to describe epifauna and differences among epifaunal communities of the three habitat types (ridge, plateau, basin). Analyses were done separately for ROV and trawl data sets.

Abundance and biomass of epifauna were estimated for each of the six trawl stations from the area swept (distance towed × net opening), and values normalized to individuals per 1000 m^2. Abundance for the four ROV stations with functioning lasers was estimated from counts of taxa per image area and converted to individuals per 1000 m^2. Proportional abundance was calculated for all ROV stations based on counts of animals calculated per picture and summed per station for each taxon/morphotype. Number of taxa and Simpson diversity index were calculated for each station for both ROV and trawl samples. The Simpson diversity index was chosen over other diversity indices (e.g., Shannon-Wiener index) since it is less sensitive to variation in abundances (Magurran, 2013), and was calculated based on the formula:

$$D = 1 - (\sum n_i (n_i - 1)/N (N - 1))$$

where n_i = the number of individuals in *i*th species; and N = the total number of individuals. D ranges from 0 (low diversity) to 1 (high diversity). Morphotypes were treated as species in diversity estimates (Magurran, 2013). It was not possible to scale number of taxa and the Simpson index to transect length, which may have caused some bias in comparisons among the habitat types.

Assessment of differences in epifaunal community characteristics among habitat types

Univariate statistics - factorial analyses of variance (ANOVAs) and Student's *t*-test - were used to explore the effect of habitat type on the above-described community attributes. All univariate statistics were performed in the statistical computing software R . Prior to analyses, data were tested for normality (Shapiro–Wilk test) and homogeneity of variances (Bartlett test) (Crawley, 2007).

Multivariate statistics were used to reveal patterns in the spatial variability of epifaunal community structure among habitat types and to identify the taxa contributing most to dissimilarity among habitats. The PRIMER v 6.0 software package (Clarke and Gorley, 2001) was used to perform the multivariate analyses for community structure. Hierarchical cluster analysis was performed to check if communities from the same pre-assigned habitat type grouped together. The analysis was done on trawl-based abundance data and ROV-based proportional abundance; proportional abundance was chosen over abundance because abundance could not be determined for all ROV stations. Square-root data transformation was applied prior to calculating similarities to down-weigh the influence of dominant taxa. A similarity matrix was calculated based on the Bray-Curtis coefficient (Bray and Curtis, 1957). A similarity profile test (SIMPROF) was used to explore statistical significance of difference among cluster branches. The magnitude of differences among the habitats and the significance of differences were tested with the analysis of similarities (ANOSIM) routine. When ANOSIM detected a significant grouping (at $\alpha = 0.05$ level), a SIMPER (a similarity percentage procedure) analysis was carried out to establish the taxa contributing most to the dissimilarities among epifaunal communities of the three habitat types.

4.4.2 Biological traits distribution (Paper II)

Attributes

Biological trait modalities (i.e., “traits by station” matrixes) and functional diversity indexes were used to describe the dominant biological characteristics of epifauna across the study area and explore differences between mid-depth and deep stations. Analyses were done separately for ROV and trawl samples for the most part.

We estimated Rao’s quadratic entropy (Rao’s Q), referred to as Functional diversity (FD) from here on, and the Functional redundancy index (FR). FD measures the amount of trait *dissimilarity* between two random entities (individuals) in the community (Van der Linden et al., 2016). FD was calculated based on the “traits by taxon” and “taxa by stations” matrixes; it was calculated as a product of the distance between pairs of species in traits space and weighted by the relative abundance of species (Botta-Dukát, 2005). The index ranges from 0 to 1, where 0 indicates that communities are the same in their biological trait profiles, and a value close to 1 indicates that communities are unique in their biological trait profiles (Van der Linden et al., 2016).

FR measures the amount of trait *similarity* between species in a community (Van der Linden et al., 2016), meaning it indicates to which degree different species represent the same ecosystem functions (Petchey and Gaston, 2006; de Bello et al., 2007). FR is the relationship between FD and species diversity (Ricotta et al., 2016), and was calculated as the ratio of FD to the taxonomically based Simpson index. In order to obtain a regularly increasing index, the formula was converted to 1–(FD/D) (Van der Linden et al., 2016). FR ranges from 0 (where all species have different trait-categories) to 1 (where all species display the same trait-categories) (de Bello et al., 2007).

Assessment of dominant trait modalities and their distribution

We selected four traits often used to describe deep-sea fauna in the literature - size, larval development, adult movement, and feeding habit – to investigate their dominant trait modalities across the entire study area and to test if common deep-sea paradigms hold true for our study area. For this, we used the “traits by stations” matrix based on presence/absence of taxa combined for ROV and trawl samples.

All nine traits were used for the rest of the traits analysis. To investigate differences in functional structure of epifauna between mid-depth and deep station(s) in terms of trait modality distribution we first used a multivariate fuzzy correspondence analysis (FCA, Chevenet et al., 1994) on trawl and ROV data sets. In addition, we identified what traits contribute most to the difference in the functional structure among stations by acquiring correlation ratios of each trait along the fuzzy principal axes (Chevenet et al., 1994). We then used a univariate non-parametric Kruskal–Wallis test to check whether there was a significant difference of trait modalities and functional diversity indexes between mid-depth and deep stations.

All statistical analyses were performed using the software R (R Development Core Team, 2017) with the package ade4 (Dray and Dufour, 2007) for the FCA and calculation of FD; FR was calculated manually in Excel.

4.4.3 Effect of environmental characteristics on epifaunal community structure and traits distribution (Paper I and II)

The potential influences of environmental factors on taxonomic **(Paper I)** and functional **(Paper II)** community structure were investigated with a canonical correspondence analysis (CCA) using the package ‘vegan’ (Oksanen et al., 2013) in the statistical computing software R (R Development Core Team, 2017). Again, analyses were done separately for ROV and trawl data sets.

The CCA was performed on proportional abundance data of taxa and morphotypes **(Paper I)** and on the “traits by stations” matrixes based on proportional abundance **(Paper II)**. As environmental variables, we included water depth, bottom water salinity and temperature, grain size composition, number of rocks in ROV images, concentration of benthic pigments in sediment (phaeopigments and Chl *a*), carbon content in sediment, and C/N ratio. A forward selection procedure was used to identify environmental variables explaining most of the variability in the biological data. Monte Carlo permutation tests were used to determine the statistical significance of the model and the individual terms (Oksanen et al., 2013). In addition, the CCA ordination shows the environmental variables as arrows roughly oriented in the direction of maximum variation in value of the corresponding variable (Ter Braak, 1986).

For **Paper I**, we also tested for correlation between univariate epifaunal characteristics and environmental characteristics with a parametric Pearson's correlation analysis (when data were normally distributed) or a non-parametric Spearman's rank correlation analysis (when data were not normally distributed). For epifaunal characteristics, we used total abundance, total biomass, number of taxa from trawl surveys, and number of taxa from ROV surveys. As environmental characteristics, we used water depth, bottom temperature, sediment grain size, and number of stones per picture.

4.4.4 Pelagic-benthic coupling comparison between years (Paper III)

To assess differences in pelagic-benthic coupling between the sampling years, we used $\delta^{13}C$ and $\delta^{15}N$ values of pelagic and benthic food web components, namely pPOM, sPOM, zooplankton, and benthos. For this, we evaluated the structure and size of isotopic niches of the food web components and the proximity of niches of the pelagic and benthic food web components for each of the two sampling years. In addition, differences in $\delta^{15}N$ and $\delta^{13}C$ values of each food web member were tested between the sampling years.

For visual inspection of isotopic niche structure, we generated bi-plots of $\delta^{13}C$ versus $\delta^{15}N$ values on station-averaged values per consumer taxon (benthos, zooplankton) and end-member (pPOM, sPOM) for each year. In addition, isotopic niche width was calculated as Standard Ellipse Areas corrected for small size (SEA_C) for each food web component by year (Jackson et al., 2011). To compare the isotopic niches of food web components between years statistically, we used a Bayesian approach to calculate 100 000 posterior iterations of SEA (Parnell et al., 2010; Reid et al., 2016) that produced a range of probable SEAs (Bayesian SEA = SEA_B) for each of the food member from each year. This enabled robust statistical comparison of SEA_B between the sampling years by calculating the probability of difference between them (Jackson et al., 2011; Reid et al., 2016). These analyses were conducted using the SIBER package (Stable Isotope Bayesian Ellipses in R; (Jackson et al., 2011)) in R 4.0.3. statistical software (R Development Core Team, 2017).

To evaluate the isotopic proximity of pelagic and benthic food web members in different years, we calculated the overlap of their SEAc as the percentage of ellipse area shared by two components using SIBER (Jackson et al., 2011). In addition, the isotopic distances of $\delta^{15}N$ ($\delta^{13}C$) between different food web components were calculated manually by subtracting the mean $\delta^{15}N$ ($\delta^{13}C$) of one food web component from that of another food web component.

Univariate analyses were used to test for differences between years in the station means of $\delta^{15}N$ and $\delta^{13}C$ values of each food web component. The Shapiro-Wilk test was applied to test for normality, followed by the Bartlett-test to verify the equality of variances. The following tests were used for the comparison: a two-sample *t*-test (if the distribution was normal and variances were equal), a Welch's two sample *t*-test (if the distribution was normal, but the variances were not equal), and a Wilcoxon rank sum test (if the distribution was not normal). This analysis was conducted in R (R Development Core Team, 2017).

4.4.5 Supplementary exploratory analysis of trophic structure

Beyond **Paper III**, I performed additional exploratory analyses on the full isotope data set collected for benthic species in Chukchi Borderland in 2016. To enable comparison of the years for **Paper III**, part of the benthic samples collected in 2016 had to be excluded from the analysis to match the samples collected in 2005. The excluded part of the data might, however, help to enhance the currently limited knowledge on Arctic deep-sea food web structure. Therefore, I explored these data, yet with no formal statistical analysis.

I first compared the isotopic niche of benthos included in the analysis for Paper III and of that excluded from the analysis by generating a bi-plot of $\delta^{13}C$ versus $\delta^{15}N$ values on station-averaged values by taxon. The isotopic niche of benthos was indicated on the plot by computing confidence ellipses (i.e., bivariate confidence intervals) (Fox and Weisberg, 2011). Then, the data were plotted to differentiate between samples from mid-depth and deep stations by computing the confidence ellipses for the two depth strata used in Paper II on a bi-plot of $\delta^{13}C$ and $\delta^{15}N$ values. In addition, the bi-plots without ellipses were generated for each phylum to explore potential trends in isotopic composition of taxonomic groups within phyla.

Trophic position (TP) of each benthic consumer was also calculated based on its nitrogen isotopic distance to *Calanus glacialis,* as a baseline. Station averages of $\delta^{15}N$ for *C. glacialis* and individual benthic consumers were used for the analysis. The following equations was used:

$$TP_{C.\ glacialis} = ([\delta^{15}N_{consumer} - \delta^{15}N_{C.\ glacialis}]/3.4) + 2 \qquad (2)$$

where 3.4 is the assumed average isotopic enrichment in $\delta^{15}N$ per trophic level in marine environments (Post, 2002; Jake Vander Zanden and Fetzer, 2007). This enrichment level was chosen to be consistent with previous food web studies in the Arctic region (e.g., Iken et al., 2010; Divine et al., 2015; Roy et al., 2015; Bell et al., 2016), although variation in enrichment factor among marine invertebrates is acknowledged (Caut et al., 2009).

4.4.6 Maps

To illustrate the difference in sea-ice cover between the sampling years, we plotted average sea-ice concentration data derived from satellite Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave at a grid cell size of 25 × 25 km (Cavalieri et al., 1996). The concentration is defined as the fraction of the area of the grid cell covered by sea ice and is given in percentage from 0 (no ice) to 100 (fully covered by ice) percent ice (https://nsidc.org/cryosphere/seaice/data/terminology.html). Average sea ice concentration for July and September (minimum ice month) was downloaded from the National Snow and Ice Data Centre (https://nsidc.org/data/NSIDC-0051/versions/1). The data were then imported into ArcGIS 10.5 (ESRI, 2011) software and projected spatially. All maps presented in the paper were generated using the ArcGIS (ESRI, 2011).

5 Results

5.1 Paper I: Epifaunal communities across marine landscapes of the deep Chukchi Borderland (Pacific Arctic)

Results of **Paper I** showed that environmental conditions at the bottom of the CBL generally resemble those in most deep-sea environments. CBL was characterized by low bottom water temperature that decreased with depth from - 0.3 to 0.7 °C. Bottom salinity ranged between 34.84 and 34.93 PSU, which corresponds to salinities of Atlantic and Arctic bottom water masses. Sediments were mainly silty based on sediment grain size analysis, though the images indicated interspersed hard substrate. The hard substrate (drop-stones) was mostly found at ridge and plateau stations. Lebensspuren were numerous at all stations indicating low current velocity. The pockmarks on the Chukchi plateau were inactive with no signs of gas bubbling or obvious bacterial deposits. Sediment pigment analysis showed very low concentration of chlorophyll (< 0.1 µg pigment/g dry sediment) and phaeopigments (< 0.8 µg pigment/g dry sediment) across all stations but station 1, located on the Northwind Ridge and closer to the Chukchi shelf.

This environment was inhabited by epifauna of relatively low abundance and biomass. Total epifaunal abundance estimates ranged from ~2300 ind/1000 m^2 to 14300 ind/1000 m^2 based on ROV samples and from ~ 34 ind/1000 m^2 to 2000 ind/1000 m^2 based on trawl samples, and biomass (from trawl stations only) ranged from ~103 to 900 g ww/1000 m^2 (Fig. 5A) Analysis of ROV images indicated Cnidaria, Annelida and Echinodermata to be the most important in terms of relative abundance. Based on trawl catches, Echinodermata and Arthropoda showed higher abundances and biomass than other phyla. In total, 152 taxa and morphotypes were identified from the ROV (78 taxa) and trawl (86 taxa) samples with 34 taxa common to both sampling tools. This study adds at least 16 taxa to the previously documented species list in this area. The most taxonomically rich phyla were Echinodermata, Cnidaria and Arthropoda (Fig. 5B).

The first two hypotheses of **Paper I** were partly confirmed with depth and food availability affecting epifaunal community structure and differentiating deep basin communities from mid-depth plateau/ridge habitats. Compared to shallower plateau/ridge stations, deep basin communities had significantly lower numbers of taxa and abundances based on the images, and lower biomass based on trawl catches. In addition, basin stations were characterized by significantly different community structure from the plateau/ridge habitat, with a swimming polychaete (possibly *Pelagomacellicephala*), poriferans (*Radialla sol*, *Polymastia*), and the holothuriod *Elpidia* being the most common basin taxa. Despite the presence of (inactive) pockmarks on the plateau and contrary to our expectations, results did not indicate a significant difference of epifaunal community structure in terms of diversity (trawl and ROV samples), and biomass and abundance (trawl samples) between plateau and ridge habitats. Similarly, cluster analysis did not indicate significant differences between plateau and ridge epifaunal community composition (Fig. 5C). Plateau/ridge stations were generally characterized by high occurrence of the brittle star *Ophiopleura borealis* and the sea star *Pontaster tenuispinus*. However, image analysis pointed to differences between western and eastern parts of the ridge/plateau habitat complex in terms of proportionally abundant taxa (Fig. 5D, E). This difference was driven by food availability and presence of hard substrate. Specifically, the eastern part of the study area was dominated by polychaetes of the families Ampharetidae and Sabellidae that were positively correlated with sediment chlorophyll concentration. The western part of the study area was dominated by morphotype 10, which resembled Cnidaria polyps (either *Atolla* or *Nausithoe* sp.) and was positively correlated with number of drop-stones. The drop-stones were also associated with enhanced diversity of mostly sessile species.

Mapping of the biogeographic affinity of epifauna showed the majority of CBL epifauna was of Arcto-boreal Atlantic affinity, in terms of both number of taxa and faunal abundance. The next most common biogeographic affinities were Arcto-boreal and Arctic affinities, while Arcto-boreal Pacific affinity was very rare, which confirms the third hypothesis of **Paper I**.

The present study also revealed geographic range extensions of four mollusks and five poriferan species, as well as a depth range extension of one mollusk species. Two mollusks found in the CBL might prove to be new species. These results contribute to the yet incomplete biodiversity inventory of the Arctic deep sea. Overall, our study documented current biodiversity, community composition, and aspects of the ecology of CBL epifauna. It contributes to the limited knowledge of Arctic deep-sea benthos and strengthens existing baseline data that are urgently needed given the climate change related transformations of the Arctic Ocean.

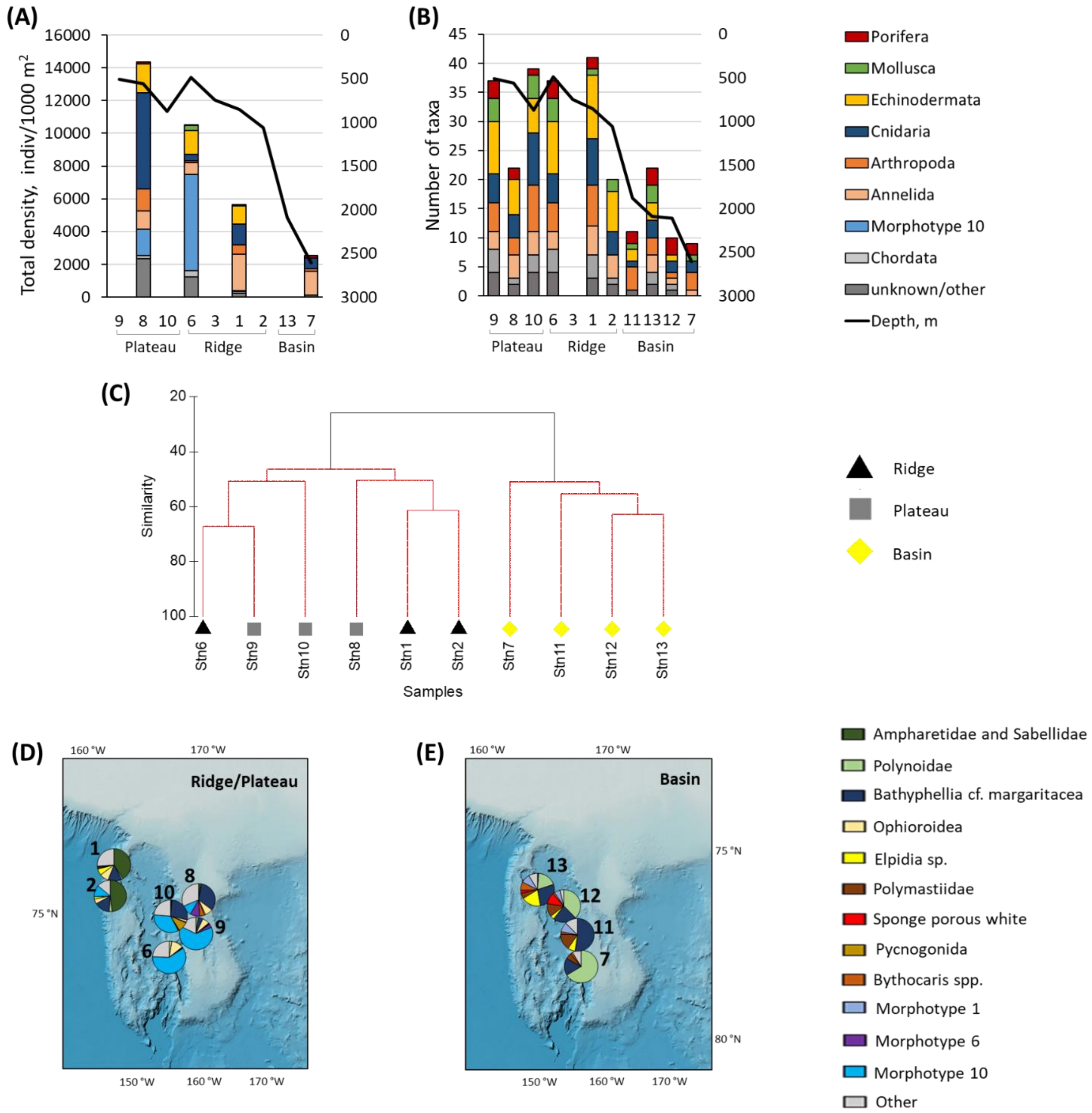


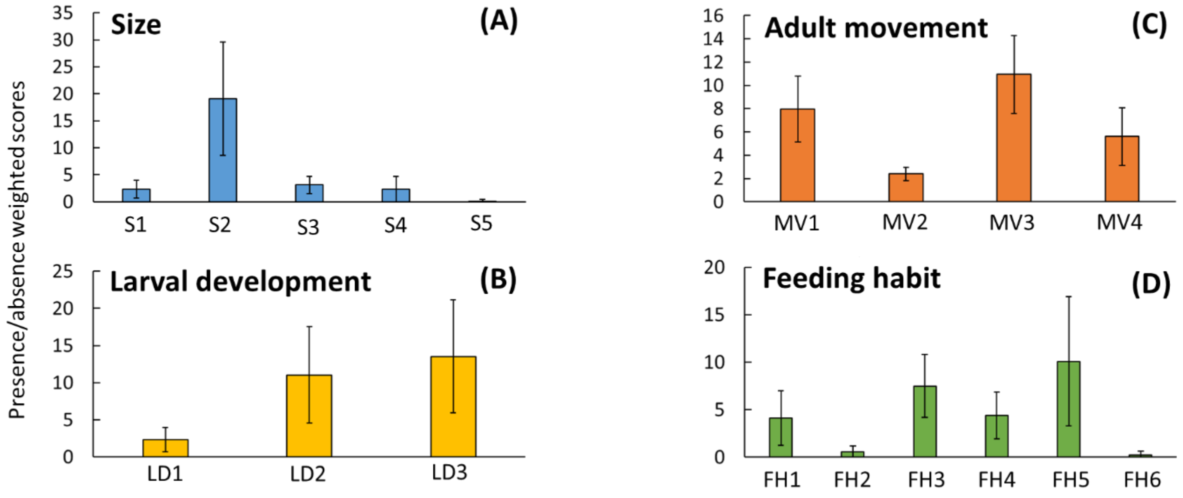
Figure 5. Total abundance, number of taxa and community composition of epifauna based on ROV samples collected in the Chukchi Borderland in 2016. (A) Total abundance by phylum (and morphotype 10 and unknown) of epifauna and (B) number of taxa per phylum at ridge, per phylum at ridge, plateau, and basin stations; different colors represent different phyla/taxa and the black line represents depth (m). (A) has fewer bars than (B) due to a laser pointer failure that did not allow us to calculate abundance at all ROV stations. No ROV imagery was taken at st. 3. (C) Hierarchical cluster diagram based on Bray-Curtis dissimilarity of epifaunal relative abundances at different stations. Black lines indicate statistically significant differences (SIMPROF, α = 0.05); red lines indicate intervals where clusters are not significantly different; triangles – ridges, squares – plateau, diamonds – basins. (D) and (E) represent proportions of dominant taxa at the ridge/plateau (D) and basin (E) stations. Different colors indicate different taxa and morphotypes. Numbers in bold print are station numbers.

5.2 Paper II: Functional pattern of benthic epifauna in the Chukchi Borderland, Arctic deep sea

Results of **Paper II** generally supported our first hypothesis with CBL epifaunal trait modalities corresponding largely to the current view of global deep-sea fauna. Specifically, small sized organisms ("small-medium" *size* trait modality) were most frequently encountered in CBL epifauna, while “large” organisms were rare (Fig. 6A). The most important *larval development* type was "direct" development followed by "lecitotrophic" larvae, while "planktotrophy" was rare (Fig. 6B). The most frequent modality of *adult movement* was "crawling", which together with "swimming" were more frequent than "sessile" epifauna (Fig. 6C). As in other deep-sea areas, "deposit feeders" were common, though not the dominant *feeding mode,* contrary to our expectations. Instead, “predators” were most frequent in the epifauna of the study area, followed by “suspension feeders” (Fig. 6D). This analysis expands our view of potentially dominant feeding modes in the deep sea.

Trait modality composition differed between mid-depth and deep stations, with depth and sediment organic carbon content explaining most of the variability of the analyzed biological traits in epifauna of the two depth strata, which confirms the second hypothesis of **Paper II**. The deep basin stations were characterized by a more homogeneous environment, likely leading to lower availability of functional niches, where varieties of trait modalities could be expressed. Indeed, fauna inhabiting basins had fewer but shared trait modalities, which was reflected in lower FD and higher FR compared to mid-depth stations. The majority of epifauna present in the basins were “mobile”, “free-living”, “swimming” organisms (Fig. 6E). Surprisingly, “suspension feeding” was most common in basins despite typically low bottom currents at great depths, also indicated by highly abundant traces of life on the seafloor of CBL basin stations. In addition, “opportunists/scavengers” were more common at basin stations than at mid-depth stations. “Internal fertilization” was also more common at deeper stations than at mid-depth stations. The mid-depth stations had a more heterogeneous environment and higher number of stones than deeper basins. This heterogeneity likely resulted in higher availability of functional niches reflected in a more variable set of trait modalities and a higher FD index compared to deeper stations. Overall, and in contrast to the deeper stations, fauna of mid-depth stations included mostly “attached”/”sessile” “predators” and “deposit feeders” In addition, our data also suggest that the increasing distance from the adjacent Chukchi shelf corresponded with spatial patterns of trait modality distribution. Specifically, higher proportional abundances of “tube-dwelling”, “sessile” and “deposit-feeding” epifauna was found at mid-depths at Northwind Ridge stations. These trait modalities were associated with higher food input as indicated by higher sediment pigment values and carbon content. Farther north, “upright” and “attached” “predators” were found in in areas of high drop-stone abundance. Occasionally, mobile predators were observed in the vicinity of the drop-stones.

This study is the first to apply biological trait analysis to epifaunal communities in the Arctic deep sea. Therefore, the study adds to the very limited information on the ecology of deep-sea benthos and can be used for assessment of sensitivity of fauna to anthropogenic activities that are currently widely discussed in light of Arctic sea-ice reduction.



Trait/Modality	Modality code
Size	
Small (<10 mm)	S1
Small-medium (10-50 mm)	**S2**
Medium (50-100 mm)	S3
Medium-large (100-300 mm)	S4
Large (>300 mm)	S5
Larval development	
Planktotrophic	LD1
Lecithotrophic	LD2
Benthic/direct	**LD3**
Adult movement	
Sessile/none	MV1
Burrower	MV2
Crawler	**MV3**
Swimmer	MV4
Feeding habit	
Surface deposit feeder	FH1
Subsurface deposit feeder	FH2
Filter/suspension feeder	FH3
Opportunist/scavenger	FH4
Predator	**FH5**
Parasite/commensal/symbiotic	FH6

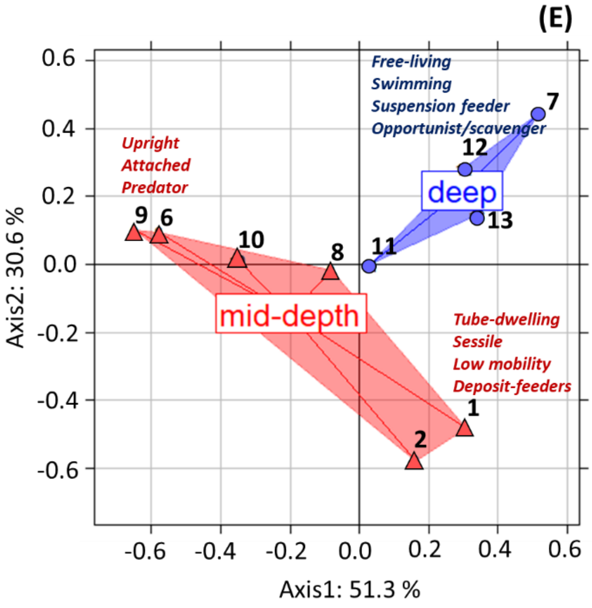


Figure 6. Occurrence of trait modalities of epifauna across the study area and results of fuzzy correspondence analysis (FCA) in Chukchi Borderland in 2016. A – D modality occurrence based on presence/absence of taxa for combined ROV and trawl data and averaged across all stations ± SD; (A) body size, (B) larval development, (C) adult movement, and (D) feeding habit; note that y-axes have different scales. Trait modality codes are defined in the legend table below the occurrence plots. (E) FCA on all the nine biological traits weighted by epifaunal proportional abundances from ROV samples ordinated by stations. Numbers are station numbers. Modalities in italics indicate common traits for the two depth strata (note, the actual trait modalities coordinates for FCA analysis can be found in Paper II). Red – mid-depth stations. Blue – deep stations.

5.3 Paper III: Reduced efficiency of pelagic-benthic coupling in the Arctic deep sea during lower ice cover

Findings of **Paper III** confirm the hypothesis of tighter pelagic-benthic coupling in the year of higher sea-ice extent (2005) than in the year of lower sea-ice extent (2016). Specifically, the results showed higher overlap of isotopic niches and generally shorter $\delta^{15}N$ and $\delta^{13}C$ isotopic distances between pelagic (pPOM and zooplankton) and benthic (sPOM and benthos) food web members in 2005 compared to 2016 (Fig. 7A).

Results also showed significantly higher $\delta^{13}C$ values of pPOM and zooplankton in 2005 than in 2016 (Fig. 7C). The higher $\delta^{13}C$ values might indicate potentially higher contribution of sea-ice algae that are often enriched in^{13}C, which could have been more abundant in the earlier year with higher sea-ice extent. The inferred sea-ice algal signal was, however, not reflected in $\delta^{13}C$ values of sediment and benthic samples collected in our study. Therefore, some evidence indicates the possibility of ice algae playing a role in the pelagic-benthic coupling difference, but clear conclusions are difficult based on a single sampling period in each year.

The benthic isotopic niche was wider in 2005 than in 2016 (Fig. 7A). This difference was largely driven by a larger range of $\delta^{15}N$ in 2005 than in 2016; which may be an indication of more variable sources of food available to, and consumed by, benthos that year. In addition, mean $\delta^{15}N$ of sPOM and benthos was significantly lower in 2005 than in 2016 (Fig. 7B), which indicates that organic matter available for benthos was generally less reworked in 2005 than in 2016 as microbial degradation can enhance $\delta^{15}N$ values.

In summary, our findings indicate potential difference in pelagic-benthic coupling between years characterized by different sea-ice settings, with stronger decoupling in the year of lower sea-ice extent. While limited in sample size, this study is the first to suggest that valuable insights on cryo-pelagic-benthic coupling can be drawn from isotopic niche analysis in the Arctic deep sea.

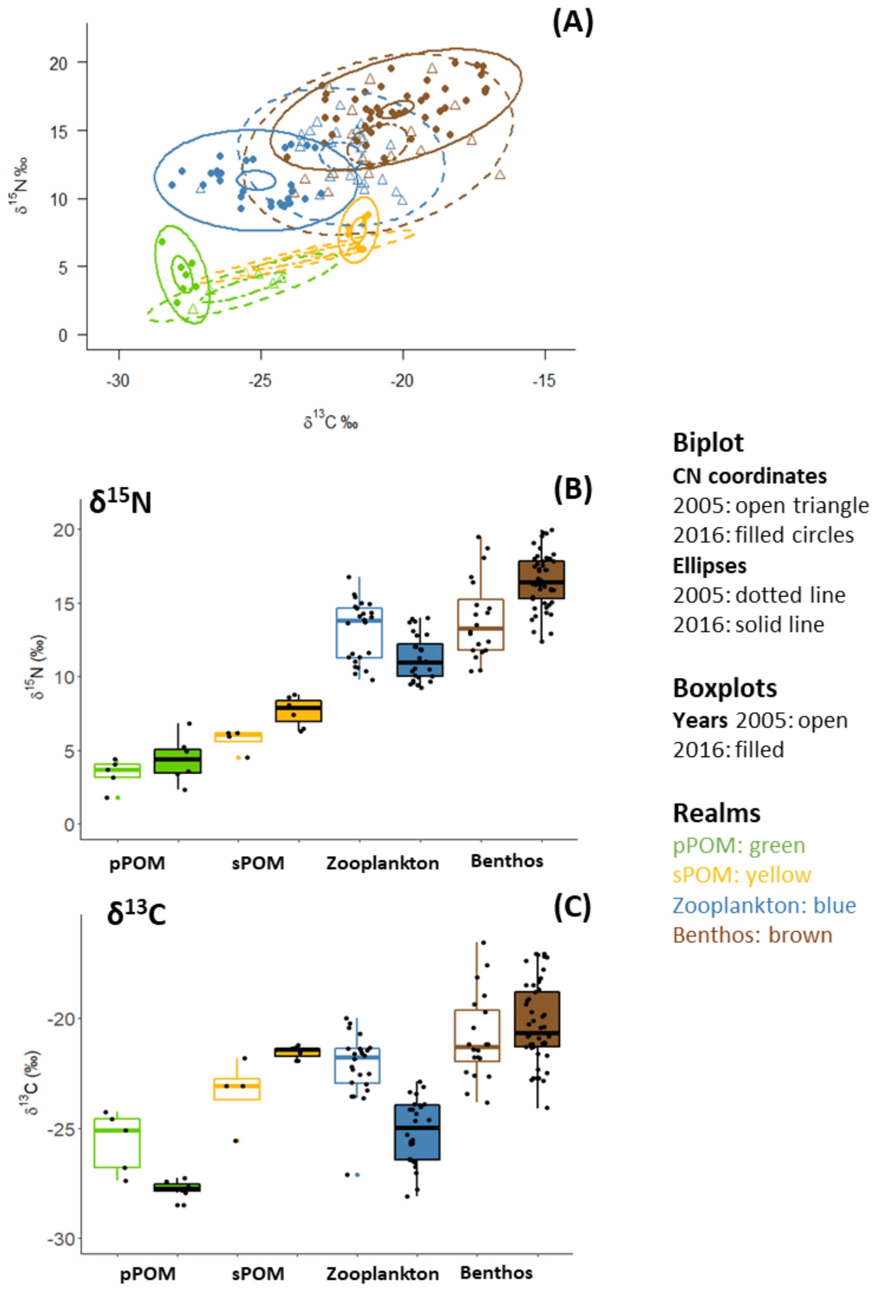


Figure 7. Isotopic niches of compared food web components (end members and zooplankton and benthic consumers) and mean values of $\delta^{15}N$ and $\delta^{13}C$ (‰) per food web component in the Chukchi Borderland in 2016 and 2005. pPOM and sPOM stand for particulate organic matter and sediment organic matter, respectively. Food web components are indicated by colors: green (pPOM), yellow (sPOM), blue (zooplankton), and brown (benthos). (A) Biplot of $\delta^{13}C$ and $\delta^{15}N$ isotope values (‰) for assemblages in the Chukchi Borderland in 2005 and 2016; outer ovals are sample size corrected standard ellipses (SEA_C) containing 95% of the data, inner small ovals indicate 95% confidence intervals around the bivariate means. Open triangles are means of samples collected in 2005 and filled circles in 2016. Dotted outlines enclose assemblages collected in 2005 and solid lines represent those collected in 2016. (B) Mean values of $\delta^{15}N$ and (C) mean values $\delta^{13}C$ (‰) per food web component in 2005 (open boxplots) and 2016 (filled boxplots).

5.4 Supplementary results: Exploratory analysis into epifaunal food web in the CBL

Supplementary results showed a slightly wider isotopic niche of organisms of the entire 2016 data set compared to that used for **Paper III** (Fig. 8A). The difference was, however, not substantial with a $\delta^{15}N$ range of 12 – 21‰ versus 12 – 20‰, and a $\delta^{13}C$ range of -27 to - 16‰ versus -24 to - 17‰ for the entire data set and that included in **Paper III**, respectively. Therefore, adding data to the considerably condensed 2016 data set used for **Paper III** would not have changed our results of low overlap and generally high $\delta^{15}N$ and $\delta^{13}C$ isotopic distances between pelagic food web components (pPOM and zooplankton) and benthos.

Isotopic composition of benthos was relatively similar between the mid-depth and deep stations, though minor differences between the depth strata were observed for $\delta^{13}C$ values. Benthos collected from mid-depths spanned 9‰ (-17 to -26‰) in $\delta^{13}C$ and was slightly closer to the pelagic baseline, while deep station species spanned 7‰ (-16 to -23‰) in $\delta^{13}C$ and were mostly closer to the benthic baseline (Fig. 8B). $\delta^{15}N$ values of benthos were similar between mid-depth (12 – 21‰) and deep (13 – 20‰) samples. However, it should be noted that most samples for isotope analysis were collected at mid-depth (220 samples), while considerably fewer samples were collected at deep stations (53 samples).

$\delta^{15}N$ values of benthic consumers were overall high and ranged from 12 – 21‰ with an average $\delta^{15}N$ of 17‰. The benthic food web of CBL comprised five trophic levels with the majority of taxa occupying the 3rd trophic level or higher.

Echinodermata showed the highest range of $\delta^{15}N$ values, followed by Arthropoda and Annelida, yet the ranges may be biased by unequal sampling effort (Fig. 8C). Based on lower $\delta^{15}N$ values some Ophiuroidea, Annelida, Amphipoda and an Ascidiacea utilized relatively fresh food available at the CBL seafloor. Asteroidea, in contrast, had the highest $\delta^{15}N$ values, indicating consumption of highly reworked organic material or predation feeding mode. Arthropoda followed by Cnidaria and Echinodermata had the highest $\delta^{13}C$ range. Cirripedia, some Amphipoda, an Octocorallia, some Ophiuroidea and Ascidiacea were closer to pelagic phytoplankton baseline, while Demospongia, some Bivalvia and Annelida were closer to the benthic baseline (Fig. 8C).

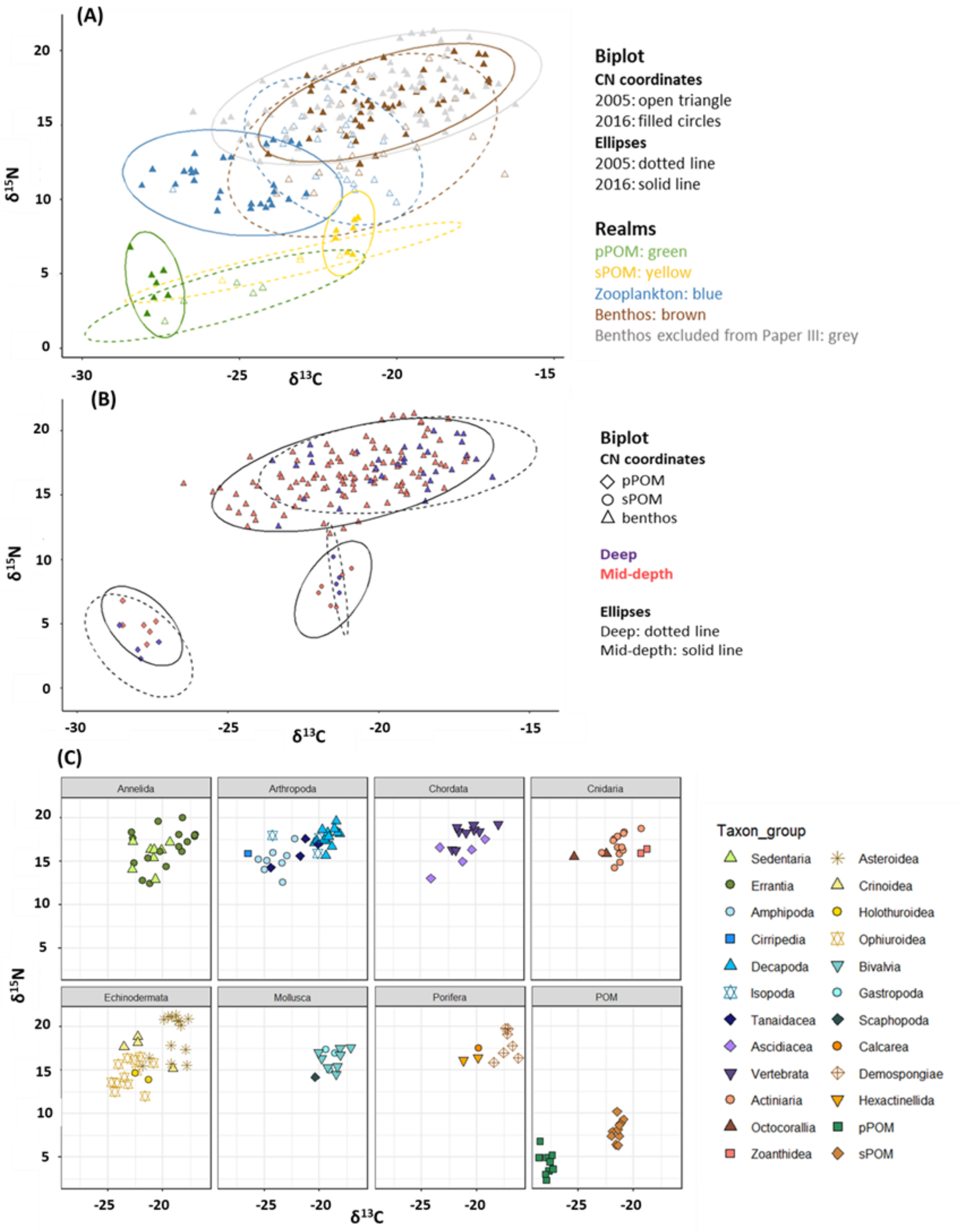


Figure 8. Biplots of station means of $\delta^{13}C$ and $\delta^{15}N$ values (‰) for benthos in the Chukchi Borderland in 2005 and 2016. pPOM and sPOM stand for particulate organic matter and sediment particulate organic matter, respectively. (A) Biplot indicating isotopic values of benthos excluded from the analysis of Paper III (in grey). Other food web components are indicated by green (pPOM), yellow (sPOM), blue (zooplankton), and brown (benthos included in Paper III). Dotted outlines enclose assemblages collected in 2005 and solid lines represent those collected in 2016. Open triangles are means of samples collected in 2005 and filled circles in 2016. (B) Biplot indicating difference between benthos collected at mid-depth and deep stations in 2016. Samples collected at mid-depth are in red and enclosed in dotted outlines, samples collected at deep stations are in blue and enclosed by solid lines. pPOM indicated by diamond-shaped symbols, sPOM by circles and benthos by triangular. (C) Biplot of benthic taxa by phylum and particulate organic matter collected in 2016. Various colors and shapes are certain taxonomic groups within those phyla, as indicated in the figure legend.

6 Discussion

Knowledge about Arctic deep-sea ecosystems is currently limited owing to difficulties related to sampling logistics in this area. However, ongoing climate change that modifies the Arctic Ocean and opens up opportunities for anthropogenic activities, raises an urgent need for baseline data collection on Arctic deep-sea ecosystems. This need is in part filled by the present thesis which focused on one of the least studied Arctic deep-sea regions – the CBL – and enhances knowledge on a poorly studied ecosystem component – benthic epifauna. Specifically, taxonomic and biogeographic epifaunal composition was described and quantitative assessment of abundance and biomass of taxa present in the region was done (**Paper I**). CBL epifauna was also described in terms of dominant behavioral, life history and morphological characteristics with BTA, which was applied to epifauna of the Arctic deep sea for the first time (**Paper II**). Environmental factors shaping epifaunal communities and function in CBL were identified (**Papers I**, **II**, and **III**). **Paper III** compared pelagic-benthic coupling between a year of higher (2005) and lower (2016) sea-ice cover and indicated potential impacts of climate change on Arctic deep-sea food webs. Finally, **Supplementary results** complemented the limited knowledge on epifaunal food webs in the Arctic deep sea.

6.1 General characteristics of CBL epifauna: a short comparison to other Arctic deep-sea areas

6.1.1 Who is there and how many?

The few available studies from the Arctic deep sea report low epifaunal biomass and abundance (Tables 1, 2), that are largely explained by energy limitations experienced by fauna in this environment (Iken et al., 2005). Epifauna of the CBL was most likely food limited as evidenced by considerably lower pigment concentration **(Paper I)** compared to Arctic shelves (e.g., Morata and Renaud, 2008; Link et al., 2013). The low values support studies on POC flux showing maximum POC flux in the Northwind Abyssal plain (0.24–0.32 g C m^{-2} $year^{-1}$; Watanabe et al., 2014) are at least an order of magnitude lower than on the adjacent Chukchi Sea shelf (4 – 166 g C m^{-2} $year^{-1}$; Grebmeier et al., 2006). Similar to other deep-sea studies, low food availability was reflected in overall low biomass and abundance of epifauna in our study region (173 to 906 g ww/1000 m^2; 329 - 2029 ind/1000 m^2 based on trawls and 2743 – 14 457 ind/1000 m^2 based on ROV, **Paper I**) with values much lower than on Arctic shelves (Tables 1, 2). The biomass estimates (**Paper I**) were, however, within the range registered for the Nansen and Amundsen Basins and generally comparable to values reported from the Alaska Beaufort Sea slope (Table 1). The estimates of epifaunal abundance acquired from ROV images (**Paper I**) were generally higher than those reported from the Nansen and Amundsen Basins and from the previous quantitative study of the CBL and Canada Basin, but mostly lower than estimates from slopes of East Greenland and north of Svalbard, and the HAUSGARTEN observatory located in Eastern Fram Strait (Table 2). Abundance estimates acquired by trawl in our study (**Paper I**) were overall comparable to those from deep Beaufort Sea (Table 2).

A total of 152 taxa and morphotypes were registered during our survey (with 49 taxa documented from 154 m^2, where the laser pointers were still functioning, **Paper I**). The total number of taxa registered in our study area is comparable with those registered from adjacent shelves rather than from other Arctic deep-sea areas (Table 3), though direct comparison is difficult given areas of different sizes were sampled in different studies and actual epifaunal species richness is likely higher in both the study region and the adjacent shelves. Nevertheless, the present study contributed considerably to the taxonomic inventory of the CBL area with at least 16 taxa not previously documented from the same area by Bluhm et al. (2005) and MacDonald et al. (2010). In addition, our study documented geographic range extensions for five sponge and five mollusc species, and depth range extension for one bivalve species (**Paper I**). Two bivalves (*Hyalopecten* c.f. *frigidus* and *Bathyarca* c.f. *imitata*) caught in our samples might prove to be new species. The most speciose phyla across the study area were Echinodermata, Arthropoda and Cnidaria (**Paper I**), which corresponds well with previous findings from the Arctic deep sea (e.g., Soltwedel et al., 2009; Rybakova et al., 2013; Rybakova et al., 2019).

Common, in terms of abundance and biomass, epifaunal taxa across the CBL belonged to Cnidaria (mostly, Anthozoa), Annelida (Polynoidae, Sabellidae and Terebellidae), Echinodermata (Ophiuroidea, Asteroidea and Holothuroidea), Arthropoda (Decapoda, Amphipoda and Pycnogonida), and Porifera (**Paper I**). In general, taxonomic composition was similar to that previously reported from other Arctic deep-sea studies (e.g., MacDonald et al., 2010; Sswat et al., 2015; Rybakova et al., 2019). Most intriguingly, taxonomic composition was in fact highly similar to epifaunal communities described for the Eurasian Basin and Atlantic sector of the Arctic deep sea (e.g., Mayer and Piepenburg, 1996; Piepenburg et al., 1996; Meyer et al., 2013; Rybakova et al., 2019), except for Morphotype 10. This morphotype resembled

Table 1. Biomass estimates of epifauna at different Arctic deep-sea and shelf locations, ww is wet weight.

Region	**Biomass range or mean value, ww/1000 m^2**	**Depth range, m**	**Sampling year**	**Sampling tool**	**Reference**
			Arctic deep sea		
Chukchi Borderland	173 - 906	486 – 2 610	2016	Plumb-staff beam trawl	Our study
Eastern Central Arctic Basins: Nansen and Amundsen Basin	210 – 3 940	3571 - 4384	2012	Agassiz trawl	Rybakova et al. (2019)
Alaska Beaufort Sea slope	37 – 1 599	1000	2013 - 2015	Plumb-staff beam trawl	Ravelo et al. (2020)
			Arctic shelves		
North-eastern Chukchi Sea	570 – 644 100	23 - 58	2009, 2010	Plumb-staff beam trawl	Ravelo et al. (2014)
Chukchi Sea	1 628 – 217 023	31 - 101	2004, 2007, 2008	Beam trawl	Bluhm et al. (2009)
Beaufort Sea	5 999 and 7 789	36 - 230	2013 - 2015	Plumb-staff beam trawl	Ravelo et al. (2020)
Beaufort Sea	58 – 501 031	13 - 220	2011	Plumb-staff beam trawl	Ravelo et al. (2015)

Table 2. Abundance estimates of epifauna at different Arctic deep-sea and shelf locations.

Region	**Abundance range or mean value, ind/1000 m^2**	**Depth range, m**	**Sampling year**	**Sampling tool**	**Reference**
			Arctic deep sea		
Chukchi Borderland	2 273 - 14 346	486 - 2610	2016	ROV	Our study
Canada Basin and Chukchi Borderland	100 – 5 800	940 – 3 800	2005	Digital camera platform	MacDonald et al. (2010); (Link et al., 2013)
Eastern Central Arctic Basins: Nansen and Amundsen Basin	900 – 7 800	3571 - 4384	2012	Towed Ocean Floor Observation System (OFOS)	Rybakova et al. (2019)
East Greenland continental slope	5 000 – 30 000	751 – 2785	1994	Still camera described in Piepenburg & von Juterzenka (1994)	Mayer and Piepenburg (1996)
Continental margin west of Svalbard (HAUSGARTEN)	11 000 – 38 000	1200 - 5500	1997, 2002	OFOS	Soltwedel et al. (2009)
Eastern Fram Strait (HAUSGARTEN)	7 410 - 26 740	2309 - 2788	2002, 2004, 2007, 2011	OFOS	Bergmann et al. (2011), Taylor et al. (2016)
Chukchi Borderland	342 – 2 029	486 – 2610	2016	Plumb-staff beam trawl	Our study
Alaska Beaufort Sea slope	97 – 3 383	1000	2013 - 2015	Plumb-staff beam trawl	Ravelo et al. (2020)
Upper slope north of Svalbard	1 000 – 37 300	250 - 450	2010 - 2011	Sonde equipped with both a video and a still camera and Agassiz trawl	Sswat et al. (2015)
			Arctic shelves		
Continental shelf and deep shelf troughs north of Svalbard	2 000 – 42 600	50 - 250	2010 - 2011	A sonde equipped with both a video and a still camera, and Agassiz trawl	Sswat et al. (2015)

East Greenland shelf break	~ 200 000	190 – 377	1994	Still camera described in Piepenburg & von Juterzenka (1994)	Mayer and Piepenburg (1996)
Chukchi Sea	229 - 70 879	31 - 101	2004, 2007, 2008	Beam trawl	Bluhm et al. (2009)
North-eastern Chukchi Sea	150 – 548 860	23 - 58	2009, 2010	Plumb-staff beam trawl	Ravelo et al. (2014)
Beaufort Shelf	40 – 275 590	13 - 220	2011	Plumb-staff beam trawl	Ravelo et al. (2015)
Laptev Sea	100 - 79 500	15 - 44	1993, 1995	Still camera (PhotoseaThf 70 D)	Piepenburg and Schmid (1997)

Table 3. Number of epibenthic taxa registered in different Arctic deep-sea and shelf locations. Note, Chukchi Borderland number of taxa included morphotypes

Region	**Total number of species**	**Area sampled, m^2**	**Reference**
Arctic deep sea			
Chukchi Borderland	152 (78 from ROV and 86 from trawl)	154 at four stations, unquantified at 8 additional stations	Our study
Canada Basin and CBL	67	10 526	MacDonald et al. (2010)
Canada Basin and CBL	15		Bluhm et al. (2005)
Nansen Basin and Amundsen Basins	58	16 190	Rybakova et al. (2019)
East Greenland continental slope	91	297	Mayer and Piepenburg (1996)
Eastern Fram Strait, HAUSGARTEN	20 - 29	768	Bergmann et al. (2011); Meyer et al. (2013); Taylor et al. (2016)
Arctic shelves			
Chukchi Sea	165		Bluhm et al. (2009)
NE Chukchi Sea	239		Blanchard et al. (2013)
Alaska Beaufort Shelf / shelf and upper slope	133 / 332		Ravelo et al. (2015), Ravelo et al. (2020)

medusa polyps and could be either *Atolla* or *Nausithoe* sp., both of which have been recorded in the CBL during pelagic ROV dives (Raskoff et al., 2010; and for 2016 cruise, R. Hopcroft, pers. communication). A previous benthic study of the CBL and adjacent Canada Basin also recorded these Coronatae tubes (then identified as *Nausithoe* sp.), though in considerably lower number (MacDonald et al., 2010).

The analysis of faunal biogeography (**Paper I**) showed strong dominance of species of Atlantic affinity (over 50% of total species number and over 70% of total abundance). Concurrently, the share of Pacific affinity species was small (0 – 6% of total species number and less than 1% of total abundance). Prevalence of species of Atlantic affinity in the CBL is consistent with the study of epifauna by Ravelo et al. (2020) from the Beaufort Sea slope and with the study on bivalve biogeography by Krylova et al. (2013) from the Nansen and Amundsen Basins, and Norwegian and Greenland Seas. In addition, results of a previous study in the CBL and adjacent Canada Basin showed high prevalence of Atlantic boreal macrofaunal species (Bluhm et al., 2005). One of the likely explanations of the pattern observed is a strong dominance of Atlantic water in the Arctic deep sea that is possible since the only deep-water connection to the Arctic is from the North Atlantic via Fram Strait. At the same time, an exchange of water with the deep North Pacific is constrained by the shallow Bering Sea being the only present-day connection to the Pacific. Indeed, the salinity profiles in our study indicated the CBL seafloor lies within Atlantic and Arctic bottom-water layers (**Papers I** and **II**). Another possible – or additional - explanation for the pattern of biogeographic affinities observed in our study could be the evolutionary history of the Arctic Ocean, in particular changes in glacial ice cover during the Pleistocene (reviwed in e.g., Bluhm et al., 2011; Petryashov et al., 2013; Renaud et al., 2015). In short, the glaciation of Arctic shelves was uneven between Atlantic and Pacific sides, with extensive glaciation down to the deep ocean on the Atlantic side and only partly glaciated shelves on the Pacific side (Nesis, 1984; Briggs, 2003; Maggs et al., 2008). As a result of the glaciation, Atlantic fauna had to find refugia in deeper unfrozen areas or be extirpated, while Pacific shelf fauna could partly survive in areas not influenced by ice (Nesis, 1984; Maggs et al., 2008). After the glaciation, species adapted to depth reinvaded from the Atlantic, while the Pacific Arctic was reinvaded by the fauna from the shallow refugia and through the shallow Bering Strait (Nesis, 2003; Maggs et al., 2008; Dilman, 2009). This explains the current-day dominance of eurybathic fauna on the Atlantic side of the Arctic and the prevalence of stenobathic species on the Pacific Arctic shelves (reviewed in Bluhm et al., 2011). The majority of the CBL fauna was in fact eurybathic with 80% of species considered for the biogeographic analysis shared with Arctic shelves (Sirenko, 2001; Piepenburg et al., 2011) (**Paper I**). It has previously been suggested that endemism is high in the Arctic deep sea (80%, Vinogradova, 1997). Recent studies confirmed the high level of endemism for epifauna in the Nansen and Amundsen Basins (55%, Rybakova et al., 2019) and for bivalves in the Canada Basin (50%, Krylova et al., 2013). In our study, however, the level of endemism was not as high, with 14 – 28% of total species number and only 2 – 9% of total species abundance (**Paper I**). Only taxa collected from the trawl and identified to species level were included in the analysis of biogeographic affinity; including more species in the analysis could potentially yield higher estimates of endemism.

CBL epifauna was characterized by low abundance and biomass, generally comparable with other Arctic deep-sea areas, but much lower than those observed on Arctic shelves. Taxonomic composition was generally similar to that previously described for the Arctic deep sea, yet species richness was higher with, for example, Morphotype 10 (*Atolla* or *Nausithoe* Scyphozoa) described only for the CBL and Canada Basin so far. Consistent with both water mass distribution today and Arctic history, the majority of epifauna had boreal-Atlantic biogeographic affinity, while the share of boreal-Pacific fauna was small. The share of Arctic endemic species in CBL was lower than reported from Arctic Basins.

6.1.2 What ecological characteristics are common for epifauna in the CBL?

Besides low abundance and biomass, the limited energy available at the CBL seafloor was also reflected in dominance of small-sized epifauna (**Paper II,** Fig. 9), which is consistent with current paradigms on decreasing benthic body size with depth (Rex and Etter, 1998; Rex et al., 2006; Wei et al., 2010). Specifically, small-medium size (between 10 and 50 mm) was most frequent in CBL epifauna. The low occurrence of the smallest size category in the study is unsurprising given that we targeted epibenthic megafauna, which is often ≥ 10 mm. An opposite trend - of larger body size than in shallow areas – has been described for some deep-sea taxa (Timofeev, 2001; Danovaro et al., 2014) but only fit for one very large pycnogonid *Colossendeis proboscidea* observed in our study area (**Papers I, II**). Frequency of organisms with large body size was the lowest in CBL (**Paper II**).

Even though the deep sea is food limited, patchy particle flux in the form of phytodetrital (Billett et al., 2001) and ice-algal flux events (Boetius et al., 2013) as well as whale or fish falls (Klages et al., 2001; Higgs et al., 2014) do occur in this environment with some regularity. The ability to move is, therefore, a useful adaptation to finding scarce and patchy food (Thistle, 2003; Danovaro et al., 2014). Mobile fauna was, indeed, among dominant epifaunal characteristics in previous Arctic deep-sea studies (Table 4) and our results confirmed this paradigm (**Paper II,** Fig. 9). Examples included echinoderms (Ophiuroidea, Asteroidea, and Holothuroidea), arthropods (Decapoda, Amphipoda, and Pycnogonida), fishes, as well as mobile polynoid polychaetes (**Paper I**). Perhaps the previously unknown swimming behavior of the brittle star *Ophiostriatus striatus* (**Paper II**) is an adaptation to assess patchy food falls as this species has previously been found in association with fresh and detrital algal aggregations in the Arctic deep sea (Boetius et al., 2013; Rybakova et al., 2019). Though mobility seems to be more useful in the food-limited environment, an unexpectedly high occurrence of sessile species was also observed in our study (**Paper II**) despite the prevalence of soft-bottom sediments (**Paper I**). Such high occurrence of sessile fauna was also described in other deep-sea studies and explained by the presence of drop-stones (Jones et al., 2007b; Soltwedel et al., 2009). Similarly, drop-stones were found to be common in the CBL (**Paper I**) with a majority of sessile fauna occupying these stones. Examples included ascidians, sponges, stalked cirripeds and crinoids, and cnidarians (**Paper I**). Some few sessile species inhabited soft sediments, for example the anthozoan *Bathyphellia* cf. *margaritacea* (**Paper I**), though this species has been reported as flexible in terms of substratum choice (Sanamyan et al., 2009; Schulz et al., 2010). Other species often found in soft sediments were Porifera of the Polymastiidae family (**Paper I**), though these species are able to develop root like structures, and cement small particles of sediments to create their own hard substrate or use small sized hard substrate (Barthel and Tendal, 1993).

Predominant feeding strategies may represent adaptations to scarce and pulsed food input that is often of low nutritional quality. Deposit feeding has been suggested to be the best strategy to collect and process scarce detritus in the deep sea (Fabiano et al., 2001; Thistle, 2003); this feeding mode was also often a dominant epifaunal feeding strategy in the Arctic deep sea (Table 4). In our study, deposit feeding was common, though predatory and suspension feeders had higher frequency across the study area (**Paper II,** Fig. 9). Both predatory and suspension feeding modes are, in fact, common and, in some cases, dominating in the

Table 4. Common mobility and feeding habit traits registered for Arctic deep-sea locations.

Region	**Fauna**	**Depth**	**Mobility**	**Feeding habit**	**Reference**
Arctic deep sea					
Chukchi Borderland	Epifauna	486 - 2610	Mobile, sessile	Predators, suspension feeders	Our study
Faroe–Shetland Channel	Epifauna	1006 – 1660	Tube-dwelling/Sessile	Suspension feeders and deposit feeders	Jones et al. (2007b)
Canada Basin and CBL	Epifauna	940 – 3800	Mobile		MacDonald et al. (2010)
Canada Basin and CBL	Epifauna	800 - 2800	Mobile	Suspension feeders on ridges	Bluhm et al. (2005)
Mouth of Kangerdlugssuaq Fjord in Arctic Greenland	Epifauna	270 - 720	High mobility (disturbed by icebergs area) Mobile and sessile (less disturbance)		Jones et al. (2007a)
Eastern Fram Strait (HAUSGARTEN)	Epifauna	1257 - 1325	Mobile	Deposit feeders, predators/scavengers	Meyer et al. (2013)
Eastern Fram Strait (HAUSGARTEN)	Epifauna	1200 - 5500	Mobile and sessile	Deposit feeders (shallower depth) Suspension feeders (greater depth)	Soltwedel et al. (2009)
Eastern Fram Strait (HAUSGARTEN)	Epifauna	2351 – 2788		Suspension feeders and deposit feeders	Taylor et al. (2016)
Fram Strait	Infauna and epifauna	1000 – 5500	Burrower Tube-dwelling	Predators Surface deposit feeders Suspension feeding	Käß et al. (2021)
Bering Sea	Infauna	2603 - 3873	Mobile and surface crawler	Carnivore/scavenger	Liu et al. (2019)

Arctic deep sea (Table 4). While high occurrence of suspension feeders in the CBL might be surprising given the low current velocities at the bottom (**Paper I**), epifauna overcome this constraint by positioning themselves on drop-stones (e.g., Actiniaria, Porifera, Cirripedia) or other organisms (e.g., anemone on stalks of Crinoidea, Annelida tubes or on mobile fauna such as Gastropoda *Colus* spp.) (**Paper I**). By elevating themselves into the benthic boundary layer, suspension feeders reach slightly faster currents that carry food particles (Vogel, 2020). Some mobile fauna can also suspension feed, e.g. the polychaetes Macellicephalinae that swim above the bottom (**Paper I**) feeding on suspended particles (Zhirkov, 2001). Overall, most epifauna of the CBL exhibited more than one feeding modality (**Paper II**).

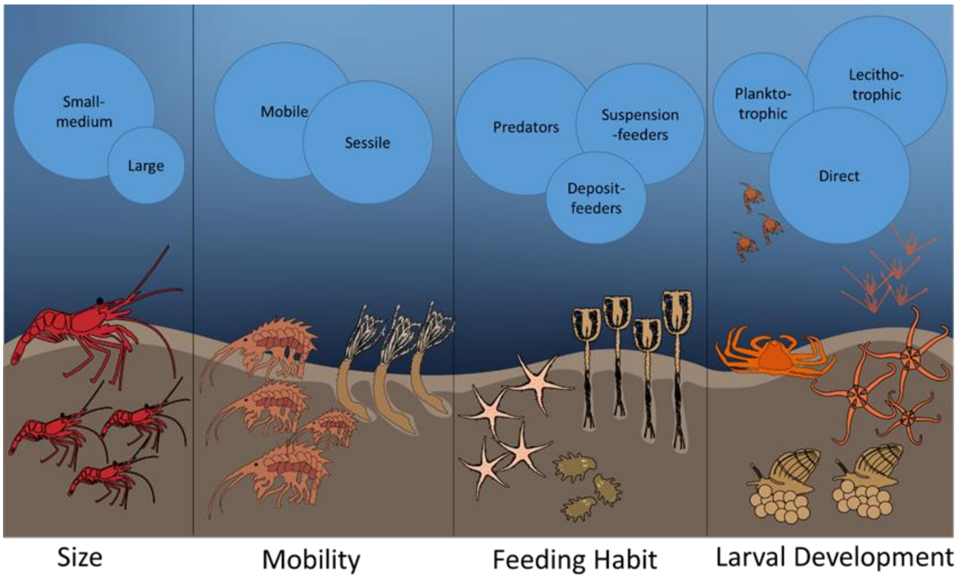


Figure 9. Schematic representation of trait modalities (blue bubbles) considered for the first hypothesis of Paper II. Bubble size illustrates relative importance of a given trait modality according to the results of the paper. Organisms are examples from the study area illustrating trait modalities and are placed underneath a given modality.

Food webs of the Arctic deep-sea are generally poorly studied, a gap partially filled by our stable isotope data **(Paper III and supplementary results)** and compilation of feeding modes in the BTA conducted in **Paper II**. The **Supplementary results** indicated an overall long food web with five trophic levels (TL) calculated based on *Calanus glacialis* as a TL2 baseline. This length corresponds well to previous reports from the Arctic deep sea (Iken et al., 2005; Bergmann et al., 2009) and is at least one trophic level longer than reported from some Arctic shelves (e.g., Iken et al., 2010; Feder et al., 2011; Connelly et al., 2014; Divine et al., 2015). These results indicate that most CBL epifauna relied mainly on degraded organic matter. **Supplementary results** of the thesis matched some of the feeding modes assigned to CBL epifauna based on the literature. Specifically, most taxa coded as predators were, indeed, characterized by high δ^{15}N values. For example, Asteroidea (e.g., *Icasterias panopla*, *Bathybiaster vexillifer*) had the highest δ^{15}N values, followed by other predators such as the decapod *Sclerocrangon boreas* and fishes (e.g., *Lycodes sagittarius*, *Rhodichthys regina*). Interestingly, some of the species coded as suspension feeders had quite high δ^{15}N values as well. This was particularly true for sponges of the Polymastiidae family, while δ^{15}N values of anemones were more variable. Suspension feeders can rely on a wide range of food items, varying in size (from bacteria to zooplankton) and quality (Gili et al., 2001). Suspension feeders can also utilize re-suspended organic matter that is often already reworked in the deep-sea environment (Iken et al., 2001). Though the majority of the epifauna in the CBL relied on refractory material or prey items themselves carrying refractory signatures, some fauna seemed to take advantage of relatively fresh detritus as indicated by their low δ^{15}N and δ^{13}C values. Examples include suspension feeders such as the cirriped *Catherinum* sp., the octocoral *Gersemia* sp., and the ascidian *Ciona* sp. Interestingly, the amphipod *Amathillopsis spinigera*, coded as a predator in the BTA, rather seemed to rely on relatively fresh organic matter. In addition, mobile animals including holothuroids (*Elpidia* sp., *Kolga* sp.), and ophiuroids (*Ophiopleura borealis*, swimming *Ophiostriatus striatus*) are, indeed, able to find relatively fresh food as indicated by their low δ^{15}N signatures. This supports our assumption regarding the usefulness of mobility in the energy-limited deep sea (**Paper II**). In addition, a wide range of δ^{15}N signatures within the same taxon might also point to the ability of species to utilize various sources of food.

Results of our study showed direct development to be the most frequent reproductive strategy of CBL epifauna followed by lecithotrophic larval development (**Paper II,** Fig. 9). In general, this finding supports the traditional view of benthic reproduction for high latitude and deep sea (Thorson, 1950; Mileikovsky, 1971). Both development types are advantageous for the deep sea due to juveniles being less dependent on either limited or variable food availability (Mileikovsky, 1971). However, most of the literate data available for reproductive strategies of Arctic deep-sea epifauna is either relatively old or non-existent on the species level. A lot of epifauna species from the CBL were, therefore, coded for reproduction based on closely related deep-sea taxa, which highlights the need for species- and habitat-specific studies and prevents us from drawing solid conclusions on true patterns and plasticity of life-history traits in Arctic deep-sea benthos.

The majority of CBL epifauna was small-medium sized and mostly mobile, though sessile fauna was also common. BTA showed most species were predators and suspension feeders, which does not contradict other deep-sea studies, though does not confirm most studies that show a prevalence of deposit-feeders. The food web was longer than on adjacent shelves with 5 TLs present and the majority of fauna occupying TL3 or higher, which indicated that fauna of CBL replies mostly on refractory material. The faunal reproduction was characterized by relatively equal proportion of direct and indirect (mostly through lecithotrophic larvae) development.

6.2 Depth and regional heterogeneity effects on epifaunal structure and function

In the CBL, depth was among the most important factors driving epifaunal community structure (**Paper I**) and function (**Paper II**) resulting in significant difference between epifauna of deep basin and mid-depth (plateau and ridge) stations (Fig. 10). Changes in epifaunal communities with depth might be explained by changes in environmental factors co-varying with depth (e.g., food availability, sediment composition, and temperature) (Soltwedel et al., 2009; Sswat et al., 2015). Indeed, in contrast to the shallower plateau and ridge stations, the CBL basins had a more homogenous environment in terms of seabed morphology and sediment characteristics, with generally higher mud content, few or no drop-stones, and persisting lebensspuren indicating very low bottom current speed (**Paper I**). The bottom temperature was also lower in basins than at mid-depth stations. The difference in food availability was, however, not pronounced between mid-depth and deep stations, at least based on indicators measured in our study (sediment pigments, total organic carbon in sediments, and C/N ratios) (**Papers I, III**). The difference in environmental settings between basins and mid-depth stations was reflected in significantly lower abundance and species number, acquired from ROV images, at basin stations than at plateau and ridge stations (**Paper I**). In addition, the single basin station sampled by trawl showed the lowest biomass of all trawl locations sampled (**Paper I**).

Besides, CBL epifaunal taxonomic community composition (**Paper I**) and trait modality composition (**Paper II**) changed with depth, which is consistent with previously described bathymetric changes in epifaunal taxonomic dominance (Mayer and Piepenburg, 1996; Sswat et al., 2015; Rybakova et al., 2020) and benthic macrofaunal trait modality profiles (Liu et al., 2019). The most common taxa in the basins, including polychaetes of the Macellicephalinae sub-family, the holothuroid *Elpidia* sp., poriferans of the Polymastiidae family (*Radiella sol* and *Polymastia* sp.), and the ubiquitous anthzoan *Bathyphellia* cf. *margaritacea* (**Paper I**) all are typical Arctic deep-sea taxa. This pattern of dominance was particularly similar to the one observed in the Nansen and Amundsen Basins, except for the high abundance of polymastiids (Rybakova et al., 2019). Proportions of "free-living", "mobile" and "swimming" modalities were higher in basins than at mid-depth stations (**Paper II**) with the highest proportional abundance of the very fast swimming Macellicephalinae polychaetes at the deepest, most isolated and among the most food limited basin stations (station 7), which again stresses the necessity to be mobile (**Papers I, II**).

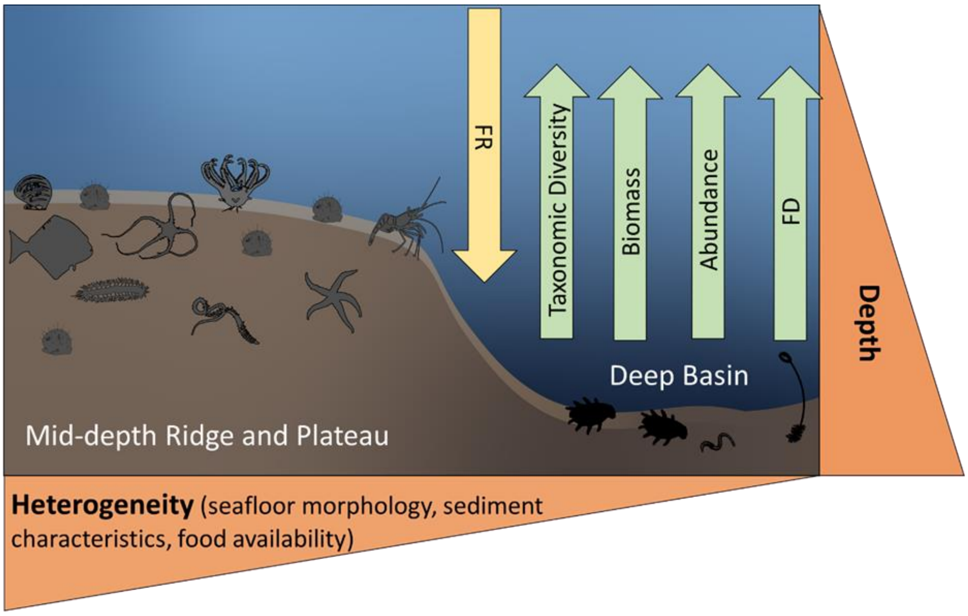


Figure 10. Epibenthic community trends related to water depth and habitat heterogeneity. Taxonomic diversity, biomass, abundance and functional diversity (FD) were higher at mid-depth stations (ridge and plateau features) than in deep basins, while functional redundancy (FR) was higher at basin stations. Habitat heterogeneity and food availability varied among regions.

Another characteristic feature of the basin stations was the higher proportion of suspension feeders and opportunists/scavengers compared to the mid-depth stations (**Paper II**). Opportunistic and scavenging feeding becomes increasingly more useful with depth as scavengers have a high ability to detect sparse carrion across large distances (Premke et al., 2006), while opportunists could take advantage of almost whatever they come across (Drazen and Sutton, 2017). However, the higher proportion of suspension feeders than opportunists/scavengers was surprising as it was previously reported only from Arctic deep-sea regions, where currents were stronger or where drop-stones were present (Soltwedel et al., 2009), though suspension-feeders can also be abundant in the absence of these conditions (Rybakova et al., 2019) as was also observed in our study (**Papers I**, **II**). Perhaps adaptations that allow suspension feeders to maximize food capture (e.g., generating feeding currents; Gili et al., 2001; Siegl et al., 2008; Weisz et al., 2008), combined with laterally transported subsidies of organic matter from the Chukchi shelf by the Chukchi Slope Current (that reaches the Northwind Basin; Boury et al., 2020) could explain the prevalence of this feeding type. Finally, the very low temperature at greater depth (**Paper I**) reduces metabolic rates of benthic invertebrates that can be extremely low under such conditions (Gatti, 2002).

Results of our study did not detect significant difference in epifaunal diversity, abundance, and biomass between plateau and ridge habitats of the mid-depth layer (**Paper I**). However, taxonomic composition (**Paper I**) and trait modality distribution (**Paper II**) changed from the western to the eastern side of mid-depth CBL locations. The main factors driving this difference were food availability and the presence of drop-stones (**Papers I, II,** Fig. 10). The western side (ridge stations 1 and 2) was characterized by higher food availability (**Paper I**) likely due to the relative proximity to the productive Chukchi shelf, from where nutrient-rich Pacific-origin water is partly transported to the Northwind Ridge (Watanabe et al., 2017). The higher food input associated with high proportions of “sessile”, “low mobility”, and “tube-dwelling” modalities (**Paper II**), in part represented by the polychaete families Ampharetidae and Sabellidae (**Paper I**) is, in fact, characteristic for areas with higher food availability (Degen, 2015). High frequency of deposit feeders at these stations further points to higher availability of deposited organic matter. The eastern side of mid-depth CBL stations was characterized by a high number of drop-stones (**Paper I**) that enhance complexity of epifaunal communities (Meyer et al., 2016; Ziegler et al., 2017) as indicated by species richness being positively correlated with the number of stones in our study (**Paper I**). The drop-stones were associated with high proportions of Morphotype 10 (likely Coronatae polyps), polychaete tubes, sponges, and anemones (**Paper I**), which resulted in high proportions of “attached” and “upright” trait modalities at these stations (**Paper II**). The drop-stones were also associated with high proportions of “predators” that were both “attached” or “mobile”. The attached predators (e.g., anemones, Morphotype 10, **Paper I**) likely used the stones to elevate themselves and enhance capture of prey (**Paper II**). The mobile fauna (e.g., arthropods and brittle stars) registered in the vicinity of the stones were likely attracted by high prey availability attached to the stones (**Papers I**) or feeding on organic matter produced by the drop-stone community (MacDonald et al., 2010; Schulz et al., 2010). In addition, stones might offer a shelter for mobile fauna in otherwise open soft-bottom seafloor.

Image analysis did not confirm the presence of chemosynthetic communities or outgassing in the pockmarks of the CBL plateau (**Paper I**), consistent with the previous study of a single inactive pockmark in the CBL (MacDonald et al., 2010). Yet inactive pockmarks may still host increased biological abundance and taxonomic richness (Webb et al., 2009b; Zeppilli et al., 2012), a phenomenon that has been explained by pockmarks stimulating turbulent re-suspension and increased settling of organic matter, leading to higher food input and increased larval settlement (Webb et al., 2009b; MacDonald et al., 2010). While epifaunal abundance within pockmarks could not be calculated in the present study, species richness was among the highest at pockmark stations 9 and 10, and epifaunal abundance was highest at station 8 located in a large groove linked to a pockmark. Though the image analysis did not indicate a distinct epifauna community present in pockmarks, the video records (not quantitatively analyzed) revealed high numbers of anemones on the slope towards the center and inside of the shallower pockmark (station 9), while high numbers of pycnogonids (small unidentified and bigger *Colossendeis proboscidea*) were observed in the deeper pockmark (station 10).

Higher heterogeneity of the ridge and plateau stations, providing more ecological and functional niches at this depth layer, resulted in significantly higher FD compared to the deep stations (**Paper II,** Fig. 10). The lower FR at mid-depth stations, might, however, indicate that these areas are less resilient to ongoing and future change and potential human use as functions may be lost when species loss occurs (Loreau, 2008; Van der Linden et al., 2016). Similar conclusions regarding resilience were reached in studies on Arctic benthic macrofauna (Kokarev et al., 2017; Liu et al., 2019; Sutton et al., 2020). In addition, high abundance of modalities “sessile”, “attached”, and “upright” at this depth layer (**Paper II**) point to higher vulnerability of mid-depth epifauna to habitat disturbances (e.g. from trawling or seafloor mining) or decreases in food availability (Degen and Faulwetter, 2019). In contrast, higher FR at deep stations could be related to the homogeneity of the abyssal environment, to which epifauna are adapted with fewer and shared trait modalities. High FR and high abundance of modalities “mobile” and “swimming” could be interpreted as lower sensitivity to perturbations and higher ability for dispersal after disturbance (Degen and Faulwetter, 2019). However, it is premature to conclude that deep basins in CBL are resilient to disturbances because epifaunal abundances were very low in the basins and sampling effort in the basins was also low.

Supplementary results on food web structure did not show a clear difference in epifaunal stable isotope signature between mid-depth and deep stations with no increase in δ^{15}N values with depth. The absence of difference might be related to the degradation pattern of organic matter with depth. Specifically, our depth range excluded shallow regions (<250 m) where particulate organic matter undergoes the most significant changes and is usually rapidly degraded by zooplankton and bacteria (Schlitzer, 2000; Iversen et al., 2010), while further degradation can be suppressed in deeper layers due to lower bacterial activity (Herndl and Reinthaler, 2013) and zooplankton densities (Kosobokova and Hopcroft, 2010). However, absence of statistical difference might also be related to low sampling efforts in particular for basin stations.

Depth was a main environmental parameter driving differences in epifauna between mid-depth and deep stations. Deep basins had lower epifaunal abundance, diversity, and biomass and different taxonomic and trait modality patterns from the mid-depth stations.

Epifauna did not differ significantly between ridge and plateau habitats. Instead, a difference in taxonomic and trait modality composition was observed between western and eastern sides of CBL. Food availability (west of CBL, near the shelf) and higher availability of hard substrate (east of CBL) determined this difference.

Heterogeneity of the seafloor morphology likely defined functional difference with higher FD at mid-depth provided by higher availability of functional niches. FR was, instead, lower at mid-depth stations, which along with specific trait modality patterns may render these stations less resilient to disturbances.

These was no clear difference in food web structure between mid-depth and deep stations, likely owing to the great depth considered in the study, where degradation of organic matter is not as intense as in upper water layers.

6.3 Gear consideration

The ROV video records provided us with information on epifaunal community composition that was otherwise not available with the trawl or ROV image data alone. In addition, behavioral characteristics not always easily observed on images were caught by video (e.g., swimming behavior by the ophiuroid *Ophiostriatus striatus* and polychaetae of the Macellicephalinae sub-family). Similarly, there were some differences in results from trawl and ROV sampling. The trawl was less efficient in sampling certain taxa compared to ROV images, including annelids, cnidarians and some other generally sessile animals. In contrast, mobile fauna was more often caught by trawl and missed on images, for example brittle stars and sea stars that were often buried in the top sediment layer. Total abundances calculated from ROV images were 6 - 7 times higher than those calculated from trawl catches. Therefore, it is advisable to use an ROV to quantify epifaunal abundance. In summary, combining both ROV and trawl deployments is advantageous to obtain the most comprehensive view of faunal community composition and their biological traits, yet trawl deployments should be limited from a conservation standpoint.

6.4 Pelagic-benthic coupling and potential alterations in epifaunal communities under climate change

One of the most apparent biological effects of sea-ice reduction is the potential decrease in sea-ice algal abundance and hence their assimilation into the food web (Fig. 11). Thus, we hypothesized that potentially higher ice algal uptake in 2005 (higher sea-ice extent) would be reflected in higher δ^{13}C values compared to 2016 (lower sea-ice extent) as sea-ice algae are often more enriched in ^{13}C compared to phytoplankton (Hobson et al., 2002; Tamelander et al., 2006). While a study caveat admittedly is that we were unable to directly sample ice algae, our results indirectly supported this hypothesis through significantly higher δ^{13}C values of pPOM and zooplankton consumers in 2005 than in 2016 (**Paper III**). This potential difference was, however, not the case for benthic samples, instead little or no difference was observed in δ^{13}C between years in sPOM and benthos (**Paper III**). We suspect that either ice algal POM had not reached the seafloor and been assimilated into the benthic food web yet; or it had been consumed in transit downwards; or was highly patchy and missed in our sampling; or was not as detectably enriched in ^{13}C as assumed (though pPOM and zooplankton give evidence the latter is not the case). Temporally resolved and more comprehensive sampling of carbon sources and consumers could shed light on this issue.

The second hypothesis tested in **Paper III** was that pelagic-benthic coupling was tighter in 2005, when sea-ice extent was higher, compared to 2016. Despite the ambiguous results described above regarding the role of ice algae, results of the **Paper III** strongly supported our hypothesis in that they showed much higher overlap between pelagic (pPOM and zooplankton) and benthic (sPOM and benthos) isotopic niches in 2005 than in 2016. It is likely that multiple causes or a combination of those are connected to the difference in pelagic-benthic coupling observed in our study (**Paper III**). The amount of primary production in the surface waters partly determines the amount of organic matter that can reach the seafloor (Grebmeier and Barry, 1991). In fact, overall phytoplankton production decreased in our study region in recent years (much in contrast to elsewhere) despite the reduced sea-ice cover due to strong freshening of the Canada Basin (McPhee et al., 2009; Rabe et al., 2011), which strengthens stratification and prevents nutrient renewal in the euphotic zone (McLaughlin and Carmack, 2010; Nummelin et al., 2016). To our knowledge, there are no studies measuring ice algal biomass or modelling its changes from 2005 and onwards in our study region. However, based on the potential evidence discussed above and on the fact that ice-habitat, which is necessary to retain ice primary production, has reduced, we might also assume a decrease in ice-algal biomass in recent years.

In addition to the amount of primary production, the strength of pelagic-benthic coupling also depends on the fate of organic matter during sinking to the seafloor (Graf, 1989), specifically grazing intensity. High grazing intensity by zooplankton results in higher retention of organic matter in the water column and reduced downward carbon flux (Wassmann and Reigstad, 2011). An increase in grazing efficiency might be expected in scenarios of increased local zooplankton abundance or increased zooplankton abundance with advection of the warmer Pacific waters into the basin (Hirche and Kosobokova, 2007; Kędra et al., 2015). Zooplankton density in the Canada Basin, however, is low compared to shelf regions (Kosobokova and Hopcroft, 2010; Abe et al., 2020), which may lead to overall low grazing efficiency in the study area. Scarce inter-annual zooplankton studies over the Canada Basin region (Rutzen and Hopcroft, 2018; Abe et al., 2020) suggest that there was no significant inter-annual variation in zooplankton populations between 2007 and 2017, though Abe's et al. (2020) models suggest a negative effect on zooplankton abundance with a continuous decline in primary production in the region. It has not been evaluated if advection of zooplankton from the Pacific into the CBL region has increased in recent years. The few expatriates from the North Pacific found in the Canada Basin (Kosobokova and Hopcroft, 2010; Hunt et al., 2014) are thought not to be viable or have no reproduction success in the high Arctic Ocean due to unfavorable conditions (Nelson et al., 2014). Thus, these species would rather contribute as additional biogenic material sinking to the seafloor than as additional grazers. It remains speculative how zooplankton communities may have contributed to the difference in pelagic-benthic coupling observed in our study.

Sinking velocity of organic matter is another factor affecting pelagic-benthic coupling by determining extent of biological degradation and, thus, affecting the amount and quality of food reaching the seafloor. Sinking velocity, in turn, is affected by primary producer composition, and their sinking speed or ability to maintain buoyancy. For example, small-celled species are more resistant to sinking (Li et al., 2009; Metfies et al., 2016) and, thus undergo higher biological degradation and generally contribute less to organic matter flux (Reigstad and Wassmann, 2007; Wolf et al., 2016; Dybwad et al., 2021). In contrast, larger and silicified diatoms tend to sink faster, contributing more and fresher organic matter input to the seafloor (McMahon et al., 2006; Søreide et al., 2010; Boetius et al., 2013; Fernández-Méndez et al., 2014). In the study region, the phytoplankton community had increased proportions of small-celled (flagellate) phytoplankton and decreased importance of larger-celled phytoplankton (diatoms) between 2004 and 2014 (Li et al., 2009; Zhuang et al., 2018). In addition, the ice loss and thinning in the study area (Frey et al., 2015; Perovich et al., 2020) might also have resulted in a decrease in larger and heavier sea-ice diatoms as seen elsewhere (Rózańska et al., 2009; Hop et al., 2020). All in all, these changes in primary producer community structure might imply a reduction in overall flux of relatively fresh organic matter in recent years including our study period, perhaps explaining the observed difference in pelagic-benthic coupling and particularly the lower ^{15}N values of benthic consumers in 2005 than in 2016 (**Paper III**).

Pulling together evidence from all thesis papers, a relatively weak benthic-pelagic coupling was indicated by high $\delta^{15}N$ values of benthic consumers (**Paper III**) and low sediment pigments concentration (**Paper I**), low epifaunal abundance and biomass compared to adjacent shelf regions (**Paper I**), and generally small size of epifauna (**Paper II**). The results of **Paper III** point to de-coupling of pelagic and benthic realms with ice loss and decrease of organic matter quality available for benthos. The weakening of the coupling likely leads to decreases in organic matter flux and changes in benthic community composition.

The future development of benthic communities in response to climate change is unclear. Here, some plausible different scenarios are described, which could form the basis for further study.

1) One might expect continued decrease in pelagic-benthic coupling in the CBL with climate change resulting in less carbon flux to the seafloor and only highly degraded organic matter available for benthos. Inter-annual studies in the eastern Fram Strait indicated decreased epifaunal abundances in years of lower food availability at the sea bottom (Bergmann et al., 2011; Meyer et al., 2013), coincident with a decrease in diversity of feeding types (Bergmann et al., 2011). We might expect a similar response of epifauna in our study area, where continued benthic-pelagic coupling reduction could result in mobile epifauna migration to areas with higher food availability, while sessile fauna might decrease in abundance due to lower recruitment related to lack of carbon supply. Thus, with climate change, benthic communities of CBL might have lower taxonomic and functional diversity, low abundance and biomass, but high functional redundancy due to dominance of fewer but shared traits.
2) Even if vertical transport of organic matter was reduced or unchanged, lateral transport can provide food to benthic communities (Fig. 11 C). For example, advection of detritus from the Bering Strait has been found to support benthos of the adjacent Chukchi shelf in addition to vertical flux, positively affecting faunal biomass (Grebmeier et al., 2015). Increased influx of nutrient-rich Pacific water into the Arctic Ocean has been observed in recent years (Woodgate, 2018), including transport to our study area through the Chukchi Slope Current (Watanabe et al., 2015; Boury et al., 2020), potentially providing food subsidies to the benthos in the CBL. Continued

increase in lateral transport can be expected with climate change if the volume increase through Bering Strait continues. In this scenario, the increased food availability might result in higher benthic abundance, biomass, and perhaps functional diversity. In fact, epifaunal abundance observed in the present study was slightly higher compared to a few abundance estimates previously acquired from the CBL (MacDonald et al., 2010). However, the limited number of samples and slight variation in sampling locations constrain direct temporal comparison.

3) We might expect increased anthropogenic activities over deep areas in a seasonal ice-free Arctic with negative effects on benthic communities. Low food flux and low bottom temperature result in slow growth rates, reproduction, and recruitment of deep-sea fauna (e.g., Glover and Smith, 2003), making deep-sea benthos vulnerable to human impacts. Some effects from anthropogenic activities on deep-sea benthos have been already documented. For example, trawling negatively affects biodiversity and abundance, in particular for sessile species, and damage habitats (Koslow et al., 2001; Roberts, 2002; Clark et al., 2016). Similarly, the oil spill from the Deepwater Horizon resulted in lower faunal diversity, high evenness, and decreased abundance (Montagna et al., 2013; Reuscher et al., 2020). Therefore, the CBL fauna can also experience negative effects from anthropogenic activities.

Overall, deep-sea ecosystems are so poorly studied and understood that both impacts from human activities or climate change cannot be effectively predicted (Smith et al., 2008; Sweetman et al., 2017). For the CBL, more sampling stations and repeated measurements would be essential to provide an adequate answer concerning how CBL epifauna will change with climate change or human exploitation.

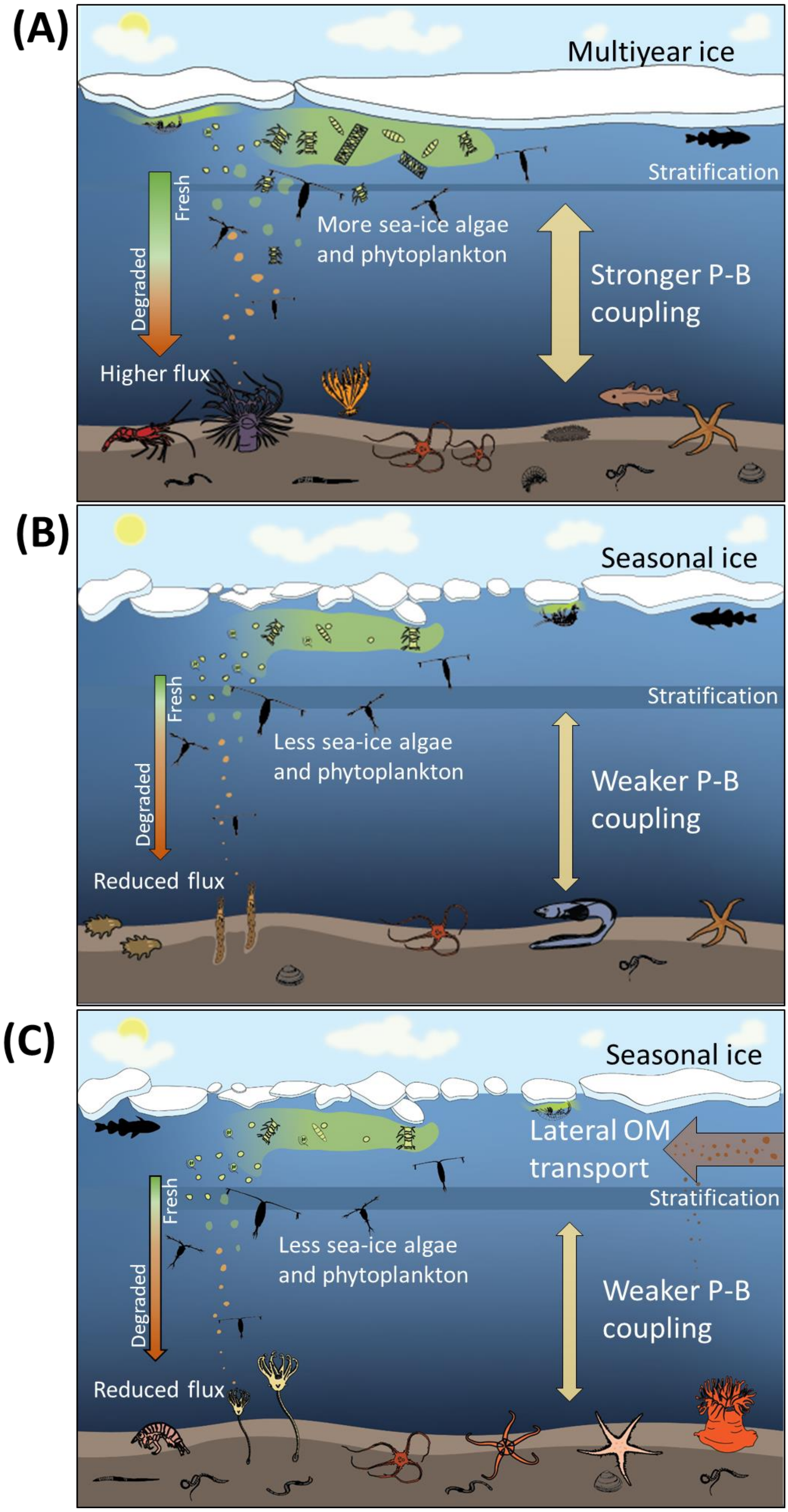


Figure 11. Conceptual figure depicting pelagic-benthic coupling scenarios where (A) and (B) are underlying hypotheses in Paper III. (A) Pelagic-benthic coupling in 2005, (B) Pelagic-benthic coupling in 2016, (C) Pelagic-benthic coupling in 2016 supplemented with lateral transport of organic matter. P-B = Pelagic-benthic, OM = organic matter. The scenarios are discussed in section 6.4.

7 Conclusions and outlook

Limited knowledge on structure and function of Arctic deep-sea ecosystems hinders the development of sustainable management strategies at a time when ongoing climate change opens up opportunities for exploitation of Arctic deep-sea resources. For example, the CBL has already been categorized as having fishable depth (Dupuis et al., 2019) and oil and gas reserves have also been quantified in this area (Bird et al., 2008). Results of the present thesis are, therefore, timely and should be used in assessments of ecosystem resources and functional state. The results suggest CBL epifauna might be vulnerable to potential disturbances. In addition, high proportions of taxa with low dispersal ability among adult and larval life stages may prevent rapid adaptation to changes, and reduce the ability to recolonize and escape perturbation (**Paper II**). For example, upright and sessile fauna are sensitive to trawling (Jørgensen et al., 2019). In addition, low FR (**Paper II**) at the mid-depth stations indicates high risk of function loss with potential decrease in species diversity in response to anthropogenic disturbances. Considering the known faunal responses to fish trawling (Wassenberg et al., 2002; Blanchard et al., 2004; Jørgensen et al., 2019; Tiano et al., 2020) and oil and gas exploitation (Dijkstra et al. 2020) we might expect negative alterations in CBL communities if CBL resources will be exploited. Recovery from any disturbance in the deep-sea Arctic can be slow (Bergman et al., 2015), because at high latitudes recolonization is suppressed by low temperatures, long life cycles and high longevity (Al Habahbeh et al., 2020).

In addition to potential anthropogenic disturbances, ongoing climate change likely affects epifaunal diversity, abundance, biomass, and biogeography through its effects on quality and quantity of the food supply to the seafloor. Therefore, results documenting the current community structure are also timely as they can serve as much-needed baseline data that will allow future comparisons. **Paper III** indicated potential decoupling between pelagic and benthic realms in the later year of lower sea-ice (2016) extent compared to a decade earlier and consumption of lower quality organic matter by benthos in 2016 compared to 2005. This finding is generally consistent with physical and biological changes documented in the area. Specifically, the overall decrease in sea-ice extent and its shift from multiyear to annual sea ice (Kwok, 2018; Perovich et al., 2020) has likely resulted in a decrease of often fast-sinking sea-ice algae. Concurrently, halocline strengthening within this region (Coupel et al., 2015) has led to a decrease of primary production (Song et al., 2021) and a shift to small-celled phytoplankton (Zhuang et al., 2018). As a result, it is likely that vertical organic flux to the seafloor decreased and residence time of organic matter in the water column increased leading to less and more degraded material reaching the seafloor. Considering potential future decoupling of the pelagic and benthic realm with continued climate change, we might expect a decrease in faunal abundance, diversity, and biomass, resulting in decreased ecosystem function. Alternatively, however, food input to benthic ecosystems might be enhanced by increased *lateral* transport of Pacific water from the Chukchi Self (Corlett and Pickart, 2017) which may lead to the opposite effects on benthic communities, or offset the reduction in vertical flux. In conclusion, responses of epifaunal communities to climate or environmental changes are not straightforward to predict (Taylor et al., 2017). Clearly, more sampling efforts and time-series are needed to evaluate and predict biological responses to changes in the Arctic deep-sea environment, and to develop a conceptual mechanistic framework for functioning of Arctic deep-sea benthos.

Currently, time-series of biological and physical parameters are available only from one Arctic deep-sea area – HAUSGARTEN observatory in the eastern Fram Strait. Response to climate change might, however, differ between Eurasian and Amerasian parts of the Arctic deep sea. However, the existing long-term Distributed Biological Observatory on the Pacific Arctic shelves does not currently include deep-sea locations (Grebmeier et al., 2019). Thus, placement of a long-term observatory in the Amerasian Basins connecting to the Pacific Arctic shelves that includes measurement of environmental and biological parameters is advisable. The suite of the 30+ year observatory at Porcupine Abyssal Plain in the North Atlantic (Hartman et al., 2021), the relatively nearby, downstream HAUSGARTEN observatory (Soltwedel et al., 2005) and a much further downstream Canada Basin observatory would yield a solid trio of deep-sea observatories connected through the current regime. The CBL could serve as a location for this purpose with the already collected baseline data during the Hidden Ocean cruises. Yet it might be advisable to choose a location on the Canada Basin side of the CBL with a typical abyssal environment to avoid the heterogeneous nature of the CBL.

Our study is a first step toward filling research gaps of Arctic deep-sea ecosystem structure and functioning and provides the first regional-scale study addressing such a range of Arctic deep-sea habitats. Yet, this study has some limitations. For example, sampling is still challenging in the high Arctic with variable weather and ice conditions, which resulted in low sampling efforts, in particular for trawl samples. The spatially limited sampling efforts were particularly challenging due to heterogeneity of the study area. In addition, challenging environmental conditions make it difficult to position a ship at a desirable location, which prevented temporal comparison for some of the stations. The limitations for conducting BTA included very sparse literature on biology of Arctic deep-sea species. Recommendations for future studies, therefore, include:

- Combination of ROV and trawl tools to gain a more comprehensive view of the epifaunal community composition and characteristic traits.
- Higher spatial and temporal sampling effort.
- Increase species- and habitat-specific studies, in particular on traits such as life history and feeding modes.
- Including traits that are indicative of species vulnerability to natural or anthropogenic perturbations (e.g., fragility, temperature tolerance, life span, skeleton).

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Epifaunal communities across marine landscapes of the deep Chukchi Borderland (Pacific Arctic)

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ABSTRACT

Epifaunal communities from the poorly studied Arctic deep sea of the Chukchi Borderland region were investigated to: (1) determine differences in community structure among ridges, plateau with pockmarks, and much deeper basins as three main habitat types, (2) analyse the environmental factors that might shape these communities, and (3) investigate biogeographic affinities dominating the epifaunal communities. Epifaunal samples were collected in summer 2016 with a beam trawl (6 stations) and ROV (10 stations) from 486 to 2610 m depth. Seventy-eight and eighty-six taxa were registered from ROV images and trawl samples, respectively, with Echinodermata and Arthropoda dominating overall taxon richness. Epifaunal densities were estimated at 2273 to 14,346 ind/1000 m^2 based on ROV images but only 342 to 2029 ind/1000 m^2 based on trawl samples. Epifaunal biomass based on trawl catches ranged from 173 to 906 g wet weight/1000 m^2. There was no significant difference in density, biomass and community composition between plateau and ridge communities, though the western and eastern parts of the study area differed in plateau/ridge community properties. Abundance in the eastern part of the study area was dominated by annelids (Ampharetidae and Sabellidae), and the western part by an unknown cnidarian (likely polyps of *Atolla*). Trawl samples from both western and eastern regions were dominated by the echinoderms *Ophiopleura borealis* and *Pontaster tenuispinus*. Deep basin communities differed from shallower plateau/ridge stations by significantly lower number of taxa and densities based on the images, and by lower biomass based on trawl catches. Polynoid annelids and sponges were characteristic taxa of the basin stations. Water depth and number of stones providing hard substrate significantly influenced epifaunal community structure, with sediment pigments and grain size also being influential. Arcto-boreal-Atlantic species dominated communities in the Chukchi Borderland, presumably mediated by Atlantic water dominance in the deep water layers of the Pacific Arctic. This study adds to the limited knowledge of ecology of the Arctic deep sea and improves existing baseline data that can be used to assess future effects of climate change on the system.

1. Introduction

Deep-sea regions occupy roughly half of the Arctic Ocean area (Jakobsson, 2002), yet the understanding of Arctic deep-sea biodiversity still remains extremely limited. Recent scientific programs such as the International Polar Year 2007–2009, Census of Marine Life (e.g. Bluhm et al., 2011), and studies at the HAUSGARTEN, a biological long-term deep-sea observatory located in Fram Strait (Soltwedel et al., 2005, 2009; Bergmann et al., 2011; Meyer et al., 2013), have helped increase current knowledge of the Arctic deep-sea biodiversity. Results have shown benthic communities within the Arctic Ocean basins exhibit higher biodiversity – including numerous species new to science described in the last decades (e.g. Gagaev, 2009; Rodríguez et al., 2009) – than previously expected. A recent count estimated 1125 invertebrate taxa inhabit the central Arctic Ocean deeper than 500 m (Bluhm et al., 2011). The most abundant taxa reported were nematodes among the meiofauna, crustaceans, polychaetes, and bivalves among the macrofauna, and sponges, cnidarians, and echinoderms among the epifaunal megafauna (Bluhm et al., 2011). Despite these efforts much of the Arctic deep-sea region remains poorly known and virtually unsampled.

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*Abbreviation:*CBL, Chukchi Borderland

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Epifaunal organisms, those animals living attached to or on the sediment surface (Nichols and Williams, 2009), are currently among the least studied in the Arctic deep sea (except at HAUSGARTEN; Bergmann et al., 2011; Meyer et al., 2013), which is partly related to the difficulty of deploying trawls or photographic gear at great depths in often ice-covered waters. It is known from studies of Arctic shelf systems that epifaunal organisms contribute considerably to total benthic biomass in Arctic ecosystems and play key roles in trophic interactions, bioturbation, and remineralization (Feder et al., 2005; Piepenburg, 2005). In addition, epifaunal sensitivity to natural disturbance and human impacts (Teixidó et al., 2007; Jørgensen et al., 2011) necessitate basic knowledge of their biodiversity patterns given the ongoing sea-ice loss and the potential for enhanced deep-sea fisheries, shipping, and petroleum/mineral exploitation in Arctic deep-sea areas (Thiel, 2003). As benthic communities integrate the effects of physical, chemical and biological factors, they can be used as indicators of ecosystem status.

Globally, epifaunal community structure differs among different regions of the deep-sea floor (e.g. Levin et al., 2001) which is now recognized as a system of great complexity with diverse habitats at different spatial scales (Danovaro et al., 2014). These differences arise from environmental factors such as sediment characteristics, sea floor morphology, current flow regimes, chemical conditions, depth, and food availability (Levin et al., 2010; Bluhm et al., 2011; Pierdomenico et al., 2015). Deep-sea sediments consist mainly of silt and clay, while ridges and plateaus can have a higher sand fraction (Stein et al., 1994; Bluhm et al., 2011). Hard substrate (e.g., drop stones from ice-transport processes, carbonate outcrops at methane seeps, whale bones) and other forms of increased complexity of sea floor morphology (e.g., elevations, canyons, depressions in the sea floor) occasionally occur in the deep sea and may enhance benthic biodiversity and biomass compared to abyssal plain deep-sea environments (McClain and Barry, 2010; Pierdomenico et al., 2015; Åström et al., 2016; Meyer et al., 2016). Seafloor morphology also affects direction and strength of bottom currents transporting food particles, eggs and larvae (Buhl-Mortensen et al., 2015), even though currents are usually very slow in Arctic deep-sea systems (Macdonald and Carmack, 1991). Food availability is often the major depth-related factor driving benthic community structure and limiting biomass (Soltwedel et al., 2009; Bluhm et al., 2011; Kröncke et al., 2013). Arctic deep-sea ecosystems are usually described as oligotrophic with highly seasonal food supply to the benthos (Iken et al., 2005) resulting in decreasing benthic biomass with depth (Bluhm et al., 2011). Despite the low food availability in the deep sea benthic biodiversity can be comparatively high which has previously been discussed in light of (1) comparatively stable, 'stress-free' environmental conditions (time-stability hypothesis, Sanders, 1969) or alternatively (2) as a result of patchy food deposition enriching habitat heterogeneity (patch dynamics theory, Grassle, 1989).

This study investigates epifaunal benthic communities in the poorly studied Chukchi Borderland area (CBL) which is currently impacted by dramatic decreases in sea-ice thickness (Stroeve et al., 2005; Perovich, 2011), warming Atlantic water below the surface and halocline waters (Shimada et al., 2004), and increased Pacific water inflow through Bering Strait in surface waters (Woodgate et al., 2007). Consequently, biological change may be expected in the future. Changes in biological communities, however, would be impossible to detect given that only few benthic studies have been conducted here (Cromie, 1961; Mohr and Geiger, 1968; Hunkins et al., 1970; Bluhm et al., 2005; MacDonald et al., 2010) with only one of the epifaunal studies being quantitative (MacDonald et al., 2010). Thus, there is a need to characterize the biodiversity in the complex landscape of that area that hold the potential for high biodiversity and heterogeneity, and to gain insights into mechanisms structuring benthic habitats in the Arctic deep sea.

The CBL is bathymetrically complex (Mayer et al., 2010) in that it comprises comparatively shallow ridges, plateaus, and much deeper, isolated basins (Jakobsson et al., 2008). In addition, the Chukchi Plateau is characterized by the presence of pockmarks, i.e., rounded or elliptical depressions of < 1 to > 100 m in diameter and depth that were formed as a result of explosion of gas or fluids from decomposing organic material or leaking gas reservoirs in underlying sediment layers (Hovland and Judd, 1988; Astakhov et al., 2014). Though little is known about patterns of life within pockmarks worldwide and especially in the Arctic, endemic chemosynthetic communities and/or high density of epibenthic fauna have been documented for both active and inactive seeps (Gibson et al., 2005; Webb et al., 2009a; MacDonald et al., 2010; Åström et al., 2016). Finally, the CBL region also is hydrographically complex in that Pacific surface and deeper Atlantic water meet here (Woodgate et al., 2007). This layering of these water masses results in cosmopolitan Arctic boreal and Atlantic boreal species dominating over Pacific affinities in the macro-infauna of the Canada Basin and CBL (Bluhm et al., 2005). However, biogeographic patterns and transitions in epifaunal communities of the CBL have not yet been mapped.

The aim of the present study is to investigate epifaunal communities in the heterogeneous CBL area using bottom trawl samples and remotely operated vehicle (ROV) imagery. The specific objectives are: (1) to compare epifaunal community structure, taxonomic diversity, and distribution patterns across ridge, plateau and basin locations of the CBL; (2) to identify environmental parameters that may influence epifaunal community characteristics; and (3) to evaluate biogeographic affinities of epifauna in the study area. Given the large difference in depth between basin and plateau/ridges, and the presence of pockmarks on the Chukchi Plateau, we specifically tested the hypothesis that (1) epifaunal community structure differs among plateau, basin and ridge locations, with the highest diversity and density at pockmarks plateau locations and the lowest at deep basin locations. Considering the hydrological complexity of the study area with increasing importance of Atlantic origin water with increasing depth, the second hypothesis tested was that (2) the CBL epifaunal species inventory represents a gradient of declining Pacific-affinity proportion with increasing depth.

2. Material and methods

2.1. Study area

The study was conducted in the CBL, north of Alaska between 74 and 78°N and 158 - 165°W during the Hidden Ocean III expedition (HLY1601) on the USCGC *Healy* in July–August 2016 (Fig. 1, see http://oceanexplorer.noaa.gov/explorations/16arctic/welcome.html). The CBL occupies a roughly rectangular area of 600 × 700 km, ranging in depth between ~300 and 3000 m, and extends into the Amerasian Basin north of the Chukchi Sea (Hall, 1990). Dynamic geological formation processes have led to the present-day CBL that consists of north-trending topographic highs, including the Northwind Ridge and Chukchi Plateau that surround the isolated Northwind Basin, which also contains several small ridges (Fig. 1) (Hall, 1990; Jakobsson et al., 2008; Mayer et al., 2010). On the Chukchi Plateau, pockmarks were first discovered in 2003 (Gardner et al., 2007) with later surveys revealing many more, typically of 300–400 m in diameter and 30–50 m deep (Mayer et al., 2010). It was suggested that these pockmarks were formed under the effect of pulsed fluid flows with the last modification occurring about 30–15,000 years ago (Astakhov et al., 2014).

Waters of Arctic, Atlantic and Pacific origin interact over the complex CBL bottom topography (Perovich et al., 2003; Woodgate and Aagaard, 2005). The Pacific-origin water comprises the Polar Mixed Layer and upper halocline originating from Bering Sea and Alaska Coastal water entering the Chukchi Sea via the shallow and narrow Bering Strait (McLaughlin et al., 2004; Steele et al., 2004; Woodgate, 2013). The influence of Pacific water decreases with depth and increasing latitude, being virtually absent north of the 2000 m isobath at ~79°N (Woodgate and Aagaard, 2005). The lower halocline is of Atlantic origin and enters the area from the Eurasian Basin via Fram

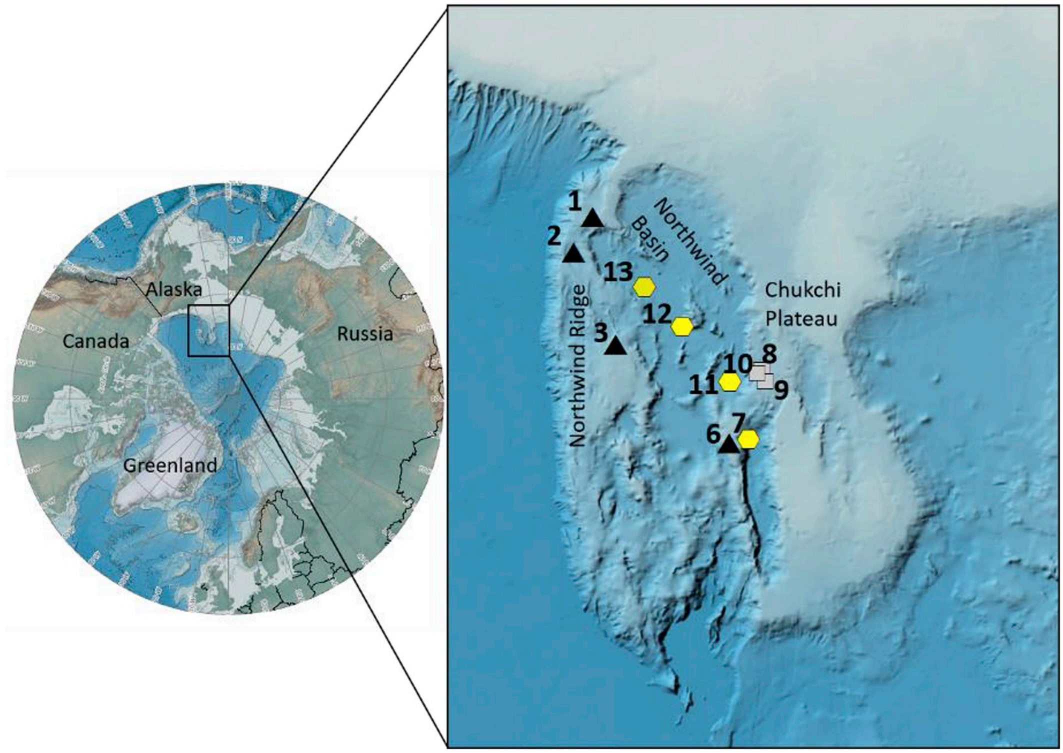


Fig. 1. Study area and stations sampled for epifauna during Hidden Ocean: Chukchi Borderland expedition in 2016; stations symbols indicate different type of topography (triangular – ridge, square – plateau, diamond – basin).

Strait and the Barents Sea (Woodgate and Aagaard, 2005). Underneath it, the Atlantic layer water consists of Fram Strait Branch water and Barents Sea Branch water (McLaughlin et al., 2004; Woodgate et al., 2007). The Arctic Ocean deep-water layer originates from the Greenland Sea; it enters from the Fram Strait and spreads across the Eurasian Basin, finally reaching the Canada Basin (Bluhm et al., 2015).

Sampling stations were chosen to represent the three main habitat types: ridges, basins, and plateau with pockmarks (Fig. 1, Table 1). Ridge stations located on the Northwind Ridge (stations 1, 2) and on one of the ridges in the Northwind Abyssal Plain (station 6), ranged in depth from 486 to 1059 m. Three plateau stations (stations 8, 9, 10) were sampled relatively close to each other, and their depth ranged from 508 to 873 m. For stations 9 and 10, it was possible to investigate epifaunal communities on the plateau surrounding a pockmark and within the pockmark. Station 8 was in a large groove that was linked to a pockmark. The basin stations were located within the Northwind Basin (stations 11, 12, 13) and isolated from station 7 by a ridge. The depth of the basin stations ranged from 1882 to 2610 m (Fig. 1, Table 1).

Table 1

Information on stations where ROV images and the beam trawl samples were collected. Note the low number of images used for the analysis of the station 8 was due to limited time for the bottom ROV dive at this particular station. The high number of images used for the analysis for station 9 is due to two stations (9a and 9b) being combined. Bottom temperature, salinity and fluorescence values are given; O – no samples are taken, X – samples are taken.

Station	1	2	3	6	7	8	9	10	11	12	13
Latitude, °N	74.32	74.71	75.64	77.06	77.07	76.63	76.59	76.43	76.4	75.93	75.4
Longitude, °W	−159.42	−158.48	−158.82	−161.82	−162.53	−164.06	−163.98	−163.47	−162.26	−161.45	−160.73
Temperature, deg C	0.07	−0.05	0.28	0.70	−0.30	0.41	0.48	0.06	−0.29	−0.28	−0.29
Bottom salinity, PSU	34.87	34.88	34.86	34.84	34.93	34.86	34.85	34.84	34.92	34.92	34.92
Fluorescence, mg/m^3	0.40	0.39	0.39	0.40	0.38	0.39	0.40	0.39	0.38	0.37	0.38
Depth, m	853	1059	746	486	2610	557	508	873	1882	2107	2091
Mean sediment Phaeo, µg pigment/g dry sediment	0.773	0.298	0.088	0.145	0.117	0.192	0.197	0.240	0.192	0.185	0.266
Mean sediment Chl, µg pigment/g dry sediment	0.098	0.039	0.010	0.016	0.012	0.023	0.021	0.026	0.020	0.020	0.027
Sediment organic carbon, %	1.26	1.14	0.81	0.63	0.77	0.98	0.78	0.88	1.09	1.13	1.25
Mud, %	93	96	96	97	98	99	99	95	98	99	100
Sand, %	7	4	4	3	2	1	1	5	2	1	0
Topography	Ridge	Ridge	Ridge	Ridge	Basin	Plateau	Plateau	Plateau	Basin	Basin	Basin
ROV	X	X	O	X	X	X	X	X	X	X	X
Trawl	X	X	X	O	O	O	X	X	O	O	X
Number of pictures analyzed	100	80	0	98	99	39	180	69	79	80	80
Mean area per image, ROV	0.8 ± 0.4			0.8 ± 0.6	0.3 ± 0.1	0.3 ± 0.2					
Average amount of stones per picture	0.3	0.0		1.0	0.0	0.6	0.8	0.1	0.0	0.0	0.1
Trawl transect length, m	1577	1589	2280				713	1246			1689

2.2. Biological sampling

Epifaunal communities (including invertebrates and demersal fishes) were investigated with two main tools, the ROV Global Explorer (www.deepseasystems.com/) and a plumb-staff beam trawl. The ROV was used to perform a photographic survey of the seafloor at each of ten stations, with two dives each at stations 1 and 9 for a total of 12 ROV dives (Table 1). Analyses were performed on 24-megapixel images collected with a downward-looking DSSI DPC-8800 digital camera. The ROV was equipped with DSSI Ocean Light Underwater LED lights. Forward looking 10x and 3.8x zoom 4K video cameras were used to guide the photographic surveys, control distance from the sea floor, and collect taxonomic vouchers with the suction sampler and manipulator arm. We kept the ROV to a linear transect as much as possible but deviations from straight lines occurred at some stations due to variable drift speeds and bottom currents, irregular topography and occasional inspection and collection of taxa of interest, which might have led to a slight biases in estimation of taxonomic abundance and diversity. Still images were taken every 5–8 s, depending on drift speed. Four digital laser pointers, one located at each corner of a fixed distance of a 10 - cm square, were used to estimate the photographed area at four stations, after which they stopped functioning. The average bottom time of the ROV dives was 3:29 h, and the average distance between start and end point during bottom time was about 3800 m (distance measured with ArcMap from ESRI software).

Trawl samples were collected at six stations with one haul per station to compare abundance estimates to those from ROV images and to verify taxonomic identification inferred from ROV images (Table 1). The 3.05 m modified plumb-staff beam trawl was equipped with rubber rollers on the footrope (Abookire and Rose, 2005), a 7 mm mesh net with 4 mm in the cod end, and had an effective mouth opening of 2.26 × 1.20 m. Trawling at all stations was performed for a target duration of about 30 min at a target speed of 1.5 knots speed over ground. Actual trawl duration and speed varied due to challenges of trawling under the local environmental conditions, resulting in actual distance swept ranged from 713 to 2280 m. Trawl bottom time was estimated from a time depth recorder (TDR, Star Oddi) affixed to the net. The TDR also showed whether the trawl stayed at seafloor. Trawl hauls were rinsed of sediments over a 2 mm mesh on deck. Organisms were sorted and identified to the lowest possible taxonomic level. All organisms were counted and weighed by taxon to 1 g accuracy. Vouchers of taxa that were difficult to identify on board were preserved in 10% formalin or 190 proof ethanol. The vouchers were later sent to expert taxonomists for further detailed identification (see acknowledgments). Taxon names were verified using WoRMS (http://www.marinespecies.org/, on 30.10.2018).

2.3. Environmental sampling and processing

At each station, a range of environmental variables was collected with a SBE9/11 + CTD and an Ocean Instruments BX 650 0.25 m^2 box corer (Table 1). Water temperature, salinity and fluorescence of the water were measured with the CTD package as close to the bottom as possible, on average around 20 m from the bottom. Sediment samples were collected from box core samples. The upper surface (0–1 cm) of the sediments was subsampled and frozen at −20 °C for later determination of grain size composition, organic carbon content, and concentration of sediment chlorophyll *a* and phaeopigments. Only cores with intact surface layers were used for sediment analyses. Sediment grain size was analyzed on a Beckman Coulter Particle Size Analyzer LS 13320 at the Geology Laboratory of UiT The Arctic University of Norway in Tromsø. The samples were pre-treated with HCl and H_2O_2 to remove calcium carbonate and organic material, respectively. Each sample was analyzed three times and mean grain-size values were calculated. Sediment organic carbon (%) was determined on a Costech ESC 4010 elemental analyzer at the stable isotope facility at the University of Alaska Fairbanks, USA. Concentration of sediment chlorophyll *a* and phaeopigments (μg pigment/g dry sediment) was measured at the University of Alaska Fairbanks. Pigments were extracted with 5 ml of 100% acetone for 24 h in the dark at −20 °C. A Turner Designs TD-700 fluorometer was used to measure pigment concentration. The fluorescence of the sample was read before and after acidification with HCl (final concentration of HCl was 0.003N) for determination of phaeopigments (Arar and Collins, 1997; Jeffrey and Welschmeyer, 1997).

2.4. Image analysis

A subset of the useable images of the sea floor was chosen from each station for the image analysis. Images that were overlapping, blurred, had suspended sediment, were poorly illuminated, or that were far off the seafloor were classified as unusable. In total, 940 images were manually analyzed for faunal densities and proportional organism abundances. Faunal densities were determined at the four stations (stations 1a, 6, 7, 8) where laser pointers were still functioning so that total image area could be determined. The mean area per image varied from 0.2 to 0.8 m^2 (Table 1). For remaining stations proportional organism abundances were determined. Typically, 70–100 pictures per station were analyzed (Table 1). Image processing and analyses were performed with ImageJ (https://imagej.nih.gov/ij/, (Rasband, 2009).

All putative taxa present in the study area were used to create a taxonomic image library. Taxa were identified to the lowest possible level based on a combination of the ROV imagery, the voucher collection, and additional identifications by experts (see acknowledgments). Where identification was difficult, taxa were named morphotypes (taxa that are distinguishable on the basis of their gross morphology (Oliver and Beattie, 1996)). The image library allowed for standardization of taxonomic identification and nomenclature, in particular in case of morphotypes.

All taxa and morphotypes present on the images were counted per image. In addition, lebensspuren, burrows, colour of the sediments, and presence of stones were noted. Stones larger than a few cm were counted, and their approximate size and associated fauna were recorded. The average number of stones per picture was calculated and included in the statistical analyses.

2.5. Biogeographic affinity

Invertebrates and fishes collected in the trawl hauls were assigned to one of the following biogeographic groups: (1) Arctic – occurring only in the Arctic, (2) Arcto-boreal-Pacific – found in Arctic and boreal Pacific waters, (3) Arcto-boreal-Atlantic – found in Arctic and boreal Atlantic waters, (4) Arcto-boreal – found in Arctic and in both Atlantic and Pacific boreal waters, and (5) other – occurring also outside of boreal and Arctic zones. Biogeographic affinities were assigned based on the best current distribution information available in the published literature (Zhirkov, 2001; Vassilenko and Petryashov, 2009; Stepanjants et al., 2012), internet sources (OBIS: http://www.iobis.org/ , Encyclopedia of Life: http://eol.org/, WoRMS: http://www.marinespecies.org/), and expert knowledge by collaborating taxonomists (all sources listed in Table S2). The list of taxa analyzed for biogeographic affinities included 44 taxa identified to species level; all taxa not identified to species level were excluded from this analysis. Percent of species from different biogeographic regions was presented based on densities and number of taxa by station. Data collected by the ROV were not used in this analysis due to considerably fewer taxa identified to species and given weighting by density was not possible for all ROV stations.

2.6. Statistical analysis

For the six trawl stations, biomass and density were estimated from

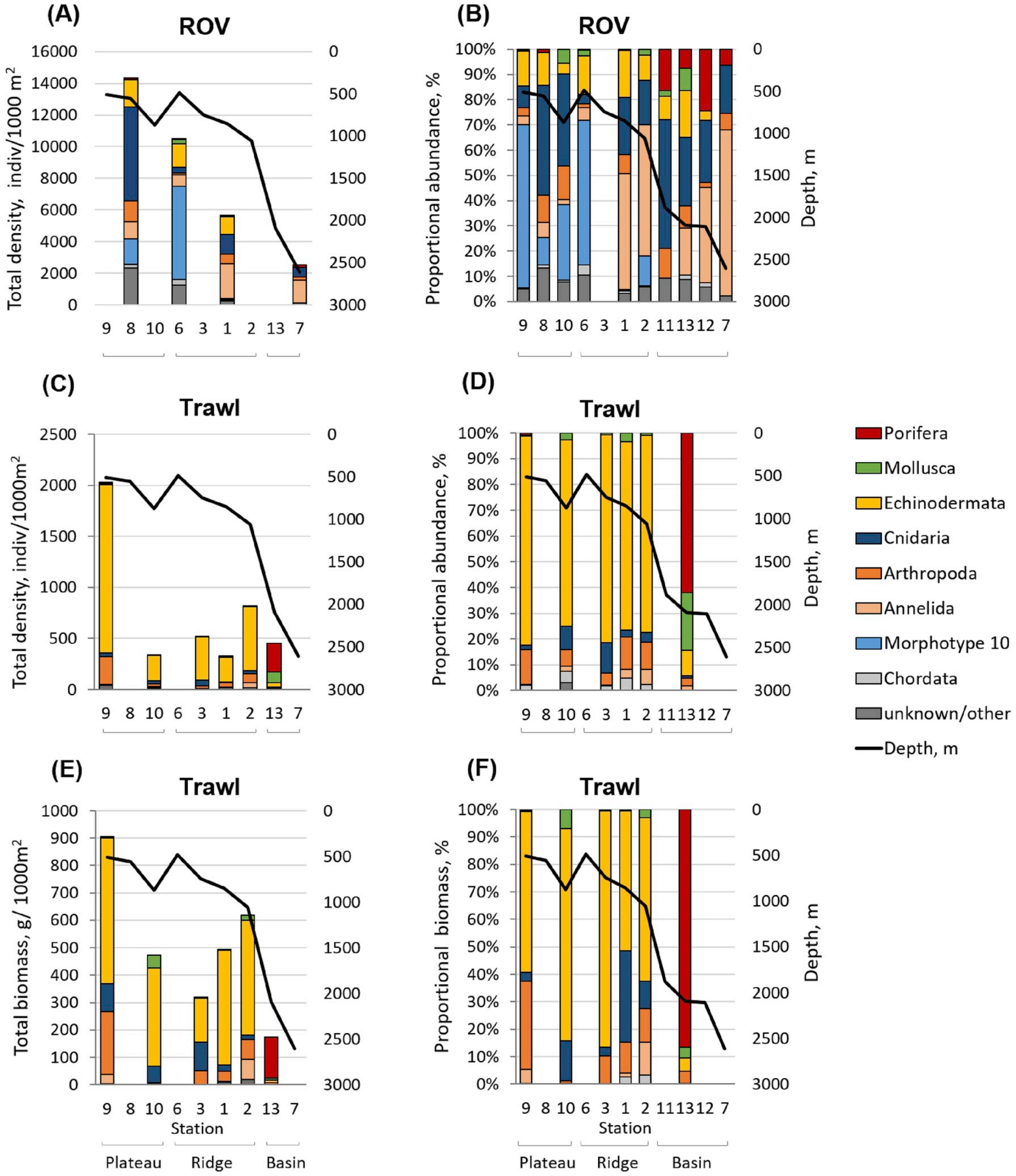


Fig. 2. Total density and biomass and proportional abundance and biomass of epifauna at different stations based on trawl and ROV samples; total density (A) and proportional abundance (B) based on ROV samples, total density (C) and proportional abundance (D) based on trawl samples, total and proportional biomass based on trawl samples (E, F, respectively); note the scale is different in A, C and E, (A) has less bars than (B) due to laser pointers problem that did not allow us to calculate density and biomass.

area swept as follows: distance towed × net opening; then estimates were normalized to individuals 1000 m^{-2}. For the four ROV stations where laser pointers were functioning, taxa counts were also converted to density as individuals 1000 m^{-2}. In addition, counts were converted to proportional abundance for all ROV stations. The Simpson diversity index (D) was calculated since it is less sensitive to variation in densities than other commonly used diversity indices (e.g., Shannon-Wiener index) (Magurran, 2013). The Simpson index was calculated based on the formula:

$$D = 1 - \left(\sum n_i(n_i - 1)/N(N - 1)\right)$$

where n_i = the number of individuals in *i*th species; and N = the total number of individuals. Thus, D ranges from 0 to 1, and lower values indicate lower diversity. Morphotypes were treated as species in diversity estimates (Magurran, 2013). The diversity measures were not scaled to transect length, which might have caused a slight bias in comparisons.

Factorial analyses of variance (ANOVAs) were used to compare ROV-based number of taxa and Simpson index values among three habitat types (ridge, plateau and basin). For trawl stations, comparison of number of taxa, Simpson index, density and biomass for ridge and plateau stations was conducted with the Student's *t*-test. This test was also used to compare Simpson index values of ridge and plateau stations between trawl and ROV samples. Prior to analyses, data were tested for normality (Shapiro–Wilk test) and for homogeneity of variances

Table 2
ANOVA results comparing number of taxa and Simpson index for ridge, plateau and basin stations based on ROV samples; and *t*-test results comparing: (1) number of taxa, Simpson index, density, and biomass for ridge and plateau stations, (2) Simpson index of plateau and ridge stations for trawl and ROV samples; statistically significant results are indicated with asterisks.

Variable	df	*F*-value/t-value	*P*-value
ROV			
***F*-value**			
Number of taxa	2	6.4	0.03*
Simpson index	2	0.2	0.8
Trawl			
t-value			
Number of taxa	3	0.5	0.6
Simpson index	3	0.5	0.6
Density	3	0.8	0.5
Biomass	3	1.0	0.4
Simpson index (ROV vs trawl)			
Plateau stations	2	0.9	0.5
Ridge stations	2	1	0.4

(Bartlett test) (Crawley, 2007). The analyses were performed in the statistical computing software R (RDevelopment, 2012).

The epifaunal community composition was analyzed by means of multivariate statistics including hierarchical cluster analysis using the PRIMER v 6.0 software package (Clarke and Gorley, 2001). Density data collected with the trawl were used for the analyses. Proportional abundance data were used for all ROV stations since density could not be determined for all stations. Square-root data transformation, which down-weighs the influence of dominant taxa, was applied prior to calculating similarities. The abundance data were grouped *a priori* as ridge, basin, and plateau with pockmark. A similarity matrix was calculated based on the Bray-Curtis coefficient (Bray and Curtis, 1957). A similarity profile test (SIMPROF) was used to explore statistical significance of difference among cluster branches. The magnitude of differences among ridge, plateau and basin categories and the significance of potential differences were tested with the analysis of similarities (ANOSIM). Statistical significance of the ANOSIM global R statistic was assessed by a permutation (999 times) test. When ANOSIM detected a significant grouping (at $\alpha = 0.05$ level), a SIMPER (a similarity percentage procedure) analysis was carried out to establish taxa contributing most to the dissimilarities between epifaunal communities.

The potential influence of environmental factors on epifaunal community structure was tested with canonical correspondence analysis (CCA) using the package 'vegan' (Oksanen et al., 2013) in the statistical computing software R (RDevelopment, 2012). In the CCA ordination biplot, the environmental variables are presented as arrows that are roughly oriented in the direction of maximum variation in value of the corresponding variable (Ter Braak, 1986). Water depth, bottom temperature, sediment grain size (clay and silt fraction combined), number of stones per picture, sediment pigments, and sediment organic carbon were included in the analysis, and correlated with the square root transformed proportional abundance of the taxa. Environmental variables included in the model were obtained with a forward selection procedure. Monte Carlo permutation tests were used to determine the statistical significance of the model and the individual terms.

In addition, correlations between univariate epifaunal characteristics from trawl surveys (total density, total biomass, and number of taxa), ROV surveys (number of taxa) and physical-chemical characteristics of water and sediments (water depth, bottom temperature, sediment grain size, number of stones per picture) were evaluated using parametric Pearson's correlation analysis (when data were normally distributed) and non-parametric Spearman's rank correlation analysis (when data were not normally distributed). Maps presented in the paper were generated using ArcMap 10.5 software (ESRI).

3. Results

3.1. Epifaunal community structure, taxonomic diversity and distribution patterns

3.1.1. Epifaunal density and biomass

A total of 2721 individuals was recorded across all stations from ROV images, of which 1584 individuals were classified into eight phyla (Cnidaria, Annelida, Echinodermata, Arthropoda, Porifera, Mollusca, Chordata, Nemertea; phyla are listed from most to least abundant, Fig. 2, Tables S1) and 1137 individuals were classified into 10 morphotypes of uncertain phyla (Table S1). At the four ROV stations where laser pointers were present, densities showed a clear increasing trend with decreasing depth from 2273 ind/1000 m^2 at the basin station 7 at 2610 m depth to 14,346 ind/1000 m^2 at the plateau station 8 at 557 m depth (Fig. 2A). Relative composition of the number of individuals per phylum obtained from all ROV stations showed different phyla dominated across the study area. Annelida were most numerous at two ridge stations (stations 1 and 2) as well as at three basin stations (stations 12, 13, and 7), where they comprised 18–66% of the total abundance (Fig. 2B). Cnidaria were numerous at all stations, but dominated at the plateau stations 8 and 10 and basin station 11, where they comprised 37–51% of the total abundance. Epifaunal communities at ridge station 6 and plateau station 9 were dominated by morphotype 10, possibly *Atolla* polyps, which was also a co-dominant community member at plateau station 10 (Fig. 2B).

A total of 2505 individuals were registered in six trawl samples and represented nine phyla: Echinodermata, Arthropoda, Porifera, Cnidaria, Mollusca, Chordata, Annelida, Sipuncula and Nemertea (phyla are listed from most to least abundant; Fig. 2 Table S1). Total density and biomass were variable across stations with no significant difference indicated by the Student's *t*-test for biomass and densities between ridge and plateau stations (Table 2). Densities calculated from the trawl samples were 6–7 times lower than those calculated from the ROV images (Fig. 2 A, C). The highest and lowest total densities were found at the two plateau stations and varied from 342 ind/1000 m^2 at station 10 to 2029 ind/1000 m^2 at station 9 (Fig. 2 C). The biomass ranged from 173 g/1000 m^2 at the basin station 13–906 g/1000 m^2 at the shallow plateau station 9 (Fig. 2 E).

Results of the relative composition of phyla from trawls suggested certain taxa were missed by the trawl compared to ROV samples taken at the same stations. For example, the relative abundance of Annelida and Cnidaria was generally much lower in trawls than in ROV images. Also, in contrast to the ROV samples, morphotype 10 was encountered only once in trawl catches at station 9. The by far dominating phylum, in terms of relative abundance and biomass, at the plateau and ridge stations was Echinodermata with 72–80% of relative abundance and 51–86% of relative biomass, followed by Arthropoda and Cnidaria (Fig. 2D, F). The only basin station 13 sampled by trawl was markedly different from the rest of the stations in that it was dominated by Porifera with 62% and 87% of relative abundance and biomass, respectively, and Mollusca with 23% of relative abundance (Fig. 2 D, F).

3.1.2. Epifaunal diversity

In total, 152 taxa and morphotypes were identified from the trawl and ROV samples, with at least 34 taxa common to both sampling tools. From the ten ROV stations combined, 78 taxa including morphotypes were registered, mostly within Echinodermata (16 taxa), Cnidaria (15), Arthropoda (12), and Chordata (10, 8 of which were fishes) (Fig. 3 A, S1 Table). In general, the total number of taxa was significantly higher at the plateau and ridge stations than at the basin stations (Table 2). The number of taxa ranged from 41 to 40 taxa at ridge station 1 and plateau station 10, respectively, to 9 taxa at basin station 7. The relatively low number of taxa at station 8 might be a result of fewer images available for the analysis at this station (Fig. 3 B, Table 1). The high number of images analyzed at station 9 (where two stations (9a, 9b)

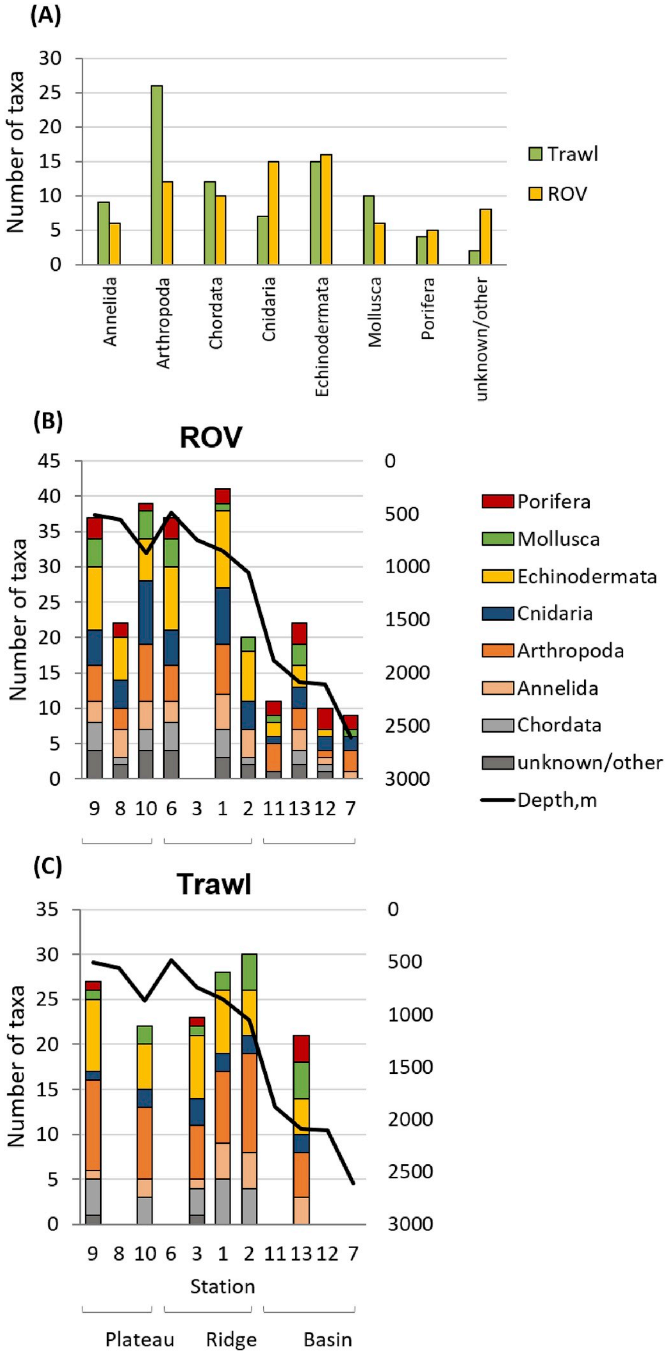


Fig. 3. Number of taxa per phylum based on ROV and trawl samples across all stations (A) and at different stations based on ROV (B) and trawl (C) samples.

combined), however, did not appear to affect diversity estimates at this station. Echinoderms together with Arthropoda and Cnidaria were most diverse at the plateau and ridge stations. The number of taxa per phylum was relatively evenly distributed at the basin stations (Fig. 3B).

Eighty-six taxa were recorded from the six trawl stations. Patterns of diversity for taxa per phylum were relatively similar to those observed from ROV images (Fig. 3A). The most diverse phyla in the trawl samples were Arthropoda (24 taxa), Echinodermata (15 taxa), Chordata (12, 9 of which were fish taxa), and Mollusca (10) (Fig. 3A). The total number of taxa varied from 21 at basin station 13 to 30 taxa at ridge station 2, with no significant difference between ridge and plateau stations (Table 2). The majority of taxa across all trawl stations were Arthropoda and Echinodermata (Fig. 3C). Particularly low diversity was found in the trawl catch at ridge station 3 based on the Simpson's diversity index though there were no statistically significant differences among different stations for either trawl and ROV samples (Table 2). The Simpson's diversity index was slightly lower in trawl catches than ROV images at all stations where both gears were employed (Fig. 4), but these differences were not statistically significant either (Table 2).

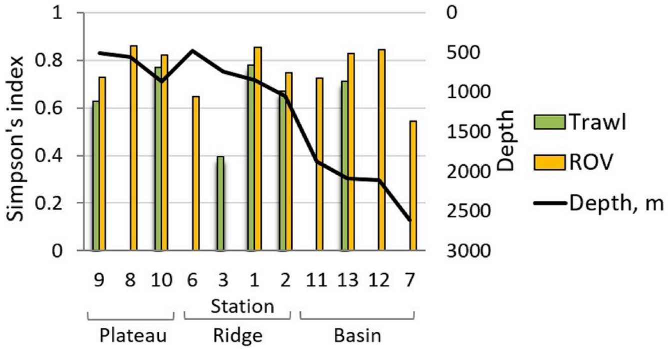


Fig. 4. Simpson's index for epibenthic community from ROV and trawl samples.

Several species found in the CBL represented geographic and depth range extensions compared to literature values. The bivalve *Yoldiella intermedia* (M. Sars, 1865) extended its depth range from a previous maximum of 1150 m (Sirenko et al., 2004) to 2037 m depth at station 13 in our study. Geographic range extension was registered for four mollusks, and five sponges: *Rhinoclama filatovae* F. R. Bernard, 1979, *Tindaria compressa* Dall, 1908, *Hyalopecten* c.f. *frigidus* (Jensen, 1904), *Bathyarca* c.f. *imitata* (E. A. Smith, 1885), (all Mollusca), and *Radiella sol* Schmidt, 1870, *Grantia phillipsi* Lambe, 1900, *Scyphidium septentrionale* Schulze, 1900, *Stylocordyla boralis* (Lovén, 1866), and *Hyalonema (Cyliconema) apertum simplex* Koltun, 1967 (all Porifera). *Hyalopecten* c.f. *frigidus* and *Bathyarca* c.f. *imitata* might prove to be new species.

3.1.3. Community structure

Results of the hierarchical cluster analysis on relative abundances obtained from ROV images revealed two main clusters of 74% dissimilarity (SIMPROF, $p = 0.05$, Fig. 5). The first cluster included all basin stations, while the second cluster included both plateau and ridge stations (Fig. 5). Similarly, ANOSIM showed a significant difference between basin stations and combined plateau and ridge stations, though no significant difference was found between ridge and plateau stations (Table 3). SIMPER analysis for the two main clusters (basin and ridge/plateau) determined that the difference between ROV communities was mainly due to morphotype 10, and polychaetes belonging to the

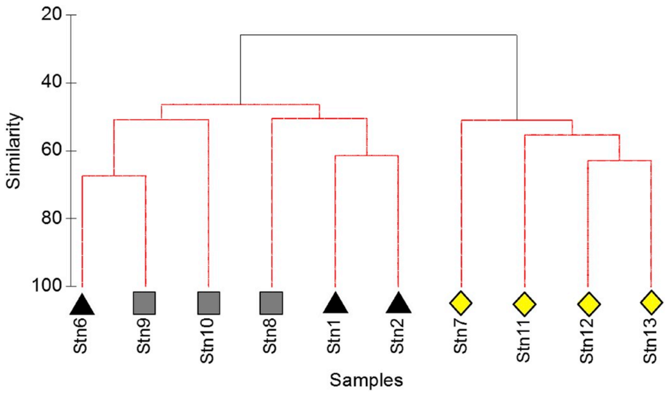


Fig. 5. Hierarchical cluster analysis based on Bray-Curtis dissimilarity of epifauna relative abundance at different stations based on the ROV samples. Black lines indicate statistically significant differences (SIMPROF, P = 0.05); red lines indicate intervals where clusters are not significantly different; triangular – ridges, square – plateau, diamond – basins.

Table 3
Results of ANOSIM test of epifanuna community, based on square root transformed relative abundance obtained from the ROV images, at the ridge (R), plateau (P), and basin (B) stations.

	Withing group comparison	Pairwise test		
		R/B	P/B	R/P
R global	0.80	0.99	0.99	< 0.10
P-value	0.005	0.029	0.029	0.1

Table 4
Results of SIMPER analysis showing the five taxa contributing most to dissimilarities among combined ridge/plateau and basin communities.

Taxa	Contribution %
ROV	
Morphotype 10 (c.f. *Atolla* sp.)	9
Polynoidae	8
Ampharetidae	5
Polymastiidae	4
Bathyphellia cf *margaritacea*	4
TRAWL	
Radiella sol	11
Ophiopleura borealis	9
Pontaster tenuispinus	8
Bathyarca nucleator	5
Elpidia sp.	4

Polynoidae and Ampharetidae families (Table 4).

Cluster analysis performed for the trawl samples (not shown) indicated similar differences as for ROV samples, with the one basin station sampled clustering separately from the ridge and plateau stations (SIMPROF, $p = 0.05$). The average dissimilarity between the two main clusters was 93%. Species contributing most to dissimilarities between the two clusters were the sponge *Radiella sol,* the brittle star *Ophiopleura borealis,* and the sea star *Pontaster tenuispinus* (Table 4).

Based on the ROV images, relative abundance of dominant taxa changed across the study area indicating marked difference between ridge/plateau and basin communities. In addition, ridge/plateau communities differed between the eastern and the western side of the study area (Fig. 6 A). The geographically close ridge communities at stations 1 and 2 (east) were dominated by polychaetes of the families Ampharetidae and Sabellidae, which comprised more than 40% of relative abundance at each station (Fig. 6 A, C, D). The subsequent most common taxa were the anthozoan *Bathyphellia* cf *margaritacea* (14–16%) and ophiuroids, especially *Ophiopleura borealis* (5–9%) (Fig. 6 A, E, F). Ridge station 6 and plateau stations 8, 9 and 10 in the western study region were characterized by high proportions of morphotype 10 (possibly, *Atolla* polyps) particularly at stations 9 and 6 (57–64%, Fig. 6 A, G1). In addition, morphotype 6 (possibly a sponge) was regularly found, and was attached to stones at these stations (up to 10%) (Fig. 6 A, G2). At stations 6, 8, and 9 ophiuroids, especially *Ophiostriatus striatus* (4–7%) were also regularly occurring (Fig. 6 A, H). Similar to the geographically distant ridge stations 1 and 2, the anthozoan *B.* cf *margaritacea* was common at plateau stations 8, 9, and 10 (5–35%) and dominated at station 8 (34%, Fig. 6 A, E). Characteristic for only ridge station 6 were an ascidian *Ciona* sp. (3%) (Fig. 6 I) and morphotype 5 (5%), resembling "holes" in the seafloor (Fig. 6 J). Characteristic of plateau station 10 (within a pockmark) were small unidentified pycnogonids as well as the large pycnogonid *Colossendeis proboscidea* (10%) (Fig. 6 A, K). The latter was not observed in other parts of the study area and was particularly numerous at this station based on the video records (personal observations). In addition, video recordings from the ROV indicated a considerable increase in number of anemones on the slope towards the center of pockmark and inside of the pockmark at the plateau station 9 (personal observation).

Basin stations, for the most part, differed in dominant taxa from ridge/plateau stations (Fig. 6 B), with the exception of *B.* cf *margaritacea*, which was common almost everywhere and contributed 17–51% to relative abundance at basin stations (Fig. 6 B, E). A polychaete of the family Polynoidae (possibly genus *Pelagomacellicephala*) was the second most common taxon at all basin stations except station 11(17–51%) (Fig. 6 B, L). Porifera were recorded at all basin stations with Polymastiidae contributing most to total abundance at stations 11 and 12 (16–13%) and an unknown white sponge (11%) at station 12 (Fig. 6 B, M, N). At stations 11, 12 and 13, the sea cucumber *Elpidia* sp. occurred regularly (4–17%) as did morphotype 1, resembling a gastropod with an oval, laterally compressed shell (6–9%) (Fig. 6 B, O, P). In addition, the shrimps *Bythocaris* spp. were recorded at all basin and ridge/plateau stations, but contributed most at station 13 (8%, Fig. 6 B, R). Proportional abundance of fish taxa never exceeded 2% at any station, with *Lycodes* spp. being most common and recorded at most stations (Fig. 6 S).

Based on the trawl samples, the most abundant species of the plateau/ridge stations were the brittle star *Ophiopleura borealis* and the sea star *Pontaster tenuispinus. O. borealis* dominated at the shallower stations 9, 3 and 1 (43–56% relative abundance), while *P. tenuispinus* was dominant at the deeper stations 10 and 2 (43–56%). Other abundant taxa at the plateau/ridge stations were other ophiuroids (e.g., *Ophiacantha bidentata*, *Ophioscolex glacialis*) and the shrimp *Bythocaris* spp. Porifera of the family Polymastiidae (*Radiella sol* and *Polymastia* sp.) contributed 62% to total abundance at the basin station 13, followed by the bivalve *Bathyarca* c.f. *imitata* and the sea cucumber *Elpidia* sp. (11% and 8%, respectively). As with the ROV images, *Lycodes* spp. were found at all trawl stations (except station 13), with highest relative abundance at the pockmark station 10, though it never exceeded 3%.

3.2. Environmental parameters and epifaunal communities

Bottom temperatures gradually decreased with increasing water depth from 0.7 °C at station 6 to - 0.3 °C at station 7. Salinity ranged between 34.84 and 34.93 PSU at stations 10 and 7, respectively. Concentration of chlorophyll (0.010–0.098 µg pigment/g dry sediment), phaeopigments (0.088–0.773 µg pigment/g dry sediment) and percent carbon content (0.81–1.26%) in sediments were similarly low across all stations but station 1, where concentrations of phaeopigments and chlorophyll was higher (Table 1).

The sediments at all stations were almost entirely composed of mud (95–100% of silt and clay combined) (Table 1). This was generally in agreement with the images, which showed most of the stations were characterized by fine, usually light-colored sediments (Fig. 7), but images also showed interspersed hard substrate. Station 6 was covered by numerous, dark-colored pebbles a few mm size on top of fine-grained sediments (Fig. 7 B, Table 1). Stones (larger than a few cm) were present at most plateau/ridge stations except station 2 (Fig. 7 C). In contrast, there were no stones registered at the basin stations except station 13. The number of stones was highest at station 6 and 9 (Table 1).

Lebensspuren of different shapes and sizes were observed at all stations. They were particularly numerous inside the pockmark at station 10 and the isolated basin station 7 (Fig. 7D and E). In general, the most recognizable traces were those left by gastropods (relatively wide, long and straight lines, Fig. S1A), fish (two lines with "dots" occurring in two parallel rows with undisturbed sediments in between, Fig. S1B), and an unidentified animal leaving narrow, non-linear tracks more or less concentrated in one spot (Fig. S1C). At the plateau/ridge stations, many tracks from sea stars or ophiuroids were present (Fig. S1D). Abundant lebensspuren at basin station 11 were small near-circular holes with a tail, which were also present but less numerous at some other stations (Fig. 7F). There was no sign of chemosynthetic activity at any of the pockmark plateau stations such as gas bubbling or obvious

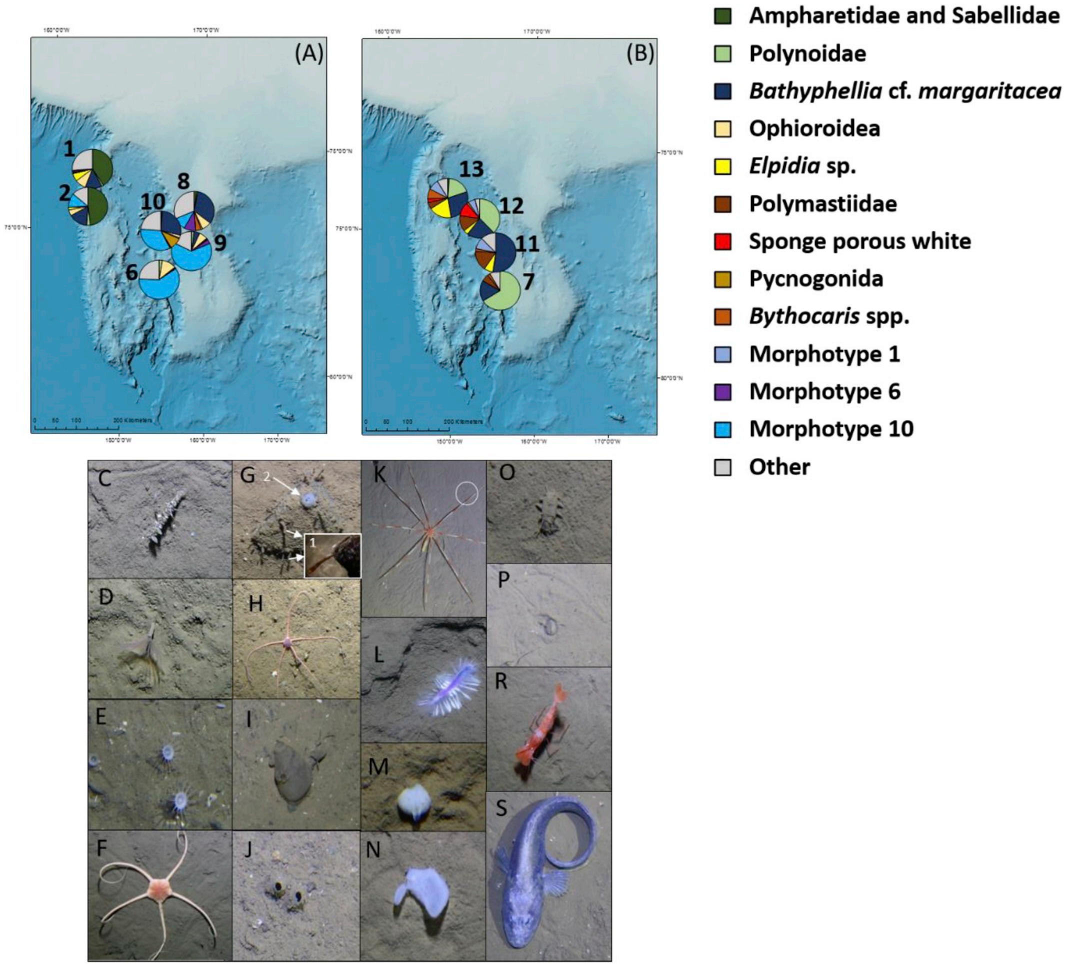


Fig. 6. Proportions of dominant taxa at the ridge and plateau (A) and basin (B) stations based on ROV images (upper panels), and images of the dominant taxa (lower panel), C- Ampharetidae, D – Sabellidae, E– *Bathyphellia* cf *margaritacea*, F – *Ophiopleura borealis*, G (1) - morphotype 10, G (2) - morphotype 6, H – *Ophiostriatus striatus*, I – *Ciona* sp., J – morphotype 5, K – Pycnogonida (*Colossendeis proboscidea* and a small unidentified pycnogonid, circled), L – Polynoidae (possibly genus *Pelagomacellicephala*), M – Polymastiidae, N - white sponge, O – *Elpidia* sp., P – morphotype 1, R – *Bythocaris* sp., S - *Lycodes frigidus*.

bacterial deposits. In addition, burrows of unknown origin and patches of sediment of different coloration indicating recent sediment disturbance/movement, were registered at the stations 1, 2, 9 and 11 (Fig. S2).

There was no significant correlation between abundance, biomass or number of taxa obtained and any of the environmental variables at the six trawl stations. For the ten ROV stations, the number of taxa was negatively correlated with depth ($r^2 = -0.75$, $p = 0.012$) and positively correlated with the number of stones per picture ($r^2 = 0.73$, $p = 0.017$) (Table 5). The main taxa associated with the stones on the images were morphotype 10, tubeworms in a white calcareous tube (possibly Serpulidae), morphotype 6, and various anemones (Figs. 8 and 9). At the ridge/plateau stations, brittle stars were often observed by arms sticking out from beneath the stones.

The CCA biplot showed the position of benthic taxa in relation to the environmental variables at different stations (Fig. 10). The environmental variables water depth, percent mud, amount of stones per picture, and sediment chlorophyll *a* showed significant relationships with epifaunal community composition ($p = 0.001$) and explained 65% of variance, with the first ordination axis explaining 32% and the second ordination axis explaining 18% of the variance in epifaunal community composition at the sampling stations. Among these, depth and amount of stones were the strongest predictors (Table 6). Stations and associated taxa separated into two main groups: basin stations on the right side of the plot and ridge/plateau stations on the left (Fig. 10). Basin stations were characterized by greater depth and finer sediments. The ridge and plateau stations were spread along the second axis on the ordination plot, mostly reflecting the west-east gradient of stations. Ridge station 6 and plateau stations 8 and 9 grouped together and were characterized by a high number of stones. Ridge stations 1 and 2 and plateau station 10 were associated with high sediment chlorophyll *a* concentrations and had coarser sediments (Fig. 10). Polynoidae and Porifera were closely associated with greater depth. Ampharetidae, Sabellidae and *Ophiopleura borealis* were associated with high sediment chlorophyll *a* concentration. Morphotype 10 was positively associated with the amount of stones.

3.3. Biogeographic affinities

The majority of species identified to species level across all trawl stations were of Arcto-boreal-Atlantic affinity (Table S2). They represented 50–59% of the total number of taxa per station. Species occurring only in the Arctic region were represented with 14–28% of the number of taxa. Arcto – boreal taxa comprised 11–29% of all taxa and were not observed at basin station 13. Pacific-boreal taxa were present only at the two shallower ridge/plateau stations 3 and 9, and with only 6% of total number of species. Taxa occurring with “other” biogeographic affinity were present at the deepest station 13 (25%) and at the relatively shallow ridge station 1 (6%), (Fig. 11A).

In terms of relative abundance, trawl communities were by far dominated by Arcto-boreal-Atlantic species. They represented >90% of total abundance at the deeper stations (basin station 13 and ridge

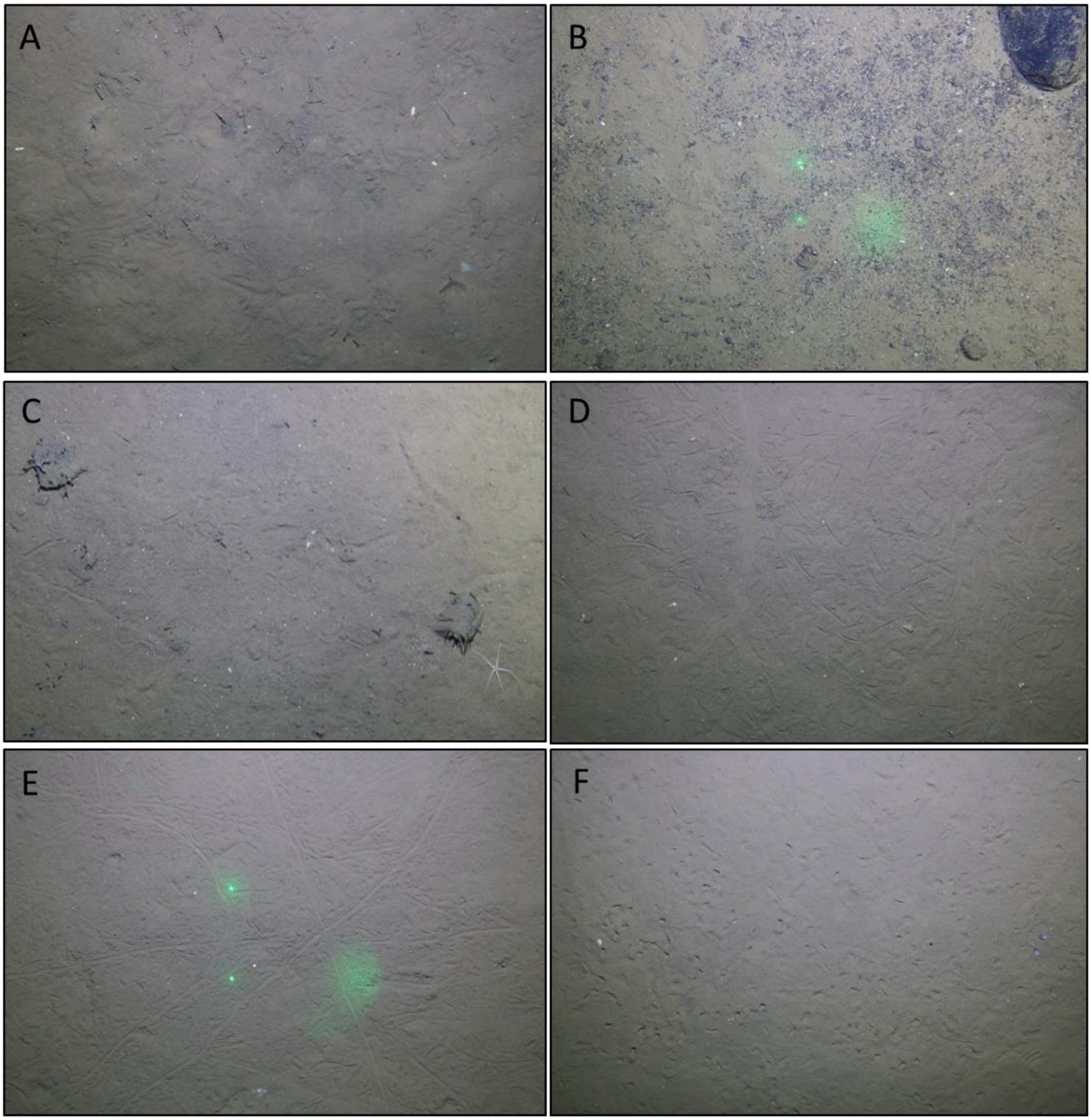
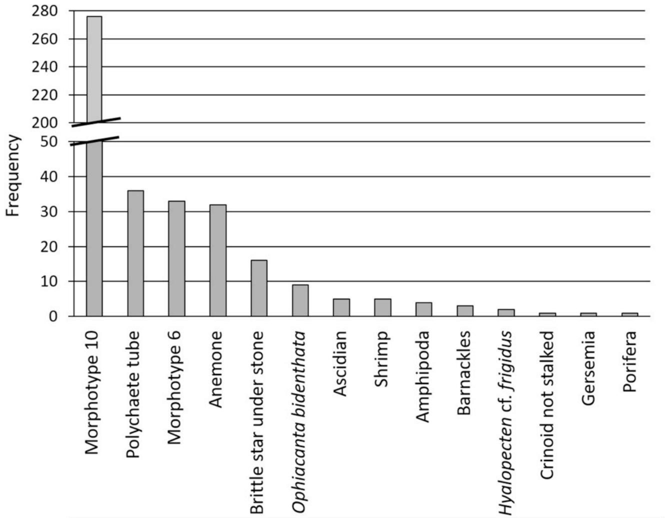


Fig. 7. Examples of the images taken in the CHB. Ridge stations: (A) Station 1 showing dense polychaete tubes, (B) Station 6 showing coarse sediment; Plateau stations: (C) Station 9 showing stones on the seafloor, (D) Station 10 showing numerous lebensspuren; Basin stations: (E) Station 7 showing very dense lebensspuren, (F) Station 11 showing near-circular lebensspuren.

station 2) and 77–87% at the remaining stations. The contribution of Arcto-boreal species increased with decreasing depth from 2 to 15%. The contribution of Arctic species to total abundance was low at the deeper stations (2–4%), and did not exceed 9% at the shallower stations. The contribution of Arcto-boreal-Pacific taxa was less than 1%, and contribution of species occurring outside of boreal and Arctic areas ("other") did not exceed 2% of total abundance (Fig. 11B).

Table 5
Pearson's and Spearman's correlation coefficients between biological variables (density, biomass for trawl and number of taxa for both trawl and ROV samples) and environmental variables. Significant relationships are shown in bold; *$p < 0.05$, **$p < 0.01$

	Depth	Bottom Temperature	%Mud	%Carbon	Phaeopigments	Chlorophyll	Number of stones
TRAWL							
Total density	−0.31	0.31	0.64	−0.71	−0.49	−0.49	
Total biomass	−0.71	0.69	−0.01	−0.42	0.14	0.14	
Number of taxa	−0.44	0.20	−0.37	−0.20	0.54	0.54	
ROV							
Number of taxa	**−0.75****	0.63	−0.63	−0.15	0.55	0.54	**0.73***



Total number of occurrences													
718	94	29	66	75	13	28	21	19	13	34	1	3	41

Fig. 8. Frequency of occurrence of different taxa on stones from all stations combined. The total number of occurrence of these taxa is shown in the table below the figure. Note that the y-axis is broken between 50 and 200.

4. Discussion

Our study in one of the least known parts of the Pacific Arctic deep sea revealed marked epifaunal community differences among habitat types, partly supporting the first hypothesis tested. We found lower density, diversity (in ROV observations but not in trawl samples) and biomass (in trawl samples), as well as different taxon composition in the deep basin compared to the shallower ridge and plateau fauna. However, there was no significant difference between ridge and plateau epifaunal communities, although western and eastern parts of the CBL

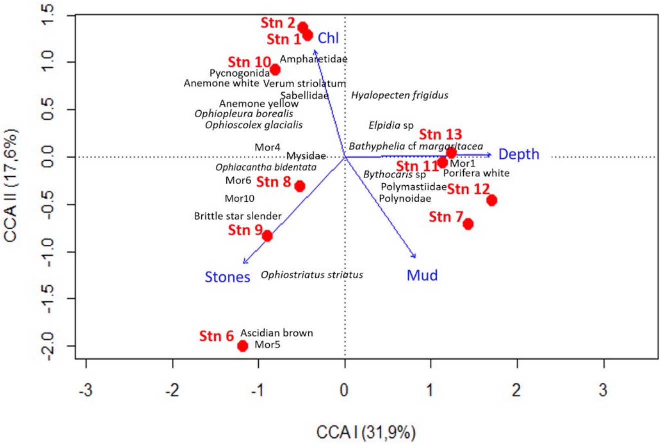


Fig. 10. Canonical correspondence analysis (CCA) based on relative abundance of taxa obtained from the ROV images ordinated with normalized environmental variables (depth, temperature, amount of stones per picture, chlorophyll concentration in the sediments, and percent of mud (clay and silt sediment fractions combined); chl – chlorophyll, Mor – morphotype.

Table 6
Results of the CCA on square root transformed proportional abundance obtained from the ROV images, at ridge, plateau, and basin stations.

Explanatory variables/model	Df	F-ratio	P-value
Full model	4	1.9	0.001***
Depth	1	0.5	0.001***
Amount of stones per picture	1	0.2	0.048*
Mud	1	0.1	0.51
Chlorophyll *a*	1	0.7	0.17

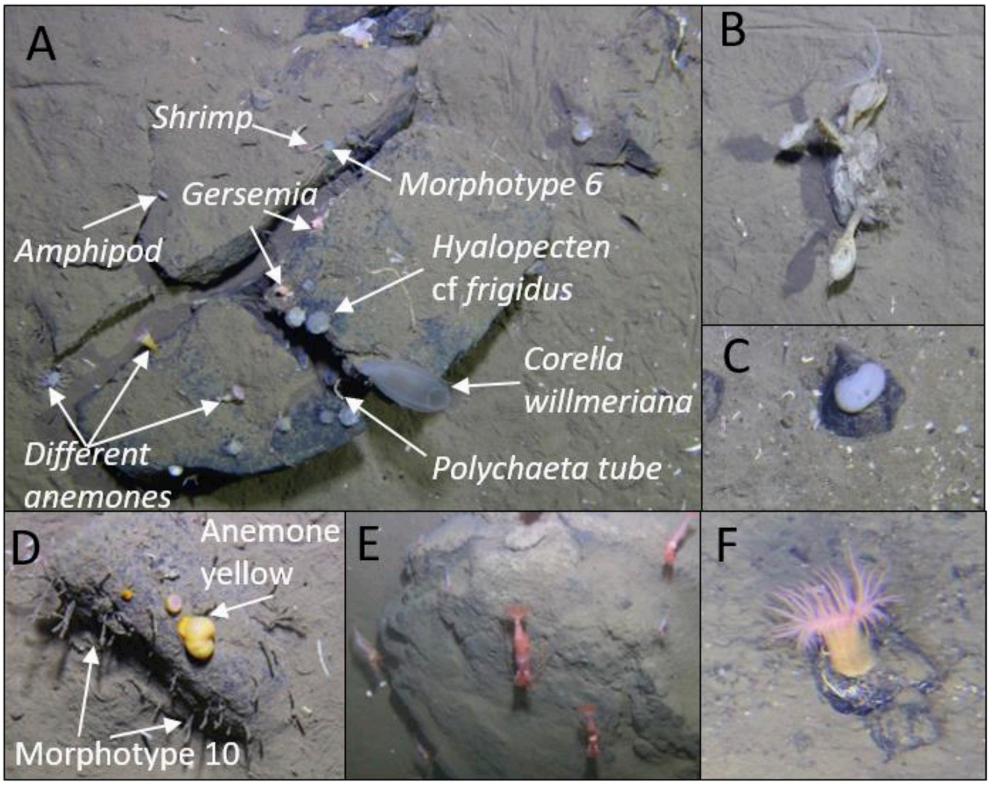


Fig. 9. Examples of fauna associated with the stones, A: Shrimp, *Gersemia* sp., Amphipoda, *Hyalopecten* c.f. *frigidus*, *Corella willmeriana*, Polychaete tubes, and various anemones on the stone, station 10; B: *Verum striolatum*, station 10; C: Morphotype 6, station 10; D Morphotype 10 and a yellow anemone, station 10; E: *Bythocaris* sp., station 13; F: pink anemone, station 6. In color in both print and online version.

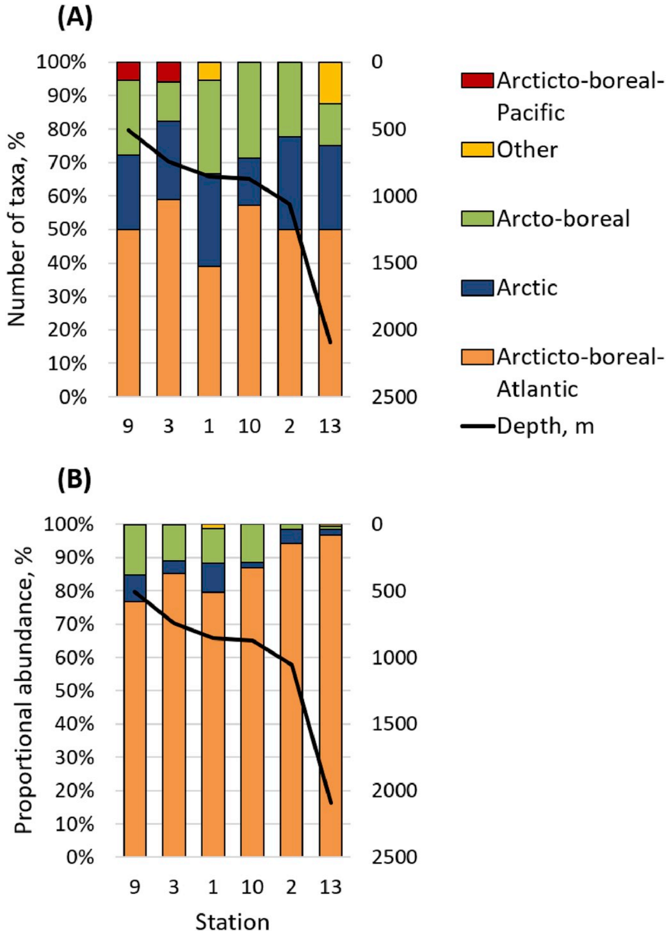


Fig. 11. Proportion of different biogeographic groups of the epifauna taxa collected by trawl in the Chukchi Borderland area based on number of taxa (A) and proportional abundance (B).

differed in plateau/ridge community properties. As is typical with deep-sea studies, water depth and availability of hard substrate in the form of stones were the strongest predictors of benthic community structure, along with sediment grain size and indicators of food availability. Results of the study supported our second hypothesis as Arcto-boreal-Atlantic taxa dominated species richness and biomass; the latter increased with increasing water depth while taxa with Pacific affiliations were essentially absent.

4.1. Epifaunal community structure, taxonomic diversity, distributional pattern

4.1.1. General characteristics of the epifaunal communities

The total number of taxa/morphotypes found across the CBL in the present study was 78 (ROV) and 86 (trawl) with a grand total of 134. This is higher compared to the previous records from the same area, where 15 (with only 4 stations analyzed from video, Bluhm et al., 2005) and 67 (MacDonald et al., 2010) epifaunal taxa were documented. Most of the taxa from the CBL are found throughout the Arctic deep sea and shelf (Bergmann et al., 2011; Taylor et al., 2016). The most speciose phyla across the study area were Echinodermata, Arthropoda and Cnidaria, which is typical of Arctic deep-water epifaunal communities (e.g. Mayer and Piepenburg, 1996; Soltwedel et al., 2009).

In general, knowledge on Arctic deep-sea epifaunal biomass is extremely sparse and mostly restricted to continental slopes (Piepenburg and Schmid, 1996; Ravelo et al., 2015; Ravelo, Bluhm, Foster, Iken, unpubl. data). Our study adds to this limited knowledge with epifaunal biomass measured from trawl catches ranging from 173 to 906 g ww/1000 m^2. The values obtained are generally within those registered from the Alaska Beaufort Sea slope, where biomass varied from 37 to 5250 g ww/1000 m^2 between 500 and 1000 m with values mostly below 700 g ww/1000 m^2 at stations at 1000 m (Ravelo, Bluhm, Foster, Iken, unpubl. data). Our epifaunal biomass estimates from the CBL tended to be one to two orders of magnitude lower than the highest values recorded on Arctic shelves (Bluhm et al., 2009; Anisimova et al., 2010; Ravelo et al., 2015). At least in part, these differences are related to gear bias as was obvious from the density estimates. Total epifaunal densities from trawl samples (329 - 2029 ind/1000 m^2) were much lower than those recorded from ROV images (2743 - 14,457 ind/1000 m^2). The difference in estimates of densities obtained by trawl and ROV have previously been reported for some fish species and decapods (McIntyre et al., 2015; Ayma et al., 2016), again with higher values obtained from imagery. Trawl efficiency in the deep sea can be reduced based on difficulty of maintaining consistent bottom contact. In contrast, ROV images may provide more accurate quantitative estimates of community properties, at least for fauna easily seen on images (Rice et al., 1982). Densities reported from the single previous quantitative study of the CBL area and adjacent Canada Basin varied from 90 to 5830 ind/1000 m^2 (MacDonald et al., 2010). The total epifaunal densities reported from images at the HAUSGARTEN observatory in Fram Strait were generally higher and ranged from 120 to 54,800 ind/1000 m^2 (Soltwedel et al., 2009; Meyer et al., 2013; Taylor et al., 2017). Like biomass, densities tend to be much higher on Arctic shelves (Bluhm et al., 2009; Degen et al., 2016).

4.1.2. Habitat and regional differences

In general, epifaunal diversity, density and biomass varied across the ridge and plateau stations, but with no significant difference found between these two habitat types. The ridge stations were flat rather than steep and the pockmarks associated with the plateau stations did not indicate signs of chemosynthetic activity (see below), perhaps making the sites in these habitats quite similar. Based on the ROV images, however, the pattern of numerical taxon dominance differed across the eastern and western groups of ridge and plateau stations. Eastern communities at the Northwind Ridge were dominated in abundance by annelids of the Ampharetidae and Sabellidae have been previously observed in relatively high numbers in the deep sea of the Southern Ocean (particularly Ampharetidae, Schüller and Ebbe, 2007), and in hydrodynamically active areas with strong deep sea currents (Thistle et al., 1985) such as in Fram Strait (Sabellidae, Meyer et al., 2013). These polychaetes are sessile surface deposit feeders (Ampharetidae) and suspension feeders (Sabellidae), though they are capable of also using other feeding strategies, a plasticity that might allow them to be common in the deep sea (Fauchald and Jumars, 1979). In addition, the higher abundance of these polychaetes on the Northwind Ridge might be due to higher input of organic matter here compared to other stations (see discussion in section 4.2), which can be efficiently taken up by these families (Gambi and Bussotti, 1999; Gontikaki et al., 2011).

In the western CBL, ridge and plateau stations were characterized by high numbers of unidentified coronate tubes, (morphotype 10), a common deep sea taxon (Jarms et al., 2002). The medusa phase of the coronates *Atolla* sp. and *Nausithoe* sp. was previously reported from the pelagic realm in this area, where the abundance of *Atolla* was significantly higher (Raskoff et al., 2010). Polyp stages of coronates are morphologically very similar (Jarms, 1991), but given that *Atolla* medusae were also recorded in pelagic ROV dives (R. Hopcroft, pers. communication), we suggest that morphotype 10 might be *Atolla* polyps. These polyps need hard substrate for attachment (Jarms et al., 2002), and the higher availability of stones on the western side of the study area may explain the dominance of coronate polyps here.

Unlike at pockmarks with active gas venting, we did not find characteristic seep organisms that are known to rely on chemosynthetic energy (Hovland and Svensen, 2006; Olu-Le Roy et al., 2007; Sahling et al., 2008). A single pockmark previously investigated in the CBL also did not indicate active seepage or typical seep-associated biota (MacDonald et al., 2010). Active fluid flux is actually rarely observed in pockmarks (Webb, 2009), since many of them are relicts formed several thousand years ago (Buhl-Mortensen et al., 2015). Instead of chemosynthetic biota, increased biological abundance and taxonomic richness were previously observed in inactive pockmarks elsewhere (Webb et al., 2009b; Zeppilli et al., 2012), including the pockmark of the CBL, where abundance of epifauna, and holothurians in particular, was high (MacDonald et al., 2010). Such enhanced values have been linked to morphology of pockmarks altering hydrodynamic conditions, causing turbulent re-suspension of material and enhanced settling of organic matter, resulting in higher food supplies and increased larval settlement (Webb et al., 2009b; MacDonald et al., 2010). While densities could not be calculated in the present study, dense population of anemones were observed in the shallower pockmark (station 9, 508 m depth), possibly indicating increased water movement over the pockmark. The deeper pockmark (station 10, 973 m) was instead characterized by higher number of pycnogonids, again a taxon previously recorded in pockmarks with active seepage of gases, cold seeps, mud volcanos and under-water pingos, though these studies did not offer explanations of these observations (Hovland et al., 2005; Krylova et al., 2011; Rybakova et al., 2013; Sen et al., 2018).

4.1.3. Basin stations

Deeper locations of the CBL were characterized by lower biomass (trawl samples), density and species richness (ROV but not trawl samples), as well as different benthic community composition from the shallower ridge and plateau stations. Such changes with depth are in agreement with other studies (e.g. Southern Ocean: Linse et al., 2007; Arctic: Soltwedel et al., 2009; Sswat et al., 2015) and knowledge on bathymetric trends in global deep-sea faunal communities (Rex et al., 2006).

High proportional abundance of mobile swimming polynoid annelids and the sea cucumber *Elpidia* sp. was characteristic for the basin stations. The identified subfamily Pelagomacellicephala is characteristic of deeper waters (Levenstein, 1978; Uschakov, 1982) including the Arctic Basin (Bluhm et al., 2005; MacDonald et al., 2010). High abundance of holothurians is also typical for deep-sea communitiesboth elsewhere (Billett et al., 2001; Brandt et al., 2007) and in the Arctic (e.g. MacDonald et al., 2010). Both taxa are mobile, a useful trait allowing these taxa to respond fast to seasonally and spatially changing food input in polar deep seas (Iken et al., 2005; MacDonald et al., 2010).

Sponges were also prominent at basin stations in terms of densities and biomass (trawl samples), as well as proportional abundance (ROV samples). Indeed, sponges often occur in abyssal benthos (Barthel and Tendal, 1993) and as well as submarine canyons (Schlacher et al., 2007), the east Greenland slope (Mayer and Piepenburg, 1996), and the Angola Basin in the SE Atlantic (Kröncke et al., 2013). Sponges found in basins of the CBL were mainly the polymastiids *Radiella sol* and *Polymastia* sp. growing in a mud-dominated environment. Though Polymastiidae have previously been found to colonize hard substrate (Mayer and Piepenburg, 1996; Buhl-Mortensen et al., 2015), some develop root like structures, cement small particles of sediments to create their own hard substrate or use small sized hard substrate (Barthel and Tendal, 1993). The variable feeding strategies of deep-sea sponges such as suspension feeding (e.g. Witte et al., 1997), taking up dissolved organic matter (de Goeij et al., 2008), and carnivory (Vacelet, 2006; Ereskovsky and Willenz, 2007) might allow them to survive in oligotrophic conditions of the Arctic deep sea.

Among the most abundant taxa of the basin stations also was the common Arctic deep-sea anthzoan *Bathyphellia* cf *margaritacea*, which was found almost everywhere in the study area. The species' flexible choice of substrata (Sanamyan et al., 2009; Schulz et al., 2010) might be a reason for its wide destribution across the study area.

4.2. Environmental factors

In the CBL, depth was among the main environmental factors significantly affecting epifaunal community structure, species richness, numerically important taxa, density and biomass. This is in accordance with other studies reporting depth zonation in epifaunal community composition (Mayer and Piepenburg, 1996; Piepenburg et al., 1996; Piepenburg and Schmid, 1996; Sswat et al., 2015), and decreases in density, diversity and biomass with depth (e.g. synthesized by Bluhm et al., 2011). These changes are likely indicative of changes in environmental factors co-varying with depth (e.g., food availability, sediment composition, temperature and salinity change) (Soltwedel et al., 2009; Sswat et al., 2015).

Food availability and presence of hard substrate (stones) were the factors affecting epifauna across habitats and also contributing most to the difference between eastern and western parts of the CBL. Quality and quantity of food was previously described as the most important factor structuring deep-sea benthic communities (Soltwedel et al., 2009; Wei et al., 2010; Kröncke et al., 2013). The main source of organic matter for benthic deep-sea organisms is derived from the upper water layers (e.g. Smith et al., 2009), and benthic availability of food is strongly linked to depth, seasonality and presence of sea ice in the Arctic (e.g. Bluhm et al., 2015). Indicators of organic matter availability within sediments (benthic pigments) measured in this study suggested very low organic matter content across the study area and low-quality food for benthic organisms (Table 1). The higher benthic pigment concentrations at Northwind Ridge was probably due to organic matter transported here from the productive Chukchi shelf, which is located closest to the Northwind Ridge station. This transport is mediated through the nutrient-rich Pacific-origin water abundant in the eastern part of the Northwind Ridge in the upper ~225 m (McLaughlin et al., 2004). While pigment concentration is a point-in-time measurement largely depending on the time of sampling, long-term trends in organic carbon supply are often more closely reflected in community characteristics of macrobenthos such as density (Renaud et al., 2008) that correlates well with production regimes in upper water masses and vertical carbon flux due to their limited mobility (Grebmeier et al., 2006). Indeed, order of magnitude higher densities of macrobenthos were observed at the Northwind Ridge station compared to other stations (S. Hardy, Univ. of Alaska Fairbanks, unpublished data), along with the higher abundance of sessile Ampharetidae and Sabellidae worms in our study. The majority of epifaunal taxa, however, did not respond to the potentially higher food supply by elevated abundance or biomass at that station. This is consistent with previous epifaunal studies on the Chukchi shelf and Greenland Sea slope (Mayer and Piepenburg, 1996; Bluhm et al., 2009; Ravelo et al., 2014), where total organic content and pigment concentration were less correlated with epifauna than other environmental factors. Detectability of pelagic-benthic coupling is lower for epifaunal than sessile/less mobile macrofaunal organisms because the higher mobility of epifaunal organisms allows them to move to food patches diluting the spatial coupling (Bluhm et al., 2009).

(Drop)stones are known to support complex epifaunal communities and enhanced faunal diversity compared to the surrounding soft bottom deep-sea environment (Soltwedel et al., 2009; Meyer et al., 2016; Ziegler et al., 2017). They are often colonized by encrusting and sessile fauna like cnidarians, crinoids, barnacles, sponges (Brandt et al., 2007; MacDonald et al., 2010; Schulz et al., 2010; Meyer et al., 2016). This habitat enhancement was also indicated in our study, where species richness was positively correlated with the number of stones. The most abundant taxon associated with stones in our study was a sessile coronate polyp (morphotype 10; section 4.1.1). Mobile fauna (e.g., arthropods and brittle stars in our study) in the vicinity of stones are likely feeding on organic matter produced by the dropstone community (MacDonald et al., 2010; Schulz et al., 2010).

Finally, grain size composition also affected epifaunal community composition in the CBL, which is in accordance with, for example, studies from the Chukchi Sea where the importance of sediment grain size for epibenthic distribution and taxon richness has been shown (Feder et al., 1994; Bluhm et al., 2009). Although sediments grain size composition of the CBL actually varied little the highest mud content was observed in basins and the highest sand fraction on the Northwind Ridge. This pattern indicates higher current velocities at Northwind Ridge than in the basin, which was also evident by more abundant lebensspuren in the basins and higher abundance of the suspension feeding sabellid polychaetes and stalked crinoids (the latter seen in video records).

4.3. Biogeographic affinities

The biogeographic pattern of the CBL fauna was characterized by strong (over 50% of total number of species and over 70% of total abundance) dominance of species with Atlantic affinity across the entire study area. The share of species of only Pacific affinity was small at shallow stations (6% of total number of species and 1% of total abundance), and zero deeper than 850 m. Prevalence of species of Atlantic affinity in deep Arctic areas is consistent with earlier studies from the Beaufort Sea (Ravelo, Bluhm, Foster, Iken, unpubl. data), Arctic Basins and Norwegian and Greenland Seas (bivalves, though in the Canada basin, endemic species were more important; Krylova et al., 2013). This pattern reflects the current geomorphology, bathymetry and oceanography, as well as the evolutionary history of the Arctic Ocean, including changes in geological settings and glaciation events over time (e.g. reviewed in papers of Bluhm et al., 2011; Jirkov, 2013; Petryashov et al., 2013; Renaud et al., 2015).

The near absence of Pacific taxa might be explained by a limited connection to the Pacific Ocean. The deep-water connection between the Arctic and Pacific oceans closed 80–100 million years ago (Dunton, 1992). Currently, the Arctic Ocean connects to the Pacific via the shallow Bering Strait (around 50 m deep), which partly acts as a barrier for dispersal of benthic organisms adapted to deep water. On the contrary, the more saline, denser Atlantic water dominates in the Arctic deep sea with the only deep-water connection to the Arctic via Fram Strait (about 2500 m deep). The water mass distribution and circulation pattern strongly contribute to dominance of Atlantic affinity species over Pacific affinity in the study area.

Additional possible underlying reasons for the observed biogeographic pattern are the multiple glaciation events during the Pleistocene, an asymmetry in glacial ice cover, and the consequent reinvasion of fauna in the Atlantic and Pacific parts of the Arctic (Nesis, 1984; Vermeij, 1991; Briggs, 2003; Nesis, 2003; Maggs et al., 2008; also reviewed by Dilman, 2009). The Pacific Arctic shelves were only partly glaciated, providing refugia and allowing fauna to survive and maintain their presence on the shelf (Nesis, 1984, 2003; Maggs et al., 2008). After the glaciations, the Pacific Arctic was reinvaded by the fauna from the shallow refugia and through the shallow Bering Strait, which explains why most of the current Pacific species are stenobathic and therefore almost absent from the CBL. On the Atlantic side of the Arctic, shelves were covered by ice down to the deep ocean (Nesis, 1984, 2003; Maggs et al., 2008). Thus, shallow water fauna on the Atlantic side of the Arctic could not survive glaciation and had to find refugia in deeper unfrozen areas or be extirpated. After the glaciation, species adapted to depth reinvaded from the Atlantic, which is a reason why we find more eurybathic fauna on the Atlantic side of the Arctic (Nesis, 1984, 2003; Fedyakov and Naumov, 1987; Maggs et al., 2008; Piepenburg et al., 2011). CBL fauna was in fact also eurybathic indicated by the fact that around 80% of the fauna used for the biogeographical analysis in our study (Table S2) is shared with Arctic shelves (Piepenburg et al., 2011; Sirenko, 2013).

5. Summary and conclusions

Our results suggest taxon richness, biomass and density of epifauna decrease with depth in the CBL leading to marked differences between basin and plateau/ridge communities. These changes were mainly driven by depth. No statistically significant differences in community metrics were observed between ridge and plateau stations. Regional differences in numerically dominant taxa, however, were recorded between western and eastern ridge/plateau stations, which were attributed to differences in food supply and hard substrate availability. The majority of epifaunal species of the CBL were of Atlantic-boreal affinity documenting stronger biogeographic influence of Atlantic than Pacific waters on CBL communities. In addition, the study contributes to the yet incomplete biodiversity inventory of the Arctic deep sea with at least nine species showing new distribution records and more than 16 taxa added to the previously documented species list from this area.

This documentation of the current biodiversity and community structure of Arctic deep sea fauna and its interaction with the environment is urgently needed given that the Arctic is changing due to climate change. The environmental changes most prominent in the study area include: decrease in sea ice cover with most pronounced changes in the Pacific sector of the Arctic (Perovich, 2011); decrease in sea ice thickness, much of which occurred in the CBL region (Perovich et al., 2003; Stroeve et al., 2005); increased inflow of warming Atlantic water into the Pacific Arctic (Shimada et al., 2004; McLaughlin et al., 2011); and the rising volume of fresher and warmer Pacific water inflow reaching the Chukchi shelf (Woodgate and Aagaard, 2005; Woodgate et al., 2010). It is anticipated that these changes, along with effects such as acidification, atmospheric changes, and potentially increased human impact, might significantly affect community composition, diversity and functioning of the Arctic ecosystems in the future. For example, a shift in benthic species composition (Grebmeier et al., 2006); decrease in diversity of ice-associated taxa (Melnikov et al., 2001); northward faunal range expansion of fishes (Mueter and Litzow, 2008), decrease in phytoplankton cell size in the Canada Basin (Li et al., 2009) and increased primary production across much of the Arctic Ocean (Arrigo et al., 2008) have been documented. These observations are based on time series and are therefore mostly restricted to shallow areas. The lack of Arctic deep-sea data restrict the evaluation of biological responses to large-scale change in the Arctic environment. In order to provide adequate answers concerning how Arctic deep-sea ecosystems will change, long-term observations are needed. Currently, the HAUSGARTEN observatory in Fram Strait is the only Arctic deep-sea research observatory, where biological and physical parameters are being documented. Response to environmental change may vary between Atlantic and Pacific parts of the Arctic deep sea. Thus, placement of a long-term observatory in the Pacific sector of the Arctic deep sea that includes measurement of environmental and biological parameters at different trophic levels is advisable. We suggest the CBL is an ideal location for this purpose because of the prominent climate-related alterations in that region which could act as a Pacific counterpart to the Atlantic HAUSGARTEN long-term observatory.

Contribution of authors

KI and BB conceived the study idea, KI obtained the funding for field work, KI and IZ conducted the field work. IZ conducted the image analysis with input by BB, PR and KI, IZ conducted the data analysis and most writing with all authors participating in data interpretation and article preparation., All authors have approved the final article.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2019.06.011.

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Paper II

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Functional Pattern of Benthic Epifauna in the Chukchi Borderland, Arctic Deep Sea

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Assessment of Arctic deep-sea ecosystem functioning is currently an urgent task considering that ongoing sea-ice reduction opens opportunities for resource exploitation of yet understudied deep-sea regions. We used Biological Trait Analysis to evaluate ecosystem functioning and test if common paradigms for deep-sea fauna apply to benthic epifauna of the deep-sea Arctic Chukchi Borderland (CBL). We also investigated the influence of environmental factors on the functional structure of the epifauna. The analysis was performed for 106 taxa collected with a beam trawl and a Remotely Operated Vehicle from 486 to 2610 m depth. The most common trait modalities were small-medium size, mobile, benthic direct and lecithotrophic larval development, and predatory feeding, which mostly supports the current view of epifauna in the global deep sea. Functional composition of epifauna differed between two depth strata (486–1059 m and 1882–2610 m), with depth and sediment carbon content explaining most of the functional variability. Proportional abundances of the modalities free-living, swimming, suspension feeders, opportunists/scavengers, internal fertilization and globulose were higher at deep stations. Functional redundancy (FR) was also higher there compared to the mid-depth stations, suggesting adaptation of fauna to the more homogeneous deep environment by fewer and shared traits. Mid-depth stations represented higher functional variability in terms of both trait modality composition and functional diversity, indicating more variable resource use in the more heterogeneous habitat. Food input correlated positively with the proportional abundance of the modalities tube-dwelling, sessile and deposit feeding. Areas with drop stones were associated with higher proportional abundance of the modalities attached, upright, and predators. Comparatively low FR may render the heterogeneous mid-depth area of the CBL vulnerable to disturbance through the risk of loss of functions. Across the study area, high occurrence of taxa with low dispersal ability among adult and larval life stages may prevent rapid adaptation to changes, reduce ability to recolonize and escape perturbation.

Keywords: Arctic deep sea, benthic epifauna, biological trait analysis, functional composition, ROV

Abbreviations: CBL, Chukchi Borderland; FD, functional diversity; FR, functional redundancy.

INTRODUCTION

The deep ocean floor covers around 65% of the surface of the earth, yet it is the least explored ocean habitat. While we have begun to identify trends in deep-sea biodiversity patterns such as mid-depth peaks and latitudinal declines in diversity, and a generally higher level of rarity and endemism compared to shelf communities (Levin et al., 2001; Stuart et al., 2003; Renaud et al., 2006; Rex and Etter, 2010; Bluhm et al., 2011), still little is known about functional characteristics of deep-sea ecosystems. This is a serious gap, because deep-sea regions experience increasing anthropogenic influences (e.g., deep-sea fisheries, oil and gas exploration, mining, marine debris), and are at the same time subjected to the influences of climate change, in particular in polar regions (Smith et al., 2008; Ramirez-Llodra et al., 2011; Levin and Le Bris, 2015; Tekman et al., 2017). These impacts may bring changes in environmental properties, biodiversity and functioning of deep-sea ecosystems (Danovaro et al., 2008; Levin and Le Bris, 2015; Sweetman et al., 2017). Understanding of the current state of deep-sea ecosystem functioning and assessing its potential vulnerability to human impact and climatic changes is, thus, essential.

In contrast to shallower marine ecosystems, the deep sea is generally thought to be a more stable environment with constantly low bottom water temperature (typically, 0.01–4°C, but down to sub-zero values in the Arctic), high pressure, and low current velocity and resuspension (e.g., Gage and Tyler, 1991; Thistle, 2003; Tyler, 2003; Sweetman et al., 2017). More than 75% of the sea floor is covered by visually homogeneous abyssal plains, interrupted by geological structures such as ridges, canyons, hydrothermal vents, and cold seeps that add substantial heterogeneity to the habitat, biota and processes (Ramirez-Llodra et al., 2010; Levin and Le Bris, 2015). Deep-sea benthic communities are driven to a large extent by the amount of energy provided to the system from surface production (Iken et al., 2001, 2005). Only ∼0.5–2% of the surface production typically reaches the deep-sea floor and by that time is dominated by heavily reworked detrital organic material (Fischer et al., 2000; Ramirez-Llodra et al., 2010). Food limitation is particularly extreme in the central Arctic basins where the high latitude and seasonal or permanent sea ice control light penetration into the upper water column, and stratification limits the availability of nutrients during the short productive seasons (Leu et al., 2015; Randelhoff and Guthrie, 2016). Consequently, primary production in the oligotrophic Arctic basins is low (typically 1–15 g C m^{-2} year^{-1}) with low levels of vertical flux of generally $\leq$1 g C m^{-2} year^{-1} below 120 m depth, and often less than half of that reaching the deep-sea floor (Wiedmann et al., 2020). These levels are considerably lower than other deep-sea areas, where pelagic primary production is highly variable, but often exceeds 20–50 g C m^{-2} year^{-1} (Karl et al., 1996; Levin and Gooday, 2003; Emerson, 2014).

Environmental conditions shape the biological characteristics of deep-sea benthic communities. Early studies suggested that benthic "associations governed by constantly limited food availability are composed of small individuals on the average" (size-structure hypothesis, Thiel, 1975). Indeed, recent studies confirmed that organisms of comparatively smaller size dominate at greater depth (Rex et al., 2006; Wei et al., 2010), though organisms of all sizes can inhabit the benthic environment in the deep sea (e.g., Billett et al., 2001; Ruhl and Smith, 2004; Bluhm et al., 2011; Rybakova et al., 2019). Low food availability and quality on the deep-sea seafloor, and low ambient current velocity are typically reflected in high proportions of deposit-feeding fauna (Iken et al., 2001, 2005; Bergmann et al., 2009). While suspension feeders, predators and scavengers are also represented in the deep sea (e.g., Premke et al., 2006; Cartes et al., 2008; Bergmann et al., 2009; Zhulay et al., 2019), suspension feeders tend to be less frequent due to the generally low currents and thus low amount of suspended material (Thistle, 2003), and low frequency of predators likely is due to low densities of prey (e.g., Thistle, 2003; Bluhm et al., 2011). In addition, scarce food may result in a dominance of mobile taxa that are more efficient in finding food (Iken et al., 2001; Thistle, 2003; Boetius et al., 2013) than sessile taxa that can only be supported in regions with enough particle flux and stronger currents (Degen, 2015). Both pioneering and recent studies suggested that deep-sea benthic fauna present a rich assortment of reproductive modes and life-history traits, including direct development, brooding, lecithotrophic, and planktotrophic larvae (Mosely, 1880; Thorson, 1950; Pearse and Lockhart, 2004; Arellano and Young, 2009; Bennett et al., 2012; Berecoechea et al., 2017; Martinez and Penchaszadeh, 2017; Lauretta et al., 2020; Rivadeneira et al., 2020).

In summary, based on the current literature, the general view of the typical deep-sea fauna is one of taxa of small size, non-sessile, often deposit feeding and developing either directly or indirectly. These and other biological characteristics of species, also referred to as traits (Bremner et al., 2005), can be used to assess ecosystem functioning, that is the maintenance and regulation of ecosystem processes (Naeem et al., 1999), including organism-environment interaction (Bremner et al., 2006; Degen et al., 2018). Seafloor fauna are heavily involved in ecosystem processes such as consumption and transfer of organic matter to higher trophic levels, organic matter decomposition, nutrient renewal, productivity and habitat provision (e.g., Danovaro et al., 2008; Loreau, 2008; Thurber et al., 2014). These processes depend, directly or indirectly, on morphological, behavioral and life history traits that species exhibit in a community (Usseglio-Polatera et al., 2000; Bremner et al., 2003; Oug et al., 2012). Thus, an assessment of these traits can provide a deeper insight into functional structure and variation than is possible with a taxonomic description of a community alone (Bremner et al., 2003; Petchey and Gaston, 2006; van der Linden et al., 2012; Pomerleau et al., 2015). Biological trait analysis (BTA) (cf. Bremner et al., 2003) can assess functional characteristics of a given community as well as ecosystem vulnerability through metrics such as functional diversity (FD) (i.e., diversity of trait categories called modalities), and functional redundancy (FR) (i.e., a measure of the degree to which species exhibiting the same trait modalities (Bremner et al., 2003; Petchey and Gaston, 2006; van der Linden et al., 2012). Studies investigating Arctic ecosystem function using the BTA approach have advanced our understanding of functional structure of benthic communities

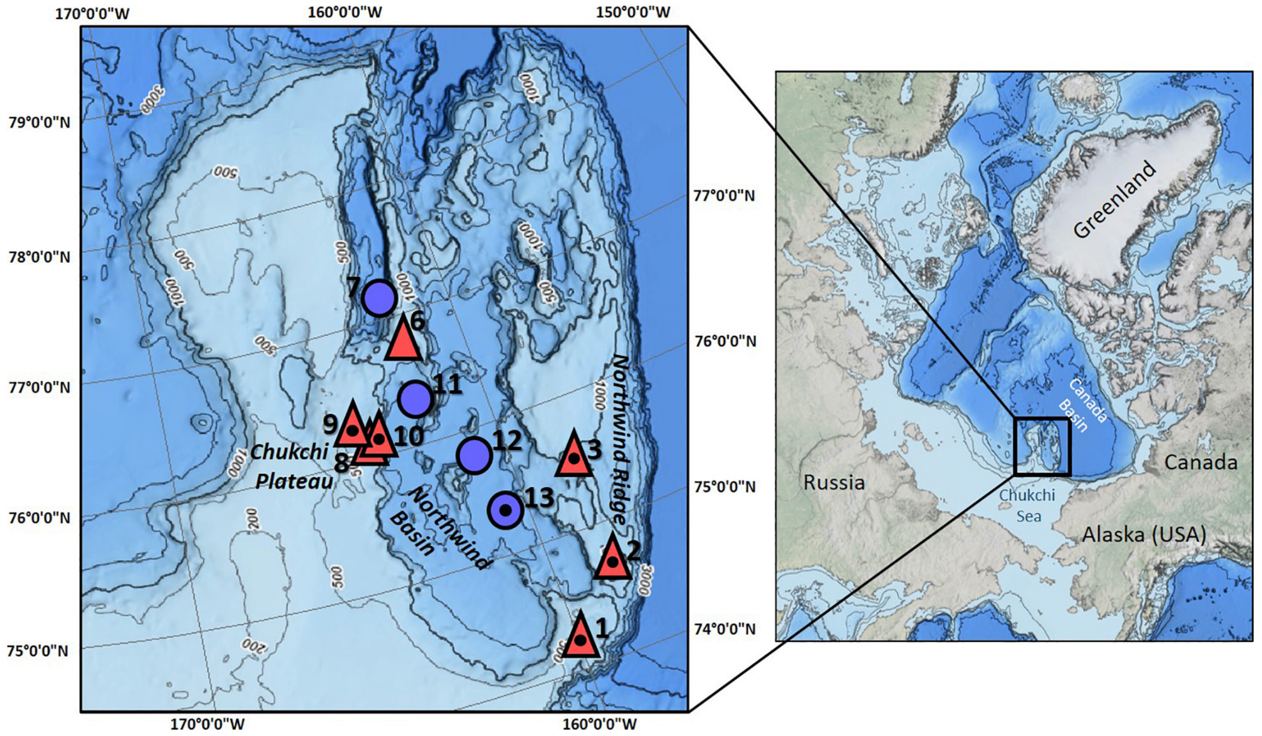

FIGURE 1 | Study area and stations sampled in the Arctic Chukchi Borderland. Red triangles are mid-depth stations, blue circles are deep stations; numbers in bold print are station numbers; small numbers along isobaths indicate water depth. All stations were sampled by ROV, except station 3. Stations that were additionally sampled by trawl are indicated by a dot inside of the triangle/circle.

mostly on the shelves and for macrofauna (i.e., mostly infaunal taxa $\geq$0.5 or 1 mm) (Cochrane et al., 2012; Krumhansl et al., 2016; Kokarev et al., 2017; Rand et al., 2018), while few studies have so far focused on biological traits of epifaunal megafauna (i.e., invertebrates and demersal fish on top of the sediment and typically $\geq$ ca. 5 mm) (Sutton et al., 2020) or deep ecosystems (Degen, 2015; Liu et al., 2019). Functional patterns have not been examined for epifaunal communities anywhere in the Arctic deep sea.

The goal of this study was, therefore, to characterize Arctic deep-sea epifauna using a biological traits approach in the Chukchi Borderland (CBL) in the Amerasian Arctic deep sea, an area of complex habitats created by plateau and ridge areas at mid-depths, surrounding or bordering deeper basins (Jakobsson et al., 2008). Specifically, the objectives of the present study were to: (1) identify dominant trait modalities represented in the epifauna of the study area; (2) describe variability in functional structure of epifaunal communities between mid-depth (plateau and ridge) and deeper (basin) areas; and (3) identify environmental factors influencing the functional structure of epifaunal communities in the study area. We tested the following hypotheses: (1) current deep-sea paradigms suggesting that deep-sea benthic communities are dominated by small-sized, non-sessile deposit-feeders or scavengers, with equal representation of direct and indirect development, hold true for the epifauna in the CBL; and (2) given that environmental conditions change with depth, there is a difference in functional structure between mid-depth and deep communities. Specifically, we proposed that (a) trait-modality composition changes with depth strata; (b) the more heterogeneous mid-depth habitats provide higher diversity of niches reflected in higher FD, while the more homogeneous deep-basin stations are likely to have lower FD but higher FR; and (c) depth, food availability and food quality strongly influence distribution of trait modalities across the study area.

MATERIALS AND METHODS

Study Area and Field Sampling

The community composition data underlying this study were collected in the CBL, north of Alaska (7–78°N, 158–165°W) onboard USCGC *Healy* in July–August 2016 (**Figure 1**). The CBL extends from the Chukchi shelf into the Canada Basin, covering a depth gradient from ~300 to 3000 m. It consists of the Northwind Ridge and Chukchi Plateau where stations were grouped as "mid-depth" (486–1059 m), and of the isolated Northwind Basin where stations were grouped as "deep" (1882–2610 m) (**Figure 1** and **Table 1**; Jakobsson et al., 2008; Mayer et al., 2010). Waters of Arctic, Atlantic, and Pacific origins interact in the CBL study area with Pacific-origin water comprising the Polar Mixed Layer and upper halocline (McLaughlin et al., 2004; Steele et al., 2004; Woodgate, 2013). The lower halocline is of Atlantic origin, arriving from Fram Strait and the

TABLE 1 | Station information for ROV images and beam trawl samples collected in the Arctic Chukchi Borderland.

Stations group/ station number		Depth, m	Latitude, °N	Longitude, °W	Temperature, °C	Bottom salinity, PSU	Mean sediment Phaeo, μg pigment/g dry sediment	Mean sediment Chl, μg pigment/g dry sediment	Sediment organic carbon,%	Mean C/N ratio	Mud,%	Gear	Number of images analyzed
Mid-depth*	6	486	77.06	−161.82	0.70	34.84	0.15	0.02	0.63	3.90	97	ROV	98
	9	508	76.59	−163.98	0.48	34.85	0.20	0.02	0.78	5.51	99	ROV, Trawl	180
	8	557	76.63	−164.06	0.41	34.86	0.19	0.02	0.98	6.52	99	ROV	39
	3	746	75.64	−158.82	0.28	34.86	0.09	0.01	0.81	6.92	96	Trawl	
	1	853	74.32	−159.42	0.07	34.87	0.77	0.10	1.26	7.98	93	ROV, Trawl	100
	10	873	76.43	−163.47	0.06	34.84	0.24	0.03	0.88	5.90	95	ROV, Trawl	69
	2	1059	74.71	−158.48	−0.05	34.88	0.30	0.04	1.14	8.11	96	ROV, Trawl	80
Deep**	11	1882	76.40	−162.26	−0.29	34.92	0.19	0.02	1.09	6.81	98	ROV	79
	13	2091	75.40	−160.73	−0.29	34.92	0.27	0.03	1.25	8.05	100	ROV, Trawl	80
	12	2107	75.93	−161.45	−0.28	34.92	0.19	0.02	1.13	7.15	99	ROV	80
	7	2610	77.07	−162.53	−0.30	34.93	0.12	0.01	0.77	4.85	98	ROV	99

Stations are listed by increasing depth. Note the low number of images for station 8 was due to limited bottom time. The high number of images for station 9 is due to two stations (9a and 9b) being combined.

**Mid-depth stations are within the Atlantic Water layer (salinity 33.5–34.9 PSU) and range in depth between 486 and 1059 m.*

***Deep stations are within Deep Water layer (salinity ≥34.9 PSU) and range in depth between 1882 and 2610 m.*

Barents Sea (Woodgate and Aagaard, 2005). Underneath it and characterizing the "mid-depth" stations is the Atlantic water layer (McLaughlin et al., 2004; Woodgate et al., 2007; Bluhm et al., 2015), while "deep" stations are in the Arctic Ocean deep-water layer originating from the Greenland Sea and spreading across the Eurasian Basin to the Canada Basin (Bluhm et al., 2015).

Epifauna (including invertebrates and demersal fishes) was sampled with the ROV Global Explorer (Oceaneering International), which performed a photographic survey of the seafloor at ten stations (**Table 1**), as described in Zhulay et al. (2019). 24-megapixel still images were collected with a downward-looking DSSI DPC-8800 digital camera along transects every 5–8 s. Four digital laser pointers, one located at each corner of a fixed distance of a 10-cm square, served as a size reference for the imaged area and size of organisms at four stations (stations 1, 6, 7, and 8), after which they stopped functioning. In addition, epifauna was sampled with a single trawl sample at six stations (stations 1, 2, 3, 9, 10, and 13, **Table 1**) using a 3.05 m modified plumb staff beam trawl (Abookire and Rose, 2005) equipped with a 7 mm mesh net with 4 mm in the cod end. Ca. 30 min hauls at ∼1.5 knots speed over ground were taken with bottom time estimated from a time depth recorder (Star Oddi) affixed to the net. Organisms were sorted, identified to the lowest possible taxonomic level, and counted. Select taxonomic vouchers were further identified by expert taxonomists (see section "Acknowledgments") and taxon names were verified using WoRMS (http://www.marinespecies.org/, on September 10, 2020). The proportional abundance of each taxon was then calculated for each trawl station.

At each station, near-bottom water temperature and salinity were measured with a SBE9/11 + CTD at ∼20 m above the bottom. Sediment surface samples (0–1 cm) from box core samples were taken and frozen at −20°C for later determination of grain size composition, carbon and nitrogen content, and concentration of sediment chlorophyll *a* and phaeopigments (Zhulay et al., 2019). Sediment grain size was analyzed from samples pre-treated with HCl and H_2O_2, to remove calcium carbonate and organic material, on a Beckman Coulter Particle Size Analyzer LS 13320 at the Geology Laboratory of UiT The Arctic University of Norway in Tromsø. Sediment organic carbon and nitrogen (%) were determined on a Costech ESC 4010 elemental analyzer at the stable isotope facility at the University of Alaska Fairbanks (UAF). The C/N ratio, an indicator of food quality with higher values indicating lower food quality (e.g., Dorgelo and Leonards, 2001; Iken et al., 2010), was then calculated for each station. Concentrations of sediment chlorophyll *a* and phaeopigments (μg pigment/g dry sediment) were measured on a Turner Designs TD-700 fluorometer after pigment extraction with 5 ml of 100% acetone for 24 h in the dark at −20°C at UAF. The fluorescence of the sample was read before and after acidification with HCl (final concentration of HCl was 0.003 N) for determination of phaeopigments (Arar and Collins, 1997; Jeffrey and Welschmeyer, 1997).

Image Analysis

A subset of the useable ROV images of the sea floor were manually analyzed from each station (39–180 per station, 940 images in total) (**Table 1**, Zhulay et al., 2019). Image processing and analyses were performed with the ImageJ[1] (Rasband, 2009). Taxa were identified to the lowest possible level based on a combination of morphological features visible on the ROV imagery, the voucher collection from trawls, and additional identifications by taxonomic experts (see acknowledgments). Taxa that could not be identify were excluded from this analysis due to difficulties related to assigning trait modalities to these organisms. All taxa present on the images were counted per image and proportional abundance of taxa per station was calculated. Rocks larger than two cm were counted and the average number

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[1] https://imagej.nih.gov/ij/

of rocks per picture was included in the statistical analyses as an environmental factor.

Biological Traits

Nine commonly used traits represented by a total of 39 modalities were chosen for the present analysis following established definitions by Bremner et al. (2006), Costello et al. (2015), Degen et al. (2018), and Sutton et al. (2020) (**Table 2**). The traits reflected morphology (adult size, body form), behavior (living habitat, mobility, adult movement, feeding habit, substrate affinity) and life-cycle characteristics (larval development and reproduction) (**Table 2**; reviewed by Martini et al., 2020a). For the purpose of this study, modalities of larval development trait were based on the published concept for Arctic traits analysis (Degen and Faulwetter, 2019) that assumes that planktotrophs disperse farther than lecithotrophs although many exceptions are known to occur in the deep sea (Young, 2003). Every trait was coded for every taxon identified based on: (1) observations made from trawl-collected material during the cruise and/or from ROV images (i.e., traits directly measured *in situ*, also referred as realized traits, c.f. Martini et al., 2020a) for size, body form, adult movement, living habit, and substrate affinity or (2) information inferred from published literature (referenced in **Supplementary Table 1**), online traits databases (e.g., polytraits, Faulwetter et al., 2014; the Arctic Traits Database, Degen and Faulwetter, 2019) and relevant web pages (e.g., FishBase[2], Sea Life Base[3]) (i.e., traits acquired from other sources, also referred as potential traits, c.f. Martini et al., 2020a) for the rest of the traits. The size of organisms was measured on board from specimens collected at each station in the trawl samples or from the ROV images with the ImageJ software (Rasband, 2009). Size measurements from ROV images were possible at the four stations where the digital laser pointers were functioning and where the positioning of a given organism was suitable for those measurements. The average adult size of a given species across all stations was used for the analysis. As information about biology and behavior of many epifaunal taxa in the Arctic deep sea remains limited or is at times non-existent at the species level, coding of these taxa was conducted based on information available for closely related species in the same genus or family (following, e.g., Faulwetter et al., 2015; Rand et al., 2018; Sutton et al., 2020). In a few cases, modalities common at even higher taxonomic rank (such as direct development in Peracarida) were applied. For coding a "fuzzy coding" procedure (Chevenet et al., 1994) was used, resulting in a "traits by taxon" matrix (**Supplementary Table 2**). The "fuzzy coding" procedure allows taxa to be coded with multiple modalities to different degrees using a 0–3 code, with 0 indicating no affinity, 1 and 2 indicating partial affinity, and 3 indicating the highest affinity for a given modality. This approach was proposed to account for variation encountered within a species (Chevenet et al., 1994) and when incorporating information from species in the same genus or family (Charvet et al., 2000). While including higher taxonomic levels may introduce uncertainty to the results, their suitability has been documented for biological traits analysis as well as taxonomic community analysis, especially in multivariate analyses that showed that the functional structure of communities could be conserved (Bournaud et al., 1996; Bowman and Bailey, 1997; Dolédec et al., 1998). To give the same weight to each taxon and trait, the fuzzy codes (0–3) were converted to proportions for each trait modality totaling to 1 (e.g., Bolam et al., 2017).

A total of 106 invertebrate and fish taxa were used for BTA, of which 53 taxa occurred in the ROV images and 77 taxa in trawls with 26 taxa common to both sampling gears. In addition to the "traits by taxon" matrix, "taxa by stations" (i.e., presence/absence of taxa or proportional abundances of taxa at each station) and "traits by stations" (i.e., trait composition at each station, obtained by multiplying the "taxa by stations" and "traits by stations" matrices and indicated by presence/absence or proportional abundance weighted scores) matrices were generated (following Beauchard et al., 2017; Degen et al., 2018). Three "taxa by stations" (**Supplementary Tables 3–5**) and three "traits by stations" (**Supplementary Tables 6–8**) matrices were compiled for subsequent analysis: presence/absence of taxa based on ROV and trawl samples combined across all stations, and one each with proportional abundances acquired from either ROV or trawl samples. Proportional abundance was chosen over absolute abundance due to the above-mentioned failure of the laser pointers that made it impossible to calculate absolute abundances for all ROV stations. Proportional abundance was also used for trawl samples for consistency.

Data Analysis

To test our first hypothesis, namely that epifaunal organisms in the CBL are predominantly small-sized, non-sessile deposit-feeders or scavengers with equal representation of direct and indirect development, we included the four traits: size, larval development, adult movement and feeding habit. The "traits by stations" matrix was used to test this hypothesis; it was based on presence/absence data of taxa collected with both the ROV and the trawl (**Supplementary Table 6**).

To test the second hypothesis, namely that a difference in functional structure exists between mid-depth and deep communities, all nine traits were used. To investigate differences in the overall functional composition of epifauna and visualize potential differences between these two depth strata, we applied a fuzzy correspondence analysis (FCA, Chevenet et al., 1994). FCA is an extension of a regular correspondence analysis that is suitable for fuzzy coded traits data of discrete variables (Chevenet et al., 1994). FCA is based on the "traits by stations" matrix (**Supplementary Tables 7, 8**) and identifies and visualizes traits and their modalities contributing most to the difference in the functional structure among stations (Bremner et al., 2006), and provides correlation ratios of each trait along the fuzzy principal axes, representing the amount of variance of a certain trait modality explained by a given axis (Chevenet et al., 1994). Correlation ratios greater than 10% were considered as the traits contributing most to variation among the stations following Conti et al. (2014). A Kruskal–Wallis test was used to test for significant differences in proportional abundance of trait modalities between mid-depth and deep stations using

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[2] www.fishbase.org

[3] http://www.sealifebase.org

TABLE 2 | Overview of traits and their modalities used in the present paper.

Trait	Modality	Modality code	Definition
Size	Small (<10 mm)	S1	<10 mm
	Small-medium (10–50 mm)	S2	10–50 mm
	Medium (50–100 mm)	S3	50–100 mm
	Medium-large (100–300 mm)	S4	100–300 mm
	Large (>300 mm)	S5	>300 mm
Body Form	Globulose	BF1	Round or oval
	Vermiform	BF2	Worm-like or thin, elongate body form
	Dorsoventrally compressed	BF3	Flattened from dorsal and ventral sides
	Laterally compressed	BF4	Flattened from side to side
	Upright	BF5	Upstanding, vertical
Reproduction	Asexual	R1	Budding and fission
	Sexual-external fertilization	R2	External fertilization, eggs and sperm deposited on substrate or released into water (broadcast spawners)
	Sexual-internal fertilization	R3	Internal fertilization, but no brooding, eggs deposited on substrate, indirect or direct development
	Sexual-brooding	R4	Internal or external fertilization, eggs or larvae are brooded, indirect or direct development
Larval development	Planktotrophic	LD1	Generally pelagic for several weeks, larvae feed and grow in water column
	Lecithotrophic	LD2	Shorter larval period, larvae with yolk sac pelagic or benthic
	Direct	LD3	Direct development (i.e., no larva), benthic[1]
Living habit	Free-living	LH1	Not limited to any restrictive structure at any time. Able to move freely within and/or on the sediments
	Crevice dwelling	LH2	Inhabit crevices in coarse/rock substrate and/or biogenic substrate
	Tube dwelling	LH3	Inhabit tubes
	Burrowing	LH4	Inhabit permanent or temporary burrows in the sediment, or burrow in the sediment
	Epizoic	LH5	Live on or in other organisms
	Attached	LH6	Adherent to a substratum
Adult movement	Sessile/none	MV1	No movement as adult
	Burrower	MV2	Movement in the sediment
	Crawler	MV3	Movement along on the substratum via movements of its legs, appendages or muscles
	Swimmer	MV4	Movement above the sediment
Mobility	None	MO1	No movement as adult
	Low	MO2	Slow movement
	Medium	MO3	Medium movement
	High	MO4	High movement, swimmer or fast crawler
Feeding habit	Surface deposit feeder	FH1	Active removal of detrital material from the sediment surface
	Subsurface deposit feeder	FH2	Removal of detrital material from within the sediment matrix
	Filter/suspension feeder	FH3	Capture and ingestion of food particles suspended in water
	Opportunist/scavenger	FH4	Use different types of food sources/feeds on dead organic material
	Predator	FH5	Preying (hunting or killing) upon other organisms
	Parasite/commensal/symbiotic	FH6	Obtain nourishment and shelter on or in another organism (a host) with a harm to the host/without significant harm to a host/with mutual benefit from an interaction
Substrate affinity	Soft	SA1	Sand or mud
	Hard	SA2	Rocks, gravel
	Biological	SA3	Epizoic or epiphytic life style
	None	SA4	Hyper-benthos

Slightly adjusted from Bremner et al. (2006), Degen et al. (2018), Costello et al. (2015), and Sutton et al. (2020).

[1] *Brooders of juveniles are included here.*

the "traits by stations" matrix from ROV data (**Supplementary Table 7**). Only one trawl sample was available from deep stations preventing statistical comparisons.

We then visualized which of the available environmental variables explained most of the variation in the functional structure of the epifaunal communities using a canonical correspondence analysis (CCA) performed on the "traits by stations" matrices for ROV (**Supplementary Table 7**) and trawl (**Supplementary Table 8**) samples. For environmental data, we included water depth, bottom water salinity and temperature, grain size composition, number of rocks in ROV images, concentration of benthic pigments in sediment (phaeopigments

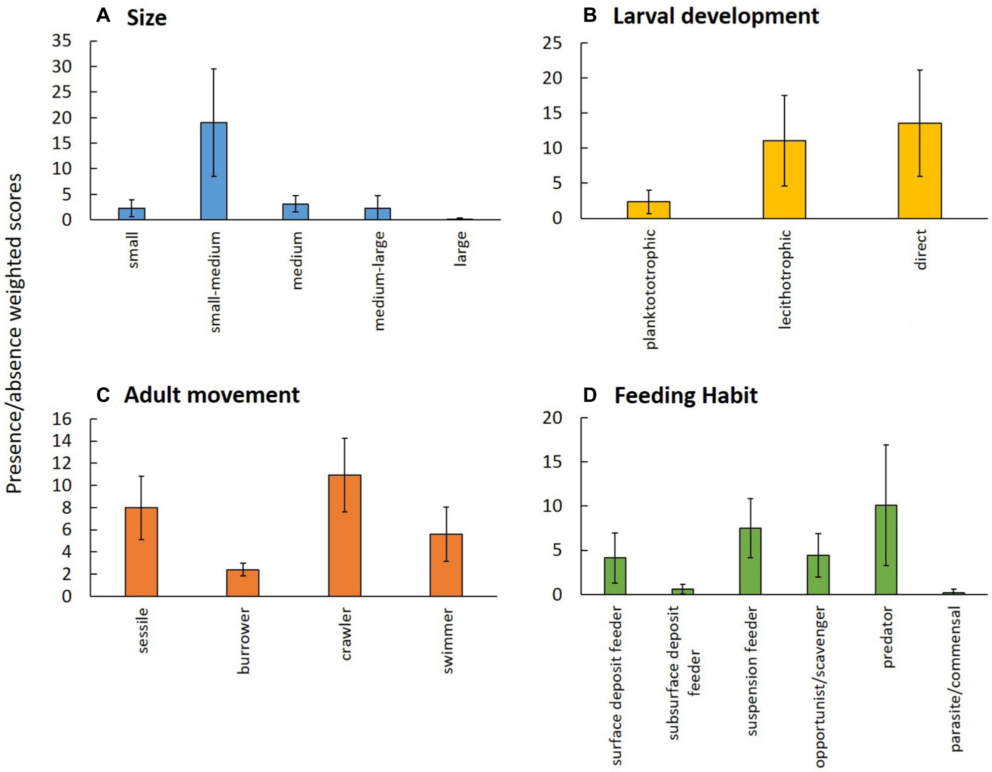

FIGURE 2 | Occurrence of trait modalities based on presence/absence of taxa for combined ROV and trawl data of epibenthos from the Chukchi Borderland and averaged across all stations ± SD; **(A)** body size, **(B)** larval development, **(C)** adult movement, and **(D)** feeding habit; note that *y*-axes have different scales. Trait modalities are defined in **Table 2**.

and Chl *a*), carbon content in sediment, and C/N ratio. A forward selection procedure was used to identify environmental variables explaining most of the variability in the trait-by-station data. These variables were then used in the model, whereas other factors were overlaid on the plots as passive factors. The significance of the models and environmental variables were tested with Monte Carlo permutation tests (Oksanen et al., 2013).

As part of hypothesis two, we tested for differences in functional diversity and redundancy between depth strata for both ROV and trawl-based data. FD was estimated using Rao's quadratic entropy (Rao's Q), which is a measure of trait dissimilarity (Rao, 1982; Botta-Dukát, 2005). Rao's Q ranges from 0 to 1, where 0 means low FD (i.e., communities are the same in their biological trait profiles) and 1 means high FD (i.e., communities are unique in their biological trait profiles) (Van der Linden et al., 2016). FD was calculated based on the "traits by taxon" (**Supplementary Table 2**) and "taxa by stations" (**Supplementary Tables 4, 5**) matrices.

FR is the relationship between FD and species diversity (Ricotta et al., 2016), and was calculated as the ratio of FD to the taxonomically based Simpson index (D, calculated using equation (1)).

$$D = 1 - ((\Sigma n(n-1)/N(N-1)), \tag{1}$$

where n is the total number of organisms of a particular species, and N is the total number of organisms of all species. In order to obtain a regularly increasing index, the formula was converted to: 1–(FD/D) (Van der Linden et al., 2016). FR defines to which degree different species represent the same ecosystem functions (Petchey and Gaston, 2006; de Bello et al., 2007) and ranges from 0, where all species have different trait-categories, to 1, meaning all species display the same trait-categories (de Bello et al., 2007). A Kruskal–Wallis test was used to check for significant differences in FD and FR between mid-depth and deep ROV stations.

All statistical analyses were performed using the software R (R Core Team, 2017) with the package ade4 (Dray and Dufour, 2007) for the FCA and calculation of FD index, and the package vegan (Oksanen et al., 2013) for the CCA analyses. A schematic representation of the hypotheses tested and methods used to test the hypotheses, along with figure and table numbers representing results of the tests, is given in the **Supplementary Figure 1**.

RESULTS

Trait Modality Composition

The body size modality "small-medium" was the most frequent in the epifauna across the study area, while size "large" was rarest

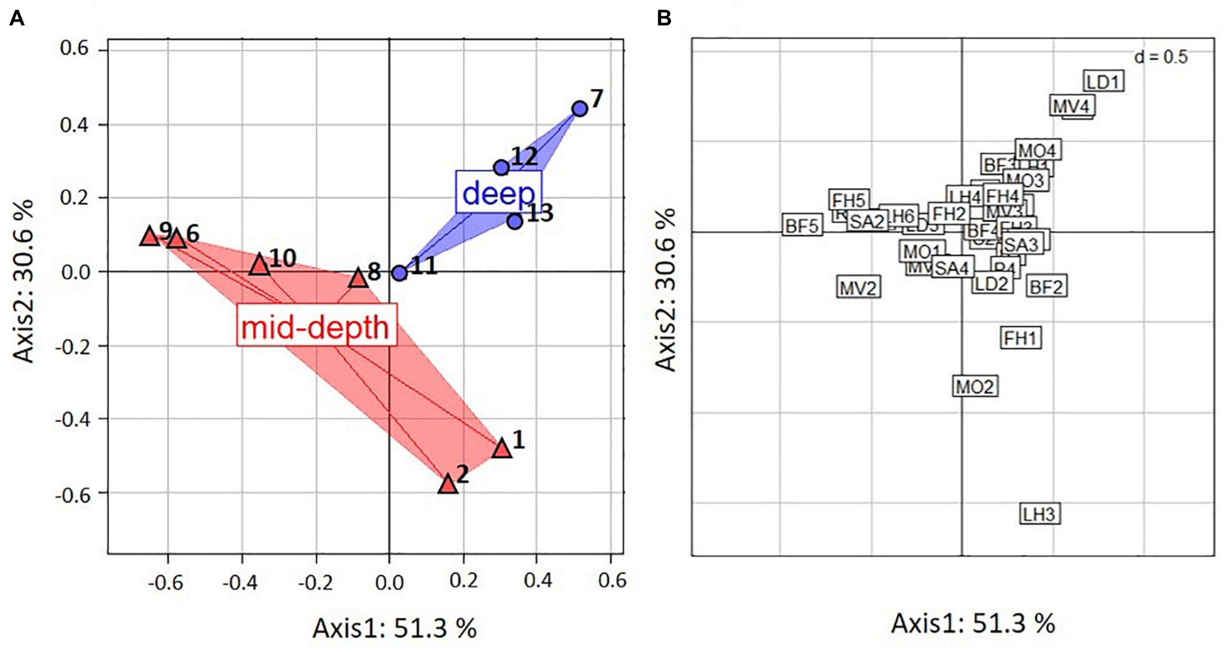

FIGURE 3 | Results of fuzzy correspondence analysis (FCA) on the biological traits of epifauna from the Chukchi Borderland weighted by taxa proportional abundances from ROV samples, **(A)** ordination by stations, where numbers are station numbers, **(B)** ordination by traits, where trait modality codes are abbreviated by two letter-one number combinations and explained in **Table 2**. Red – mid-depth stations. Blue – deep stations.

(**Figure 2A**). The most frequent larval development was "direct" followed by "lecithotrophic," while the occurrence of the modality "planktotrophic" was much lower (**Figure 2B**). Non-sessile adult movement modalities combined were more frequent than sessile forms. Individually, "crawlers" were dominant, though "sessile" was second most frequent and since this study focused on epifauna, "burrowers" were expectedly least frequent in the data set (**Figure 2C**). Feeding habit "predators" was most frequent, followed by "suspension feeder." The least frequent modalities of feeding habit were "parasite/commensal" and "subsurface deposit feeder" (**Figure 2D**).

Functional Structure of Epifaunal Communities

The FCA showed substantial variation in functional composition across all stations. The first two axes of the FCA accounted for 81.9% of the variability in distribution of trait modalities, with 51.3% for the first and 30.6% for the second axis (**Figure 3A**). Most of the variation along the first axis was explained by body form (BF) (31%), reproduction (R) (20%), living habit (LH) (14%), feeding habit (FH) (18%), and substrate affinity (SA) (19%) (**Table 3**).

Trait modality composition generally differed between mid-depth and deep stations (**Figure 3A**). Deep stations 7, 12, and 13 were located on the upper right hand side of the FCA plot and corresponded to higher proportional abundance of modalities "swimming" (MV4), "sexual-internal fertilization" (R3) and "planktotrophic larval development" (LD1) (**Figures 3A,B**). Mid-depth stations 6, 9, and 10, located on the lower left hand side of the FCA plot, were characterized by higher proportional abundance of "upright body form" (BF5), affinity for hard substrate (SA2) and "predators" (FH5) (**Figures 3A,B**). Variation along the second axis was driven mostly by living habit (LH) (32%) and mobility (MO) (10%) (**Table 3**). These traits separated mid-depth stations 1 and 2 from the rest of the stations (**Figure 3A**), and the two stations were characterized by higher proportional abundance of modalities "low mobility" (MO2), "sessile" (MV1), "deposit feeding" (FH1), and "tube-dwelling" (LH3) (**Figure 3B**). Deep station 11 and mid-depth station 8 were not differentiated from the remaining stations based on the traits used. In general, results for the trawl

TABLE 3 | Correlation ratios of each biological trait on the first two axes of the fuzzy correspondence analysis for ROV samples of epibenthos in the Chukchi Borderland.

Traits	Axis 1	Axis 2
Size	0.06	<0.01
Body form	**0.31**	0.06
Reproduction	**0.20**	0.06
Larval development	0.09	0.09
Living habit	**0.14**	**0.32**
Adult movement	0.09	0.09
Mobility	0.08	**0.10**
Feeding habit	**0.18**	0.07
Substrate affinity	**0.19**	<0.01

Correlation coefficients higher than 10% are in bold.

TABLE 4 | Results of Kruskal–Wallis test comparing proportional abundance of modalities at deep and mid-depth stations for ROV data of epibenthos in the Arctic Chukchi Borderland.

Trait modalities	p-value	Trait modalities	p-value
S1	0.20	MV1	0.06
S2	0.20	MV2	–
S3	0.21	MV3	0.06
S4	0.83	MV4	0.03*
S5	–	MO1	0.14
BF1	0.03*	MO2	0.03*
BF2	0.39	MO3	0.06
BF3	0.39	MO4	0.03*
BF4	0.52	FH1	1
BF5	0.02*	FH2	0.67
R1	0.14	FH3	0.03*
R2	0.67	FH4	0.03*
R3	0.01*	FH5	0.14
R4	0.67	FH6	–
LD1	0.06	SA1	0.20
LD2	0.83	SA2	0.13
LD3	0.09	SA3	0.45
LH1	0.03*	SA4	0.64
LH2	–		
LH3	0.01*		
LH4	0.29		
LH5	–		
LH6	0.39		

Asterisks indicate significant results ($p \leq 0.05$). Trait modalities are defined in ***Table 2****.*

data supported those from the ROV (**Supplementary Figure 2** and **Supplementary Table 9**). The difference was that higher proportional abundance of modalities "sessile" (MV1) and "small size" (S1) was observed at the single deep trawl station, while mid-depth trawl stations were characterized by high proportional abundance of modalities "free-living" (LH1), "crawlers" (MV3), "dorsoventrally compressed" (BF3), and "medium size" (S3) (**Supplementary Figure 2**).

Results of the Kruskal–Wallis test indicated significant differences between mid-depth and deep stations for body form (BF), feeding habit (FH), reproduction (R), and lifestyle and mobility traits [adult movement (AM), living habit (LH), and mobility (MO)]. Deep stations were characterized by significantly higher proportional abundance of the body form "globulose" (BF1), feeding habits "suspension feeder" (FH3) and "opportunist/scavenger" (FH4), reproduction "sexual-internal fertilization" (R3), and higher proportional abundance of "free-living" (LH1), "highly mobile" (MO4), and "swimmer" (MV4) modalities (Kruskal–Wallis test; **Table 4** and **Figure 4**). Mid-depth stations had significantly higher proportional abundance of the body form "upright" (BF5), living habit "tube-dwelling" (LH3), and mobility "slow movement" (MO2) (Kruskal–Wallis test; **Table 4** and **Figure 4**). The Kruskal–Wallis test was not run on trawl data because only one deep station was sampled by trawl, but boxplots for the trawl data indicated generally similar patterns to those from the ROV data. Differences included higher proportional abundance of modalities "attached" and "sessile" at the single deep trawl station than at deep ROV stations, and higher proportional abundance of modalities "free-living" and "crawling" at the mid-depth trawl stations (**Supplementary Figure 3**).

Significantly lower FD and higher FR were found for deep ROV stations compared with mid-depth stations ($p = 0.03$ for both, **Figure 5**). Though the lack of station replication prevented statistical analysis for the trawl samples, the trends in FD and FR were similar to the ROV results, though the difference in FD and FR between the two depth strata was less distinct (**Supplementary Figure 4**).

Environmental Factors Influencing Functional Structure of Epifaunal Communities

Results of the CCA for the ROV samples showed that depth and sediment organic carbon content were the most important factors explaining variability in the distribution of trait modalities (**Table 5**). These environmental factors explained 64% of the total variation. Depth was positively associated with "dorsoventrally" compressed (BF3) and "globulose" (BF1), "internal fertilization" (R3), "free-living" (LH1), "swimming" (MV4), and "suspension-feeding" (FH3), modalities (**Figure 6**). High carbon content was positively associated with the modalities "vermiform" (BF2), "sexual-external fertilization" (R2), "sexual-brooding" (R4), "tube-dwelling" (LH3), and "surface deposit-feeding" (FH1) (**Figure 6**).

Results of the CCA for trawl samples also indicated depth as the most important factor influencing the functional composition of epifaunal communities, with temperature also being a significant factor (**Supplementary Table 10**). Both factors were used to constrain the CCA, resulting in 92.9% of the total variation explained. In contrast to the ROV data, depth was positively associated with "sessile" (MV1) and "attached" (LH6), and substrate affinity "hard" (SA2). Temperature was positively associated with "predators" (FH5) and "opportunist/scavenger" (FH4) modalities, and substrate affinity "biological" (SA3) (**Supplementary Figure 5**).

DISCUSSION

Trait Modalities Composition Across the Deep-Sea CBL

Body size of organisms affects many ecological functions including energy and nutrient cycling, and secondary production (Degen et al., 2018). One of the most common characteristics of deep-sea benthos is the small size of most species (Rex and Etter, 1998). Our study results are consistent with this paradigm and hence with our hypothesis, in that the second smallest (small-medium size, 10–50 mm) organism category had the highest occurrence, while large organisms ($\geq$50 mm) had the lowest occurrence in epifaunal communities across the CBL. Low occurrence of the smallest size category is unsurprising given that we targeted epibenthic megafauna (typically $\geq$10 mm).

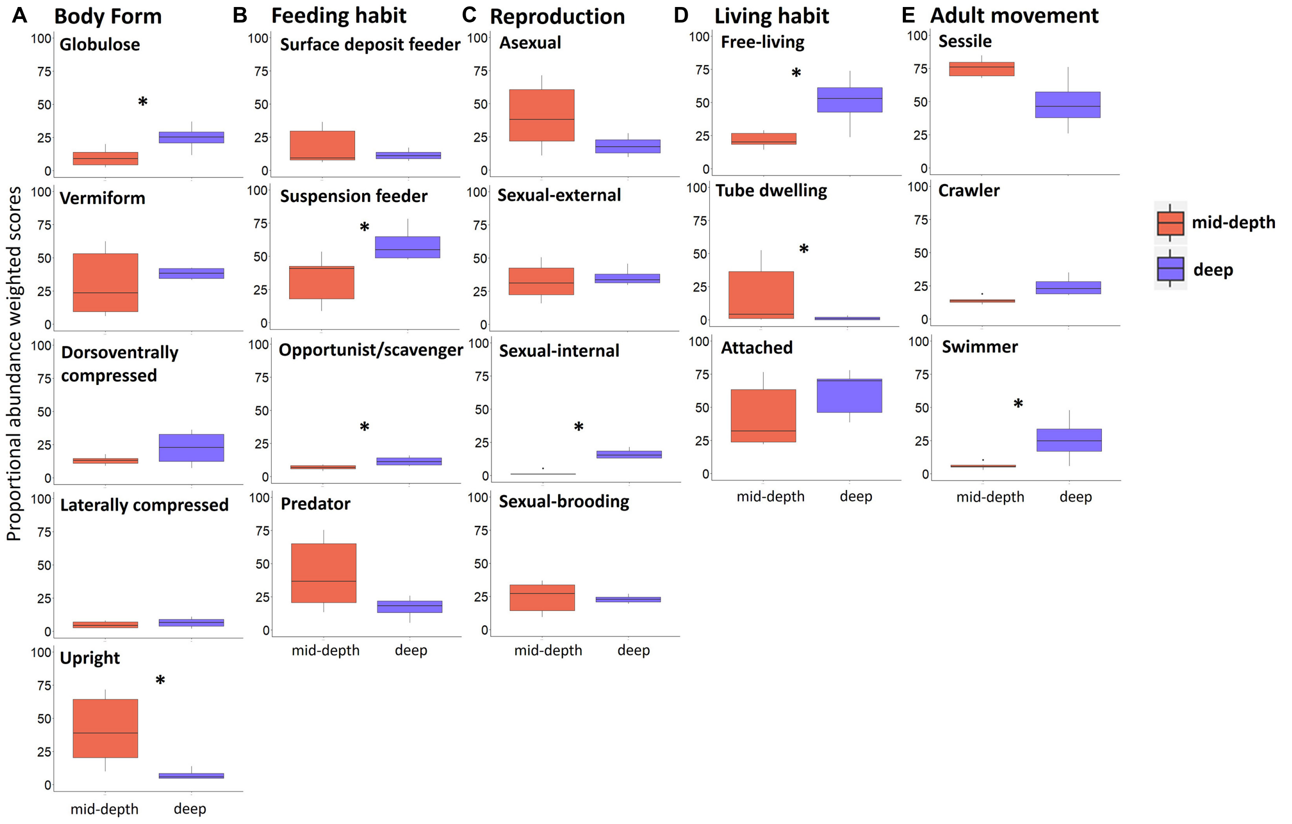

FIGURE 4 | Boxplots comparing modalities of different traits (weighted by proportional abundance) for mid-depth (in red) and deep stations (in blue) based on ROV samples of epifauna from the Chukchi Borderland; **(A)** body form, **(B)** feeding habit, **(C)** reproduction, **(D)** living habit, and **(E)** adult movement. Note traits with significant difference between depth strata and traits contributing most to variability among stations based on the Fuzzy Correspondence Analysis results are shown; modalities of these traits with low proportional abundance are not shown. Asterisks indicate significant difference between mid-depth and deep stations ($p < 0.05$, Kruskal–Wallis test). Trait modalities are defined in **Table 2**.

A series of studies reporting reduced average body size with depth for deep-sea meiofauna (Soltwedel et al., 1996; Soetaert et al., 2002; Kaariainen and Bett, 2006) and macrofauna (Rex et al., 1999; Kaariainen and Bett, 2006) generally support Thiel's size-structure hypothesis (Thiel, 1975) for these groups. This decrease in body size with depth has also been found for epifauna (Rex et al., 2006; Wei et al., 2010). Opposite to this trend, some deep-sea taxa with larger body sizes than in shallow areas have also been documented (Rex and Etter, 1998), in some cases resulting in gigantism. This phenomenon, often attributed to low temperature and high oxygen availability that causes slow growth rate and longevity (Shirayama and Horikoshi, 1989), has been found for deep-sea isopods, amphipods, pycnogonids, ostracods, and anemones (Timofeev, 2001; Danovaro et al., 2014) but in our study, only the very large pycnogonid *Colossendeis proboscidea* could fit this concept.

Overall, we confirm our hypothesis that the majority of epifauna found in our study was non-sessile; most were crawlers but swimmers were also found. Not unexpectedly, burrowers were less common, given the focus of the study was epifauna. As a consequence of the ability to move organisms can escape from disturbance (natural or anthropogenic), disperse or migrate (Beauchard et al., 2017; Degen and Faulwetter, 2019) and increases the chance of finding scarce and patchy food compared to sessile or less mobile organisms. Still, movement rates of epibenthic megafauna are generally lower in the deep sea compared to shelves (Thistle, 2003; Ruhl, 2007). For example, deep-sea brittle stars and holothurians move at 1–3 cm min^{-1} and 1–2 cm min^{-1}, respectively, compared with 15–45 cm min^{-1} and 7 cm min^{-1}, respectively, in shallow waters (summarized in Thistle, 2003). When stimulated, for example by food, however, many deep-sea animals can move faster (Premke et al., 2006; MacDonald et al., 2010; Taylor et al., 2016). For example, we observed unusual swimming behavior in the brittle star *Ophiostriatus striatus*, perhaps an adaptation to access patchy food falls (Boetius et al., 2013). ROV observations such as ours, hence, increase our often scarce knowledge of traits of deep-sea taxa. Besides mobile taxa, we did also find an unexpectedly high occurrence of the modality sessile in our study, especially obvious in ROV imagery. Sessile taxa in our study area, including ascidians, sponges, stalked cirripedes and crinoids, and zoanthid and nephtyid cnidarians were in part present on the numerous drop stones providing hard substrate for these organisms (Zhulay et al., 2019).

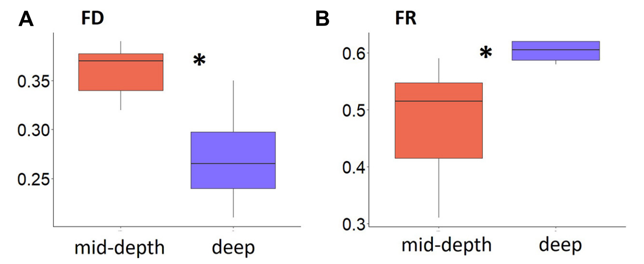

FIGURE 5 | Boxplot of functional diversity indices for epifauna from the Chukchi Borderland, **(A)** Functional Diversity (FD) (represented by Rao's Q) and **(B)** Functional Redundancy (FR) for mid-depth and deep ROV samples. Asterisks indicate significant differences between mid-depth (red) and deep (blue) stations ($p < 0.05$, Kruskal–Wallis test). Note the scales of the *y*-axes are different.

TABLE 5 | Results of canonical correspondence analysis using Monte-Carlo permutation test, performed on a traits by stations matrix for ROV samples of epibenthos in the Arctic Chukchi Borderland.

	p-value	*F*-value
Full model (depth + carbon)	0.001***	6.10
Depth	0.001***	7.40
Carbon	0.002**	4.79

*Asterisks indicate statistical significance (**$p \leq 0.01$, ***$p \leq 0.001$).*

Trophic structure of the Arctic benthic deep-sea communities is poorly studied (but see Iken et al., 2005), though feeding habits influence energy flow, nutrient cycling, secondary production, organic matter decomposition, and nutrient regeneration (Bremner, 2008; Degen et al., 2018). We do know that the major food source is organic detritus originating mostly from the upper productive zone (Fabiano et al., 2001; Thistle, 2003). This organic material often undergoes strong transformation while sinking, decreasing nutritional value and particle size (Thistle, 2003). The paradigm that deposit feeding is among the best strategies to collect and process this organic detritus efficiently (Thistle, 2003) has indeed been supported for both macrofaunal and megafaunal deep-sea communities (Kröncke, 1998; Iken et al., 2005; Rex and Etter, 2010). The deposit feeders were also common yet not dominant in our study area, only partly confirming our hypothesis. Predators and suspension-feeders, however, were more common among our epifaunal taxa. This is contrary to a trend of decreasing proportions of predatory asteroid and gastropod species with depth (Carey, 1972; Rex et al., 1990). Our findings, however, are in agreement with other studies that found that predation is in fact common in oligotrophic seas or in areas with little food input (Kröncke and Türkay, 2003; Wieking and Kröncke, 2003; Vacelet, 2008), and are supported by high nitrogen isotope values in certain taxa of our study area (Iken et al., 2005). One theory states that prey can be more easily detected in the deep sea compared to shallow water environments, as "flow in the benthic boundary layer is slow and thus chemical gradients and pressure waves produced by prey should be more persistent and provide better information for prey location" (Thistle, 2003). Facultative predation is even known for specific deep-sea species of, for example, sponges (Vacelet, 2006; Godefroy et al., 2019; Martini et al., 2020b), and bivalves (Morton, 2016; Morton and Machado, 2019), suggesting feeding modes may be unusual, highly plastic and require more study. A stable isotope-based assessment for the study area is ongoing and will provide more clarification of the species' feeding modes and trophic levels.

The high occurrence of suspension feeding taxa among the CBL epifauna was initially surprising. Higher current and particle fluxes, proving food for suspension feeders, tend to occur on elevations and slopes (Clark et al., 2010) including the Chukchi Slope Current in the CBL (Corlett and Pickart, 2017) and were suggested to provide food for suspension feeders from the nearby Chukchi shelf to the Northwind Ridge (Bluhm et al., 2005). In addition, suspension feeders on the above-mentioned drop stones can extend above the substrate and into the benthic boundary layer, where the currents are slightly faster and carry food particles (Vogel, 1996). Besides on stones, some taxa (in particular anthozoans) were elevated above the seafloor in other ways, namely either on stalks of crinoids or polychaete tubes or, in the case of most hormathiid anemones (*Hormathia* spp., *Allantactis parasitica*) on gastropod shells (usually *Colus* spp.).

Scavengers were also represented in the study area, although not as highly occurring as reported in some deep-sea areas including the Eurasian Arctic (Klages et al., 2001; Premke et al., 2006). It is unsurprising that parasites/commensals were the least occurring feeding type in the study area given our study focused on epifaunal megafauna of which few are parasitic. Smaller external and internal parasites are in fact occurring in Arctic megafauna, especially in demersal fish (Klimpel et al., 2006), but were invisible on the ROV images. We did encountered taxa such as ribbon worms, isopods and sea leeches, which generally contain parasitic forms on fishes and arthropods (Køie, 2000; Mantelatto et al., 2003; Ravichandran et al., 2009), but we did not observe them on a potential host. Commensalism was encountered for some hormatiid anemones attached to shells of gastropods, a widespread strategy increasing probability of contact with food particles, while providing protection to the host (Buhl-Mortensen et al., 2015). Similar commensal relationships were observed for other anthozoans and the amphipod *Amathillopsis spinigera* that were often found in association with sessile tubeworms and stalked crinoids. Clearly, more research is needed on parasitic and commensal biotic interactions in the deep-sea.

Little is known about larval development in the Arctic Ocean in general. Recent molecular studies, however, have documented the presence of pelagic larvae of more species than previously acknowledged for the Arctic (Ershova et al., 2019) and the deep sea (Kersten et al., 2019), and detailed studies in the deep sea have added species-specific observations (e.g., Mercier and Hamel, 2008; Martinez and Penchaszadeh, 2017; Montgomery et al., 2017). This trait is important for ecological functions such as dispersal, recolonization, recovery, tolerance to stress, and link between pelagic and benthic realms (Degen and Faulwetter, 2019). In the present study, direct development dominated as a single modality, yet given the sparse species-specific literature, generalizing this conclusion

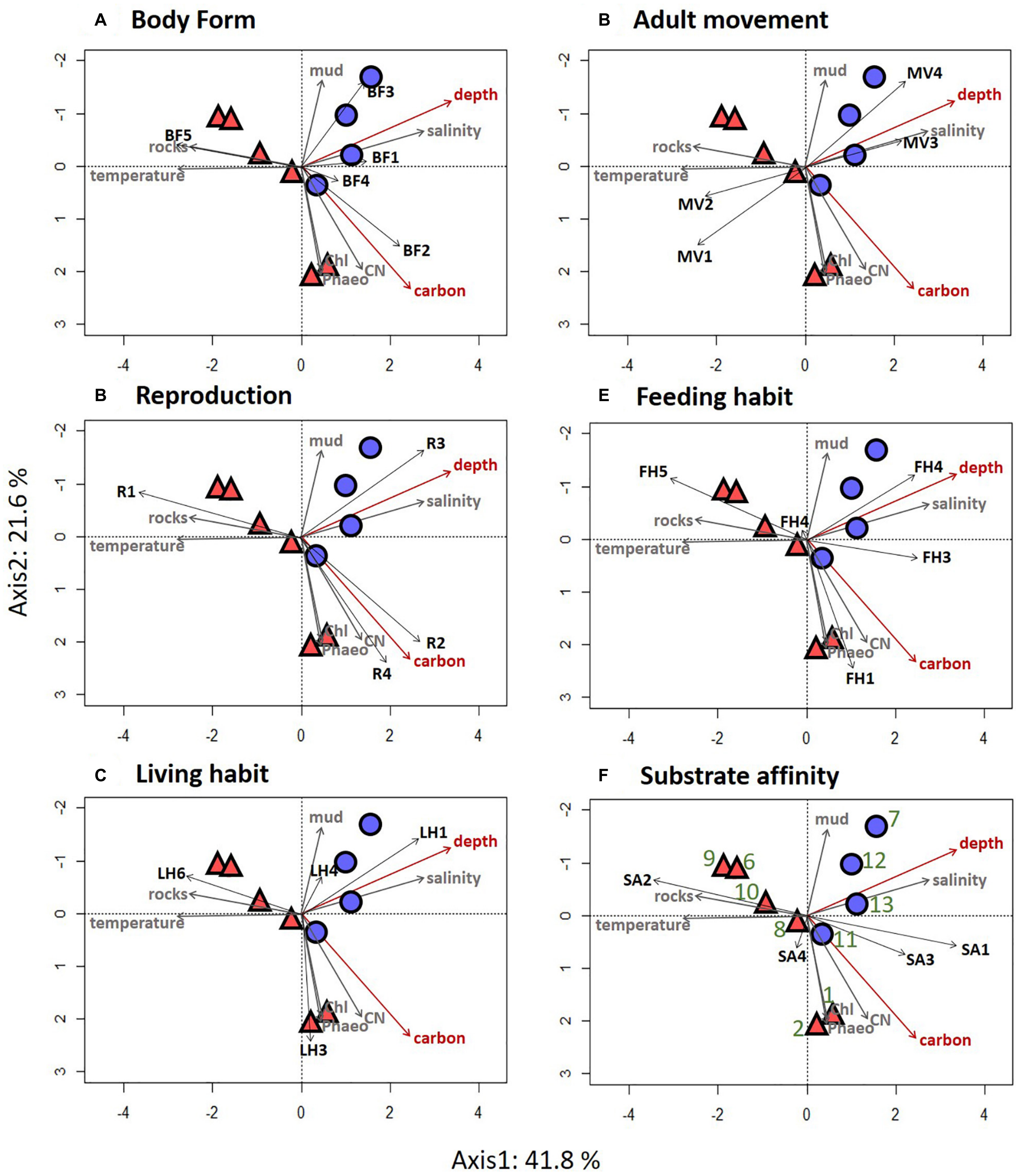

FIGURE 6 | Results of the canonical correspondence analysis (CCA) performed on the traits by stations matrix for ROV data of the epifauna from the Chukchi Borderland. Traits identified as most important in the Fuzzy Correspondence Analysis are presented; **(A)** body form, **(B)** reproduction, **(C)** living habit, **(D)** adult movement, **(E)** feeding habit, and **(F)** substrate affinity. Passive environmental factors are overlain on the figure panels in gray color; environmental factors in red are those that were used to constrain the CCA. Mid-depth stations are present in red triangles and deep stations are present in blue circles. Station numbers are identified in green on the last CCA plot. Trait modality codes are abbreviated by two letter-one number combinations and explained in **Table 2**.

for the Arctic is premature. Nevertheless, advantages of this development type include, for example, protection from various unfavorable environmental conditions in the pelagic realm and settling on unfavorable substrate, and experiencing little planktonic predation. Most important for the deep sea, juveniles are less dependent on either limited or variable food availability (Mileikovsky, 1971). Yet indirect development, including planktotrophic and lecithotrophic larvae, was almost equally prevalent in the epifaunal taxa of our study area, which, in general, supports our hypothesis. This finding is consistent with a growing number of studies documenting the occurrence of pelagic larvae in both polar waters (Schlüter and Rachor, 2001; Fetzer and Arntz, 2008; Kuklinski et al., 2013; Brandner et al., 2017; Ershova et al., 2019) and deep-sea areas (Scheltema and Williams, 2009; Kersten et al., 2019). Among larval development types, lecithotrophs were most common in our study area. This is similar to findings in the NE Greenland, the deep-sea of the NE Atlantic, and Antarctica, where more than 70% of echinoderms were found to reproduce with pelagic larvae, the majority of which were lecithotrophs (Pearse, 1994). Development with pelagic larvae allowing dispersal over broader areas is an advantage, in particular for species with limited mobility (Fetzer and Arntz, 2008; Stübner et al., 2016), which were found in high numbers in our study area. In a work by Mercier and Hamel (2008), depth-related shifts in life history strategies and a simultaneous combination of brooding and broadcast-spawning with lecithotrophic larvae were reported in a deep-sea asteroid. This finding also stresses the need to species- and habitat-specific work to help close many knowledge gaps that currently limit final conclusions on true diversity and plasticity of life-history traits in deep-sea benthos.

In summary, our investigation of functional traits of deep-sea epifauna from the CBL area generally supported our first hypothesis that small, non-sessile organisms are the most common, with a relatively equal proportion of direct and indirect (mostly through lecithotrophic larvae) development. The hypothesized predominance of deposit feeding, however, was not found in the observed species pool, though that feeding mode was more prominent in the proportional abundance-weighted data set. That modality is common in infaunal taxa, which we did not cover here (Gage and Tyler, 1991; Iken et al., 2001; Mamouridis et al., 2011). Our analysis of trait modalities highlights instead that there is no single way to live successfully under deep-sea conditions, but rather that, similar to shallower areas, multiple strategies are in fact viable.

Functional Differences Between Epifauna at Deep and Mid-Depth Stations

Trait Modality Composition at Mid-Depth and Deep Stations

Our hypothesis that functional traits of epibenthic communities would change with increasing depth in the CBL was generally confirmed. In particular, epifauna of deep stations reflecting more homogeneous habitat (Zhulay et al., 2019) had significantly higher proportional abundance of the modalities free-living, swimming, suspension feeders, opportunists/scavengers, internal fertilization and globulose compared to the mid-depth stations, which were characterized by complex habitat structure including ridges, a plateau with pockmarks, and rocks. In addition, our data also suggest that the increasing distance from the productive Chukchi shelf corresponded with spatial patterns of functionality in addition to the depth-related patterns.

The higher proportional abundance of modalities free-living and mobile/swimming at greater depths is consistent with generally decreasing food availability with increasing depth in deep-sea areas, both globally and in the Arctic (Thistle, 2003; Wiedmann et al., 2020). In the study region, this decrease is reflected in an annual POC flux on the adjacent Chukchi Sea shelf being at least an order of magnitude higher (4–166 g C m^{-2} $year^{-1}$; Grebmeier et al., 2006) than in the Northwind Abyssal plain (0.24–0.32 g C m^{-2} $year^{-1}$; Watanabe et al., 2014). Indeed, the deepest and most food limited basin station (station 7) had the highest proportional abundance of the modality swimming. Conversely, lower proportional abundance of free-living and mobile/swimming (i.e., more sessile, attached) modalities at mid-depth stations coincided with higher food availability at lower depths in general. This pattern was, however, not robust as trawl samples in fact showed a higher proportional abundance of the modality mobile at the mid-depth stations compared to the ROV data, where the modality crawling was most abundant. Mobile fauna is often caught with trawls (Brandt et al., 2016), while trawls can be less reliable in assessing density of some sessile fauna compared to ROV approach (Chimienti et al., 2018). The combination of both tools, thus, allowed us to get more comprehensive insights into the functional structure of benthic communities.

Suspension feeding was surprisingly more abundant at deeper stations in our study, where numerous persisting lebensspuren confirmed low bottom current velocity (Zhulay et al., 2019). The question arises as to what and how these organisms eat. In fact, suspension feeders are able to feed on a wide range of food items, ranging in size (from bacteria to zooplankton) and quality (Gili et al., 2001). Bacterial abundance and biomass do not decline with depth in the global ocean, thus becoming relatively more important in deeper layers (Rex et al., 2006; Wei et al., 2010) and, potentially, serving as food for benthic organisms in our study area. In addition, deep-water zooplankton communities in the Arctic Deep Water may provide a food source, though their abundances are low (less than 1 ind m^{-3}) (Kosobokova and Hirche, 2000; Kosobokova et al., 2011). Adaptations that allow suspension feeders to maximize food capture even at slow current velocity might also play a role including generating feeding currents and associations with microbial communities (Gili et al., 2001; Siegl et al., 2008; Weisz et al., 2008). Finally, little maintenance energy was documented for Antarctic deep-water sponges (Gatti, 2002). Besides suspension-feeding, proportional abundance of opportunists/scavengers was also significantly higher at greater depths. These feeding strategies become increasingly more useful with depth as scavengers have an ability to detect sparse carrion across large distances (Premke et al., 2006), while opportunists can take advantage of almost whatever they come across in the food-poor environment (Drazen and Sutton, 2017). In turn, predation and deposit feeding were more common at the mid-depth stations, with deposit feeding being the dominant modality in the trawl samples. This might point to higher availability of deposited organic matter or prey at these mid-depth stations.

Proportional abundance of the modality internal fertilization was significantly higher in the deep compared to mid-depth stations. This pattern is consistent with previous studies where internal fertilization was common (Young, 2003). In an environment where chances of finding a mate are low, internal fertilization may have a higher success rate than external fertilization once a mate has indeed been found.

In addition to the depth pattern, substantial variability found in trait modality patterns was likely related to variable distance to the productive shelf rather than to depth alone. Evidence for this effect is for example the high proportional abundance of modalities tube-dwelling, sessile and deposit feeding at mid-depths stations at Northwind Ridge (stations 1, 2), which were associated with higher food input, likely from productive waters from the Chukchi shelf, as indicated by sediment pigment values and carbon content. In the same mid-depth range, higher proportional abundance of the modality predators farther north in the study area (stations 6, 9, and 10) was associated with a high amount of drop stones, where attached and upright predators took advantage of the presence of stones and elevated themselves to increase capture of prey. Additionally, mobile predators were occasionally observed in the vicinity to the stones, likely attracted by the enhanced amount of prey attached to the stones (Zhulay et al., 2019).

Functional Metrics and Ecosystem Vulnerability at Mid-Depth and Deep Stations

Both FD and FR indices showed changes with depth, where deep stations had lower FD and higher FR compared to the mid-depth stations, supporting our hypothesis. The depth-related FD trend was in agreement with results from the Arctic Nansen Basin (Degen, 2015), but contrary to a study from the Bering Sea (Liu et al., 2019), although the direct comparison of values obtained in different studies is no appropriate due to different authors using different traits or different numbers of traits in their calculations. Since FD indicates "the range of things organisms do in an ecosystem" (Petchey and Gaston, 2006; van der Linden et al., 2012), higher FD at the mid-depth stations indicates that these communities support more diverse ecological functions than those at greater depths. It seems likely that this pattern is linked to the more heterogeneous habitat structure at mid-depth stations providing more functional niche space for epifaunal organisms compared to the more homogeneous deeper abyssal plain. In contrast, higher FR at the deeper stations is, in turn, likely related to the homogeneity of the abyssal environment to which epifauna appear to have adapted by fewer and shared trait modalities. Low FR at mid-depth stations may render these areas less resilient to ongoing and future change and potential human use as functions may be lost when species loss occurs (Loreau, 2008; Van der Linden et al., 2016), a conclusion consistent with studies on Arctic benthic macrofauna (Kokarev et al., 2017; Liu et al., 2019; Sutton et al., 2020). In addition, modalities such as sessile, attached, and upright body form at these stations point to higher vulnerability of mid-depth epifauna to predation, disturbances or decreases in food availability (Degen and Faulwetter, 2019). The higher FR at deeper stations in addition to high proportional abundance of modalities mobile/swimming might indicate lower vulnerability to disturbances, higher flexibility to perturbation, and higher ability for dispersal after disturbance (Degen and Faulwetter, 2019). It is important to note, however, this conclusion is potentially biased by low faunal densities and low sampling effort. It is, therefore, premature to conclude that deeper communities in the CBL are resilient.

In support of our second hypothesis, data indicated an overall difference in functional structure of epifauna between mid-depth and deep stations in terms of trait composition, FD, and FR. In addition, depth, carbon content in sediments (reflecting food availability), and bottom temperature (reflecting difference in water masses) were the main predictors of the functional structure of epifaunal communities, which generally supported our second hypothesis.

PERSPECTIVE AND OUTLOOK

Currently, we have limited ecological information on structure and function of deep-sea ecosystems in general, and in the Arctic Ocean in particular. Despite this lack, exploitation of Arctic deep-sea resources is now discussed widely in light of sea-ice cover decline. It is important to gain sufficient knowledge prior to any potential exploitation to assess and understand potential risk of human impacts and develop sustainable management strategies for possible resource use. The results generated in this study are, thus, very timely and can directly serve current assessments of biological and ecosystem resources and functions in the Central Arctic Ocean (CAO) by Scientific Experts on Fish Stocks of the Central Arctic Ocean (FisCAO) (fish stock assessment, Dupuis et al., 2019), the Working Group for Integrated Assessment of the Central Arctic Ocean (WGICA) (fisheries, ICES, 2020), and the International Union for Conservation of Nature (IUCN) (deep-sea mining plans and threats) (Cuyvers et al., 2018). Within FisCAO, the CBL is categorized as having fishable depth. In many places across the world's oceans the documented negative effects from seabed fishing include reduced biodiversity, body size and biomass and particularly strong effects on fragile, upright and epifaunal taxa (Wassenberg et al., 2002; Blanchard et al., 2004; Jørgensen et al., 2019; Tiano et al., 2020), and shifts toward opportunistic species (Blanchard et al., 2004). Recovery from such and other impacts can be slow (Bergman et al., 2015), especially in high latitudes where recolonization is depressed by low temperature, long live cycles and high longevity (Al-Habahbeh et al., 2020). Indeed, the presence of upright body forms in the mostly sessile species visible in our imagery, in particular at the northern mid-depth stations, indicated a vulnerability of the system to trawling, as was also suggested for example for the Barents Sea shelf (Jørgensen et al., 2019). In addition, oil and gas reserves have also been quantified in this area (Bird et al., 2008). It has been made clear that the onset of such multiple pressures in deep sea habitats results in an urgent need for biodiversity and trait-based characterization of deep-sea fauna (Costa et al., 2020), a need we directly address in the present study. Our trait-based evaluation of CBL epifauna points to potentially high sensitivity of benthic community function to disturbances especially at mid-depths as indicated by high FD and low FR. In addition, rapid climate change may have a greater impact on sessile taxa reproducing with larvae of low dispersal ability than mobile species or species with high larval dispersal (Young et al., 1997). Thus, traits analysis can offer insight into resilience and recovery capacity of taxa after disturbance.

Our study forms the first step toward filling research gaps of Arctic deep-sea system functioning and vulnerability, though study limitations include the poorly known biology of many of the taxa encountered, as well as spatially limited sampling in a heterogeneous area. We strongly recommend further study that: (a) enhances spatial and temporal coverage; (b) uses traits generated from the actual species in question, as higher taxonomic levels contain different species, which may have distinctive trait modalities (Cochrane et al., 2012; van der Linden et al., 2012); (c) includes more traits, in particular those that might be helpful to indicate potential effects of direct human impact such as trawling or climate-change related impacts such as warming and acidification on organisms (e.g., fragility, temperature tolerance, life span, skeleton); and (d) generates trait information from the area of interest as, due to plasticity of organisms, modalities can change in response to local environmental settings (Bremner, 2005).

DATA AVAILABILITY STATEMENT

The datasets generated and analyzed for this study can be found in the DataverseNO https://doi.org/10.18710/OGOAWN.

AUTHOR CONTRIBUTIONS

KI and BB conceived the study idea. KI obtained the funding for fieldwork. KI and IZ conducted the fieldwork. IZ conducted the image analysis with input by BB, PR, and KI. IZ and RD compiled biological trait information with the input by BB and KI, and conducted the statistical analysis. IZ and BB conducted most writing with all authors participating in data interpretation and article preparation. All authors have approved the final article.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.609956/full#supplementary-material

Supplementary Figure 1 | Schematic representation of the hypotheses, methods used to test the hypotheses and number of figures/tables representing results. Trait modality codes are abbreviated by two letter-one number combinations and explained in **Table 2**.

Supplementary Figure 2 | Results of the fuzzy correspondence analysis on the biological traits of epifauna from the Chukchi Borderland weighted by taxa proportional abundances from trawl samples, **(A)** ordination by stations, where numbers are station numbers, **(B)** ordination by traits, where trait modality codes are abbreviated by two letter-one number combinations and explained in **Table 2**. Red – mid-depth stations. Blue – deep stations.

Supplementary Figure 3 | Boxplots comparing modalities of different traits (weighted by proportional abundance) for mid-depth (in red) and the single deep station (grey line) based on trawl samples of epifauna from the Chukchi Borderland; **(A)** body form, **(B)** feeding habit, **(C)** reproduction, **(D)** living habit, and **(E)** adult movement. Note traits contributing most to variability among stations based on the Fuzzy Correspondence Analysis results are shown; modalities of these traits with low proportional abundance are not shown. Asterisks indicate significant difference between mid-depth and deep stations ($p < 0.05$, Kruskal–Wallis test). Trait modalities are defined in **Table 2**.

Supplementary Figure 4 | Boxplot of functional diversity indices for epifauna from the Chukchi Borderland, **(A)** Functional Diversity (FD) (represented by Rao's Q) and **(B)** Functional Redundancy (FR) for mid-depth (red) and deep trawl samples of epifauna from the Chukchi Borderland. Note the scales of the *y*-axes are different.

Supplementary Figure 5 | Results of canonical correspondence analysis performed on the traits by stations matrix for trawl data of the epifauna from the Chukchi Borderland. Traits identified as most important in the FCA analysis are presented; **(A)** body form, **(B)** reproduction, **(C)** living habit, **(D)** adult movement, **(E)** feeding habit, and **(F)** substrate affinity. Passive environmental factors are overlain on the figure panels in gray color; environmental factors in red are those that were used to constrain the CCA. Mid-depth stations are present in red triangles and deep station is present in blue circles. Station numbers are identified in green on the last CCA plot. Trait modality codes are abbreviated by two letter-one number combinations and explained in **Table 2**.

Supplementary Table 1 | Literature and other sources used to collect trait information for epifauna sampled in the Arctic deep Chukchi Borderland (also available at Arctic Trait Database: https://www.univie.ac.at/arctictraits/index.php).

Supplementary Table 2 | Traits by taxon matrix for epifauna sampled in the Arctic deep Chukchi Borderland using fuzzy coding.

Supplementary Table 3 | Presence and absence of epifaunal taxa at each station sampled in the Arctic deep-sea Chukchi Borderland with a remotely operated vehicle and a beam trawl.

Supplementary Table 4 | Proportional abundance of epifaunal taxa at each station sampled in the Arctic deep-sea Chukchi Borderland with a remotely operated vehicle.

Supplementary Table 5 | Proportional abundance of epifaunal taxa at each station sampled in the Arctic deep-sea Chukchi Borderland with a beam trawl.

Supplementary Table 6 | Traits by stations matrix based on presence/absence of epifaunal taxa sampled in the Arctic deep-sea Chukchi Borderland with a remotely operated vehicle and a beam trawl.

Supplementary Table 7 | Traits by stations matrix based on proportional abundance of epifaunal taxa sampled in the Arctic deep-sea Chukchi Borderland with a remotely operated vehicle.

Supplementary Table 8 | Traits by stations matrix based on proportional abundance of epifaunal taxa sampled in the Arctic deep-sea Chukchi Borderland with a beam trawl.

Supplementary Table 9 | Correlation ratios of each biological trait of epibenthos in the Arctic Chukchi Borderland with the first two axes of the fuzzy correspondence analysis for trawl samples ($n = 6$). Correlation ratios higher than 10% are in bold.

Supplementary Table 10 | Results of canonical correspondence analysis using Monte–Carlo permutation test, performed on a trait by station matrix for trawl samples of epibenthos in the Arctic Chukchi Borderland. Asterisks indicate significant results ($p \leq 0.05$).

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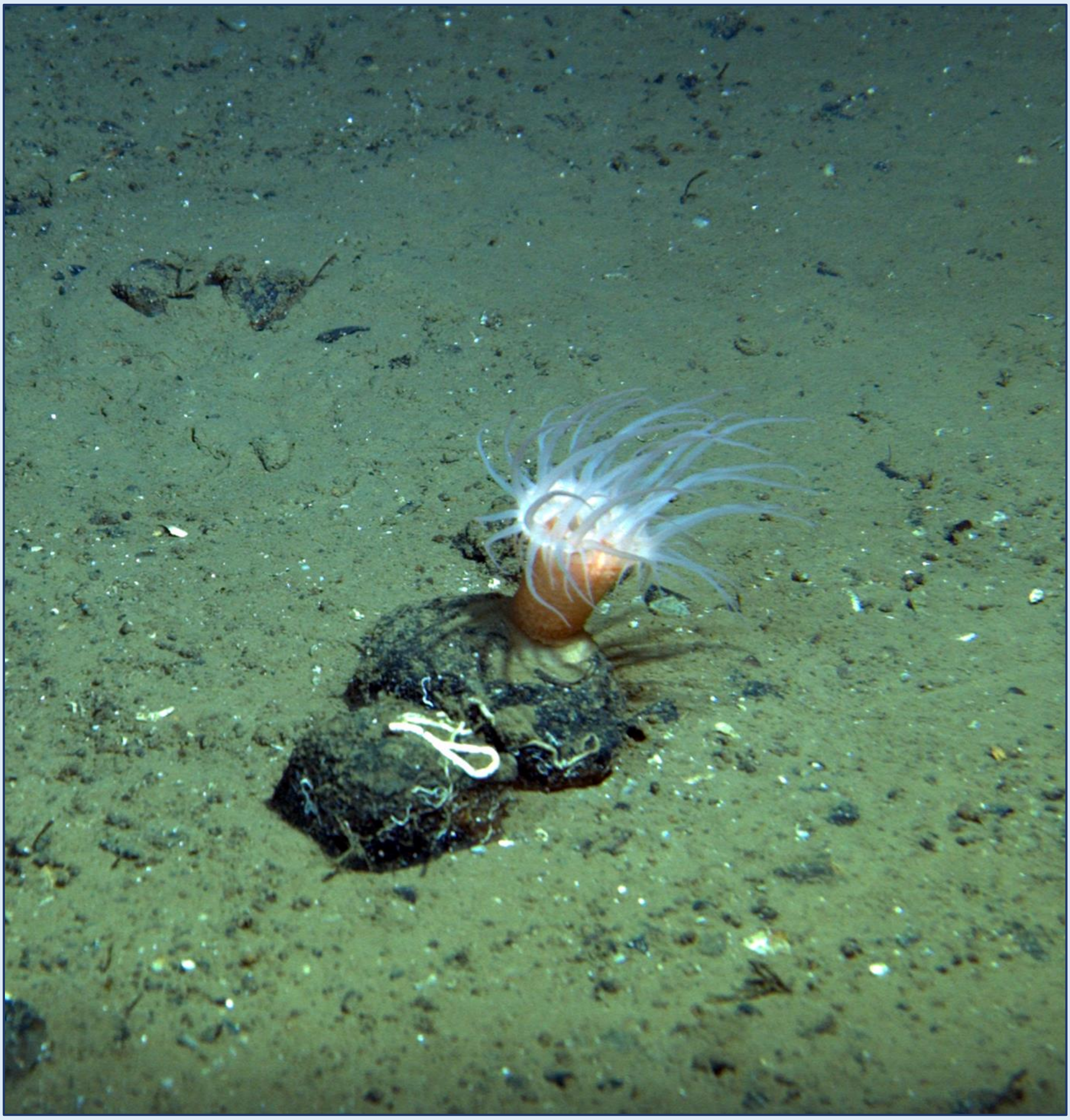
Paper III

Zhulay, I., Iken, K., Renaud, P.E., Kosobokova, K., Bluhm, B.A. Reduced efficiency of pelagic-benthic coupling in the Arctic deep sea during lower ice cover. Manuscript



Reduced efficiency of pelagic-benthic coupling in the Arctic deep sea during lower ice cover

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Abstract

Pelagic-benthic coupling connects surface water production to seafloor habitats via energy, nutrient and mass exchange. Massive ice loss and warming in the poorly studied Arctic Chukchi Borderland are thought to affect this coupling. The strength of pelagic-benthic coupling was compared between two years, 2005 and 2016, varying in climate settings, based on $\delta^{13}C$ and $\delta^{15}N$ stable isotope values of end members and pelagic and benthic consumers. Considerably higher isotopic niche overlap and generally shorter isotopic distance were found between pelagic and benthic food web components in 2005 than in 2016. Results also indicated more refractory food consumed by benthos in 2016 and fresher food reaching the seafloor in 2005. Higher $\delta^{13}C$ values of pelagic particulate organic matter and zooplankton indirectly suggested a higher contribution of ice algae in 2005 compared to 2016. The difference in pelagic-benthic coupling between the two years is consistent with increasing retention of energy within the pelagic system, perhaps due to strong stratification in the Amerasian Basin in the recent decade. Weaker coupling to the benthos can be expected to continue with climate change and ice loss in the study area, though monitoring of the area is needed to confirm this prediction.

Key words: Food webs, Arctic, deep sea, pelagic-benthic coupling, climate change

1. Introduction

The deep sea is considered to be the world's largest sink for biogenic carbon (Klages et al., 2004). Important insights into the global carbon cycle can, therefore, be gained by understanding the processes connecting marine realms through dynamics of organic matter, nutrients and energy cycling in deep-sea ecosystems (Gage, 2003; Griffiths et al., 2017). Pelagic-benthic coupling is considered to be tight when organic matter from surface production sinks to the seafloor with little reworking in the water column. Organic fluxes to the seafloor and strength of pelagic-benthic coupling vary in different ocean regions and largely depend on biological and physical processes in the overlying water column (e.g., Grebmeier and Barry, 1991; Wassmann et al., 2006; Olli et al., 2007; Pape et al., 2013). One of the least studied regions in terms of trophic structure and carbon flux is the Arctic Basin (Iken et al., 2005).

The Arctic Basin region is characterized by strong seasonality, with seasonal and regional multiyear ice cover and the polar night lasting for up to six months jointly constraining light availability needed for primary production (Rysgaard et al., 2001; Nicolaus et al., 2012). In addition, nutrient concentration in the surface water is often low in the Arctic Basin, mostly due to strong stratification (Bluhm et al., 2015). Therefore, the amount of pelagic primary production here is among the lowest recorded in the world, with average estimates of 1 to 25 g C m^{-2} y^{-1} (Arrigo et al., 2008; Wassmann et al., 2010). In addition to phytoplankton, sea-ice algae can contribute significantly to total primary production in this region. For example, Gosselin et al. (1997) found that ice algae contributed more than 50 % to the total primary production in the Arctic Basin, a fraction that is much higher than their contribution of 4 – 30 % on seasonally ice-covered shelves (Legendre et al., 1992; Carmack et al., 2006). Other nutrient inputs, such as from advection of terrestrial matter and shelf production (Cooper et al., 1999; Bell et al., 2016) or from large food falls (Klages et al., 2001; Premke et al., 2006), may be of local importance but are overall minor contributions for the Arctic Basin as a whole (Bluhm et al., 2015).

The combined primary production sources serve directly as food sources for ice-associated and pelagic fauna. Their grazing intensity, in turn, has a strong impact on the amount and composition of organic matter reaching the seafloor (Olli et al., 2002; Riser et al., 2008). Specifically, high grazing efficiency leads to a decrease in sedimentation of phytoplankton, while little grazing facilitates higher sedimentation of intact phytoplankton cells and aggregates to the deeper water layers. The particulate organic matter (POM) can settle out in the form of intact cells, phytodetritus, fecal pellets, zooplankton carcasses, and marine snow (Grebmeier and Barry, 1991; Gage, 2003; Iken et al., 2005). During the descent, the POM undergoes additional biodegradation by bacteria and heterotrophs (Klages et al., 2004; Mintenbeck et al., 2007). The amount and quality of material reaching the seafloor also depends on the water depth as stronger vertical flux attenuation is expected in deeper areas of the Arctic Ocean (Piepenburg, 2005). Indeed, only a very small portion of carbon produced at the surface is estimated to reach the bottom of the Arctic deep sea (1 – 10 %, Neuer et al., 2002; Klages et al., 2004; Danovaro et al., 2014; Wiedmann et al., 2020). Thus, typically very little and largely reworked organic particles reach the benthic fauna in the central Arctic, although export of fresh ice algal production has occasionally been observed (Boetius et al., 2013). Therefore, benthic trophic pathways in deeper areas of the Arctic Ocean have generally been described as longer than in shallower regions, with up to five trophic levels recorded for benthic species in the few published studies from Arctic and sub-Arctic deep-sea environment (Iken et al., 2005; Bergmann et al., 2009).

The presence or absence of sea ice may alter the strength of pelagic-benthic coupling in the Arctic marine ecosystems. Based on work on Arctic shelf systems, pelagic-benthic coupling is traditionally considered tighter in areas where sea ice is present (Carroll and Carroll, 2003), although extremely high particle flux to the seafloor has recently also been observed during low sea ice cover on the Chukchi Sea shelf (O'Daly et al., 2020). Usually, the formation of a stratified water layer from early sea ice melt allows primary production to start at a time when pelagic grazing intensity is low, and when seasonal zooplankton populations are not well established yet (Carroll and Carroll, 2003; Bluhm and Gradinger, 2008). In addition, ice algal production is mostly represented by large-sized diatoms that contribute significantly to a relatively fast transport of undisturbed organic matter to the seafloor (Ambrose et al., 2005; Moran et al., 2012). Similar connections between sea ice presence and stronger pelagic-benthic coupling have been observed (Boetius et al., 2013) or modeled for the Arctic deep sea (Wassmann and Reigstad, 2011).

The Arctic sea ice, however, is undergoing significant thinning and decrease in extent (Stroeve and Notz, 2018; Perovich et al., 2020), with a decrease in multiyear ice by more than 50% since the 1999 (Kwok, 2018). This decline is due to the Arctic currently experiencing strong warming of about three times the global average (Steele et al., 2008; Polyakov et al., 2010). Thinning of sea ice allows higher light penetration and, thus, can enhance primary productivity (Nicolaus et al., 2010; Arrigo et al., 2012). In fact, increases in primary production are currently documented (Dybwad et al., 2021) or predicted (Frey, 2018; Ardyna and Arrigo, 2020) in different areas of the Arctic Ocean. However, small-sized primary producers (e.g., flagellate species) are expected to dominate in warmer, fresher, and nutrient-poor water (Morán et al., 2010; Metfies et al., 2016). This is especially the case in the Amerasian Basin, the focus area of the present study, where the nutrient-poor Beaufort Gyre contains a large amount of freshwater (Polyakov et al., 2020). Smaller phytoplankton cells are more resistant to sinking (Li et al., 2009; Metfies et al., 2016). In addition, pelagic grazing pressure can increase in response to increased primary production (Lalande et al., 2007), as well as due to increased advection of zooplankton with Pacific and Atlantic water into the Arctic Ocean (Hirche and Kosobokova, 2007), leading to higher retention of organic matter in the water column. Thereby, physical and biological alterations related to climate change can lead to a weakening of pelagic-benthic coupling and a decrease in deposition of (fresher) carbon to already food-limited benthic fauna.

In this study, we aim to assess potential changes in pelagic-benthic coupling in the Arctic Chukchi Borderland within the Canada Basin between two years characterized by different sea-ice settings (2005 and 2016, Fig.1). The Arctic system was already under the influence of lowered sea ice cover from climate change in 2005, though signs of warming were not as pronounced in the early 2000s as in most of the following years, including 2016 (Perovich et al., 2020) (Fig.2). Average sea-ice extent for September consisted of ~6.9 million km^2 until 2005, while it never exceeded 5.2 million km^2 in the following years, including 2016, when the September sea-ice extent was 4.1 million km^2 (Richter-Menge et al., 2006; Richter-Menge et al., 2016; Perovich et al., 2020, Fig. 1, 2). In addition, a continuous decline in sea-ice thickness and, hence, increased dominance of first-year ice over multiyear ice, was registered over the last decades and including the period of our study (Perovich et al., 2017; Kwok, 2018). In the present study, we tested the hypothesis that pelagic-benthic coupling was tighter in the early 2000s (when more sea ice was present; represented here by 2005) compared to later, lower ice years (represented by 2016). Following earlier studies on pelagic-benthic coupling in Arctic regions (Hobson et al., 1995; Iken et al., 2005; Iken et al., 2010), we used stable carbon and nitrogen isotope analysis of POM end members and pelagic and benthic consumers to investigate pelagic-benthic coupling, specifically by comparing food source use and trophic niche space between the two years. This approach is based on the well-established concept that nitrogen stable isotope ratios indicate trophic position of organisms as tissues is progressively enriched in the heavier isotope with increasing trophic level in a reasonably predicable manner (Post, 2002). Thus, lower δ^{15}N values of benthic taxa can be expected in a food web where pelagic-benthic coupling is tight. Carbon stable isotopes ratios are indicative of carbon end member utilization based on different isotopic ratios of different primary producers or habitats (Zanden and Rasmussen, 2001; Post, 2002). For example, sea-ice algae are often characterized by more enriched ^{13}C compared to phytoplankton (on average by 4-5 ‰, though highly variable; Hobson et al., 2002; Tamelander et al., 2006).

Thus, higher carbon isotope values can be found in areas where ice algae are a main food source. Both trophic markers (^{15}N and ^{13}C) combined describe trophic niches in isotope biplot space (Jackson et al., 2005). A high overlap of isotopic niches of pelagic and benthic members in a given food web can indicate tighter coupling between these two realms. We hypothesized a decrease in pelagic-benthic coupling strength would be reflected in a lower overlap of pelagic and benthic isotopic niches, higher δ^{15}N values of benthic organisms, as well as lower $\delta\,^{13}$C values from reduced ice algal uptake associated with lower ice extent.

2. Material and Methods

2.1. Study area and sampling stations

To assess pelagic-benthic coupling, samples were collected during the “Hidden Ocean” expeditions onboard the US Coastguard icebreaker *HEALY* between 28 June and 25 July 2005 (expedition HLY05-02) and 2 July and 10 August 2016 (expedition HLY16-01) (Table 1). Sampling stations were located between 74 – 76 °N and 158 – 163 °W (Fig. 3). In 2005, five stations were sampled at depths ranging from 621 to 2090 m (Table 1, Fig. 3). In 2016, eight stations were sampled at depth varying between 486 and 2107 m (Table 1, Fig. 3).

The study area is characterized as relatively cold, fresh, and oligotrophic due to high input of freshwater to the surface water layer from melting sea ice and rivers that collects in the Beaufort Gyre (Lee et al., 2019). Additional input of nutrients to this oligotrophic environment is possible through the connection to the nutrient-rich Pacific Water and productive Amerasian shelves (i.e., Chukchi and western Beaufort Sea shelves) (McLaughlin et al., 2011; Watanabe et al., 2015). The hydrography of the region is complex with Pacific, Atlantic, and Arctic water masses meeting and mixing here (e.g., McLaughlin et al., 2004; Woodgate, 2013). In addition, the Chukchi Borderland itself has complex topography (Jakobsson et al., 2008), which can influence, for example, the flow of the bottom waters. Details of circulation in this area are still not well understood (Boury et al., 2020; Li et al., 2020).

The study area is located in the region of the most dramatic sea ice melt in the Arctic with more intensive melt since 2007 (Hutchings and Faber, 2018). This melt is mainly related to increased influxes of warm Atlantic Water and lower-salinity waters from the Pacific (Woodgate et al., 2010; Carmack et al., 2015). In addition, the Chukchi Borderland has shifted from a multiyear ice-covered area to a seasonal ice region in recent years (Watanabe et al., 2015).

2.2. Sample collection

Pelagic POM (pPOM) was collected at each station in both years from the chlorophyll maximum layer from Niskin bottles attached to a SBE9/11 + CTD rosette equipped with an *in-situ* fluorometer. The chlorophyll maximum layer varied from 30 to 60 m depth in 2005 and from 50 to 70 m in 2016. Two to three water samples per station were collected from different bottles of the same CTD cast, totaling 13 pPOM samples in 2005 and 21 pPOM samples in 2016 (Table 1). The collected water samples were then filtered onto pre-combusted, 25 mm diameter GF/F filters. Large organisms visible by eye on the filters (e.g., meso-zooplankton) were removed.

Sediment POM (sPOM) was collected into a sterile plastic bag from the top ~1 cm sediment from 0.06 m^2 box core samples at 3 stations in 2005 and from 0.25 m^2 box core samples at each of the 7 stations in 2016 (Table1). One replicate sediment sample per station was collected per year.

Zooplankton consumers were collected at 5 stations with a multi-net (Midi, Hydrobios, 150 μm) in 2005 and at 6 stations with the same Multinet in 2016. Five zooplankton species common to the upper water column in the Arctic Basin and representing different taxonomic groups with different food preferences were chosen for the analysis: the copepods *Calanus glacialis* (grazer), *Calanus hyperboreus* (grazer), *Paraeuchaeta glacialis* (predator), the amphipod *Themisto abyssorum* (predator/omnivore), and the chaetognath *Eukrohnia hamata* (predator, but see Grigor et al. (2020)). Often, mass of individual zooplankton organisms was insufficient for isotopic analysis; thus, several individuals of the same species were pooled by station. A total of 71 zooplankton samples were collected in 2005 and 66 in 2016. Replication varied from 1 to 3 samples of each zooplankton species per station.

Epifaunal benthic consumers, including some demersal fish, were sampled with a 7 mm mesh (4 mm cod end) beam trawl and a remotely Operated Vehicle (ROV *Global Explorer*, Deep-Sea Systems Inc. in 2005, and Oceaneering International in 2016) in both years. The ROVs were equipped with a suction hose and a manipulator arm enabling targeted sample collection. Infaunal benthic consumers were collected with a 0.25 m^2 box core in both years. All benthic samples were washed to remove sediments (2 mm mesh size for beam trawl, 0.3 mm for box core samples) and fauna were identified to the lowest taxonomic level possible. Vouchers of invertebrate taxa were collected when identification was uncertain and identified later by experts (see acknowledgements). Taxon names were verified with WoRMS (www.marinespecies.org, 13.12.2021). Benthic consumers were then subsampled for muscle tissue, where possible, to represent a tissue with slow turnover rate (e.g., Weems et al., 2012). Where muscle tissue was not distinguishable or unavailable, tissue was sampled from body walls (e.g., anemones), tube feet (e.g., asteroids), and entire organisms were collected when body mass was small (e.g., some worms, small amphipods). A total of 29 and 85 benthic organism samples were collected in 2005 and 2016, respectively, with replication varying from 1 to 3 per species per station. All samples collected for isotope analysis were frozen at –20°C immediately after collection until laboratory analyses.

2.3. Laboratory analysis

pPOM filters were fumed with concentrated hydrochloric acid (HCl) vapor for 48 hours and dried before analysis. sPOM samples were thawed and each sample was homogenized by mixing. Approximately 1 ml of the sediment was treated with 1 N HCl until bubbling stopped and then rinsed with distilled water until pH of the sediments was close to neutral, after which the samples were freeze dried before analysis (following Iken et al., 2010; Bell et al., 2016). All organism tissue samples were dried at 60 °C for 24 h prior to the laboratory analysis. Lipids in zooplankton tissue samples were removed with repeated use of a 2:1 ratio of chloroform:methanol to avoid interpretation bias in lipid-rich zooplankton (Mintenbeck et al., 2008). The samples were then re-dried at 60°C for 24 h. Tissue samples that contained high carbonate concentrations were acidified with 1 N HCl for carbon isotope analyses to prevent the bias introduced by inorganic carbon in $\delta^{13}C$ values. The acid was removed by rinsing with distilled water after bubbling had ceased; then, samples were dried again at 60 °C for 24 h.

All carbon and nitrogen stable isotope analyses were performed at the Alaska Stable Isotope Facility at the University of Alaska Fairbanks on a Thermo Finnigan Delta Isotope Ratio Mass-Spectrometer with Vienna PDB as standard for carbon and atmospheric N_2 as standard for nitrogen. Instrument error was < 0.2 ‰ for $\delta^{13}C$ and <0.4 ‰ for $\delta^{15}N$ in 2005, and < 0.2 ‰ for both $\delta^{13}C$ and $\delta^{15}N$ in 2016. Sample isotopic ratios were expressed in the conventional δ notation as parts per thousand (‰) according to the following equation:

$$\delta X = [(\mathrm{Rsample}/\mathrm{Rstandard}) - 1] \times 1000 \qquad (1)$$

where X is ^{13}C or ^{15}N of the sample, and *R* is the corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

2.4. Statistical analysis

For the analysis of potential differences in benthic-pelagic coupling between sampling years we included only station pairs that were geographically close to each other and located in similar bathymetric features (e.g. basin/ridge) (Fig. 3, Table 1), and either the same or closely related taxa in both years. To provide a general overview of the difference in isotopic niche structure between the two sampling years, bi-plots of $\delta^{13}C$ versus $\delta^{15}N$ were generated based on station-averaged values of each of the two carbon end-members (pPOM, sPOM) and each of the consumer groups (zooplankton and benthos). The isotopic niche widths of these four food web components (pPOM, sPOM, zooplankton, and benthos) were then compared between the two years. For this, we calculated Standard Ellipse Area corrected for small sample size (SEA_c containing 95% of data, Jackson et al. 2011), and Bayesian Standard Ellipse Areas (SEA_B), i.e., posterior estimates of SEAc (Jackson et al., 2011). The Bayesian approach, an approach similar to a bootstrap, was used to incorporate uncertainty of estimates and to allow robust statistical comparison of posterior probabilities (Parnell et al., 2010; Reid et al., 2016). SEA_B of each end-member and consumer group were compared between the sampling years by calculating the probability of difference between them (Jackson et al., 2011; Reid et al., 2016). Following Reid et al. (2016) and Włodarska-Kowalczuk et al. (2019), we considered a probability higher than 95% a meaningful difference. The overlap of SEAc of different food web components was calculated as the percentage of ellipse area shared by two components in order to test the hypothesis that benthic-pelagic coupling (expressed here as isotopic niche proximity) was tighter (=stronger overlap in SEAc) in 2005 than 2016. These analyses were conducted using the SIBER package (Stable Isotope Bayesian Ellipses in R; (Jackson et al., 2011)) in R 4.0.3. statistical software (Team, 2017).

Isotopic distances of $\delta^{15}N$ and $\delta^{13}C$ between different food web components as a measure of pelagic-benthic coupling were calculated by subtracting the mean $\delta^{15}N$ ($\delta^{13}C$) of one food web component from the mean $\delta^{15}N$ ($\delta^{13}C$) of another food web component. This metric was used to test the hypothesis that distance between food web components was lower in 2005 than in 2016.

To test the hypothesis that $\delta^{15}N$ was overall lower in benthos (reflecting fresher food reaching the seafloor through tighter pelagic-benthic coupling) and $\delta^{13}C$ was higher (reflecting higher input of generally more carbon-isotopically enriched ice algae) in 2005 than in 2016, the means of $\delta^{15}N$ and $\delta^{13}C$ of each food web component were compared. The following tests were used for the comparison: a two-sample *t*-test (if distribution was normal and variances were equal), a Welch's two sample *t*-test (if the distribution was normal, but the variances were not equal), and a Wilcoxon rank sum test (if the distribution was not normal). The Shapiro-Wilk test was applied to test for normality, followed by the Bartlett-test to verify the equality of variances. Values are presented as mean ± standard error (SE) in the text and tables. The analysis was conducted in R (Team, 2017).

To illustrate the difference in sea-ice cover between the sampling years, we plotted average sea-ice concentration data derived from satellite Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave at a grid cell size of 25 × 25 km (Cavalieri et al., 1996). The concentration is defined as the fraction of the area of the grid cell covered by sea ice and is given in percentage from 0 (no ice) to 100 (fully covered by ice) percent ice (https://nsidc.org/cryosphere/seaice/data/terminology.html). Average sea ice concentration for July and September (minimum ice month) was downloaded from the National Snow and Ice Data Centre (https://nsidc.org/data/NSIDC-0051/versions/1). The data were then imported into ArcGIS 10.5 (ESRI, 2011) software and projected spatially. All maps presented in the paper were generated using the ArcGIS (ESRI, 2011).

3. Results

The $\delta^{15}N$ range of pPOM and sPOM was higher in 2016 with higher values of $\delta^{15}N$ in 2016 than in 2005 (Fig. 4 A, 5 A). Specifically the $\delta^{15}N$ of pPOM ranged from 1.4 to 5.1 ‰ in 2005 and from 1.9 to 7.6 ‰ in 2016, and $\delta^{15}N$ for sPOM ranged from 4.5 to 6.2 ‰ in 2005 and from 4.7 to 10.2 ‰ in 2016. The $\delta^{15}N$ range of zooplankton consumers was, instead, higher in 2005 than in 2016 (8.1 to 17.2 ‰ and 8.3 to 14.7 ‰ in 2005 and 2016, respectively). The $\delta^{15}N$ range of benthic consumers was slightly higher in 2005 than in 2016, though ^{15}N values were generally higher in 2016 (10.4 to 19.5 ‰ and 12.4 to 20.5 ‰ in 2005 and 2016, respectively, Table S1).

$\delta^{13}C$ values of pPOM and their ranges were slightly higher in 2005 than in 2016, with values varying from -24.0 ‰ to -27.7 ‰ in 2005 and from -28.9 ‰ to -26.0 ‰ in 2016 (Fig. 4 A, 5 B). A similar pattern of higher $\delta^{13}C$ values and $\delta^{13}C$ range in earlier year was observed for zooplankton consumers, where $\delta^{13}C$ ranged from -27.8 to -19.7 ‰ in 2005 and from -28.6 to -21.7 ‰ in 2016. In contrast, $\delta^{13}C$ values of sPOM were generally lower in 2005 and varied from -25.6 ‰ to -23.1 ‰ in 2005 and from -22.4 to 20.4 ‰ in 2016. $\delta^{13}C$ values of benthos were similar between the years and ranged from -24.8 to -16.6 ‰ and from -24.6 to -16.2 ‰ in 2005 and 2016, respectively (Table S1).

Isotopic niche size, measured as standard ellipse area (SEAc), of the benthic component differed between 2005 and 2016 with a wider niche in 2005 (Fig. 4 A, B, Table S1). This difference was confirmed by high probability of difference (96%) between posterior Bayesian estimates of standard ellipse areas (SEA_B) for the benthos components between years. Compared to the benthos, the isotopic niche size of zooplankton was slightly more similar between years, with an 86% probability of difference and this probability was below the threshold of 95% considered a meaningful difference in the present study (Fig. 4 A, B, Table S1).

SEAc overlap between consumer groups and between endmembers was also different for the two years. Specifically, overlap between benthos and zooplankton was considerably higher in 2005 (57.9%) than in 2016 (5.5%). The SEAc overlap between sPOM and pPOM was generally low, but also higher in 2005 (4.8%) than in 2016, when SEAc did not overlap (Fig. 4 A, Table S2).

$\delta^{15}N$ isotopic distances between pairs of food web components were mostly smaller in 2005 compared to those in 2016 (Table 2). The exception was the isotopic distance between pPOM and zooplankton, which was higher in 2005 compared to 2016 (Table 2). For $\delta^{13}C$, the same trend of shorter isotopic distances between the food web components in 2005 versus 2016 was also evident between the following pairs: pPOM and sPOM, pPOM and benthos, zooplankton and benthos (Table 2). On the contrary, $\delta^{13}C$ isotopic distance was higher between pPOM and zooplankton, and sPOM and benthos in 2005 compared to 2016 (Table 2).

Mean $\delta^{15}N$ values of sPOM and benthos collected in 2005 were significantly lower than those collected in 2016 (Fig. 5, Table 3). Mean $\delta^{15}N$ values of pPOM, however, did not differ significantly between the two years, though mean $\delta^{15}N$ of pPOM in 2005 was slightly lower than in 2016. For zooplankton, instead, the mean $\delta^{15}N$ was significantly higher in 2005 than in 2016 (Fig. 5, Table 3). Mean $\delta^{13}C$ values of pPOM and zooplankton in 2005 were significantly higher than those in 2016. Conversely, mean $\delta^{13}C$ of sPOM was significantly lower in 2005 compared to 2016. There was no significant difference between the years for mean $\delta^{13}C$ of benthic organisms (Fig. 5, Table 3).

4. Discussion

The degree to which water column and benthic processes are coupled influences benthic community composition, production, and elemental cycling rates (Graf, 1989; Grebmeier and Barry, 1991; Renaud et al., 2008). This is particularly true in the energy-limited deep sea, where benthos is largely sustained by production originating in the above water layers (Gooday, 2002). Based on stable isotope data collected in the Chukchi Borderland, we evaluated differences in pelagic-benthic coupling between two years characterized by different climate settings. In 2005, the ice cover was still comparatively high despite some evidence of regional warming (Richter-Menge et al., 2006), while by 2016 the Arctic had experienced a series of very low sea ice years and undergone transformations due to climate change (Perovich et al., 2020). Results of our study generally supported our hypothesis of tighter pelagic-benthic coupling in 2005 than 2016. This difference was reflected in much higher overlap of zooplankton and benthic isotopic niches in 2005 than in 2016. Similarly, pelagic and benthic food-web endmembers slightly overlapped in 2005, while no overlap was observed in 2016. These findings are consistent with shorter $\delta^{15}N$ and $\delta^{13}C$ isotopic distances between pPOM and sPOM, pPOM and benthos, and zooplankton and benthos in 2005 compared to 2016.

Multiple causes could underlie the patterns we found. Lower surface primary production in 2016 relative to 2005 (Zhuang et al., 2018; Song et al., 2021) could be a potential explanation for pelagic-benthic coupling differences between the sampling years, as primary production in part determines how much organic matter will eventually reach the seafloor. Although increased primary production has been observed in some areas of the Arctic Ocean (Ardyna et al., 2014; Arrigo and van Dijken, 2015; Ardyna and Arrigo, 2020), low values of primary production and Chl *a* concentration were in fact documented in the study area over the last few years (Coupel et al., 2015; Zhang et al., 2020; Song et al., 2021). For example, estimates of integrated primary production in the ice-free Canada Basin were about 4 times lower in 2008 (24 ± 15 mg C m^{-2} d^{-1}, Coupel et al., 2015), after the significant decline of sea-ice cover in 2007 (Perovich et al., 2008), than those in 2005 (60 mg C m^{-2} d^{-1}, Lee et al., 2010). The reduced primary production was generally attributed to exceptionally high freshening of the Canada Basin (McPhee et al., 2009; Rabe et al., 2011), that resulted in strengthening of stratification and inhibition of nutrient renewal in the euphotic zone (McLaughlin and Carmack, 2010; Nummelin et al., 2016). Both the absolute level of production as well as the stratification have implications for the amount of production settling to the seafloor, discussed below.

The source of primary production can also influence pelagic-benthic coupling. Our results showed significantly higher $\delta^{13}C$ values of pPOM in 2005 than in 2016. This may point to differences in sources of pPOM between the years, potentially the balance of ice algae and phytoplankton, the two major sources of primary production in the central Arctic Ocean (Leu et al., 2015). Specifically, based on the higher sea ice cover in 2005, we might assume that the abundance of ice algae was also higher in that year. Sea-ice algae are often characterized by more enriched ^{13}C compared to phytoplankton (on average by 4–5‰, though highly variable; Hobson et al., 2002; Tamelander et al., 2006). Therefore, the observed higher $\delta^{13}C$ values of pPOM in 2005 compared to 2016 might be an indication of a higher ice-algal contribution to pPOM in the earlier year. However, $\delta^{13}C$ values of ice POM from samples taken during the 2005 expedition did for the most part not differ from those of pPOM (Gradinger et al., 2010 and unpublished data). The absence of a difference was likely because during the late stages of ice-algal bloom, ice gets more porous and allows CO_2 exchange between water and ice, which results in similar $\delta^{13}C$ values of these two primary production sources (Iken et al., 2005; Søreide et al., 2006; Leu et al., 2015). Instead, the significantly higher $\delta^{13}C$ values of zooplankton in 2005 compared to 2016, however, might be the result of consumption of produced ice POM *earlier* in the year during the peak bloom. The turnover time between food and consumer of about 3 weeks for copepods in the Arctic (Boissonnot et al., 2016) makes it feasible that an earlier, enriched carbon isotope ice algal signal might be present in the zooplankton at our time of sampling in 2005. The potentially higher ice POM contribution in 2005 was, however, not reflected in our sediment and benthic tissue samples, unlike previous studies (Søreide et al., 2006; Tamelander et al., 2006). $\delta^{13}C$ values of benthos did not differ significantly between years, and $\delta^{13}C$ of sPOM were significantly lower in 2005 than in 2016, though the sample size of sPOM was low for both years. In summary, some bits of evidence point to the possibility of ice algae playing a role in the apparent difference in pelagic-benthic coupling between the study years, but unequivocal conclusions are difficult based on a single sampling period in each year.

Besides the amount and sources of primary production, organic matter quality and fate during sinking to the seafloor shape pelagic-benthic coupling intensity. The isotopic niche of benthos was significantly wider in 2005 than in 2016, even though fewer benthic samples were available in 2005. While not exactly the same species were sampled in all cases, only closely related taxa we included in the comparison. For comparability, fish, decapods and ophiuroids sampled in 2016 but not in 2005 were excluded and hence would not have biased isotopic niche size. The wider niche in 2005 could point to more diverse quality and sources of food available to benthos. The difference in isotopic niche was essentially driven by a larger δ^{15}N range in 2005 compared to 2016. Mean δ^{15}N of sPOM and - as hypothesized - benthos were significantly lower in 2005 compared to 2016, which indicates that organic matter available to the benthos was generally less reworked in 2005 than in 2016 since microbial degradation can result in a higher δ^{15}N value with increasing depth (Mintenbeck et al., 2007 and reference therein). Potential difference in food quality might be related to changes in primary production composition documented in the study area that likely affected sinking velocity of organic matter and its overall vertical export flux. Specifically, increased importance of small-celled (flagellate) phytoplankton and decreased contribution of large (diatoms), associated with the freshening of the area, have been documented in recent years from 2004 to 2014 (Li et al., 2009; Zhuang et al., 2018). In addition, significant ice loss and the recent seasonally ice-free nature of the study area (Frey et al., 2015; Perovich et al., 2020) might also imply a reduction in the contribution of the larger diatoms that constitute the majority of sea-ice algae (Różańska et al., 2009; Smith Jr and Sakshaug, 2013; Hop et al., 2020). Small-celled species are more resistant to sinking (Li et al., 2009; Metfies et al., 2016) and tend to contribute little to the vertical organic matter export flux (Reigstad and Wassmann, 2007; Wolf et al., 2016; Dybwad et al., 2021), (but see Le Moigne et al., 2015; Wollenburg et al., 2018), and are largely retained in the upper water column (Reigstad and Wassmann, 2007; Wolf et al., 2016). Conversely, larger and silicified diatoms tend to sink faster or form rapidly sinking aggregates at the advanced stages of their bloom (Smetacek, 1985; Jackson et al., 2005; Boetius et al., 2013; Fernández-Méndez et al., 2014) and also reflect a high quality food source (McMahon et al., 2006; Søreide et al., 2010). Therefore, diatom cell vertical flux and, thus, contribution to pelagic-benthic coupling might be both more substantial than small-celled flagellate species (Reigstad and Wassmann, 2007; Dybwad et al., 2021), and also provide higher nutritional quality; though it is unclear to what extent this shift would be measurable in the stable isotopic patterns. Thus, overall flux of relatively fresh organic matter could have decreased in 2016 compared to 2005, which might also have led to weaker coupling of benthos to primary producers in 2016.

The strength of pelagic-benthic coupling can also be determined by grazing efficiency of zooplankton, which largely depends on the density of zooplankton present at the time of primary production; at high zooplankton densities and, thus, grazing intensity, downward carbon flux is reduced (Wassmann and Reigstad, 2011). In general, zooplankton density in the Canada Basin is low compared to shelf zooplankton assemblages (Kosobokova and Hopcroft, 2010; Abe et al., 2020). Overall, density of zooplankton was relatively stable since 2003 in the Canada Basin (Rutzen and Hopcroft, 2018; Abe et al., 2020). However, some changes in zooplankton communities have been documented for the region from 2004 to 2008.

Specifically, density of short-lived grazers *Oithona similis* and *Microcalanus pygmaeus* were significantly reduced in 2007-2008, which was likely a result of decreased primary production as a response to the freshening in the study area (Hunt et al., 2014). In contrast, overall biomass of zooplankton increased between 2004 and 2008, largely due to longer-lived and larger-sized *Calanus* species (Hunt et al., 2014) potentially leaving less fresh food to settle to the seafloor. Other potential grazers might be advected from the North Pacific to the study area. Very few species found here are, however, expatriates from the North Pacific (Kosobokova and Hopcroft, 2010; Hunt et al., 2014), which are currently thought not to be viable in the Arctic Ocean or have minimal reproductive success due to potentially unfavorable conditions in the new environment (Nelson et al., 2014). These species may also serve as additional biogenic material and contribute to sedimentation of organic matter to the seafloor. However, based on the literature it is difficult to say whether the grazing efficiency and advection of zooplankton has increased in the area over the time from 2005 to 2016 (Rutzen and Hopcroft, 2018; Abe et al., 2020). Zooplankton studies have been sporadic in the study area (e.g., Hopcroft et al., 2005; Kosobokova and Hopcroft, 2010) with very limited inter-annual comparisons exist (Hunt et al., 2014; Rutzen and Hopcroft, 2018; Abe et al., 2020).

5. Summary and conclusion

Evaluation of climate change effects on pelagic-benthic coupling in the deep Arctic Ocean is difficult due to limited availability of long-term data sets. In the present study, we compared pelagic-benthic coupling in 2005, in the decade with only early signs of warming (Richter-Menge et al., 2006), and 2016, when years of intense climate warming had been documented and impacts of systems drivers observed. Our results indicate potentially stronger decoupling of benthic and pelagic realms in 2016 compared to 2005. In addition, results indicated that ice algal contribution was potentially higher in 2005, at least in pelagic particulate organic matter and zooplankton, compared to 2016, though seasonal samples were lacking that could provide firm evidence. Benthic communities received fresher organic material in 2005 than in 2016. The inferred decoupling is consistent with physical and biological changes that were observed in the region in recent years. Specifically, a shift from perennial to seasonal sea ice (Kwok, 2018; Perovich et al., 2020) has potentially resulted in an overall decrease of sea ice diatoms within this system. Additionally, strengthening of the halocline within this region (Coupel et al., 2015) has resulted in a decrease in primary production in the area (Song et al., 2021) and a shift to small-celled phytoplankton (Zhuang et al., 2018). We propose that these changes likely lead to a decrease in overall organic matter flux to the seafloor, a longer residence time of organic matter in the water column and, thus, higher level of organic matter biodegradation before it reaches the seafloor.

Further changes in pelagic-benthic coupling are likely to occur with the predicted continued decrease in sea ice (Årthun et al., 2021) and, thus, potential loss or reduction of typically fast-sinking ice-algal production. The Arctic deep sea is an allochthonous, largely heterotrophic and oligotrophic system (Gage, 2003; Tyler, 2003), where any decrease in food input, quality and quantity might lead to shifts in benthic community composition and production. In turn, these impacts affect the ocean’s biogeochemical cycles and nutrient regeneration, which are currently difficult to predict. Since ecosystem responses to climate change might vary depending on location and local environmental and biological settings, it is recommended that time-series observations, similar to those on the adjacent Chukchi Sea shelf (Grebmeier et al., 2019), be extended into the deep basin.

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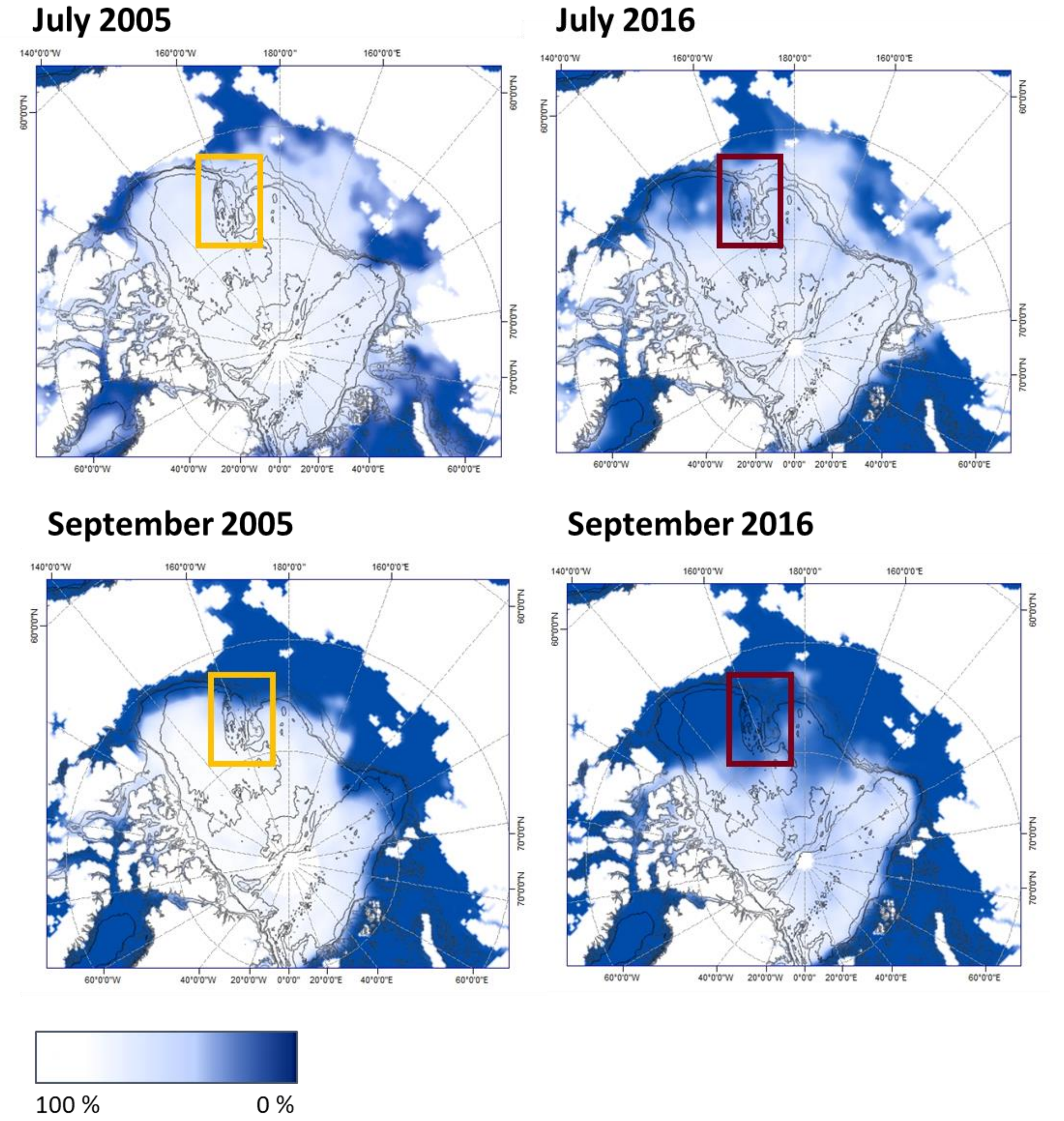
Figures



July 2005

July 2016

September 2005

September 2016

Figure 1. Comparison of sea ice concentration between 2005 and 2016, for July (upper panel, covers most of the sampling period for both years) and September (bottom panel, minimum ice month). The study area is marked by yellow and red squares for 2005 and 2016, respectively. Lowest ice concentrations are indicated by dark blue and highest concentrations are in white. Data derived from the National Snow and Ice Data Centre (NSIDC) website https://nsidc.org/data/NSIDC-0051/versions/1.

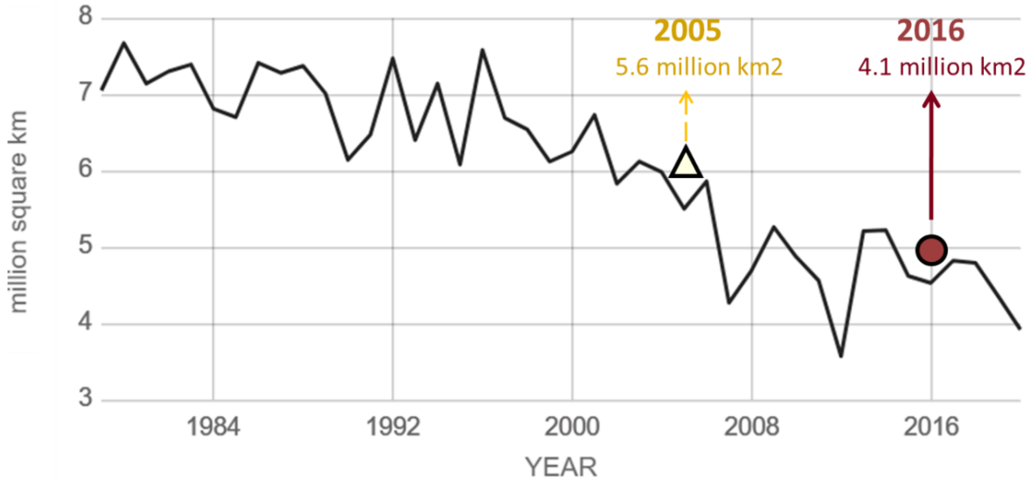


Figure 2. Arctic average September minimum ice extent (modified from climate.nasa.gov). Sampling years are indicated by white triangle (2005) and red circle (2016), numbers above the triangle and circle indicate mean sea ice extent in 2005 (in yellow) and 2016 (in red).

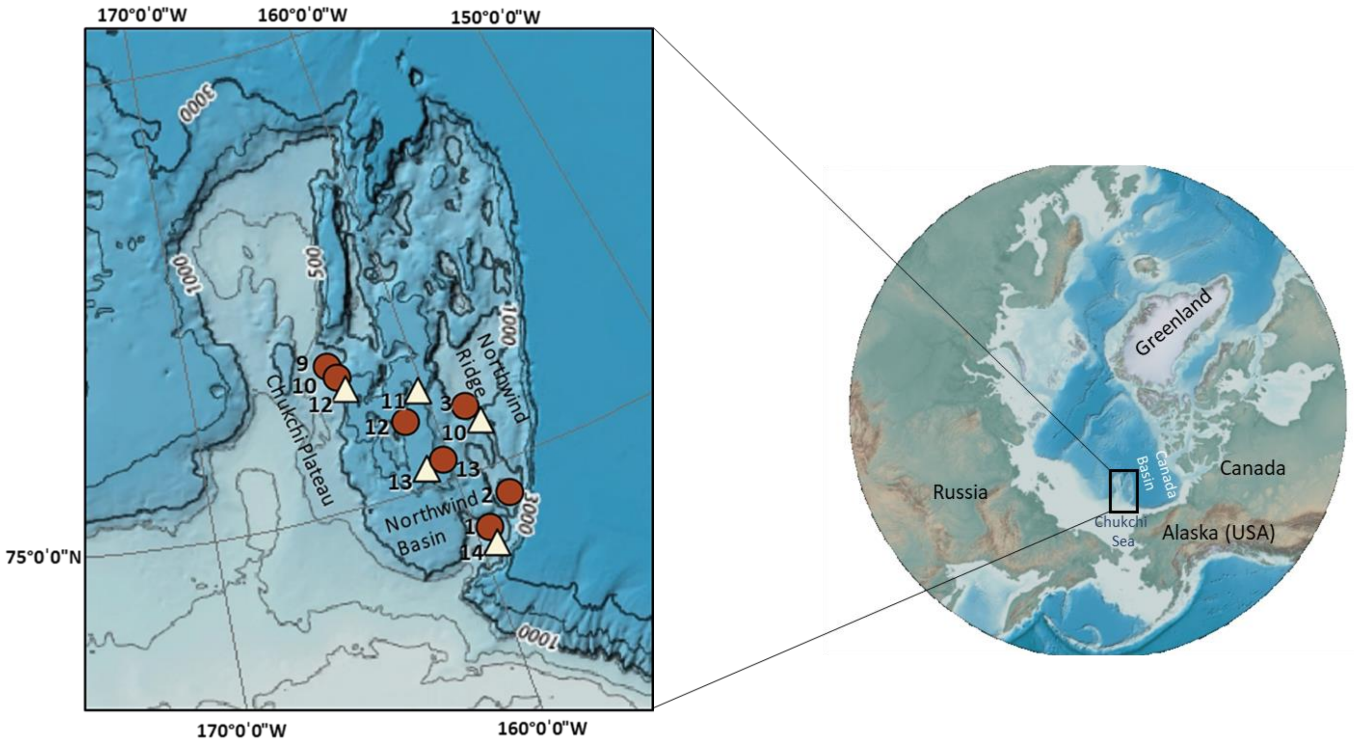


Figure 3. Study area and stations sampled in the Arctic Chukchi Borderland. Stations sampled in 2005 and 2016 are indicated by white triangles and red circles, respectively. Numbers in bold print are station numbers; small numbers along isobaths indicate water depth.

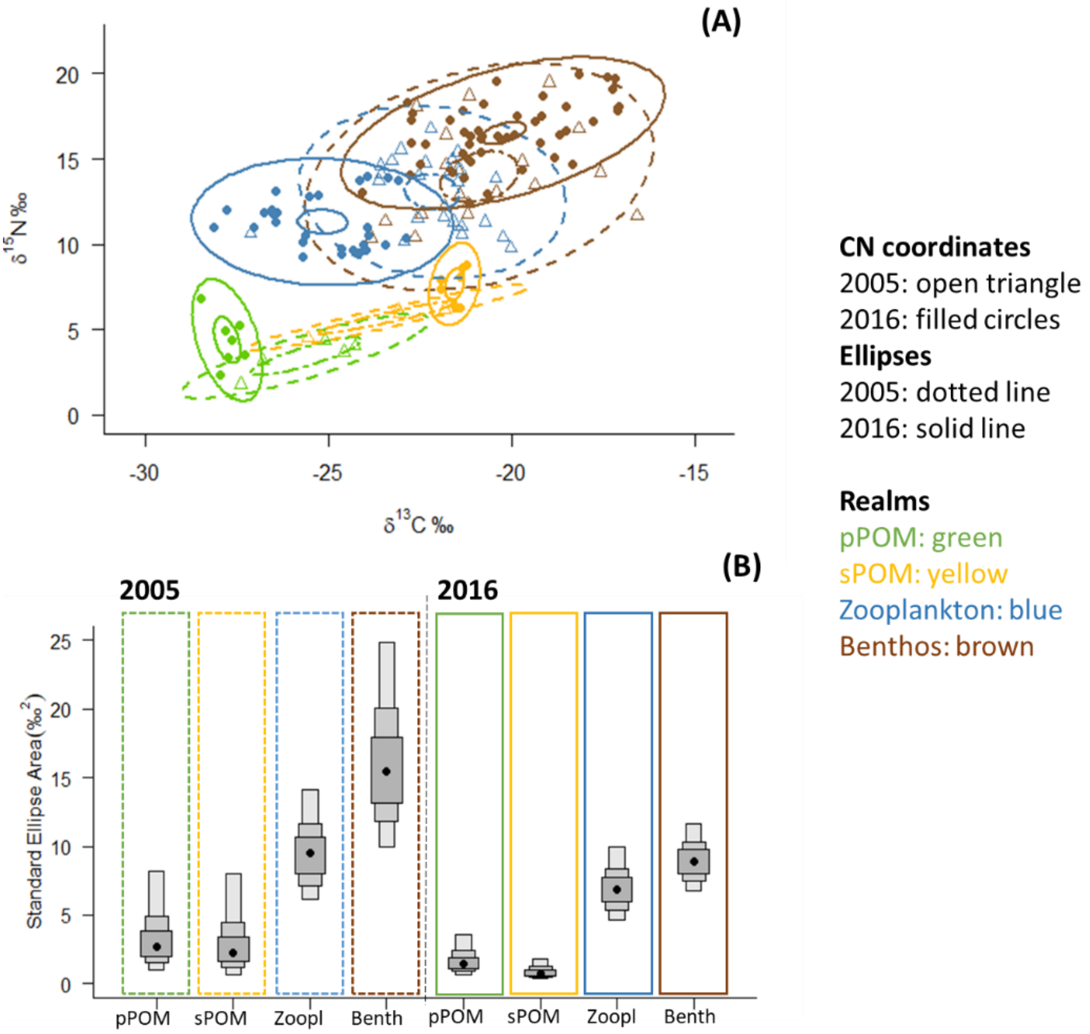


Figure 4. Isotopic niches of compared food web components in the study area. (A) Biplot of $\delta^{13}C$ and $\delta^{15}N$ isotope values (‰) for assemblages in the Chukchi Borderland in 2005 and 2016; outer ovals are sample size corrected standard ellipses (SEA_C) containing 95 % of the data. Inner small ovals indicate 95% confidence intervals around the bivariate means. Open triangles are means of samples collected in 2005 and filled circles in 2016. Food web end members and consumers are indicated by colors: green (pPOM), yellow (sPOM), blue (zooplankton), and brown (benthos). See Table 1 for pPOM and sPOM abbreviations. (B) Standard ellipse areas Bayesian estimations (SEA_B) presented as credible intervals for each of the community components for the two sampling years; black dots are the mode of the SEA_B (‰^{2}), the shaded boxes represent the 50% (dark grey), 75% (lighter grey) and 95% (lightest grey) credible intervals. Dotted outlines enclose assemblages collected in 2005 and solid lines represent those collected in 2016. Total amount of zooplankton taxa consisted five for both years, and total amount of benthic taxa consisted 13 in 2005 and 32 in 2016. Only comparable taxa were included (i.e., either the same or closely related taxa).

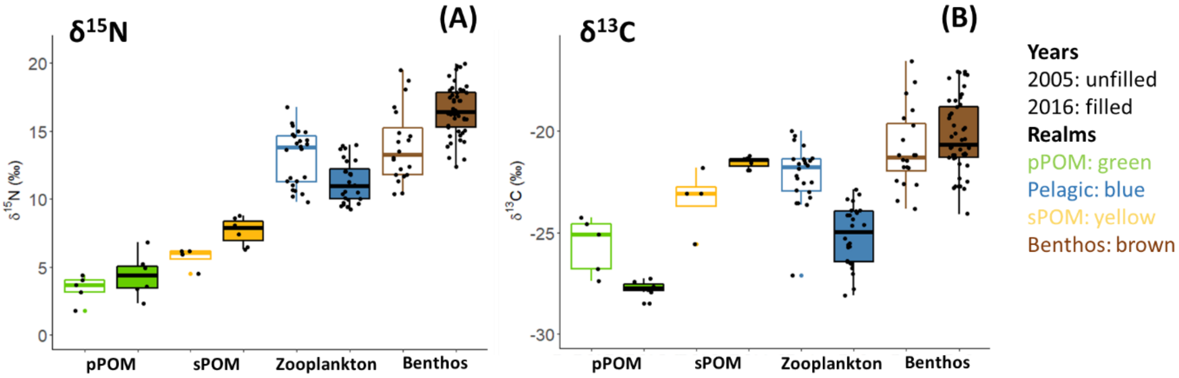


Figure 5. Mean values of $\delta^{15}N$ and $\delta^{13}C$ (‰) per food web component (pPOM in green, pelagic in blue, sPOM in yellow, and benthos in brown) in 2005 (open boxplots) and 2016 (filled boxplots), collected in the Chukchi Borderland. See Table 1 for pPOM and sPOM abbreviations. Only comparable taxa were included (i.e., either the same or closely related taxa).

Tables

Table 1. Station locations, depth and samples collected for stable isotope analysis in 2005 and 2016 in Arctic Chukchi Borderland. pPOM and sPOM stand for pelagic and sediment particulate organic matter, respectively.

Year	Station	Depth (m)	Latitude (°N)	Longitude (°W)	Pelagic	Benthic	pPOM	sPOM
2005	10	621	75.46	158.32	X		X	
	11	1374	76.01	160.41	X	X	X	X
	12	937	76.26	163.29	X	X	X	X
	13	2090	75.16	161.13	X	X	X	X
	14	749	74.18	159.54	X		X	
2016	1	853	74.37	159.53	X	X	X	X
	2	1059	74.66	158.38	X	X	X	X
	3	746	75.68	158.53	X	X	X	X
	9	508	76.51	163.78		X	X	X
	10	873	76.41	163.56	X	X	X	X
	12	2107	75.73	161.24	X	X	X	X
	13	2091	75.23	160.38	X	X	X	X

Table 2. Isotopic distances within and between means of $\delta^{15}N$ and $\delta^{13}C$ (‰) of endmembers (pPOM, sPOM) and consumers (zooplankton, benthos), in 2005 and 2016. See Table 1 for pPOM and sPOM abbreviations.

		Distance between				
		pPOM and sPOM	pPOM and zooplankton	pPOM and benthos	zooplankton and benthos	sPOM and benthos
$\delta^{15}N$						
	2005	2.1	9.6	10.5	0.9	8.4
	2016	3.3	6.9	12.1	5.2	8.9
$\delta^{13}C$						
	2005	1.7	3.5	4.7	1.3	3.0
	2016	6.2	2.6	7.5	4.9	1.3

Table 3. Comparison of $\delta^{15}N$ and $\delta^{13}C$ (‰) values from different food web components in the Chukchi Borderland between 2005 and 2016: results of parametric two sample *t*-test (t), Welch's two sample *t*-test (t) and Wilcoxon rank sum test (W) (for choice of test see methods). Numbers in bold indicate statistically significant results (p-values <0.05). See Table 1 for pPOM and sPOM abbreviations. See Figure 5 for graphical representation of means and error.

	t	W	df	n	p-value
$\delta^{15}N$					
pPOM	1.25		10	12	0.24
sPOM	3.36		9	11	**0.008**
Zooplankton		510	-	52	**0.001**
Benthos	3.86		27	69	< **0.001**
$\delta^{13}C$					
pPOM	3.95		10	12	**0.003**
sPOM		2	-	11	**0.029**
Zooplankton		630		52	< **0.001**
Benthos	1.32		67	69	0.191

Supplementary

Table S1. Food web niche metrics for different food web components (pelagic particulate organic matter (pPOM), sediment POM (sPOM), zooplankton, and benthos) collected in the Chukchi Borderland in 2005 and 2016. Number of samples (*n*), average δ^{13}C and δ^{15}N ± standard error (‰), δ^{13}C and δ^{15}N range (‰), standard ellipse area corrected for small sample size (SEA_C, ‰^{2}) that includes 95% of the data, and modes of posterior probability distribution (SEA_B).

		Means		Range			
	n	δ^{13}C	δ^{15}N	δ^{13}C	δ^{15}N	SEAc	SEA_B
2005							
pPOM	4	- 25.6±0.7	3.4±0.5	-24.0 to -27.7	1.4 to 5.1 ‰	3.0	2.7
sPOM	5	- 23.4±0.8	5.7±0.4	-25.6 to -23.1	4.5 to 6.2 ‰	1.8	2.3
Zooplankton	24	- 22.2±0.3	13.1±0.4	-27.8 to -19.7	8.1 and 17.2 ‰	10.0	9.4
Benthos	20	- 20.9±0.4	13.9 ± 0.6	-24.8 to -16.6	10.4 to 19.5 ‰	16.8	15.6
2016							
pPOM	7	- 27.8±0.2	4.4±0.7	-28.9 to -26.0	1.9 to 7.6 ‰	1.0	1.4
sPOM	7	- 21.5±0.1	7.6±0.4	-22.4 to 20.4	4.7 to 10.2 ‰	1.9	0.8
Zooplankton	28	- 25.2±0.3	11.3±0.3	-28.6 to -21.7	8.3 and 14.7 ‰	7.2	6.9
Benthos	49	- 20.2±0.3	16.5±0.3	-24.6 to -16.2	12.4 to 20.5 ‰	9.1	8.9

Table S2. Overlap of SEA_C (%) calculated for SEAs, containing 95 % of data, of different food web components (pPOM, sPOM, zooplankton, and benthos) collected in the Chukchi Borderland in 2005 and 2016.

	$pPOM_{2005}$	$sPOM_{2005}$	$Zooplankton_{2005}$	$Benthos_{2005}$	$pPOM_{2016}$	$sPOM_{2016}$	$Zooplankton_{2016}$	$Benthos_{2016}$
$pPOM_{2005}$	-							
$sPOM_{2005}$	4.8	-						
$Zooplankton_{2005}$	0	0	-					
$Benthos_{2005}$	0	0.1	57.9	-				
$pPOM_{2016}$	3.6	0.9	0	0	-			
$sPOM_{2016}$	0.4	1.8	2.6	3.7	0	-		
$Zooplankton_{2016}$	0	0	21.0	23.3	0	0	-	
$Benthos_{2016}$	0	0	27.6	50.7	0	0	5.5	-