

Department of Arctic and Marine Biology

Benthic Fauna on Ridges and Abyssal Plains in the Central Arctic Ocean: Baseline Data for Future Management

Ida Søhol Master's thesis in Biology BIO-3950, November 2024



Benthic Fauna on Ridges and Abyssal Plains in the Central Arctic Ocean: Baseline Data for Future Management

Author:

Ida Søhol

Supervisors:

Bodil Bluhm (UiT)

Eva Ramirez-Llodra (REV Ocean)







Open paper

November, 2024

Abstract

The benthos of the Central Arctic Ocean (CAO) abyss is an underworld yet to be thoroughly and systematically understood. Although 50% of the Arctic is deep sea, most research has been focused on the continental shelves and the water column. This is largely because research in the CAO is challenging, especially due to the ocean being ice-covered. Yet, today, anthropogenic pressures on the CAO are increasing with the ice cover declining, improving access for human activities. Since intense mining debates are occurring just south of this research area, it is urgent to compile information about benthic diversity also across the CAO. Existing data of benthic fauna of the CAO from decades of research provide valuable insights of benthic distribution and biodiversity in the Arctic deep-sea and substantial habitat diversity is now recognized, but spatial distribution and taxonomic knowledge gaps remain. Additional sampling and a pan-Arctic perspective are therefore essential for analyzing habitat-specific biodiversity, especially in areas that could be of interest for human use. This study is built on both a previously compiled dataset of benthic taxa records (depths >500 m), and new meiofauna samples to investigate patterns of benthic community composition and abundance compared between deep-sea ridges and deep-sea basins in the CAO from Fram Strait northwards.

My findings reveal that ridges have generally higher benthic abundance for both macro- and meiofauna, yet differences were not statistically significant. In the meiofauna, nematodes contributed most to abundance in soft sediment habitats of both ridges and basins, with >74% of total abundance in both habitats. Additionally, the similarities in benthic community structure across the CAO rather resemble geographical proximity, suggesting that neighboring regions – whether ridges or basins – generally have more benthic biota in common than similar geomorphological features do. A large fraction of benthic taxa from soft sediments at both ridges and basins that currently have only been recorded from a given ridge or basin of the CAO do also occur in other deep-sea areas outside the CAO. However, local habitat variations within ridges are recognized as a source of benthic faunal dissimilarity. Specifically, the presence of a wide range of geomorphological features (e. g. hydrothermal vents and seamounts) caused largely non-overlapping species presence among different habitats within the Gakkel Ridge, suggesting that ridge regions potentially possess benthic fauna that are not found elsewhere. This is suspected because most seamounts and vents in the CAO remain unmapped, and perhaps house more undiscovered fauna.

i

My study highlights the need for increased research efforts to develop baseline data of ridge and basin ecosystems in the CAO. Such research will critically improve the statistical power needed to assess to what extent ridge habitat heterogeneity creates unique benthic biodiversity. It is essential to attain sufficient understanding of the CAO deep-sea benthos before potential anthropogenic activities occur in these understudied ecosystems.

Acknowledgment

First and foremost, I would like to express my gratitude to my supervisors, Bodil Bluhm and Eva Ramirez-Llodra, for introducing me to this field, and for their guidance, encouragement, and expertise. Your insights and knowledge have been of great inspiration to me. I am incredibly thankful to have two power-women like you to look up to. A special thanks to my main supervisor, Bodil Bluhm, for your encouragement to this project, and for the trust you have shown me. Thank you for creating an environment for me with the freedom to explore, learn, network and develop new skills.

I extend my heartfelt thanks to Carolin Uhlir from Senckenberg for introducing me to the world of ArcGIS and welcoming me to the beautiful city of Hamburg. I will forever be greatful for gaining this new skill, and I could not ask for a better mentor – all the great discussions, problem solving and laughters made my introduction to ArcGIS so memorable!

A special thank you goes to Joel Vikberg Wernström for introducing me to meiofaunal taxonomic identification. Your expertise and attention to detail were of great help, and I am thankful to have learned more about meiofaunal taxonomy during this period.

I am also grateful to the REV Ocean team and Ocean Census Cruise team for an incredible deep-sea cruise in May 2024. This experience expanded my deep-sea knowledge and I am thankful to now know so many amazing scientists from all corners of the world. I am honored to have had the opportunity to collaborate with you.

To my best friend and study partner, Vic – thank you for being by my side through all these years of scubadiving, freediving, skiing, surfing and studying. Sharing this journey with you has made this experience unforgettable. I also wish to acknowledge friends who made everyday moments special: Hanna, Johan, Juni and Tord – thank you for the chats, coffee breaks, and laughter in between study sessions.

Lastly, a special thanks to my family: mom, dad, Oskar, Kristine and Mats, for their neverending support!

Table of Contents

1	Intro	oduction	1
	1.1	Environmental Settings	1
	1.2	Deep-sea Habitats	2
	1.3	Biodiversity in the Arctic Deep Sea	4
	1.4	Importance of Studying the Deep Sea	6
2	Aim	s and Hypotheses	8
-	Ann	and Hypotheses	
3	Mat	erial & Methods	9
	3.1	Study Area	9
	3.2	H1: Abundance of Benthic CAO Fauna is higher at ridges than in basins	
	3.2.1	Field sampling	
	3.2.2	Meiofaunal Taxonomic Identification Data Analysis	12
	2.2.5	110. CAO Di la ca Hald Haima Anna Different farm tha Alamad Dising	10
	3.3 331	H2: CAO Ridges Hold Unique taxa Different from the Abyssal Plains	13
	3.3.2	Geographic Information Systems – ArcGIS	
	3.3.3	Statistical analysis	16
4	Rest	llts	18
•	4.1	Results H1: Abundance of Benthic CAO Fauna is higher at ridges than in basins	
	4.2	Results H2: Taxon Distribution at Ridges vs. Basins	
	4.2.1	Overall data distribution	22
	4.2.2	Community similarity between ridges and basins	25
	4.2.3	Taxon-level characteristics of basins and ridges	
5	Disc	ussion	
	5.1	Benthic Abundance on Ridges vs. Basins (H1)	
	5.2	Sampling, Record and Taxa Densities	
	5.3	Geographical Proximity in Community Composition	
	5.4	Ridges reveal high Community Heterogeneity	40
	5.5	Unique Species (that are not so unique?)	42
	5.6	Sources of Uncertainty	44
	5.6.1	Geomorphological features used for mapping in ArcGIS	
	5.6.2	Sampling and Standardization Challenges	45
6	Con	clusion and Outlook	
7	Refe	rences	
8	Арр	endix 1	

List of Figures

Figure 1. Map of the Central Arctic Ocean	9
Figure 2. Map of Occurrence Records	14
Figure 3. Overview Map of Subregions	15
Figure 4. Photo panel of Meiofauna Taxonomic Identification	19
Figure 5. Meiofauna Taxa Abundance	
Figure 6. Box plot of (a) Meiofauna and (b) Macrofauna Abundance	21
Figure 7. Map of (a) Sampling Events and (b) Geographical Record Density	23
Figure 8. Map of Taxa Count	24
Figure 9. Taxa Presence on Ridges vs. Basins	24
Figure 10. Bar plot of Percentage Contribution of Total Taxa Richness	25
Figure 11. Hierarchical Clustering Dendrogram	26
Figure 12. Non-Metric Multidimensional Scaling (NMDS) Analysis (8 Regions of CAO)	26
Figure 13. Non-Metric Multidimensional Scaling (NMDS) Analysis (17 Subregions of CAO)	27
Figure 14. Species Presence of Ridge Habitats (Vent Field, Seamount, Soft-Bottom)	29
Figure 15. Map Series of the CAO Ridges and Basins	

List of Tables

Table 1. Station Table of Nansen Legacy and GoNorth Stations	. 11
Table 2. Abundance of Benthic Meiofauna Taxa	. 18
Table 3. Results of Shapiro-Wilk Test and Mann-Whitney U Test	. 20
Table 4. ANOSIM Test Results	. 28

1 Introduction

Beneath the white Arctic sea ice, an abyssal world exists with far more questions than answers. The deep ocean is the least explored and understood ecosystem on Earth, despite being the largest (Ramirez-Llodra et al., 2010). However, the little we know indicates that the deep sea provides one of the highest levels of biodiversity on Earth (Ramirez-Llodra et al., 2010). The Central Arctic Ocean seafloor differs from other deep-sea environments due to the unique conditions of the Arctic. Unlike the North Atlantic deep sea, the Arctic deep sea is predominantly ice-covered, semi-isolated from other ocean basins, and geologically relatively young (Bluhm et al., 2011a). These factors, in addition to the pronounced seasonality in light availability and primary production, create a distinct and largely unexplored ecosystem (Bluhm et al., 2011a; Vinogradova, 1997).

1.1 Environmental Settings

The complex topography of the Central Arctic Ocean seafloor is defined by three prominent mid-ocean ridges: the Gakkel Ridge, extending from NE Greenland to the Laptev Sea, separating the Nansen and Amundsen Basins; the Lomonosov Ridge, separating the Eurasian from the Amerasian Basins; and the Alpha-Mendeleev Ridge, separating the Canada and Makarov Basins (Jakobsson et al., 2020), Figure 1). The only deep-water inflow to the CAO happens through the Fram Strait (2,500 m), exchanging deep water with the Greenland and Norwegian Basins (average depth 2,000-3,000 m) (Rudels & Quadfasel, 1991). Within the intricate deep-sea bathymetry, the seafloor biomes encompass a variety of environments, including continental and island slopes, submarine canyons, abyssal plains, seamounts, ridges and plateaus, as well as deep-water biogenic beds, and chemosynthesis-based ecosystems (Keith et al., 2020). Geomorphological features such as rocky substrate, slopes and elevation gradients, play a vital role in shaping different ecosystems within the deep benthic biome by influencing the movement of ocean currents and the vertical flux of nutrients and organic matter (Keith et al., 2020). These features found on e.g. ridges and seamounts, can create resource-rich hotspots for organisms that support diverse and thriving marine communities.

The abyssal zone covers depths from 3000 to 6000 meters, and primary productivity through photosynthesis is not supported due to the lack of light (Keith, 2020). Organisms of the deep sea are adapted with traits that allow survival in conditions of complete darkness, high hydrostatic pressure, and scarce levels of nutrients and carbon (Keith, 2020). Since the

abyssal environment is characterized by a scarcity of fresh food, the structure and function of the ecosystem is heavily influenced by the quantity and quality of the detrital matter that descends from the water column (Gage, 2003; Ramirez-Llodra et al., 2024; Smith et al., 2008; Wiedmann et al., 2020). This organic material originates from deposits from the overlying water column, such as sinking sea-ice and pelagic algae, or from advection from continental margins and river inputs (Boetius et al., 2013; Gage, 2003; Ramirez-Llodra et al., 2024; Rybakova et al., 2019; Smith et al., 2008). This organic matter accumulates only in the uppermost sediment layer, while the sediment in the Arctic abyssal zone is otherwise (similar to the global ocean) predominantly inorganic (Ramirez-Llodra et al., 2024). Only ca. 1% of surface ocean production in the Arctic sinks out to the deep-sea floor (Wiedmann et al., 2020), due to strong recycling and grazing in the pelagic system, consequently weakening pelagic-benthic coupling and limiting food supply for benthic deep-sea communities (Wassmann & Reigstad, 2011).

1.2 Deep-sea Habitats

The abyssal seafloor is the largest group of benthic marine habitats, accounting for 73% of the global seafloor area (Ramirez-Llodra et al., 2010). Still, less than 1% of the biology of the abyss has been investigated (Keith et al., 2020). Being an intricate network of plains and rolling hills broken up by seamounts, and subdivided by mid-ocean ridges, island arcs and ocean trenches, the abyssal plains are mostly blanketed by a thick layer of fine sediment and clay (Smith et al., 2008). Infaunal communities, such as meiofauna, are particularly prevalent in soft sediment (Rex et al., 2006). Characteristic to soft sediment habitats, the meiofauna is primarily dominated by nematodes and foraminiferans, whereas crustaceans and bivalves dominate the macrofauna, and the megafauna exhibits dominance by echinoderms (Bluhm et al., 2011a). Globally, the abyssal biota is remarkably diverse, though densities and biomass are low (Bluhm et al., 2011a; Wei et al., 2010; Wiedmann et al., 2020). Abyssal ecosystems consist predominantly of macrofauna and meiofauna, with a significant proportion of species (in a global perspective) newly discovered and unknown to science (Keith et al., 2020). Species distribution and key ecological processes, such as community respiration and bioturbation, are linked to the flux of particulate organic carbon, and these processes influence critical ecosystem services provided by abyssal plains, including nutrient cycling and carbon sequestration (Keith et al., 2020).

Mid-ocean ridges are Earth's largest volcanic system, created by lateral spreading of ocean crust and the upwelling of basaltic lava, forming a rift valley that encircles the Earth (Harris et al., 2014). Of all ocean basins, the CAO has the largest fraction of mid-ocean spreading ridge in the abyssal zone, with these ridge features covering 4.76% of the abyssal zone (Harris et al., 2014). The ridges host a variety of habitat types, including steep rocky walls, sedimented areas, seamounts, banks, and both active and inactive hydrothermal vents (Ramirez-Llodra et al., 2024). This diversity in topography and substrate types contributes significantly to niche diversity and biodiversity in these regions (Keith et al., 2020). The interaction of these prominent topographic formations with water masses and currents increasing turbulence, mixing, and particle retention, in turn facilitates the upward movement of nutrients from vast areas of the seafloor, thereby supporting varied ecosystems (Keith et al., 2020).

Hydrothermal vents are extraordinary geothermal features found along mid-ocean ridges, back-arc basins and active seamounts, where heated fluids (up to 400°C) rich in metals and chemicals are released from chimneys (Keith et al., 2020). Biological communities in hydrothermal ecosystems are primarily sustained by chemoautotrophic microorganisms, which derive energy from the oxidation of reduced compounds in vent fluids, such as sulfide, methane, and hydrogen, alongside oxidized compounds in seawater, like sulfate, nitrate and oxygen (Juniper, 2001; Ramirez-Llodra et al., 2023; Van Dover, 2000). The energy derived from these reactions allows the microorganisms to fuel higher trophic level faunal biomass, where the specific environmental characteristics of hydrothermal vents result in low diversity but high endemism of specialized fauna (Keith et al., 2020).

Vent faunal communities in the CAO have remained unexplored until recently because of their remote, challenging and ice-covered locations (Ramirez-Llodra et al., 2023). The first evidence of hydrothermal venting on the Gakkel Ridge was found in 2001 on the AMORE expedition by Edmonds et al. (2003). In 2014, the AURORA expedition aimed to further study hydrothermal vents on the Gakkel Ridge, leading to the first images of an active black smoker, named the Aurora Vent Field (Boetius, 2015; Ramirez-Llodra et al., 2023). In 2021, another significant milestone was achieved when Ramirez-Llodra et al. (2023) documented the Aurora Vent Field as the first and only hydrothermal vent site explored on the Gakkel Ridge in the CAO to date. Using a remotely operated vehicle (ROV), researchers collected vent fluids, rocks, microbes, and fauna for detailed study of this unique chemosynthetic-based ecosystem. Their findings revealed species new to science, in addition to dense aggregations of hexactinellid sponges in the vicinity of the vent, suggesting that these habitats may play a

crucial role in supporting other marine fauna. Shrimps, anemones, crinoids, isopods, and amphipods were observed in greater abundance in areas dominated by hexactinellid sponge habitats, indicating a facilitating effect. Further investigations in taxonomy, connectivity, and biogeography of the fauna are ongoing in order to clarify the links between the Aurora Vent Field fauna and that of other vent fields (Ramirez-Llodra et al., 2023).

In addition to hydrothermal vents, the Gakkel Ridge features seamounts, often recognized as "hotspots" of marine life because of increased productivity and particle export (Morganti et al., 2022; Rogers, 2018). Seamounts are characterized as topographic elevations rising >1,000 m from the seafloor without reaching the ocean surface, housing structures like rocky outcrops and walls as well as sedimented areas (Keith et al., 2020). Other similar geographic structures but of lower elevations are called knolls, mounds and plateaus (Ramirez-Llodra et al., 2024; Rogers, 2018; Schlacher et al., 2010). Seamounts often support filter-feeding benthic communities, particularly under conditions of upwelling hydrodynamics (Morganti et al., 2022) or modified currents (Kröncke, 1994). Rocky walls can, for example, be dominated by sessile suspension-feeders, such as cnidarians, crinoids, sponges and ascidians (Keith et al., 2020) which is related to the higher current velocity at slopes (Kröncke, 1994). Only five seamounts in the deep Arctic Ocean have been studied to date, with their biological communities documented and described: Northern Mount, Central Mount and Karasik Seamount on the Langseth Ridge (Morganti et al., 2021; 2022; Ramirez-Llodra et al., 2024; Stratmann et al., 2022), Schulz Bank between Mohns and Knipovich Ridge (Hanz et al., 2022; 2021; Meyer et al., 2019; Morrison et al., 2020; Ramirez-Llodra et al., 2024; Roberts et al., 2018), and Vesteris Bank in the central Greenland Sea (Henrich et al., 1992; Ramirez-Llodra et al., 2024; Unger Moreno et al., 2021).

1.3 Biodiversity in the Arctic Deep Sea

Although only a small fraction of the abyss has been biologically investigated, great efforts have already been made that are crucial for our understanding of the biodiversity of the Arctic deep sea. Sirenko (2001) compiled the first species inventory published in 2001 containing approximately 4,800 species for the Arctic Seas, of those 712 taxa for the CAO, with the purpose of increasing knowledge of biodiversity and species composition in the poorly studied Arctic marine regions (Sirenko, 2001). Their study built on Russian and international literature, compiled material from museums and institutions, as well as unpublished data by the authors (Sirenko, 2001). Further, the Census of Marine Life Arctic Ocean Diversity

Project was established in 2004 (Gradinger et al., 2010) with the aims to assess diversity, distribution and abundance of species from the sea ice and water column to the deep basins (Bluhm et al., 2011a; Yarincik et al., 2005). This effort increased the knowledge of CAO fauna to 1,125 taxa identified occurring only in the CAO (Bluhm et al., 2011a). Additionally, the German Alfred Wegener Institute for Polar and Marine Research (AWI) recognized the importance of detecting large-scale environmental changes in the Arctic (Soltwedel et al., 2005). With the great efforts of establishing the deep-sea observatory "Hausgarten" in 1999, they represented the first open-ocean, long-term station in a polar region, providing the first long-term Arctic time-series studies (Soltwedel et al., 2005). Additionally, important work has been conducted by Russian and American drifting stations for decades (Frolov et al., 2005; WHOI, n.d.). In 2022, Vedenin et al. (2022), conducted the first large-scale regional study of bathymetric zonation of benthic fauna in the Arctic Ocean concentrating on macroand megabenthos spanning from the shallow shelf to the deep abyssal plain (Vedenin et al., 2022). A recent publication by Ramirez-Llodra et al. (2024) from the Challenger 150 Programme – a UN Ocean Decade endorsed initiative (Challenger150, n.d.) – has made a thorough work in recognizing habitat heterogeneity in the CAO. These comprehensive and systematic studies, among others, are valuable efforts that advance our understanding of the benthic biodiversity of the CAO.

The deep sea hosts a surprisingly high biodiversity, despite food scarcity, low temperatures and the generally extreme environmental conditions (Levin et al., 2001). Studies conducted by Rex et al. (2006) provided a detailed investigation of how decrease in organic carbon input with depth shapes benthic community structure along depth gradients. The oligotrophic nature of the Arctic Ocean deep sea promotes small size-groups like meiofauna, bacteria and foraminifera (Kröncke et al., 2000). Body size of all marine animals significantly decreases with depth (Rex et al., 2006), where the larger size classes are replaced with dominance of smaller size classes (Giere, 2008), likely due to the decrease in quality and quantity of food supply with increasing depth (Wei et al., 2010). Ultimately, the correlation in depth and decreased organism size is the most consistent and prominent biogeographic trend of deep-sea benthos (Rex et al., 2006). Apart from body size adaptations in the deep, macrofaunal movement and hydrodynamic patterns are important factors for sustaining biodiversity for the deep-sea infauna, by providing heterogeneity by structuring the seabed, allowing for sufficient oxygen and availability of nutrients from phytodetritus (Giere, 2008). Despite this

5

high biodiversity pattern discovered in the deep sea, declines in abundance and biomass with depth are frequent on community level (Giere, 2008).

1.4 Importance of Studying the Deep Sea

With the sea-ice melting, the vast potential for industrial activities like deep-sea mining, shipping, fishing and oil and gas are driving the growing interest in the Arctic from policy makers, governments and industry (Huntington et al., 2022; Ramirez-Llodra et al., 2024). With increased human pressure in the Arctic, the urgency of developing management and conservation plans is critical to monitor this pristine region *before* the expected increase in anthropogenic activities occur (Ramirez-Llodra et al., 2023; 2024). Deep-sea mining is still an emerging industry, unlike other industrial sectors, providing a valuable opportunity to collaborate with industry and policy makers to produce science-based management plans to minimize ecological risks (Levin et al., 2020; Miller et al., 2018).

Active hydrothermal vents discharge metal-rich fluids that precipitate at the seafloor and form polymetallic sulfides of especially copper and zinc (Van Dover et al., 2018). These metal rich features are of interest to an emergent deep-sea mining industry at a global level (Petersen et al., 2016; Van Dover et al., 2018). Prominent investigations and debates on deep-sea mining are focused on the Clarion Clipperton Fracture Zone, an area with high presence of manganese nodules in the Central Northeast Pacific ocean, regulated by the International Seabed Authority (ISA, 2024; Koschinsky et al., 2018). Additionally, the Arctic Mid-Ocean Ridge (AMOR) is also a region of interest due to its mineral resources on hydrothermal vents and metal-rich crusts, though environmental concerns are significant due to the consequences of such anthropogenic activity on the fragile and underexplored ecosystems associated with these vent features (Amon et al., 2022; Levin et al., 2020). Consequently, it is crucial to assess whether the ecological significance, international obligations, and other insights regarding the value of active hydrothermal vent ecosystems, justify their protection over exploitation for mining purposes (Van Dover et al., 2018). The unique faunal communities found at active hydrothermal vents are of great interest due to their specialized physiological adaptations and high levels of endemicity, in addition to having significant potential for providing marine genetic resources with applications in biomedicine, biofuels, and other industries (Ramirez-Llodra et al., 2023; Van Dover et al., 2018).

6

Given the limited historical exploration, comprehensive systematic surveys that incorporate both field data collection and analytical integration processes are crucial for establishing baseline data, documenting species distribution and understanding the dynamics of Arctic deep-sea ecosystems (Olsen et al., 2016). The CAO is not connected to potential deep-sea mining areas at the moment. Yet, continuous mapping of mineral composition on ridges is, and has been, performed by multiple geological surveys carried out by science cruises, or the Norwegian Offshore Directorate with Norwegian universities highly involved in the exploration process (Energidepartementet, 2024). The Mohns and Knipovich ridges located on the AMOR have been identified as promising for mineral exploration because of their hydrothermal sulfide deposits and manganese crusts (Sokkeldirektoratet, 2023). These ridges are within Norway's national jurisdiction, and this year (2024) the government opened these areas for mineral exploration (Energidepartementet, 2024). Based on the scarcity of knowledge about the Arctic deep-sea fauna, and the increasing interest in anthropogenic activities with commercial interests in the Greenland, Iceland and Norwegian seas (GIN seas) (Olsen et al., 2016), it is of particular interest to also investigate faunal biodiversity, species composition and abundance on the CAO ridges and basins connecting to these areas in the north. Recent work by Ramirez-Llodra et al. (2024) has compiled valuable biodiversity data for each of the habitats of the CAO, but did not investigate specific biodiversity differences between regions or habitat types. My study addresses this gap by comparing biodiversity across basins and ridges and assessing region-and-habitat-specific uniqueness (e.g., vent fields, seamounts, ridges and basins), aiming to clarify biodiversity patterns that are currently underexplored in the CAO.

2 Aims and Hypotheses

The overall aim of this study is to investigate the variations in benthic fauna community composition between deep-sea basins and deep-sea ridges in the Central Arctic Ocean. Specifically, I examined variations in benthic organism abundance and biodiversity patterns between basins and ridges deeper than 500 m and north of Fram Strait. Given benthic biomass declines with water depth, and currents around ridges may facilitate production increases (Keith et al., 2020; Kröncke, 1994), and the substantial heterogeneity of benthic habitats associated with ridges (Giere, 2008; Ramirez-Llodra et al., 2024), I hypothesized:

- H1: Faunal abundance is higher at ridges than in the abyssal plains of the CAO basins.
- H2: The Arctic Ocean ridges hold unique taxa and communities different from the abyssal plains of the CAO.

My findings will provide additional data on benthic ecosystems from the deep Central Arctic Ocean, which is essential to develop robust management measures before any human impact occurs on the seafloor.

3 Material & Methods

3.1 Study Area

For this research, the area of interest is the basins and ridges in the Central Arctic Ocean known as Canada Basin, Northwind Ridge, Mendeleev Ridge, and Makarov Basin on the Amerasian side, and Lomonosov Ridge, Amundsen Basin, Gakkel Ridge and Nansen Basin on the Eurasian side (Figure 1). The Fram Strait on the Atlantic side and the Bering Strait on the Pacific side serve as the only gateways and are known to be the only places where sea water flows into the Arctic Ocean (Jakobsson et al., 2020). The Fram Strait is the only deepwater connection to the Arctic (Jakobsson et al., 2020).



Figure 1. Map of the Central Arctic Ocean with the 8 main regions of interest, and the stations of the Nansen Legacy Cruise (AeN) and the GoNorth Cruise (GN) samples used in testing H1.

3.2 H1: Abundance of Benthic CAO Fauna is higher at ridges than in basins

3.2.1 Field sampling

To investigate Hypothesis 1, meiofauna samples from Nansen Legacy Cruise 2021 (cruise number 2021710) (Fransson et al., 2022) and Go North Cruise 2023 (Cruise number KH23-249) (GoNorth, 2023) were studied for abundance estimates and coarse taxonomic identification. The two Go North (GN) samples and Nansen Legacy (AeN) sample P9 were collected on the Gakkel Ridge, while AeN samples P7 and P8 were collected from Nansen Basin, and AeN samples P10 and P11 were collected from Amundsen Basin (Figure 1, Table 1). The meiofauna samples were fixed in 70% ethanol and stained with rose bengal.

The area of the Nansen Legacy transect covered a depth range of ca. 2800-4800 m with sampling covering depths between 3087-4283 m (Fransson et al., 2022). The geographical range spanned from 81.81-87.48°N and 30.85°E-18.03°W (Table 1). Sampling was conducted between 30th of August to 18th of September 2021. The GN stations were sampled at depths of 3955 m (GN1) and 3809 m (GN2) on 22th and 26th of July 2023, respectively. Coordinates were 82.8968° N, 6.2155° W (GN1) and 81.3831° N, 4.1010° W (GN2).

To retrieve AeN meiofauna samples, a box corer was utilized with a surface area of 0.5 x 0.5 meters during the Nansen Legacy cruise (Protocol, 2021). From each P-station, three box cores were collected. The meiofauna cores were pushed into the box core samples and measured 5 cm in diameter and were sectioned into centimeter-thick layers (0-1 cm and 1-2 cm). The samples were split into two parts: one for metazoan meiofauna studies and the other for foraminifera studies. Splitting was performed at the University of Oslo by collaborators. For statistical analyses later, my samples were therefore multiplied by 2 to estimate the true abundance. Latitude, longitude, and water depth data were recorded for each sampling event. GN cores measured 5.7 cm in diameter, and a single 0-2 cm layer was sectioned off. Here, single sediment samples per site were derived from ROV push cores.

Table 1. Station Table for the Nansen Legacy (AeN) and GoNorth (GN) stations from the Nansen Basin, Gakkel Ridge and Amundsen Basin, used for meiofauna samples to address hypothesis 1.

Date	Station Name	Latitude	Longitude	Bottom	Gear	Basin/
		(deg N)	(deg E/-W)	Depth (m)	Туре	Ridge
3.9.2021	P8_1	83.8310	26.1610	4017	Box core	Basin
3.9.2021	P8_2	83.8252	26.0792	4017	Box core	Basin
3.9.2021	P8_3	83.8375	26.1442	4017	Box core	Basin
8.9.2021	P9_1	85.5469	6.1870	3623	Box core	Ridge
8.9.2021	P9_2	85.5489	5.7304	3386	Box core	Ridge
8.8.2021	P9_3	85.5308	5.2367	3494	Box core	Ridge
13.9.2021	P10_1	86.3739	-16.6770	4246	Box core	Basin
13.9.2021	P10_2	86.3951	-16.4257	4248	Box core	Basin
13.9.2021	P10_3	86.4163	-16.4282	4252	Box core	Basin
18.9.2021	P11_1	87.4900	-18.0397	4279	Box core	Basin
18.9.2021	P11_2	87.4821	-17.7250	4283	Box core	Basin
18.9.2021	P11_3	87.4848	-17.6742	4281	Box core	Basin
22.07.2023	GN Station 1	82.8968	-6.2155	3955	Push core	Ridge
26.07.2023	GN Station 2	81.3831	-4.1010	3853	Push core	Ridge

3.2.2 Meiofaunal Taxonomic Identification

To address hypothesis 1, the retrieved meiofauna samples were investigated at the Benthos lab at NFH. The upper 0-1 cm layer and the 1-2 cm layer were processed separately for all AeN replicates. Meiofauna was sorted under a Leica (Model MZ16) microscope, inspected at 10-15x magnification, and/or at 30-50x for the smallest organisms. A small amount of each sample was placed in a Bogoroy tray with the use of a pipette. This sorting dish consists of a deeper meandering system along the tray, ensuring thorough inspection of the sample and avoiding overlooking small individuals of meiofauna. An Irvine loop, a particularly thin wired loop designed for small sized animals, was used to transfer individuals to separate vials by taxon. Each individual was identified to phylum level, and to lower taxonomic levels, when possible, based on their morphological characteristics. Identification was based on the book *Meiobenthology: The Microscopic Motile Fauna of Aquatic Sediments* by (Giere, 2008), as well as taxonomic expertise assistance from PhD. student Joel Vikberg Wernström and his network.

3.2.3 Data Analysis

Statistical analyses and data visualization were performed in RStudio (version 2024.04.2+764) by R (version 4.4.0, R Core Team, 2024). The abundance and composition of samples derived from the Gakkel Ridge were compared with samples retrieved from the Amundsen and Nansen Basins. The counts from 0-1 cm layers and 1-2 cm layers were added together for the AeN samples. Mean abundances were calculated per 10 cm², the typical area to which meiofauna are standardized. Stacked bar charts were made with the "ggplot2" package (Wickham, 2016) to visualize meiofauna taxon abundance and relative abundance by taxonomic group on ridges and basins.

Then I tested if there were significant differences in meiofauna abundance on ridges and basins. For this analysis, meiofauna abundance data from Schewe and Soltwedel (1999), Schewe (2001) and Clough et al. (1997), in addition to the AeN and GN samples, were used to ensure a larger dataset to investigate differences in abundances on CAO ridges and basins. Ultimately, 28 stations on ridges and 19 stations in basins were available. To test the normal distribution of this combined dataset, I performed a Shapiro-Wilk test and consequently conducted a Mann-Whitney U Test on the non-normally distributed data. For visualization, box plots with "ggplot2" package (Wickham, 2016) were produced. The identical procedure was performed to investigate if macrofauna abundance (ind. per m²) followed the same

pattern by extracting abundance data from Kröncke (1994) and Clough et al. (1997) with a total of 24 ridge stations and 21 basin stations.

3.3 H2: CAO Ridges Hold Unique taxa Different from the Abyssal Plains

3.3.1 Data Structure

To address hypothesis 2, a larger biodiversity dataset recently compiled for the deep Arctic Ocean, considering depths of >500m (Ramirez-Llodra et al., 2024) was used to quantify biodiversity by region. Statistical analyses and mapping were performed in R Studio and ArcGIS versions.

Ramirez-Llodra et al. (2024) compiled the data from three sources: 1) non-digitized scientific literature, 2) previously unpublished field data collections, 3) open-access databases like the Ocean Biodiversity Information System (OBIS; www.iobis.org) and the Global Biodiversity Information Facility (GBIF; www.gbif.org). According to Ramirez-Llodra et al. (2024), the merged dataset was subjected to quality control following the criteria of (Saeedi et al., 2019a; 2019b) and Alfaro-Lucas et al. (2023). This included matching taxonomic names against the World Register of Marine Species (WoRMS) and reconciling synonyms, verifying pelagic and non-marine taxa based on literature, and retaining only accepted marine benthic species while removing unaccepted, pelagic, or non-marine records. Additionally, records identified at higher taxonomic levels were excluded due to uncertainties in their benthic classification. The dataset was further cleaned using R packages "robis" and "scrubr," with duplicates, dubious records, and data exceeding the Arctic Ocean's maximum depth removed. The depth accuracy of the records was validated using the International Bathymetric Chart of the Arctic Ocean (IBCAO) map, and any discrepancies between a data record and the IBCAO exceeding 1000 m were excluded. Following these rigorous quality control measures, the final dataset contained 75,404 occurrence records (Ramirez-Llodra et al., 2024).

For my study, I delineated the research area to north of Fram Strait, excluding the GIN Seas, and made the following modifications to the data set: Habitat types from bathymetric feature layers produced by Harris et al. (2014) that were not a ridge or basin were removed from the data set, and all occurrence records belonging to these features were filtered out in ArcGIS to ensure only records from areas of interests (Figure 2) for this particular study were included. The derived dataset was complemented by the meiofaunal taxonomic work from my AeN and GN samples (H1), resulting in the dataset consisting of 18,165 records in total. One "record" represents an individual taxon occurrence at a specific georeferenced location (Ramirez-Llodra et al., 2024). For investigating taxonomic composition differences within regions, each region, apart from Northwind Ridge and Nansen Basin, was divided into subregions based on geographic clusters of occurrence records assessed by eye (Figure 3).



Figure 2. Map of Occurrence Records illustrating only the habitat types of interest: ridges and basins, and all occurrence records that overlap with ridge or basin areas. Occurrence records include the compiled dataset from Ramirez-Llodra et al., 2024, in addition to the meiofauna samples from AeN and GN cruises. Geomorphological feature layers produced by Harris et al., 2014.



Figure 3. Overview Map showing the 17 subregions derived from the 8 main regions. GR = Gakkel Ridge, LR = Lomonosov Ridge, MR= Mendeleev Ridge, NW = Northwind Ridge, NB = Nansen Basin, AB = Amundsen Basin, MB = Makarov Basin, CB = Canada Basin. N of records: CB1 (141), CB2 (80), CB3 (53), CB4 (169), AB1 (182), AB2 (122), GR1 (35), GR2 (15832), LR1 (23), LR2 (635), LR3 (57), MB1 (180), MB2 (72), MR1 (134), MR2 (52), NB (108), NW (261)

3.3.2 Geographic Information Systems – ArcGIS

Geographic analyses were performed in ArcGIS Pro (version 3.1.0) by Esri (Esri, 2023). Geomorphological shapefiles imported and applied for mapping in ArcGIS were produced by Harris et al. (2014) and applied as in Ramirez-Llodra et al. (2024). According to the International Hydrographic Organization and Intergovernmental Oceanographic Commission (IHO, 2019), basins are "a depression, in the seafloor, more or less equidimensional in plan and of variable extent"; mid-oceanic ridges are "the linked major mid-oceanic mountain systems of global extent" (Harris et al., 2014), and a ridge is described as "an elongated elevation of varying complexity and size, generally having steep sides". In Harris' study, the basins are restricted to seafloor depressions that are defined by closed bathymetric contours, where basins were mapped considering the identification of the most shoal, closed, bathymetric contours (Harris et al., 2014). In the major oceans, basins are bounded by the mid-ocean spreading ridges and by the foot of slopes (Gille et al., 2004; Harris et al., 2014; Wright & Rothery, 1998). Ridges were in Harris' study confined to features greater than 1000 m in relief, and often overlapped with other categories such as plateaus, spreading ridges and seamounts (Harris et al., 2014).

To delineate the research area and remove surrounding records that were not within the area of interest, a polygon of the Central Arctic Ocean (CAO) with a limitation to north of the Fram Strait was created in ArcGIS. Further subdivided, the following regions were defined and assigned to a geomorphological feature based on the definition of Harris et al. (2014): Amundsen Basin (Basin), Canada Basin (Basin), Gakkel Ridge (Ridge), Lomonosov Ridge (Ridge), Makarov Basin (Basin), Mendeleev Ridge (Ridge), Nansen Basin (Basin) and Northwind Ridge (Ridge). To investigate whether ridges of the CAO hold unique taxa compared to abyssal plains (H2), taxon occurrence records from the compiled data set were classified to the geomorphological features of interest (Ridge or Basin), with the "spatial join" tool applied from the analysis toolbox. Each ridge and basin were then matched with the region name in which they are located. Taxon occurrence records were spatially joined with the corresponding region name, to be able to visualize species that were occurring in, or unique to, each region in the data set.

To visualize the amount of taxa (taxa count), occurrence record density and sampling effort within a defined area, equal-sized hexagon cells (hexagonal cell = 5, 000 m²) were used. This cell size is 1/10 of the size Ramirez-Llodra et al. (2024) utilized, which fit well into the geomorphological structures of this more detailed investigation. In addition, a map-series was created with one map per region showing their taxon distribution and uniqueness in terms of species in the compiled data set.

3.3.3 Statistical analysis

Statistical analyses were performed in RStudio (version 2024.04.2+764) by R (version 4.4.0, R Core Team, 2024). To investigate H2, the compiled dataset from Ramirez-Llodra et al. (2024) and including the meiofauna records generated in this thesis was transformed into presence/absence format. This approach was selected due to taxa distribution being the primary focus, for which presence/absence data is sufficient. Additionally, lack of consistent sampling effort and unit area knowledge across different data points created uncertainty of whether numbers associated with the taxon data was comparable.

16

To explore regions of similar benthic faunal characteristics, a hierarchical cluster analysis was performed using the "jaccard" distance metric with an average linkage method with the "vegan" package. This distance metric is used for measuring dissimilarity between the stations based on presence or absence of taxa (Oksanen, 2024). To further support the cluster analysis, I explored differences in community composition among the ridge and basin regions in the CAO by performing a Non-Metric Multidimensional Scaling analysis (NMDS), again with the "jaccard" distance matrix. The NMDS was also produced using the "vegan" package (Oksanen, 2024). Data visualizations were generated with the "ggplot2" package (Wickham, 2016). To test for potential statistical differences between group 'ridge' and group 'basin' an ANOSIM test (Analysis of Similarities) was then performed by using the package "vegan" (Oksanen, 2024). and "jaccard" as distance matrix. The R-value provided compared the differences in similarity ranks between and within groups, where R-values close to 1 indicate high dissimilarity between groups while values close to -1 suggest high dissimilarity within groups, and R-values near 0 indicate no difference between and within groups (Clarke, 1993). Two NMDS plots and ANOSIM tests were conducted: one investigating differences between the CAO's basins and ridges, and one investigating differences among all 8 regions of the CAO by dividing the 8 main regions into a total of 17 subregions to account for within-region variability (Figure 3). Finally, taxon distribution patterns within a single ridge, the Gakkel Ridge, were shown as species presence across different habitats of this particular ridge (Aurora Vent Field, seamount on Langseth Ridge and soft sediments from Langseth Ridge) and performed with the package "ggplot2" (Wickham, 2016).

4 Results

4.1 Results H1: Abundance of Benthic CAO Fauna is higher at ridges than in basins

A total of 206 individuals of meiofauna were identified across 6 stations. The identified meiofauna belonged to 5 phyla: Arthropoda, Nematoda, Cnidaria, Annelida and Kinorhyncha (Table 2, selection of several phyla shown in photo panel Figure 4). Within the Arthropoda, further identification to lower taxonomic levels was done for Copepoda (order), Ostracoda (class), Peracarida (order) and nauplii (copepod larval stage).

Table 2. Abundance of benthic meiofauna taxa abundance of benthic meiofauna taxa from the central Arctic Ocean in the top
2 cm of sediment at Ridges (Mean of P9, GN1, GN2) vs. Basins (Mean of P8, P10, P11). For stations P8-P11 three replicates
each were studied while only one replicate each was available for GN1 and GN2.

Taxa	Abundance Ridge (ind/10cm ²)	Standard Deviation	Abundance Basin (ind/10cm ²)	Standard Deviation	
Nematoda	12.17	0.41	5.11	1.02	
Copepoda	0.90	0.58	0.34	0.47	
Ostracoda	0.25	0.22	0.34	0.47	
Cnidaria	0.12	0.21	0.05	0.09	
Nauplii	0.05	0.09	0.05	0.09	
Annelida	0.18	0.20	0.51	0.51	
Kinorhyncha	0.00	0.00	0.42	0.42	
Peracarida	0.00	0.00	0.05	0.05	
Total Abundance	13.67		6.88		
Mean	1.71		0.86		
Standard Deviation (SD)	4.24		1.73		



Figure 4. Microscopic photographs of a selection of individuals from taxonomic identification. a) Cnidaria, b) Kinorhyncha, c) harpacticoid Copepoda, d) Nematoda, e) Cnidaria, f) Nauplii, g) Specimen believed to be a terrestrial beetle larva of the Haliplidae family, magnification unknown. (pictures of Ostracoda and Annelida not included due to lack of photographs)

Nematodes dominated the community in terms of abundance in both studied habitats, accounting for 89.0% of the individuals found on the ridge, and 74.4% of the individuals in the basins (Figure 5). Copepoda and Cnidaria contributed higher percentages on the ridges with respectively 6.6% and 0.9% on the ridges and 4.9% and 0.7% in the basins. For the remaining taxa, the basins had higher percentage abundance than the ridges: Ostracoda (4.9% over 1.8%), Nauplii (0.7% versus 0.4%), Annelida (1.3% over 7.4%), Kinorhyncha (0.0% over 6.2%) and Peracarida (0.0% over 0.7%). Total mean abundances in my data set were 40.36 ± 12.7 (SD) for the ridge, and 20.61 ± 5.19 for the basins (Table 2). A curious find included an exuvia of a beetle larva (family Haliplidae), identified by Andre Frainer (UiT) (Figure 4).



Figure 5. Meiofauna Taxa Abundance from AeN and GN samples. a) visualizes abundance count of each taxon, b) shows percentage contribution in abundance of each taxon.

Table 3. Results of Shapiro-Wilk Test to test whether the abundance data of benthic meiofauna (own data and literature) and macrofauna (literature) from the CAO was normally distributed, and Mann-Whitney U Test to test the difference between the two groups. Meiofauna (n = 19 (basin), n = 28 (ridge) and macrofauna (n = 21 (basin), n = 24 (ridge) abundance.

	Meiofauna:		Macrofauna:	
Test:	P-value:	W-/U-statistic:	P-value:	W-/U-statistic:
Shapiro-Wilk Test: Ridge	0.0257	W: 0.915	3.439e-05	W: 0.739
Shapiro-Wilk Test: Basin	0.003	W: 0.825	3.574e-07	W: 0.526
Mann-Whitney U Test	0.132	U: 196	0.432	U: 217

For the data sets containing the literature sources specified in section 3.2.3, Shapiro-Wilk Test results for both macro- and meiofauna showed low p-values (< 0.05) on ridges and basins, indicating that the data was not normally distributed (Table 3, Figure 6). Meiofauna abundance differences between basins and ridges were not significant (Mann-Whitney U test; p-value = 0.132; Table 3). Macrofauna abundance between basins and ridges also showed non-significant values (Mann-Whitney U test; p-value = 0.432; Table 3).



Figure 6. Box plot of a) meiofauna abundance and b) macrofauna abundance on basins and ridges with data from literature sources specified in section 3.2.3, in addition to AeN and GN meiofauna samples for a). The dark red symbol shows the mean of each box plot, and the bold horizontal line indicates the median. Top and bottom of the boxes represent the first and third quartile. The whiskers indicate the lowest and highest value. a) n basin = 19, mean basin = 22.18 and median basin = 9.54. n ridge = 28, mean ridge = 33.73 and median ridge = 30.50. b) n basin = 21, mean basin = 348,62 and median basin = 141.00. n ridge = 24, mean ridge = 396.29 and median ridge = 200.

4.2 Results H2: Taxon Distribution at Ridges vs. Basins

4.2.1 Overall data distribution

In total, the compiled dataset from Ramirez-Llodra et al. (2024) consists of 18,165 occurrence records, with 11,744 records identified to genus or species level, distributed over 10 phyla. Occurrence records ranged from 1 to 3,410 records per taxon. Sampling effort across the CAO was generally low, with the highest number of sampling events in certain places on Lomonosov Ridge, Amundsen Basin, Gakkel Ridge and Nansen Basin (Figure 7a). The density in benthic taxa occurrence records (Figure 7b) ranging from 1 to 15,824 records largely followed the pattern of sampling effort. The lowest total count of occurrence records was in the Nansen Basin (108) and the Makarov Basin (252), while highest numbers of occurrence records were on the Gakkel Ridge (15,867) and the Lomonosov Ridge (715).

The CAO ridges had higher values of taxa richness compared to the basins, which overall had consistently lower taxa counts (Figure 8). However, ridges also had more occurrence records (n=11,051) compared to basins (n=693). Regardless of this bias, available data suggest that taxon richness in both habitats is highest for Arthropoda, Nematoda and Annelida (Figure 9) and that the percentage contribution of each taxa is similar in both basins and ridges (Figure 10).



Figure 7. a) Map representing the count of all unique sampling events according to geographical location; b) map representing the density of records according to geographical location.



Figure 8. Map illustrating the count of taxa according to geographical locations.



Figure 9. Comparison of number of taxa by phylum between habitats (ridges and basins). The x-axis represents the 10 phyla, the y-axis represents the number of taxa within each phylum. Total occurrence records in basins = 693. Total count of taxa in basins = 159. Total occurrence records on ridges = 11,051. Total count of taxa on ridges = 195.



Figure 10. Stacked bar plot visualizing percentage contribution of total taxa richness by phylum for basins and ridges.

4.2.2 Community similarity between ridges and basins

The hierarchical clustering dendrogram for all 8 regions of the CAO visualizes a geographical clustering pattern separating the Eurasian and Amerasian sides of the CAO (Figure 11). The Amundsen Basin and Nansen Basin form a cluster together with the Gakkel Ridge that lies between them, reflecting similar species composition. The other five regions, from the Lomonosov Ridge across the entire Amerasian Basin, form a separate cluster with two subclusters. The Lomonosov Ridge and Makarov Basin form a sub-cluster with the lowest dissimilarity value of 0.6. Also within geographical proximity, the Northwind Ridge, Canada Basin and Mendeleev Ridge form the second sub-cluster.



Figure 11. Hierarchical clustering dendrogram visualizing similarities and differences between the 8 regions of the CAO with presence/absence data. The height on the dendrogram indicates the similarity, where the lower height value of a joining point illustrates a higher similarity between locations.



Figure 12. Non-Metric Multidimensional Scaling (NMDS) Analysis of benthic fauna in the 8 regions of the CAO using presence/absence data. Ridges are in red triangles-, basins are blue squares. NMDS Stress Value: 0.002

To further visualize the taxonomic similarities among the different geomorphological regions of the CAO, NMDS analysis (Figure 12) showed a similar pattern to the cluster analysis. The Gakkel Ridge is the region closest to the grouping of the Amundsen and Nansen Basin. Similarly, the Makarov and Lomonosov Ridge are placed far away from the center of the plot but close to each other. The Northwind Ridge and Canada Basin are grouped in the corner, not particularly close to one another, with Mendeleev Ridge closer to the center of the NMDS

17 substations derived from the 8 main regions show differences in species composition within regions (Figure 13). The Gakkel Ridge and the Lomonosov Ridge demonstrate that there is a high benthic community dissimilarity between the subregions, whereas Amundsen Basin, Canada Basin, Mendeleev Ridge and Makarov Basin are more similar within subregions. The Northwind Ridge and one subregion of Canada Basin (CB4) are closer together, backing up geographical proximity.



Figure 13. Non-metric Multidimensional Scaling (NMDS) Analysis of the benthic fauna in 17 subregions of the CAO using presence/absence data. Ridges are in triangles in pink-red colors, basins are squares in green-blues. GR = Gakkel Ridge, LR = Lomonosov Ridge, MR = Mendeleev Ridge, NW = Northwind Ridge, NB = Nansen Basin, AB = Amundsen Basin, MB = Makarov Basin, CB = Canada Basin. NMDS Stress Value: 0.128

To test whether there is a substantial and significant difference between the benthic community structures at the ridges and basins of the CAO, ANOSIM test was performed resulting in a p-value of 0.445 indicating no significant difference between basin and ridge communities, with an R-value of -0.021. Similarly, no substantial and significant difference was indicated among the 8 regions by the high p-value of 0.24 and low R-value of 0.11.

Table 4. ANOSIM Test Results testing differences between benthic fauna on ridges and basin, and differences between benthic fauna in the eight regions (four of them within ridges and four of them within basins).

	Ridges vs. Basins:	8 Regions:
ANOSIM statistic (R)	-0.03	0.11
P-value	0.44	0.24

Focusing in on community heterogeneity within a single ridge, no overlap in species presence was shown between three different ridge habitats on the Gakkel Ridge, with the exception of the sponge *Geodia parva* found on both seamounts on Langseth Ridge and in the soft sediments of Langseth Ridge (Figure 14). At the current stage of data availability, the Aurora Vent Field is the only habitat to have reported species within the Annelida phylum, whereas species of Arthropoda and Echinodermata have only been reported from the sediments on the Langseth Ridge. Molluscs and poriferans have been observed in all habitats. It is noteworthy that sample analysis from those regions is not complete yet (Ramirez-Llodra, pers. comm.).



Figure 14. Species Presence of Ridge Habitats (Vent Field, Seamount, Soft-Bottom). Species data was derived from Morganti et al., 2022 for the Seamounts on Langseth Ridge, and the compiled data set of Ramirez-Llodra et al. (2024) for the Aurora Vent Field and sediments on the Langseth Ridge.

4.2.3 Taxon-level characteristics of basins and ridges

152 taxa (genus and species level) are present in only one of the 8 regions of the CAO (Appendix 1). However, very few of those taxa (6) were in fact unique to the CAO with the current knowledge. Those that were, occurred both on ridges and in basins: Canada and Nansen Basins, Gakkel and Mendeleev Ridges (Figure 15). The vast majority of the taxa supposedly unique to only one region of the CAO, were commonly either distributed worldwide (54%), or in the pan-Arctic. Very few taxa also occur in the Pacific (2). Notably, some shelf taxa occurred, mostly on the Lomonosov and Northwind Ridges.

The Canada and Nansen Basins were the only basins with unique species occurrences (here: species that only occurred in a given sub-region of the CAO and nowhere else): *Bathyedithia tuberculata* (Arthropoda) in the Canada Basin and *Bathypolaria kondrashovi* and *Rullierinereis abyssalis* (Annelida) in the Nansen Basin. The Amundsen and Makarov Basins did not have unique species occurrences. Taxa richness showed Arthropoda as the most taxon rich group (63.8% in Canada Basin and 62.7% in Nansen Basin), followed by Annelida (14.8% and 14.9%) and Echinodermata (9.1% and 9%). Taxa richness ratios differed in the Amundsen and Makarov Basins from the other two basins: In the Amundsen Basin Arthropoda (62%) was the most taxon richgroup, followed by Porifera (26.9%) while in the Makarov Basin Nematoda (56.8%) dominated taxon richness, followed by Arthropoda (28.2%).

Unique species on ridges were found on the Gakkel and Mendeleev Ridges: *Cocculina aurora* (Mollusca) on the Gakkel Ridge and *Nymphodora fletcheri* (Arthropoda) and *Peosidrilus simplidentatus* (Annelida) on the Mendeleev Ridge. No unique species occurrences were found for Lomonosov and Northwind Ridges. Taxa richness on the Gakkel Ridge was dominated by Arthropoda (44.8%), Annelida (31.9%) and Echinodermata (13.8%), whereas the Mendeleev Ridge shows clear dominance of Arthropoda (90.7%). Nematoda (64.2%) and Arthropoda (27.4%) dominated taxa richness on the Lomonosov Ridge. On the Northwind Ridge, Arthropoda (70.4%) dominated taxon richness, followed by Annelida (11.8%) and Echinodermata (8.4%).

30



Figure 15. Map of each ridge and basin illustrating their benthic fauna distribution and composition. All recorded species occurrences are shown as grey dots, and the number of occurrence records is given on the bottom right of each panel. Basin and ridge areas are indicated in blue and purple, respectively. The accompanying pie chart illustrates taxa richness composition by phylum. Unique species listed are those that only occurred in a given basin or ridge and nowhere else in the global ocean. The small insert maps show the location of a given basin or ridge.











Figure 15. Continued.

5 Discussion

My main findings are listed in the order in which they are discussed and reflected upon, below:

- 1. Ridges in the CAO have generally yet not statistically significantly higher benthic abundance for both macro- and meiofauna, than basins (H1).
- Ridges have a higher taxon richness than basins, yet not statistically significantly (H2). However, ridges have also a higher sampling effort leading to a higher record density, which may add bias to the results. Taxon rich phyla included Arthropoda, Nematoda and Annelida on both ridges and in basins.
- Similarities in community composition in the four basins and at four ridges reflects geographical proximity rather than a geomorphological feature type (ridge, basin) (H2).
- 4. Ridges in the CAO reveal high within-ridge community heterogeneity compared to basins (H2).
- Most species found only in one basin or on one ridge are in fact not unique on a global scale. With the current available dataset, 6 species are unique to one single region of the CAO ridges and basins (H2).
- 6. Several knowledge gaps limit our ability to draw definitive conclusions about the benthic community composition of the CAO.

5.1 Benthic Abundance on Ridges vs. Basins (H1)

In this study, I investigated meiofauna samples from the Gakkel Ridge, Amundsen and Nansen Basins for taxonomic identification to phylum level (and lower taxon levels for Arthropoda). The abundance results show that total abundance of meiofauna taxon on the ridge is nearly twice as high compared to the basins (Table 2, Figure 5a). When literature data were integrated to increase sample size, the pattern generally persists, but the difference in meiofauna abundance revealed no statistical significance between ridges and basins (Table 3, Figure 6). The latter finding is consistent with Zeppilli et al. (2018), who found that meiofauna are abundant and a central link in the food web of the deep sea, regardless of location. However, geomorphological features of ridges enhance food availability by transport of organic material by deep-water currents, in comparison to basins, where minimal current flow is limiting transport and deposition of organic material (Kröncke, 1994). Previous studies indicate that higher meiofaunal densities are found on ridges compared to adjacent basins, with areas higher on the ridge showing higher meiofaunal densities (Schewe & Soltwedel, 1999; Vanreusel et al., 2000). These results suggest that depth also affects meiofaunal abundance (Rex et al., 2006; Wei et al., 2010).

Over 74% of the abundance on both ridges and basins in my dataset consisted of Nematoda, suggesting this phylum to be a numerically dominant group within the Arctic deep-sea meiofauna, regardless of habitat. Harpacicoid Copepoda were the second most abundant taxon on ridges, a finding consistent with Hoste et al. (2007) observing nematodes dominating abundance in all meiofaunal communities (1,200-5,500 m), followed by copepods. Nematodes are particularly prominent in the Arctic deep sea, representing 91% of the meiofaunal abundance (Vanreusel et al., 2000), yet also dominate in shallow water sediments of the Arctic (Leasi et al., 2021).

While not statistically significant, the differences in mean and median abundance values between ridges and basins were higher for meiofauna than for macrofauna (Table 3, Figure 6). For macrofauna the ridge habitat had only slightly higher mean and median abundance values than the basin, with the number of samples being similar for the two habitat features. Globally decreasing faunal abundance with increasing water depth is related to decreasing quality and quantity of organic matter that reaches the seafloor, resulting in a decrease in food availability for benthic ecosystems (Smith et al., 2008). This decrease in food availability results in a general decrease in benthic abundance in both meiofauna and macrofauna (Bluhm et al. 2011a) yet with macrofaunal biomass decreasing more rapidly with depth than meiofaunal biomass (Wei et al., 2010). Although meiofaunal and macrofaunal abundance was not significantly different between ridge and basin in the present study, Kröncke (1994) suggests that macrofaunal communities in the CAO are influenced by depth and food availability and their findings show that abundance of macrofauna is higher on ridges (the Lomonosov Ridge) and slopes than basins due to the topographic elevation and lateral transport of nutrients. Ultimately, while the statistical results do not support hypothesis 1 (and published data) the observed patterns show that ridges enhance abundance of both macro- and meiofauna due to the elevation and geomorphological characteristics of ridges. However, higher sample numbers are needed to more definitely confirm or reject my hypothesis 1.

5.2 Sampling, Record and Taxa Densities

Data comparability is limited by unequal sampling effort in the present study. Ridges have a generally higher sampling effort compared to the basins in the analyzed data set, with certain locations on the Gakkel Ridge having particularly high numbers of sampling events. Higher sampling effort on ridges compared to basins may be due to 1) ridges being shallower than basins, hence less time is used on sampling, 2) recent interest in seamounts and hydrothermal vents having increased sampling on ridges, and 3) a higher number of expeditions focused on working in the north pole, resulting in an increased sampling on the Lomonosov Ridge. The count of occurrence records predictably follows this pattern: where sampling effort has been high, the density of records is also high (Figure 7). Therefore, the number of records is generally higher on the ridges compared to the basins, biasing comparison taxon abundance and density.

Although the taxon richness differs, with ridges having higher taxon richness than basins, ridges and basins generally have the same taxon-rich phyla. Porifera and Cnidaria, however, have higher richness in the basins than on ridges. Previous studies reveal that taxon richness and biodiversity decrease with depth in the Arctic (Bluhm et al., 2011a; Käß et al., 2019; Vedenin et al., 2018; Wlodarska-Kowalczuk, 2004). The higher taxon richness on ridges could suggest that habitat heterogeneity enhances biodiversity on ridge features, consistent with Zeppilli et al. (2016) suggesting that habitat heterogeneity on ridges holds greater biodiversity and functional diversity compared to the more uniform abyssal plains. A possible method to further investigate these differences in taxa count between ridges and basins is rarefaction curves. This method was applied in a study investigating the most up to date compiled dataset for the deep Arctic Ocean, showing a higher taxon richness in basin ecosystems than on ridges (Ramirez-Llodra et al., 2024). Although my findings suggest that the opposite may be true, the obvious variations in record density and sampling effort between ridges and basins could also be the reason for these observed differences in taxon count.

5.3 Geographical Proximity in Community Composition

Based on the compiled dataset from Ramirez-Llodra et al. (2024), differences in community composition in the 8 main regions of the CAO (Canada Basin, Makarov Basin, Amundsen Basin, Nansen Basins, Northwind Ridge, Mendeleev Ridge, Lomonosov Ridge and Gakkel Ridge) can be explained by a geographical proximity rather than a geomorphological relatedness. The faunal communities on ridges appear to be closely connected to those of their surrounding basins, with the Canada Basin fauna being similar to the neighboring Northwind and Mendeleev Ridges, and the Amundsen and Nansen Basins fauna being closely connected to the Gakkel Ridge fauna (Figure 11). This finding is possibly interesting in an evolutionary perspective by offering insights into species distribution across the CAO. Previous studies (Bluhm et al., 2011a) have not confirmed that the mid-Arctic ridges result in a barrier effect for benthic species distribution of macrofauna (genus and species level). In the Arctic deep sea, Atlantic influence dominates, while modern Pacific fauna is essentially absent (Bluhm et al., 2011a) due to historical glaciation events that restricted Pacific Boreal and Pacific Boreal Arctic species primarily to Arctic shelf waters (Ravelo et al., 2020). Pacific species stayed in unglaciated parts of the Pacific Arctic shelf, allowing them to persist in the Arctic without migrating into deeper waters (Ravelo et al., 2020 and references therein). Likely due to the shallow Bering Strait, Pacific species did not develop eurybathic adaptations like Atlantic taxa, which limited deep-water colonization of species of Pacific origin (references in Ravelo et al., 2020). Despite the virtual absence of Pacific fauna related to this historical aspect, the communities from the Canada Basin and the Northwind and Mendeleev Ridges are clustered together. This community similarity is likely caused by some level of connection to the Pacific Arctic shelf (e.g. Bathyarca imitata in Canada Basin, Appendix 1) or, alternatively, due to limited access to these regions from Atlantic and global deep-sea taxa. On the other hand, the Gakkel Ridge, Amundsen and Nansen Basins are more directly influenced by Atlantic deep-water species.

The conclusion on geographical proximity driving community composition is further supported by the sampling strategies applied. Most samples have been collected from softbottom areas, with sampling gear like box corers, designed to capture soft-sediment samples. This is ultimately leaving out hard-bottom habitats present on ridges, hence gives an incomplete picture of the actual faunal diversity on ridges. Additionally, samples from the Amerasian and Eurasian basins have been identified by different experts, which could add

38

some bias in how different these regions actually are. Consequently, it is unsurprising that distinct differences between ridge and basin communities are largely absent or not statistically detectable in the data set (Figure 12). Although ridges morphologically possess more intricate and distinct physical features, it is clear that investigating soft sediment fauna may not reveal strong differences between regions of ridges and of basins.

When dividing each region into subregions, more distinctions are observed between subregions on ridges compared to the subregions of basins (Figure 13). This indicates that certain sampling areas on the ridges are characterized by more distinct faunal communities, possibly due to the more complex habitats in ridge environments. Subregions GR1 (Gakkel Ridge 1), LR3 (Lomonosov Ridge 3) and Northwind Ridge had benthic fauna dissimilar to all other subregions potentially indicating higher faunal heterogeneity within ridges than basins. As the Northwind Ridge is not divided into subregions due to the limited geographical range of the ridge, this ridge is more likely dissimilar to other subregions due to its connection to the Chukchi Sea shelf (Zhulay et al., 2019). GR1 on the other hand, includes the occurrence records found on the newly sampled Aurora Vent Field (Boetius et al., 2014; Bünz & Ramirez-Llodra, 2021). This subregion shows substantial difference from other subregions, suggesting a high habitat heterogeneity and reflecting the unique ecological characteristics of this chemosynthetic habitat (Ramirez-Llodra et al., 2023).

Additionally, similarities in species composition of subregions within basins are clear. Subregions of the Canada Basin clustered together, with the exception of subregion CB4 being less similar. This subregion is located close to the Northwind Ridge (Figure 3) as well as the Chukchi Sea shelf, and is likely more influenced by the faunal composition of this ridge and the surrounding slopes. Subregions of Amundsen and Makarov Basins are grouped closer to subregion LR2 of the Lomonosov Ridge, indicating that samples of this ridge subregion are more connected to the surrounding fauna from the basins. On the contrary, subregion LR3 of the Lomonosov Ridge shows a more distinct faunal composition. LR3 is located closest to the Atlantic Water flow path (Rudels & Quadfasel, 1991) and near the Laptev East Siberian shelves. Possibly, LR3 is in a different bathymetric range and faunal layer, causing this subregion to be different to other subregions (Vedenin et al., 2021). Half of the Unique Species List (Appendix 1) of the Lomonosov Ridge in fact belongs to subregion LR3 (14 taxa out of 30), where 6 out of 14 taxa are shelf species. Still, it is critical to consider the substantial variation in the amount of records across subregions. In this matter, LR3 only has 57 records, compared to LR2 with 635 records.

5.4 Ridges reveal high Community Heterogeneity

Ridge heterogeneity should be sufficiently considered in sampling plans in order to gain consistent and extensive knowledge of all specific ridge habitats. The observed species variations in subregions within certain ridges suggest that ridges present a higher community heterogeneity compared to basins. Heterogeneous habitats, as found on ridges globally, increase diversity by allowing for diverse assemblages to develop across different habitats, ultimately allowing more species to coexist in a certain area (Zeppilli et al., 2016). A study on the Mid-Atlantic Ridge by Priede et al. (2013) suggested that ridges are important for sustaining bathyal benthic diversity, by increasing habitat surface in the deep sea, compared to a continuous abyssal plain without ridge features. In this thesis, species presence at three ridge habitats (vent field, seamount and soft sediment) at the Gakkel Ridge were investigated, and showed only one species to overlap (the sponge *Geodia parva*) across habitats, indicating that the three features are quite dissimilar in species composition (Figure 14).

However, the scarce identification of specimens to species level in all those habitats so far could mean that several species do occur in more than one habitat of the Gakkel Ridge or at other ridges. This applies to the Aurora Vent Field (sampled in 2021) where a complete inventory is yet to be published due to postponed taxonomic identification to species level (Ramirez-Llodra, pers. comm.), suggesting that sampled but yet unidentified species from the Aurora Vent field are potentially known from other hydrothermal vents such as the Loki's Castle Vent Field at 73°N on the Mohns Ridge. Therefore, there are possibly more similarities in species occurrence between habitats than currently known, but knowledge is limited due to both sampling effort and identification efforts. Cocculina aurora (Chen et al., 2022) however, is a limpet new to science and so far only known from the Aurora Vent field. Soft bottom sediments of the Langseth Ridge include 12 species of Arthropoda and two species of Echinodermata, such as the asteroid Tylaster willei. Stratmann et al. (2022) observed T. willei to primarily exist in the Arctic and North Atlantic Oceans (OBIS, 2024), when investigating faunal composition across three seamounts on Langseth Ridge, which is highlighting the possibility for many species likely to exist in more habitats than currently observed (Figure 14).

The morphological diversity of ridges, including seamounts, vents and other physical features, are enhancing complex faunal communities. Research shows that on the Arctic seamounts on steep, rocky walls in the deeper regions below 1500 m, large sponges dominate the fauna with observed crinoids, decapods and other sponges settling directly on top of them (Meyer et al., 2019; Ramirez-Llodra et al., 2024). Sponge communities found along the Arctic Mid Ocean Ridge (AMOR) and at different active and inactive hydrothermal vents are similar to these deeper communities (Brix et al., 2022; Ramirez-Llodra et al., 2020; 2024). Morganti et al. (2022) observed a surprisingly dense benthic biomass across the peaks of extinct volcanic seamounts of the Langseth Ridge. They particularly investigated sponge communities and learned that one of the key sources of nutrition for these sponges appeared to be remnants of past seep biota, e.g. past siboglinid tubeworm communities – suggesting that these sponge grounds thrive due to the unique conditions of seamounts (Morganti et al., 2022). However, research does confirm that the physical characteristics of vent sites and seamounts allow for diverse, and possibly unique, communities to exist (Consalvey et al., 2010).

Research from Loki's Castle Vent Field on the AMOR reveals highly distinct fauna compared to other hydrothermal vents in other oceanic regions, while on higher taxonomic level, several taxa are globally common on vent sites (Eilertsen et al., 2024). So far, research reveals that both hydrothermally active and non-active sites of the AMOR possess unique and poorly studied macrofauna (Ramirez-Llodra et al., 2020). According to Eilertsen et al. (2024), the preliminary data from the Loki's Castle Vent Field on the Mohns Ridge and the Aurora Vent Field on the Gakkel Ridge is indicating that Arctic vent fauna potentially is very distinct from other ocean regions. Eilertsen et al. (2024) propose that a comprehensive dataset with high taxonomic specifics is essential to test whether the Arctic forms a distinct bioregion for vent fauna.

5.5 Unique Species (that are not so unique?)

To investigate uniqueness of benthic fauna in the CAO, the compiled data set was filtered to produce a list of species and genera that were recorded in only one of the 8 regions (Appendix 1). Although these species were unique for a given geographic region of the CAO at the current stage of knowledge, they were not necessarily unique for other regions outside of my study area. These species could occur on other habitats found in the CAO not studied here, such as continental margins or shelves, or they could be undetected in other basins or ridges due to low sampling effort in the CAO. Therefore, a thorough investigation of the taxa in the unique species list was performed in OBIS, to understand whether these species were actually unique to a specific CAO region or if they occurred in other places in the Arctic or in the global ocean.

The more detailed analysis of the distribution of species and genera confirms that the majority of species and genera in the list are not unique to the CAO region where they were recorded, with many taxa occurring worldwide and/or in other Arctic areas. Four regions possess one or more unique species based on the compiled dataset: Canada Basin (1), Nansen Basin (2), Mendeleev Ridge (2), and Gakkel Ridge (1). On the contrary, a high amount of taxa are found in many places in the world, referred to as "worldwide" distributed species in the Unique Species Table (Appendix 1). My findings are consistent with Mironov et al. (2013) indicating that all abyssal Arctic genera can be divided into two groups in terms of their distribution ranges in the World Ocean: worldwide distributed genera and genera with limited distribution. In the Arctic abyssal fauna, worldwide distributed genera dominate with a percentage of 60-65% (Mironov et al., 2013).

Some species found in the CAO basins or ridges are even normally observed in shallow waters, such as the shelf bivalve *Ennucula tenuis* (Blanchard et al., 2013) or sponges of the *Polymastia* genus, both found in the Canada Basin (Bluhm et al., 2005). This finding is in agreement with research that suggests that many Arctic deep-sea species occur over a wide depth range, also known as eurybathic species, with 61% of deep-sea species (>500 m) in the Arctic overlapping with those on the shelf (Bluhm et al., 2011b; Piepenburg et al., 2011). This could explain why a number of commonly known shelf species were observed in this compiled deep-sea data set.

42

The results of faunal similarity in geographical proximity (Figure 11 and 12) between regions in the CAO could be interpreted as contradictory to the biogeography findings from the unique species list table (Appendix 1). In the latter case, many of the taxa only found in one of 8 CAO basins/ridges are species with worldwide distribution. These regionally unique species *do* occur worldwide, but *still* have a distinct distributional pattern in the CAO. For example, species of Pacific origin are mainly located on the Arctic shelf (such as *Bathyarca imitata*), whereas species with origin from the Eurasian Arctic Basin are commonly observed in the global deep sea (Bluhm et al., 2011a; Ravelo et al., 2020; Zhulay et al., 2019). Ultimately, species distribution in the Arctic differs between taxa due to e.g. adaptation to different depth ranges (Ravelo et al., 2020; Vedenin et al., 2022). In this study, I did not investigate the distribution patterns of all taxa in the data set, but only of those taxa that exclusively occurred in *one* of my eight study regions. A thorough investigation of global distribution patterns of all CAO taxa would therefore be beneficial to perform in the future, in order to accomplish a more extensive understanding of distribution patterns of Arctic benthos.

A study performed by Krylova et al. (2013) on bivalve molluses suggests that differences in biogeographic history between species can be explained by differences in evolutionary plasticity between species; some evolutionarily flexible groups might be more successful in rapidly changing environments. As previously mentioned, some deep-sea taxa in the Arctic have not been found in shallower water, while other taxa are highly adaptive and found from the intertidal to the deep sea (Mironov et al., 2013). Findings from Krylova et al. (2013) include that the majority of deep-sea species in the Arctic are of Atlantic origin, and that deep-water basins possess higher endemism than Arctic shelves (Krylova et al., 2013). In the Nansen and Amundsen Basins, the percentage of endemics was 33%, whereas in the Canada Basin 50% of the taxa were endemic (Krylova et al., 2013). In my study, the amount of endemic species in the CAO is lower – possibly in relation to new discoveries over the past ten years, but also, due to this thesis' approach where unique taxa occurring in more than one region, have not been investigated.

5.6 Sources of Uncertainty

Inevitably, data gaps limit the robustness of interpretation of CAO deep-sea fauna. Sources of uncertainty in regards to mapping, unstandardized data and sampling effort, are therefore important to consider when reflecting upon biodiversity patterns in the deep-sea with our current state of knowledge:

5.6.1 Geomorphological features used for mapping in ArcGIS

A challenge when working with the large, compiled dataset in ArcGIS was the inaccuracy of the geographical feature layers for basins and ridges, created by Harris et al. (2014). Empty spaces or gaps between the geomorphological features are especially present on the Gakkel Ridge and its surrounding basins, as well as the east side of the Lomonosov Ridge (Figure 3). Additionally, only parts of Nansen Basin are included in the feature layer, excluding >37 records from this region. Unfortunately, in total >316 records within empty spaces between feature layers were removed from the study due to uncertainty regarding what geomorphological feature they belong to (Figure 3). When performing the extensive study of the geomorphology of all oceans, Harris et al. (2014) acknowledges errors associated with the area estimation for the geomorphological features. According to their study, the errors derive from several sources: 1) spatial distribution and accuracy in depth measurements used in producing the bathymetric model; 2) errors from the supporting data sources utilized for making the classification; 3) errors derived from the smoothing of polygons; 4) errors linked to the misclassification of features (Harris et al., 2014). The SRTM30 PLUS bathymetric model used for this study has a grid resolution of 1 km, and consequently the location of the derived feature boundaries is reflecting this resolution (Harris et al., 2014). It is thereby likely that the sporadic inaccuracy of the feature layers in the CAO derive from these listed errors that are acknowledged by the creators of these geomorphological feature layers. The boundary between features is important to define in the future, with improved data resolution and integration, to optimize mapping efforts and to avoid records being lost or records being associated with the wrong geographical feature.

5.6.2 Sampling and Standardization Challenges

As expected, previous studies (Bluhm et al., 2011a) have also shown that lack of consistency in sampling gear and taxonomic identifications challenges comparison within benthos in the CAO, and possibly masks the actual ecological patterns or potentially produces artificial patterns. Priede et al. (2013) stated that "comparisons of biodiversity and evidence of endemism are hampered by our imperfect knowledge about the deep-sea fauna", while Piepenburg et al. (2011) informed that "the quality and quantity of available information still broadly varies among both regions and taxa" across the Arctic Ocean. Additionally, concerning taxonomic misidentification between scientists, Vedenin et al. (2018) suggested that in order to exclude misidentifications, taxonomic identification should be performed by the same specialists.

Despite the efforts of creating the compiled data set for benthos of the CAO, some existing data are lacking from public databases and therefore not included in this dataset, for example a new polychaete species called *Terebellides irinae* sp. n. from the Canada Basin (Gagaev, 2009), and two new species of foraminifera: *Turrispirillina karasikensis* (n. sp.) and *Turrispirillina pervesleri* (n. sp.) discovered on the Gakkel Ridge associated with sponge grounds (Bukenberger et al., 2020). The compiled dataset of the CAO contributes significantly to our understanding of the largely underexplored deep-sea environment. However, the lack of standardization in methodology across the records weakens the reliability of comparisons of data and can possibly obscure significant biogeographic and ecological patterns. Future research efforts should consider utilizing standardized sampling gear and sufficient replication to understand the true benthic diversity (Bluhm et al., 2011a; Piepenburg et al., 2011).

6 Conclusion and Outlook

Through an investigation into taxon distribution and diversity on the ridges and basins of the Central Arctic Ocean, my thesis has provided insight into patterns of abundance, geographical similarity, ridge heterogeneity and endemism in the CAO benthos. This study has, thereby, continued scientific baselines on benthic taxon occurrences in the Arctic by investigating spatial patterns of taxa, with findings suggesting – though not statistically significant – that abundance is higher on ridges compared to the basins. Findings also include indications of taxon distribution following a geographical proximity, rather than a geomorphological relatedness. Ridges and their distinct features such as hydrothermal vents enhance habitat heterogeneity and endemism, suggesting these areas to be important for deep-sea biodiversity.

Determining the further extent of heterogeneity in ridge fauna in the CAO remains a challenge, particularly due to the implications of performing research on these remote Arctic ridges. Investigations highlight the existing scarce knowledge of Arctic benthos and the complexity of deep Arctic studies: remote locations, ice-covered areas and challenging accessibility constraint research. Additionally, taxonomic expertise is crucial to enhance correct species identification and avoid using coarse taxonomic resolution.

The CAO will become more accessible to human activity in the future, with climate change promoting sea ice retreat. As anthropogenic interest in the Arctic is increasing with deep-sea mining exploration on the AMOR (Ramirez-Llodra et al., 2020), protection of Arctic ridge habitats through sufficient science-based management is crucial. In the future, the same anthropogenic industry may be expected for the CAO. Since the data limitation in the CAO is even more limited compared to the AMOR region, studies on deep-sea fauna in the CAO are essential to provide baseline data for future management. Research on the AMOR shows that this region possesses a complex topography hosting several vulnerable marine ecosystems, such as the previously mentioned sponge aggregations (Eilertsen et al., 2024). Environmental risks of mining the deep-sea include e.g. habitat alteration or elimination of benthic fauna, sediment plumes from activity affecting other areas beyond the mining sites, disturbing both benthic and pelagic fauna, and light or noise pollution from vehicle-related disturbances (Eilertsen et al., 2024; Washburn et al., 2019).

The scarce knowledge base existing (on habitats potentially subjected to deep-sea mining) strongly advocates for the 30x30 Conservation Target supported by the United Nations Convention on Biological Diversity and part of the Kunming-Montreal Global Biodiversity Framework (CBD, 2022). The 30x30 initiative aims to protect 30% of the Earth's biome by 2030. For marine environments, this would involve establishing marine protected areas (MPAs) to safeguard vulnerable habitats, such as poorly understood deep-sea regions with unique and fragile ecosystems. With very limited biological and ecological knowledge of the AMOR region, Norway is opening its extended continental shelf for exploration and exploitation licenses. Meanwhile, researchers urge for implementation of protective measures of the novel and specialized benthic communities studied on the AMOR (Eilertsen et al., 2024). The 30x30 Conservation Target could mark the turning point where the demand of protecting vulnerable nature exceeds the push for deep-sea mining exploration. Above all, this underscores the urgent need for advancing our knowledge of Arctic deep-sea fauna *before* harmful anthropogenic activity disrupts unique and underexplored habitats.

7 References

- Alfaro-Lucas, J. M., Chaudhary, C., Brandt, A., & Saeedi, H. (2023). Species composition comparisons and relationships of Arctic marine ecoregions. *Deep Sea Research Part I: Oceanographic Research Papers*, 198, 104077.
- Amon, D. J., Gollner, S., Morato, T., Smith, C. R., Chen, C., Christiansen, S., Currie, B.,
 Drazen, J. C., Fukushima, T., Gianni, M., Gjerde, K. M., Gooday, A. J., Grillo, G. G.,
 Haeckel, M., Joyini, T., Ju, S.-J., Levin, L. A., Metaxas, A., Mianowicz, K., . . .
 Pickens, C. (2022). Assessment of scientific gaps related to the effective
 environmental management of deep-seabed mining. *Marine Policy*, 138, 105006.
- Blanchard, A. L., Parris, C. L., Knowlton, A. L., & Wade, N. R. (2013). Benthic ecology of the northeastern Chukchi Sea. Part I. Environmental characteristics and macrofaunal community structure, 2008–2010. *Continental Shelf Research*, 67, 52-66.
- Bluhm, B., Ambrose, W. G., & Bergmann, M. C., L. M., Gebruk, A. V., Hasemann, C., Iken, K., Klages, M., MacDonald, I. R., Renaud, P. E., Schewe, I., Soltwedel, T., Włodarska-Kowalczuk, M. (2011a). Diversity of the arctic deep-sea benthos. *Marine Biodiversity*, *41*(1), 87-107.
- Bluhm, B. A., Gradinger, R., Hopcroft, R. R. (2011b). Editorial Arctic Ocean Diversity: synthesis. Marine Biodiversity, 41(1), 1-4.
- Bluhm, B. A., MacDonald, I. R., Debenham, C., & Iken, K. (2005). Macro- and megabenthic communities in the high Arctic Canada Basin: initial findings. Polar Biology, 28(3), 218-231.
- Boetius, A. (2015). The Expedition PS86 of the Research Vessel POLARSTERN to the Arctic Ocean in 2014, Berichte zur Polar- und Meeresforschung = Reports on polar and marine research, Bremerhaven, Alfred Wegener Institute for Polar and Marine Research, 685, 133 p.
- Boetius, A., Albrecht, S., Bakker, K., Bienhold, C., Felden, J., Fernández-Méndez, M.,
 Hendricks, S., Katlein, C., Lalande, C., Krumpen, T., Nicolaus, M., Peeken, I., Rabe,
 B., Rogacheva, A., Rybakova, E., Somavilla, R., Wenzhöfer, F., & Party, R. P. A.-.-S.
 S. (2013). Export of Algal Biomass from the Melting Arctic Sea Ice. *Science*, *339*(6126), 1430-1432.
- CBD. (2022). Decision adopted by the Conference of the Parties to the Convention on Biological Diversity at its fifteenth meeting: Kunming-Montreal Global Biodiversity

Framework (Decision 15/4). *Convention on Biological Diversity*. Accessed 05.11.2024 through: https://www.cbd.int/doc/decisions/cop-15/cop-15-dec-04-en.pdf/>

- Challenger150. (n.d.). *Challenger 150*. Accessed on 03.09.2024 through <www. challenger150.world/>
- Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, *18*(1), 117-143.
- Clough, L. M., Ambrose, W. G., Kirk Cochran, J., Barnes, C., Renaud, P. E., & Aller, R. C. (1997). Infaunal density, biomass and bioturbation in the sediments of the Arctic Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, 44(8), 1683-1704.
- Edmonds, H. N., Michael, P. J., Baker, E. T., Connelly, D. P., Snow, J. E., Langmuir, C. H., Dick, H. J. B., Mühe, R., German, C. R., & Graham, D. W. (2003). Discovery of abundant hydrothermal venting on the ultraslow-spreading Gakkel ridge in the Arctic Ocean. *Nature*, 421(6920), 252-256.
- Eilertsen, M. H., Kongsrud, J. A., Tandberg, A. H. S., Alvestad, T., Budaeva, N., Martell, L., Ramalho, S. P., Falkenhaug, T., H., R., Oug, E., Bakken, T., Høisæter, T., Rauch, C., Carvalho, F. C., Savchenko, A. S., Ulvatn, T., Kongshavn, K., Berntsen, C. M., Olsen, B. R., & Pedersen, R. B. (2024). Diversity, habitat endemicity and trophic ecology of the fauna of Loki's Castle vent field on the Arctic Mid-Ocean Ridge. *Scientific Reports*, *14*(1), 103.
- Energidepartementet. (2024). Norge åpner opp for havbunnsmineraler [Norway opens up for seabed minerals]. *Energidepartementet/Ministry of Energy*. Accessed 10.10.2024 through ">https://www.regjeringen.no/no/aktuelt/norge-apner-opp-for-havbunnsmineraler/id3021433/.

Esri. (2023). ArcGIS Pro (Version 3.1.0) [Computer software]. In Esri Inc.

- Fransson, A., Bluhm, B., Arumi, M., Assmann, K., Bårnås G. A. M., Bratrein, M., Buvik, K., Chierichi, M., Cisielski, T., Cristea, A., van Dihn, K., Eikrem, W., Espinel, N., Gardner, J., Gawinski, C., Koenig, Z., Lundesgaard, Ø., Marquardt, M., Ntinou, I. V., ... Ziegler, A. (2022). Joint Cruise 2-2 2021: Cruise Report *(The Nansen Legacy Report Series, 30/2022.*
- Frolov, I. E., Gudkovich, Z. M., Radionov, V. F., Shirochkov, A. V., & Timokhov, L. A. (2005). The Arctic Basin: Results from the Russian Drifting Stations. Springer Praxis Books

- Gage, J. D. (2003). Food inputs, utilization, carbon flow and energetics. In P. A. Tyler (Ed.), *Ecosystems of the deep oceans*. 28. 313–380. Elsevier.
- Giere, O. (2008). *Meiobenthology: The Microscopic Motile Fauna of Aquatic Sediments*. Springer Berlin Heidelberg.
- Gille, S., Metzger, E., & Tokmakian, R. (2004). Seafloor topography and ocean circulation. *Oceanography*, *17*, 11.
- GoNorth. (2023). GoNorth Arctic Expedition 2023.
- Gradinger, R., Bluhm, B., Hopcroft, R., Gebruk, A., Kosobokova, K., Sirenko, B., & Weslawski, J. (2010). *Marine Life in the Arctic*. 183-202.
- Hanz, U., Riekenberg, P., de Kluijver, A., van der Meer, M., Middelburg, J. J., de Goeij, J.
 M., Bart, M. C., Wurz, E., Colaço, A., Duineveld, G. C. A., Reichart, G.-J., Rapp, H.T., & Mienis, F. (2022). The important role of sponges in carbon and nitrogen cycling in a deep-sea biological hotspot. *Functional Ecology*, *36*(9), 2188-2199.
- Hanz, U., Roberts, E. M., Duineveld, G., Davies, A., van Haren, H., Rapp, H. T., Reichart, G.-J., & Mienis, F. (2021). Long-term observations reveal environmental conditions and food supply mechanisms at an arctic deep-sea sponge ground. *Journal of Geophysical Research: Oceans*, 126(3), e2020JC016776.
- Harris, P., Macmillan-Lawler, M., Rupp, J., & Baker, E. (2014). Geomorphology of the oceans. *Marine Geology*, *352*, 4–24.
- Henrich, R., Hartmann, M., Reitner, J., Schäfer, P., Freiwald, A., Steinmetz, S., Dietrich, P.,
 & Thiede, J. (1992). Facies belts and communities of the arctic Vesterisbanken
 Seamount (Central Greenland Sea). *Facies*, 27(1), 71-103.
- Huntington, H. P., Zagorsky, A., Kaltenborn, B. P., Shin, H. C., Dawson, J., Lukin, M., Dahl,P. E., Guo, P., & Thomas, D. N. (2022). Societal implications of a changing ArcticOcean. *Ambio*, 51(2), 298-306.
- IHO, I. (2019). Standardization of undersea feature names. Guidelines Proposal Form Terminology. *Published by the International Hydrographic Organization*. Edition 4.2.0, October 2019.
- ISA. (2024). Clarion Clipperton Fracture Zone. International Seabed Authority. Accessed on 12.09.2024 through: https://www.isa.org.jm/maps/clarion-clipperton-fracture-zone/>.
- Jakobsson, M., Mayer, L. A., Bringensparr, C., Castro, C. F., Mohammad, R., Johnson, P., Ketter, T., Accettella, D., Amblas, D., An, L., Arndt, J. E., Canals, M., Casamor, J. L., Chauché, N., Coakley, B., Danielson, S., Demarte, M., Dickson, M.-L., Dorschel, B., .

... Zinglersen, K. B. (2020). The International Bathymetric Chart of the Arctic Ocean Version 4.0. *Scientific Data*, 7(1), 176.

- Juniper, S. (2001). The Ecology of Deep-Sea Hydrothermal Vents by C. L. Van Dover. Limnology and Oceanography, 46.
- Keith, D. A., Ferrer-Paris, J.R., Nicholson, E. and Kingsford, R.T. (eds.) (2020). The IUCN Global Ecosystem Typology 2.0: Descriptive profiles for biomes and ecosystem functional groups. *Gland, Switzerland: IUCN*.
- Koschinsky, A., Heinrich, L., Boehnke, K., Cohrs, J. C., Markus, T., Shani, M., Singh, P., Smith Stegen, K., & Werner, W. (2018). Deep-sea mining: Interdisciplinary research on potential environmental, legal, economic, and societal implications. *Integrated Environmental Assessment and Management*, 14(6), 672-691.
- Kröncke, I. (1994). Macrobenthos composition, abundance and biomass in the Arctic Ocean along a transect between Svalbard and the Makarov Basin. *Polar Biology*, 14(8), 519-529.
- Kröncke, I., Vanreusel, A., Vincx, M., Wollenburg, J., Mackensen, A., Liebezeit, G., & Behrends, B. (2000). Different benthic size-compartments and their relationship to sediment chemistry in the deep Eurasian Arctic Ocean. *Marine Ecology Progress Series*, 199, 31-41.
- Levin, L. A., Etter, R. J., Rex, M. A., Gooday, A. J., Smith, C. R., Pineda, J., Stuart, C. T., Hessler, R. R., & Pawson, D. (2001). Environmental Influences on Regional Deep-Sea Species Diversity1. *Annual Review of Ecology, Evolution, and Systematics*, 32, 51-93.
- Levin, L. A., Wei, C.-L., Dunn, D. C., Amon, D. J., Ashford, O. S., Cheung, W. W. L., Colaço, A., Dominguez-Carrió, C., Escobar, E. G., Harden-Davies, H. R., Drazen, J. C., Ismail, K., Jones, D. O. B., Johnson, D. E., Le, J. T., Lejzerowicz, F., Mitarai, S., Morato, T., Mulsow, S., . . . Yasuhara, M. (2020). Climate change considerations are fundamental to management of deep-sea resource extraction. *Global Change Biology*, *26*(9), 4664-4678.
- Meyer, H. K., Roberts, E. M., Rapp, H. T., & Davies, A. J. (2019). Spatial patterns of arctic sponge ground fauna and demersal fish are detectable in autonomous underwater vehicle (AUV) imagery. *Deep Sea Research Part I: Oceanographic Research Papers*, 153, 103137.
- Miller, K. A., Thompson, K. F., Johnston, P., & Santillo, D. (2018). An overview of seabed mining including the current state of development, environmental impacts, and knowledge gaps [Review]. *Frontiers in Marine Science*, 4. 2296-7745

- Morganti, T. M., Purser, A., Rapp, H. T., German, C. R., Jakuba, M. V., Hehemann, L., Blendl, J., Slaby, B. M., & Boetius, A. (2021). In situ observation of sponge trails suggests common sponge locomotion in the deep central Arctic. *Current Biology*, 31(8), R368-R370.
- Morganti, T. M., Slaby, B. M., de Kluijver, A., Busch, K., Hentschel, U., Middelburg, J. J.,
 Grotheer, H., Mollenhauer, G., Dannheim, J., Rapp, H. T., Purser, A., & Boetius, A.
 (2022). Giant sponge grounds of Central Arctic seamounts are associated with extinct seep life. *Nature Communications*, 13(1), 638.
- Morrison, K. M., Meyer, H. K., Roberts, E. M., Rapp, H. T., Colaço, A., & Pham, C. K. (2020). The first cut is the deepest: trawl effects on a deep-sea sponge ground are pronounced four years on. *Frontiers in Marine Science*, 7. 2296-7745
- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R.,
 Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker,
 B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista,
 H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L.,
 McGlinn, D., Ouellette, M., Ribeiro Cunha, E.,Smith, T., Stier, A., Ter Braak, C.,
 Weedon, J. (2024). vegan: Community Ecology Package (R package version 2.7-0).
 In.
- Olsen, B. R., Økland, I. E., Thorseth, I. H., Pedersen, R. B., & Rapp, H. T. (2016). Environmental challenges related to offshore mining and gas hydrate extraction.
- Petersen, S., Krätschell, A., Augustin, N., Jamieson, J., Hein, J. R., & Hannington, M. D. (2016). News from the seabed – Geological characteristics and resource potential of deep-sea mineral resources. *Marine Policy*, 70, 175-187.
- Protocol, v. (2021). Sampling Protocols: Version 9. The Nansen Legacy Report Series 25/2021. T. N. Legacy.
- Ramirez-Llodra, E., Argentino, C., Baker, M., Boetius, A., Costa, C., Dahle, H., Denny, E.
 M., Dessandier, P.-A., Eilertsen, M. H., Ferre, B., German, C. R., Hand, K., Hilário,
 A., Hislop, L., Jamieson, J. W., Kalnitchenko, D., Mall, A., Panieri, G., Purser, A., . . .
 Buenz, S. (2023). Hot vents beneath an icy ocean the aurora vent field, gakkel ridge,
 revealed. *Oceanography*, *36*(1), 6-17.
- Ramirez-Llodra, E., Brandt, A., Danovaro, R., De Mol, B., Escobar, E., German, C. R.,Levin, L. A., Martinez Arbizu, P., Menot, L., Buhl-Mortensen, P., Narayanaswamy,B. E., Smith, C. R., Tittensor, D. P., Tyler, P. A., Vanreusel, A., & Vecchione, M.

(2010). Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. *Biogeosciences*, 7(9), 2851-2899.

- Ramirez-Llodra, E., Hilario, A., Paulsen, E., Costa, C. V., Bakken, T., Johnsen, G., & Rapp,
 H. T. (2020). Benthic communities on the Mohn's Treasure Mound: Implications for management of seabed mining in the Arctic Mid-Ocean Ridge. *Frontiers in Marine Science*, 7. 2296-7745
- Ramirez-Llodra, E., Meyer, H. K., Bluhm, B. A., Brix, S., Brandt, A., Dannheim, J., Downey,
 R. V., Egilsdóttir, H., Eilertsen, M. H., Gaudron, S. M., Gebruk, A., Golikov, A.,
 Hasemann, C., Hilario, A., Jørgensen, L. L., Kaiser, S., Korfhage, S. A., Kürzel, K.,
 Lörz, A.-N., . . Saeedi, H. (2024). The emerging picture of a diverse deep Arctic
 Ocean seafloor: From habitats to ecosystems. *Elementa: Science of the Anthropocene*, *12*(1): 00140.
- R Core Team (2024) R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/>.
- Rex, M. A., Etter, R. J., Morris J. S., Crous, J., McClain, C. R., Johnson. N. A., Stuart, C. T., Derming, J. W., Thies, R., & Avery, R. (2006). Global bathymetric patterns of standing stock and body size in the deep-sea benthos. *Marine Ecology Progress Series*, 317, 1-8.
- Roberts, E. M., Mienis, F., Rapp, H. T., Hanz, U., Meyer, H. K., & Davies, A. J. (2018). Oceanographic setting and short-timescale environmental variability at an Arctic seamount sponge ground. *Deep Sea Research Part I: Oceanographic Research Papers*, 138, 98-113.
- Rogers, A. D. (2018). Chapter Four The Biology of Seamounts: 25 Years on. In C. Sheppard (Ed.), Advances in Marine Biology, 79, 137-224. Academic Press.
- Rudels, B., & Quadfasel, D. (1991). Convection and deep water formation in the Arctic Ocean-Greenland Sea System. *Journal of Marine Systems*, 2(3), 435-450.
- Rybakova, E., Kremenetskaia, A., Vedenin, A., Boetius, A., & Gebruk, A. (2019). Deep-sea megabenthos communities of the Eurasian Central Arctic are influenced by ice-cover and sea-ice algal falls. *PLOS ONE*, *14*, e0211009.
- Saeedi, H., Costello, M. J., Warren, D., & Brandt, A. (2019a). Latitudinal and bathymetrical species richness patterns in the NW Pacific and adjacent Arctic Ocean. *Scientific Reports*, 9(1), 9303.

- Saeedi, H., Simões, M., & Brandt, A. (2019b). Endemicity and community composition of marine species along the NW Pacific and the adjacent Arctic Ocean. *Progress in Oceanography*, 178, 102199.
- Schewe, I. (2001). Small-Sized Benthic Organisms of the Alpha Ridge, Central Arctic Ocean. International Review of Hydrobiology, 86(3), 317-335.
- Schewe, I., & Soltwedel, T. (1999). Deep-sea meiobenthos of the central Arctic Ocean: distribution patterns and size-structure under extreme oligotrophic conditions. *Vie et Milieu/Life & Environment*, 79-92.
- Schlacher, T. A., Rowden, A. A., Dower, J. F., & Consalvey, M. (2010). Seamount science scales undersea mountains: new research and outlook. *Marine Ecology*, *31*(s1), 1-13.
- Sirenko, B. (2001). List of species of free-living invertebrates of Eurasian Arctic seas and adjacent deep waters. *Explorations of the Fauna of the Seas*, 51, 1-129.
- Smith, C., De Leo, F., Bernardino, A., Sweetman, A., & Martinez Arbizu, P. (2008). Abyssal food limitation, ecosystem structure and climate change. *Trends in Ecology & Evolution*, 23, 518-528.
- Sokkeldirektoratet. (2023). Ressursvurdering havbunnsmineraler. Report provided by The Norwegian Petroleum Directorate on behalf of the Ministry of Petroleum and Energy on 27th of January 2023. Accessed 10.10.2024 thorugh <https://www.sodir.no/globalassets/1-sodir/fakta/havbunnsmineraler/ publikasjoner/2023/ressursvurdering-havbunnsmineraler-20230127.pdf/>.
- Soltwedel, T., Bauerfeind, E., Bergmann, N., Budaeva, N., Hoste, E., Jaeckisch, N.,
 Matthiessen, J., Mokievsky, V., Nöthig, E. M., Quéric, N. V., Sablotny, B., Sauter, E.,
 Schewe, I., Urban-Malinga, B., Wegner, J., Wlodarska-Kowalczuk, M., & Klages, M.
 (2005). HAUSGARTEN: Multidisciplinary Investigations at a Deep-Sea, Long-Term
 Observatory in the Arctic Ocean. *Oceanography* 18(3):46–61.
- Stratmann, T., Simon-Lledó, E., Morganti, T. M., de Kluijver, A., Vedenin, A., & Purser, A. (2022). Habitat types and megabenthos composition from three sponge-dominated high-Arctic seamounts. *Scientific Reports*, 12(1), 20610.
- Unger Moreno, K. A., Thal, J., Bach, W., Beier, C., & Haase, K. M. (2021). Volcanic structures and magmatic evolution of the Vesteris seamount, Greenland basin [Original Research]. *Frontiers in Earth Science*, 9. 2296-6463
- Van Dover, C. L. (2000). The Ecology of Deep-Sea Hydrothermal Vents. Princeton University Press.

- Van Dover, C. L., Arnaud-Haond, S., Gianni, M., Helmreich, S., Huber, J. A., Jaeckel, A. L., Metaxas, A., Pendleton, L. H., Petersen, S., Ramirez-Llodra, E., Steinberg, P. E., Tunnicliffe, V., & Yamamoto, H. (2018). Scientific rationale and international obligations for protection of active hydrothermal vent ecosystems from deep-sea mining. *Marine Policy*, 90, 20-28.
- Vedenin, A. A., Mironov, A. N., Bluhm, B. A., Käß, M., Degen, R., Galkin, S. V., & Gebruk, A. V. (2022). Uniform bathymetric zonation of marine benthos on a Pan-Arctic scale. *Progress in Oceanography*, 202, 102764.
- Vinogradova, N. G. (1997). Zoogeography of the Abyssal and Hadal Zones. In J. H. S. Blaxter, A. J. Southward, A. V. Gebruk, E. C. Southward, & P. A. Tyler (Eds.), *Advances in Marine Biology*, 32, 325-387. Academic Press.
- Washburn, T. W., Turner, P. J., Durden, J. M., Jones, D. O. B., Weaver, P., & Van Dover, C. L. (2019). Ecological risk assessment for deep-sea mining. *Ocean & Coastal Management*, 176, 24-39.
- Wassmann, P., & Reigstad, M. (2011). Future Arctic Ocean Seasonal Ice Zones and Implications for Pelagic-Benthic Coupling. *Oceanography*, 24(3), 220–231.
- Wei, C.-L., Rowe, G. T., Escobar-Briones, E., Boetius, A., Soltwedel, T., Caley, M. J.,
 Soliman, Y., Huettmann, F., Qu, F., Yu, Z., Pitcher, C. R., Haedrich, R. L., Wicksten,
 M. K., Rex, M. A., Baguley, J. G., Sharma, J., Danovaro, R., MacDonald, I. R.,
 Nunnally, C. C., . . . Narayanaswamy, B. E. (2010). Global Patterns and Predictions of
 Seafloor Biomass Using Random Forests. *PLOS ONE*, *5*(12), e15323.
- WHOI. (n.d.). U.S. Arctic drifting stations: 1950s-1960s. Woods Hole Oceanographic Institution. Accessed 11.10.2024 through https://www2.whoi.edu/site/beaufortgyre/history/us-arctic-drifting-stations-1950s-1960s/>.
- Wickham, H. (2016). Data Analysis. In H. Wickham (Ed.), ggplot2: Elegant Graphics for Data Analysis. 189-201. Springer International Publishing.
- Wiedmann, I., Ershova, E., Bluhm, B. A., Nöthig, E.-M., Gradinger, R. R., Kosobokova, K.,
 & Boetius, A. (2020). What feeds the benthos in the arctic basins? Assembling a carbon budget for the deep arctic ocean [Review]. *Frontiers in Marine Science*, 7. 2296-7745
- Wright, J., & Rothery, D. A. (1998). Chapter 4 The structure and formation of oceanic lithosphere. In J. Wright & D. A. Rothery (Eds.), The Ocean Basins: Their Structure and Evolution (Second Edition). 68-95. *Butterworth-Heinemann*.

8 Appendix 1

Unique Species List for each region in the study area. Species (with count) only occurring in one of the eight regions are included in this list. Distribution (according to OBIS) outside of the research area of CAO basins and ridges are commented in the "Distribution" column to the right. In this column, species that are not found elsewhere in the global ocean are categorized as "Unique".

Taxa		Count	Distribution
	Annelida:		
	Bathyfauvelia affinis	6	North-Atlantic, Fram-Strait, Canada Basin
	Bathypolaria carinata	6	Canada Basin Region
	Arthropoda:		
	Bathyedithia tuberculata	1	Unique to Canada Basin
	Bythocaris cryonesus	1	Norwegian Sea and Canada Basin
	Chalarostylis canadensis	4	Canada Basin Region and African Coast
	Dactylamblyops sarsi	10	Canada Basin Region
C	Epicalymma brittoni	1	Canada Basin (Pelagic Copepod)
	Eusirus	1	Worldwide
A N	Halirages gorbunovi	1	Fram Strait, Russian Shelf, Canada Basin
Δ	Hemilamprops	5	Worldwide
D	Macellicephala longipalpa	3	Canada Basin Region
A	Polycope afanasjevi	3	Canada Basin Region
	Polycope pseudoinornata	1	Canada Basin, Iceland
В	Chordata:		
Α	Michthyops arcticus	4	Canada Basin Region
S	Cnidaria:		
Ι	Actinostola callosa	1	Worldwide
Ν	Mollusca:		
	Bathyarca imitata	2	Japan and American Pacific Coast
	Cyclocardia	2	Worldwide
	Ennucula tenuis	1	Worldwide, shelf
	Expansicervinia glacieria	2	Canada Basin Region
	Propeamussium	1	Worldwide
	Rhinoclama filatovae	1	Japan and American Pacific Coast
	Siphonodentalium lobatum	1	Norwegian and Barents Sea, Fram Strait
	Porifera:		
	Polymastia	8	Worldwide
	Scyphidium septentrionale	1	Fram Strait

Таха		Count	Distribution
	Annelida:		
Μ	Hemipodia	3	Worldwide, Shelf
Α	Janua heterostropha	1	Worldwide, Shelf
K	Progoniada	1	Worldwide, Shelf
A	Arthropoda:		
R	Michelopagurus atlanticus	1	North Atlantic
	Cnidaria:		
V	Atolla tenella	1	Russian Shelf Region
D	Mollusca:		
	Cuspidaria obesa	6	Atlantic Ocean, Pan-Arctic
A S I N	Nematoda:		
	Linhystera	1	Worldwide, Shelf
	Sphaerolaimus	1	Worldwide
1	Viscosia	2	Worldwide

Taxa	a	Count	Distribution
	Annelida:		
	Aglaophamus malmgreni	1	Worldwide, Mostly Pan-Arctic
	Arthropoda:		
	Parakanthophoreus inermis	1	GIN Seas
	Cnidaria:		
A	Garveia	2	Worldwide
M	Symplectoscyphus	1	Worldwide
	tricuspidatus		
N D	Tubularia regalis	1	Bering Sea, Arctic Canadian Coast
D S	Echinodermata:		
S F	Elpidia glacialis	1	Worldwide
E N	Porifera:		
1	Asbestopluma	3	North Atlantic, Norwegian Sea, East-Coast
В	(Asbestopluma) pennatula		of Africa
A	Clathrina	2	Worldwide
S	Crella (Yvesia) pertusa	1	North Atlantic and Norwegian Sea
Ĩ	Forcepia (Forcepia)	1	Barents Sea and Svalbard
Ν	fabricans		
	Geodia barretti	1	Worldwide
	Geodia phlegraei	1	North Atlantic and Norwegian Sea
	Haliclona	1	Worldwide
	Sycon	3	Worldwide
	Thenea muricata	2	Worldwide
	Trichasterina borealis	1	Norwegian Sea and Svalbard

Tax	a	Count	Distribution
	Annelida:		
	Galathowenia oculata	6	Worldwide, Shelf
	Poecilochaetus	1	Worldwide, Shelf
N	Potamethus filiformis	1	North of Svalbard
A	Rullierinereis abyssalis	1	Unique to Nansen Basin
IN S	Bathypolaria kondrashovi	1	Unique to Nansen Basin
F	Arthropoda:		
N	Hyperoche medusarum	1	Worldwide, Shelf
11	Xestoleberis depressa	1	Worldwide
В	Cnidaria:		
Ā	Sarsia	1	Worldwide
S	Echinodermata:		
Ι	Pourtalesia jeffreysi	1	GIN Seas, Pan-Arctic
Ν	Mollusca:		
	Astarte montagui	1	Pan-Arctic, Shelf
	Mohnia danielsseni	1	GIN Seas
	Similipecten greenlandicus	1	Pan-Arctic, Shelf

Taxa		Count	Distribution
Μ	Annelida:		
E N	Peosidrilus simplidentatus	4	Mendeleev Ridge Region
D E	Bylgides sarsi	1	Worldwide, Shelf
L E	Arthropoda:		
E V	Archypolycope semipunctata	1	Central Arctic Ocean
R	Nymphodora fletcheri	3	Unique to Mendeleev Ridge
I D	Obtusoecia obtusata	1	Worldwide
G E	Nematoda:		
	Oxystomina	1	Worldwide

Таха		Count	Distribution
	Annelida:		
	Aphelochaeta	2	Worldwide, Shelf
	Capitella minima	3	North Atlantic, Europe
	<i>Glyphanostomum pallescens</i>	1	Pan-Arctic, Norwegian and Barents Sea
	Goniada maculata	2	Worldwide, Shelf
	Melinnopsis arctica	1	Norwegian Sea, Europe
	Nothria conchylega	1	Worldwide, Shelf
	Notomastus latericeus	1	Worldwide, Shelf
	Protomystides	1	Worldwide, Shelf
	Protula tubularia	2	Worldwide, Shelf
	Scoletoma fragilis	1	Worldwide, Shelf
	Sphaerodorum	1	Worldwide, Shelf
	Arthropoda:		
	Bythocythere constricta	3	Pan-Arctic
	Cryptocope abbreviata	2	Greenland and Canada Arctic
T.	Deflexilodes tenuirostratus	3	Pan-Arctic
Ō	Eudorella emarginata	1	Worldwide, Shelf
M	Hippomedon denticulatus	2	Worldwide, Shelf
0	Ilyarachna	1	Worldwide, Shelf
Ň	Leptostylis	1	Worldwide
0	Paradoxostoma	1	Worldwide
S	Pseudomesus brevicornis	2	Atlantic and Pan-Arctic
0	Pseudotanais affinis	8	Worldwide
V	Cnidaria:		
	Epizoanthus erdmanni	3	North Atlantic and Pan-Arctic
R	Stephanoscyphistoma	3	Worldwide
Ι	Echinodermata:		
D	Myriotrochus rinkii	1	North Atlantic, Pan-Arctic
G	Ophiacantha bidentata	1	Worldwide
Ε	Mollusca:		
	Arca	2	Worldwide, Mostly Southern Hemisphere
	Yoldiella lucida	2	North Atlantic, Shelf
	Yoldiella solidula	2	Pan-Arctic, Shelf
	Nematoda:		
	Actinonema	1	Worldwide
	Araeolaimus	1	Worldwide
	Campylaimus	6	Worldwide
	Ceramonema	1	Worldwide
	Leptolaimoides	1	Worldwide
	Longicyatholaimus	6	Worldwide
	Metaglochinema	7	Worldwide
	Meyersia	8	South and Central America
	Oncholaimus	1	Worldwide

Paracyatholaimoides	1	Worldwide
Paracyatholaimus	1	Worldwide
Paralongicyatholaimus	1	Worldwide
Pselionema	11	Worldwide
Rhabditis	1	Worldwide, Shelf
Tripyloides	1	Worldwide, Shelf
Porifera:		
Craniella infrequens	1	Worldwide

Таха		Count	Distribution
	Annelida:		
	Apomatus	3182	Worldwide
	Arthropoda:		
	Heterocyprideis sorbyana	1	Pan-Arctic
G	Oculocytheropteron nodosum	1	Pan-Arctic
A K E L R I D	Echinodermata:		
	Tylaster willei	782	GIN Seas and Fram Strait
	Mollusca:		
	Cocculina aurora	4	Unique to Gakkel Ridge
	Cuspidaria centobi	1	GIN Seas
	Exitomelita	6	Fram Strait
	Mendicula ockelmanni	1	Norwegian Sea, Fram Strait
	Policordia jeffreysi	1	Atlantic Ocean
G	Yoldiella frami	1	American, Canadian, Russian Arctic
Ē	Porifera:		
	Asconema megaatrialia	2	Atlantic Ocean, GIN Seas
	Cladorhiza	1	Worldwide
	Geodia parva	7	GIN Seas and Svalbard
	Hyalonema	28	Worldwide
	Schaudinnia rosea	624	GIN Seas and Svalbard

Таха		Count	Distribution
	Annelida:		
	Cossura	1	Worldwide
	Glycinde wireni	1	Bering Strait
	Golfingia	5	Worldwide
	Ophelina breviata	1	Worldwide
	Polyphysia crassa	1	Worldwide
N	Spirorbis	2	Worldwide, shallow waters
	Arthropoda:		
R	Amathillopsis	1	Worldwide
T	Anonyx	1	Worldwide
н	Cyclopina	2	Worldwide
W	Exiliniscus	1	Worldwide
Ï	Pardalisca abyssi	1	Pan-Arctic
Ň	Sclerocrangon boreas	1	Pan-Arctic, Shelf
D	Stegocephalus	1	Worldwide, Mostly in the Pan-Arctic
	Tmetonyx cicada	1	Pan-Arctic, Norwegian Coast/Shelf
R	Cnidaria:		
Ι	Cerianthus	1	Worldwide, Shelf
D	Nausithoe	1	Worldwide
G	Tealidium	1	Worldwide
Ε	Echinodermata:		
	Bathybiaster vexillifer	1	Worldwide
	Hymenaster pellucidus	1	Worldwide
	Icasterias panopla	1	Pan-Arctic, Shelf
	Pedicellaster typicus	1	Pan-Arctic, Shelf
	Pontaster tenuispinus	3	Pan-Arctic, Shelf
	Poraniomorpha	1	Pan-Arctic, Shelf
	(Poraniomorpha) tumida		
	Mollusca:		
	Colus sabini	1	Pan-Arctic, Shelf
	Dacrydium vitreum	1	Pan-Arctic, Shelf

