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Status and spatial patterns of demersal marine fish communities in Northeast Greenland in the period 2002 – 2022

Malou Platou Johansen

Master's thesis in Biology BIO-3950 November 2024

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Supervisors:

Arve Lynghammar, UiT The Arctic University of Norway

Laurene Pecuchet, UiT The Arctic University of Norway

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Lastly, I want to echo Snoop Dogg’s sentiment from his Hollywood Walk of Fame speech:

> ”*I want to thank me for believing in me, I want to thank me for doing all this hard work. I wanna thank me for having no days off. I wanna thank me for never quitting. I wanna thank me for always being a giver and trying to give more than I receive. I wanna thank me for trying to do more right than wrong. I wanna thank me for being me at all times”*

Abstrakti

Tunup Avannaa Kalaallit Nunaanni nuna eqqississimatitamiippoq nunarsuarmilu nuna eqqississimatitaq anginerpaajuvoq avannarlersaallunilu. Inunnik tikinneqarsimanera annikilluinnarpoq, tamannalu pinngortitami pissutsinik allanngoriartornernik mississuiffigissallugu immikkut ittumik periarfissanik pilersitsivoq. Mississuinermi TUNU-programmimi umiarsuarni mississuiviusuni R/V Helmer Hanseni R/V Kronprins Haakonilu atorlugit, 2002-mit 2022-mut aalisakkat immap naqqarmiut assigiinngiiaartarnerat, siammasinnerat aammalu piffinni assigiinngissuteqartuni ineriartornerat mississorneqarpoq. Pinngortalerisut kilisaavii atorlugit kangit, immap naqqa (sokkel) immallu itinersaap killinga (kontinentalskråning) immikkoortinneqarsimapput piffissallu agguarneqarsimallutik: 2002 – 2010 aamma 2013 – 2022.

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Abstrakt

Nordøstgrønland, hjemsted for verdens største og nordligste nationalpark, er minimalt påvirket af menneskelig tilstedeværelse og udgør derfor et unikt miljø til at studere klima-drevne økologiske ændringer. Denne specialeopgave undersøgte fordeling og tidsmæssige ændringer i bundfiskearter fra 2002 til 2022 ved brug af data indsamlet under TUNU-programmets togt med R/V Helmer Hansen og R/V Kronprins Haakon. Data blev delt op i katerierne fjord-, sokkel og kontinentalskråning og sammenlignede for to tidsperioder: 2002–2010 og 2013–2022.

Resultaterne viser en øget artsdiversitet over tid, hvor den relative andel af arktiske arter er faldet, mens arktisk-boreale arter er øget. Vidt-udbredte arter i optrådte i den sene tidsperiode (2013 – 2022), hvilket antyder forskydninger i samfundssammensætning. Stationer der er blevet fisket flere gange over årene viste øget relativ forekomst af *Boreogadus saida* og *Arctogadus glacialis* i fjordene, hvilket korrelerede med lavere temperaturer. Kontinentalsoklen synes at være udsat for "atlantificering", i det stigende temperaturer og artsrigdom blev påvist. Dette er i tråd med borealiseringstendenser, der også ses andre steder i Arktis. Artssammensætningen på kontinentalkråningen indikerede, at arter migrerede til dybere og køligere vande. Non-metric Multidimensional Scaling-analyse fremhævede dybde, temperatur og afstand-til-kysten som vigtige faktorer for artsfordeling. Disse fund understreger de igangværende økosystemskift i polarområderne og de potentielle implikationer af fortsat opvarmning.

Abstract

Northeast Greenland, home to the world's largest and most northern National Park, remains minimally impacted by human presence, providing a unique environment to study climate-driven ecological changes. This study examined the status, spatial distribution, and temporal shifts in demersal fish species from 2002 to 2022, using data collected during TUNU Programme cruises on the R/V Helmer Hansen and R/V Kronprins Haakon. Sampling was conducted with bottom trawls. Stations were divided into fjord, shelf, and slope categories and compared two time periods: 2002–2010 and 2013–2022.

Results show increased species diversity, with Arctic species' relative abundance declining while Arctic-Boreal species increased. Notably, widely distributed species appeared in the late decade, suggesting community shifts. Revisited locations exhibited increased relative abundance of *Boreogadus saida* and *Arctogadus glacialis* in fjords, correlated with lower temperatures. Shelf regions, influenced by Atlantification, showed rising temperatures and species richness, consistent with borealization trends. Slope stations indicated species migrating to deeper, cooler waters. Non-metric Multidimensional Scaling analysis highlighted depth, temperature, and distance-to-coast as key drivers in species distribution. These findings underscore the ecosystem shifts underway in polar regions and the potential implications of continued warming.

Keywords: Northeast Greenland, climate change, Atlantification, borealization, ecosystem shift.

Abbreviations

LME	Large Marine Ecosystem
PAME	Protection of Arctic Marine Environments
FAO	Food and Agriculture Organisation of the United Nations
NEW	Northeast Water Polynya
SIW	Sirius Water Polynya
AO	Arctic Ocean
NEGS	Northeast Greenland Shelf
RAC	Return Atlantic Current
WSC	West Spitzbergen Current
EGC	East Greenland Current
eDNA	environmental DNA
NMDS	Non-metric Multidimensional Scaling
AIC	Akaike Information Criterion

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1 Introduction

1.1.1 Northeast Greenland

In the East Greenlandic region, especially the northeast, biological data is scarce since it is not an area targeted by fisheries. The location is poorly known due to its geographical inaccessibility (Jensen et al., 2022), hence primeval natural conditions remain within Kalaallit Nunaanni nuna eqqissisimatitaq (Northeast Greenland National Park) (Karamushko et al., 2022). Northeast Greenland is the largest and most northerly National Park and the largest protected land area in the world (GRID-Arendal, 2014). There are no current towns or settlements within the National Park. The few people who do live in the area live at either the research, military, or meteorological stations in the area (Visit Greenland, 2024). Northeast Greenland is part of the Large Marine Ecosystem (LME) no. 3, *Greenland Sea – East Greenland*, according to the Protection of Arctic Marine Environment (PAME)'s latest revision of LMEs (2013). This is an Arctic LME where most of the region is covered by sea ice in the winter (PAME, 2013). According to the European Commission's fishing areas, which follow the Food and Agriculture Organization of the United Nations (FAO) boundaries (FAO, 2023), the study area lies within Fishing Area 27, *Northeast Atlantic*, subarea no. XIVa (European Commission, 2024).

The sea bottom topography in Northeast Greenland is often massively disturbed by moving icebergs, and along with the pack ice poses several logistical problems for sampling. Hence the number of fish species is likely underestimated due to inadequate sampling, and/or the taxonomic identification is questionable, which calls for further scientific attention (Christiansen, 2012). Northeast Greenland has five polynyas (Sørensen, 2012), where only three are recurrent (Jackson et al., and citations therein, 2022). Northeast Water (NEW) Polynya is a seasonal polynya appearing in the summertime around the 5°W and 15°W and latitudes of 77°N and 81°N. It is one of the biggest reoccurring polynyas in the Arctic. NEW polynya has shown characteristics of both being a latent and sensible heat polynya. Hirano et al. (2014) and Morales Maqueda et al. (2004) explain that latent heat polynyas form due to divergent ice motion because of the prevailing winds and/or ocean currents, whereas sensible heat polynyas develop due to high surface ocean heat fluxes (Bennett et al., and citations therein, 2024). The second largest polynya in the area is the Sirius Water (SIW) polynya which is a latent heat polynya (Jackson et al., 2022). The Île-de-France Water polynya and the Store Koldeway

Polynya are two smaller polynyas. The most southern polynya is the Scoresby Sund Polynya (Sørensen, 2012) and is at the end of my study area. High Arctic polynyas are refuge places for top predators (Jackson et al., and citations therein, 2022).

1.1.2 Oceanography

Low salinity water and sea ice from the Arctic Ocean (AO) are key characteristics of the Northeast Greenland Shelf (NEGS). The low salinity layer creates a strong upper layer column stratification, which with the low nutrient presence is the current limiting factor for primary production in the area (Gjestrup et al., 2022). These factors are also controlling the sea-ice configuration on NEGS (Hansen et al., 2023). On the NEGS, colder and fresher Arctic water meets warmer and more saline Atlantic water which travels with the Return Atlantic Current (RAC), which is a branch of the northward flowing West Spitsbergen Current (WSC) coming down. WSC is Atlantic water coming upwards from the Barents Sea (Hansen et al., 2023). A transition of Arctic water to a state resembling more that of the Atlantic is called Atlantification (Ingvaldsen et al., 2021). The East Greenland Current (EGC) is the southward flowing water mass along the NEGS which is AO water travelling southward. The upper layer of the EGC consists of 150 – 200 m of Polar water formed within the central AO. Below the Polar water are warm waters from RAC (Gjestrup et al., 2022; Hansen et al., 2023). Polar and Atlantic water originate from two different places, are different in temperature and salinity, and contain species with different biogeographic affinity. Because of the stark differences, the layer in which each water mass lays can be measured (Gjestrup et al., 2022). The total freshwater flux from Northeast Greenland has almost doubled between 1992 to 2010, and between 2007 to 2016. Potential sources are glacier meltwater and freshwater exported through the Fram Strait in a liquid or solid state. Liquid freshwater export from the central AO via Fram Strait is comprised of sea ice melt, river discharge, precipitation, and low salinity ocean water entering through the Bering Strait (Gjestrup et al., 2022). NEGS has many water masses with different structures and properties (Bennett et al., 2024). For example, Karpouzoglou et al. (2023) identified a seasonal cycle of a coastal counter current, the Northeast Greenland Coastal Counter Current, which has a northward flow during summer and reverses to a southward flow during winter (Bennett et al., and citations therein, 2024).

1.1.3 Fjord composition

Fjords with long residence time can preserve shelf signals within subsurface water, and properties within these waters can give an insight into the ongoing Arctic climate change. Kalaallit Nunaat (Greenland) fjords have two important roles: Firstly, they are the main gateways through which Sermersuaq (Greenland Ice Sheet) meltwater enters the ocean, and secondly, the bathymetry and circulation regulate warm oceanic waters to marine-terminating glaciers, contributing to submarine melting and undercutting (Gjestrup et al., and citations therein, 2022). The amount of Atlantic water entering fjords depends on the depth of the sill at the entrance as well as the depth of the Atlantic water. Fjords with shallow sills inhibit Atlantic water from entering, and fjords such as these are therefore typically modified by intermediate Polar water. Atlantic water-influenced areas tend to show greater amounts of productivity due to higher concentrations of nitrate (Gjestrup et al., 2022).

1.1.4 Arctic changes and biodiversity

The Arctic is one of the areas most affected by climate change. It is the fastest-warming region on the planet: three times faster than the rest of the world, which affects snow depth, water temperature and reduction of sea ice as well as sea ice thickness (Wassmann et al., 2011; Mueter & Litzow, 2013; Longshan et al., 2014; Fossheim et al., 2015). It is regulated by local processes such as atmospheric cooling, freshwater input, ocean mixing, and air-ice-ocean coupling. It is a major oceanic heat source for the AO (Beszczynska-Möller, 2012; Ingvaldsen et al., 2021). In the Barents Sea, the increase in Atlantic water has reduced sea ice cover, changed species distributions, and transformed the ecosystem structure (Fossheim et al., 2015; Gjestrup et al., 2022; Yurkowski et al., 2018). An increase in boreal traits has been observed in the deep sea (300 – 900 m) in Southeast Greenland and is thought to be due to food availability driven by warming (Emblemsvåg et al., 2022). The change of water entities in the Arctic is changing the biological composition as well by changing the functional traits in the marine ecosystem (Frainer et al., 2017; Polyakov et al., 2020; Yurkowski et al., 2018). Likewise, borealization, the poleward shift of fish communities in the Arctic to those more representative of boreal, Atlantic fish communities is well documented. The Barents- and Bering Seas fish community shifts, coupled with their reduction of sea ice cover are examples in which borealization has occurred (Grebmeier et al., 2006; Mueter & Litzow, 2008; Grebmeier, 2012; Fossheim et al., 2015; Kortsch et al., 2015; Frainer et al., 2017). The NEW polynya is opening earlier and closer later and is present three weeks longer than that observed in the 1980s (Bennett et al., 2024).

Biodiversity is the variation of living organisms. Fish diversity is the variation of fishes (Bluhm et al., 2011).

1.1.5 Fish species distribution in polar seas

Marine communities are expected to be more sensitive to climate change than terrestrial communities because the distribution of marine species is strongly correlated with thermal tolerances (Manes et al., and citations therein, 2021). Fishes are very sensitive to temperature changes and regulate their body temperature through behaviour such as selecting or avoiding certain temperatures, so they can optimize their living conditions (Karamushko et al., 2022). Arctic species are associated with ice-covered seas and reproduce at sub-zero temperatures. Arctic-boreal species are distributed in Arctic and sub-Arctic seas and may spawn at either subzero or positive temperatures. Boreal species are distributed throughout sub-Arctic and boreal seas but may enter Arctic seas for feeding purposes. They spawn in positive temperatures. Widely distributed species are species widespread in boreal and subtropical seas as well as below the warm waters. Many deep-sea and highly migratory species belong to this group. They occur rarely in the Arctic (Jørgensen et al., 2014). Temperate species, particularly demersal fish, cannot tolerate low temperatures of ice-associated bottom water (Mueter & Litzow, 2008). Polar seas are typically considered species-poor compared to lower latitudes (Christiansen, 2012) since species richness declines at high latitudes both in teleosts and elasmobranchs (Narayanaswamy et al., 2010; Watanabe & Payne, 2023). Arctic fish species live in very contrasting seasonal environments and tend to be benthic-eating specialists compared to larger body-sized boreal fish with a broader diet range (Emblemsvåg et al., and citations therein, 2022). Arctic species are phylogenetically closer related and subject to a strongly selective environment compared to boreal species. Though many Arctic species are slow-growing and long-lived (Christiansen, 2017), boreal species in the Barents Sea display slower life histories than Arctic and Arctic-boreal species, with later age and larger size at maturity (Wiedmann et al. 2014). Boreal species tend to be generalist feeders dependent on phytoplankton production while Arctic species tend to be specialists depending on benthic species (Frainer et al., 2017).

Boreogadus saida is a circumpolar species and most likely one of the most abundant species in the Arctic. It is associated with sea ice-covered areas, predominantly during the larvae and juvenile stages. The larger fish can occur in deep water, open water, or demersal waters. The

Boreogadus saida is a keystone species, especially in the high Arctic system where it is an important food source for ice-associated marine animals (Hop & Gjøsæter, and citations therein, 2013; Hunt Jr. et al., 2016).

Manes et al., (2021) found that endemic and native, i.e. indigenous non-endemics, species are more at risk of the effects of climate change than introduced species e.g. northward moving species. Their results also concluded that endemic species are more vulnerable compared to native species. In evolutionary terms, the Arctic is a rather young habitat and therefore holds few endemic species (Narayanaswamy et al., 2010).

Using environmental DNA (eDNA) Jensen et al. (2022) demonstrated latitudinal shifts from South Greenland to Northeast Greenland where a dominance from *Mallotus villosus* to *Boreogadus saida*. A compositional difference between Southeast and Northeast Greenland has been described by Jørgensen et al. (2015). The study of marine fish distribution within the Euro-Arctic region is of particular interest due to ocean warming and related northward shifts in the geographic range for a lot of boreal species (Christiansen, 2012). Although the effects of Atlantification and borealization are observed throughout the Arctic, the Northeast Greenland sill fjords and NEW Polynya appear to still be minimally affected and to maintain their Arctic fish communities, because these areas are less affected by the inflow of Atlantic water (Karamushko et al., 2022).

1.2 Research Aims and Objectives

This study investigates the fish community compositions in Northeast Greenlandic waters by calculating and comparing diversity indices in space and time. The temporal changes are investigated by analysing changes between two time periods: 2002 – 2010 and 2013 – 2022. The fish community data was collected on the scientific TUNU Programme cruises from 2002 – 2022.

The overarching research question studied in this thesis is:

What are the status and spatial patterns of demersal marine fish communities in Northeast Greenland in the period 2002 – 2022?

The research sub-questions include:

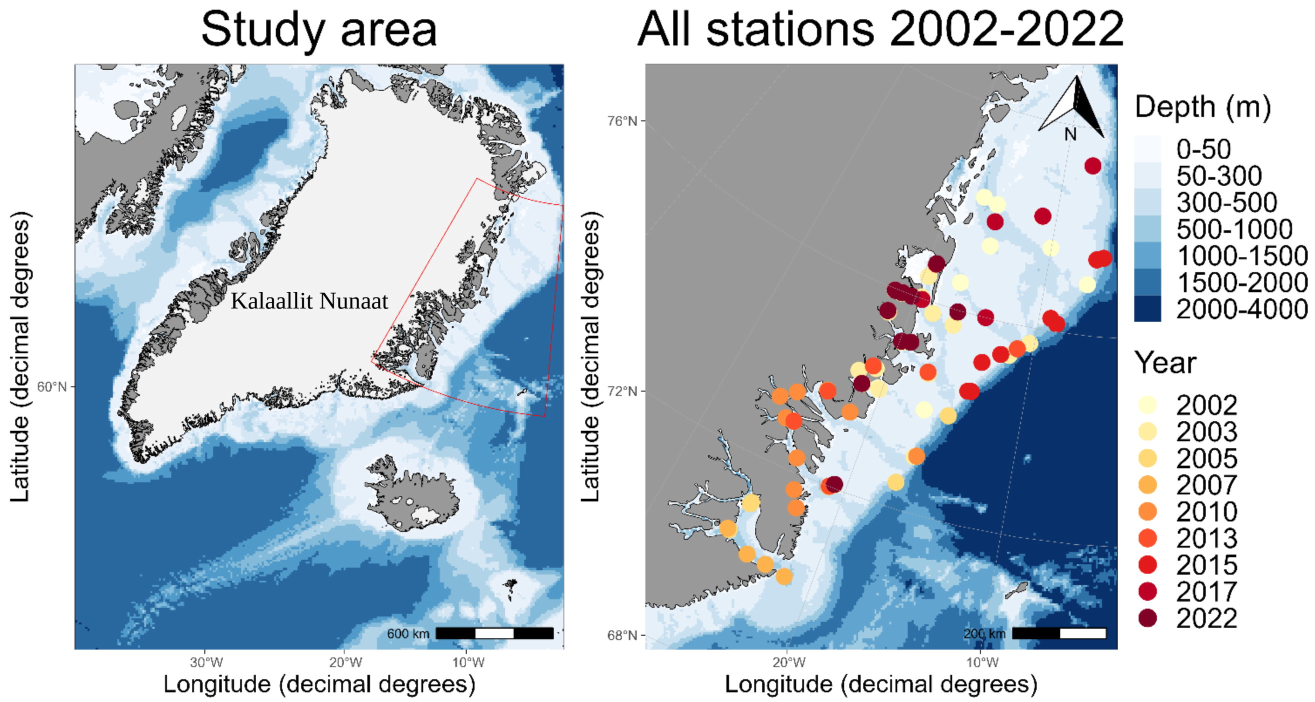
1. Are there differences in species composition between fjord, shelf, and slope communities?
2. How do the diversity indices differ in each location?
3. Are there any temporal diversity changes?
4. Are there any factors that indicate compositional differences?

2 Materials and methods

Biological data for this study are from the TUNU Programme surveys 2002 – 2022 coordinated by UiT The Arctic University of Norway (Christiansen, 2012). I have only worked with data cleaning and data analyses. Data collection and data processing have been done by TUNU Programme cruise participants, which I have not been part of.

2.1 Data collection

Sampling was conducted during summer and early autumn (July – October) using a Campelen-1800/96 NOFI fine-mesh bottom trawl (10 mm mesh size in the cod end) deployed from RV Helmer Hanssen (RV Kronprins Haakon in the year 2022), Arctic University of Norway UiT. Trawling duration varied between 5 – 30 min. Depth (m) of sampling and corresponding in situ temperature (°C) were recorded simultaneously at stations using a SeaBird sensor mounted on the gear. Figure 1 a) shows the overall sampling area, and Figure 1 b) shows where and in which years the stations were sampled.



a) b)

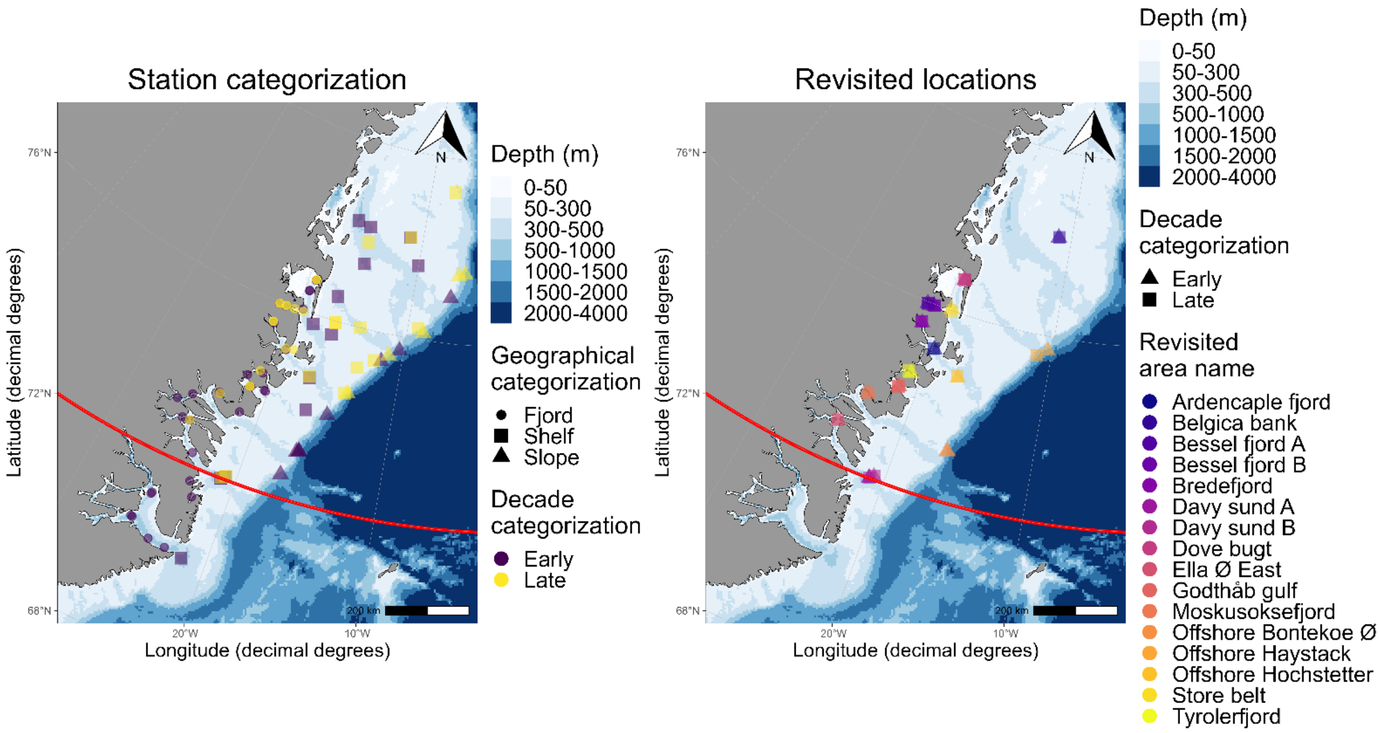
Figure 1: *a) Overview of the study area on a large map of Kalaallit Nunaat. The red outline indicates the study area. b) Zoomed in overview of study area showcasing stations trawled 2002 – 2022.*

2.2 Data processing

Hauls were sorted onboard and all fishes were identified to the species level by TUNU personnel. Abundance and weight (kg) were measured per species.

2.3 Data analyses

Data was divided into two time periods, *early (2002 – 2010)* and *late (2013 – 2022)*, to analyze temporal changes. These years were selected to have approximately equal sets of years in each decade and approximately equal number of cruises. Stations below 72°N were omitted for temporal comparisons to have approximately the same area (i.e., spatial footprint) for analyses, as stations below 72°N only consist of *early* decade stations. Three geographical categories, *fjord, shelf* and *slope*, were used to analyze the potential geographical preferences of species. Fjords in this instance are any stations surrounding land. Shelf stations are those on the shelf, and slope stations are on the slope area, i.e., deeper, according to my maps. There is a large depth range for the fjords spanning from approximately 50 m to 800 m. The shelf range is narrower being from approximately 100 m to 500 m with one outlier of about 600 m. The slope range is large, but deeper being from approximately 400 m to 1150 m. Maps with depth categorizations to the nearest hundred-meter range, in early and late time periods, can be seen in the appendix Figure 2. Station categorizations of early, late, and geographical categories can be seen in Figure 2a), where the red line indicates 72°N. The fish species are categorised by their biogeography, we selected four zoogeography categories, *Arctic, Arctic-Boreal, Boreal and Widely distributed* (Mecklenburg et al., 2018) to characterise the biogeographic composition of the fish community. Revisited locations were identified by selecting stations at locations with samples of more than one year, these stations can be seen in Figure 2b.



a) b)

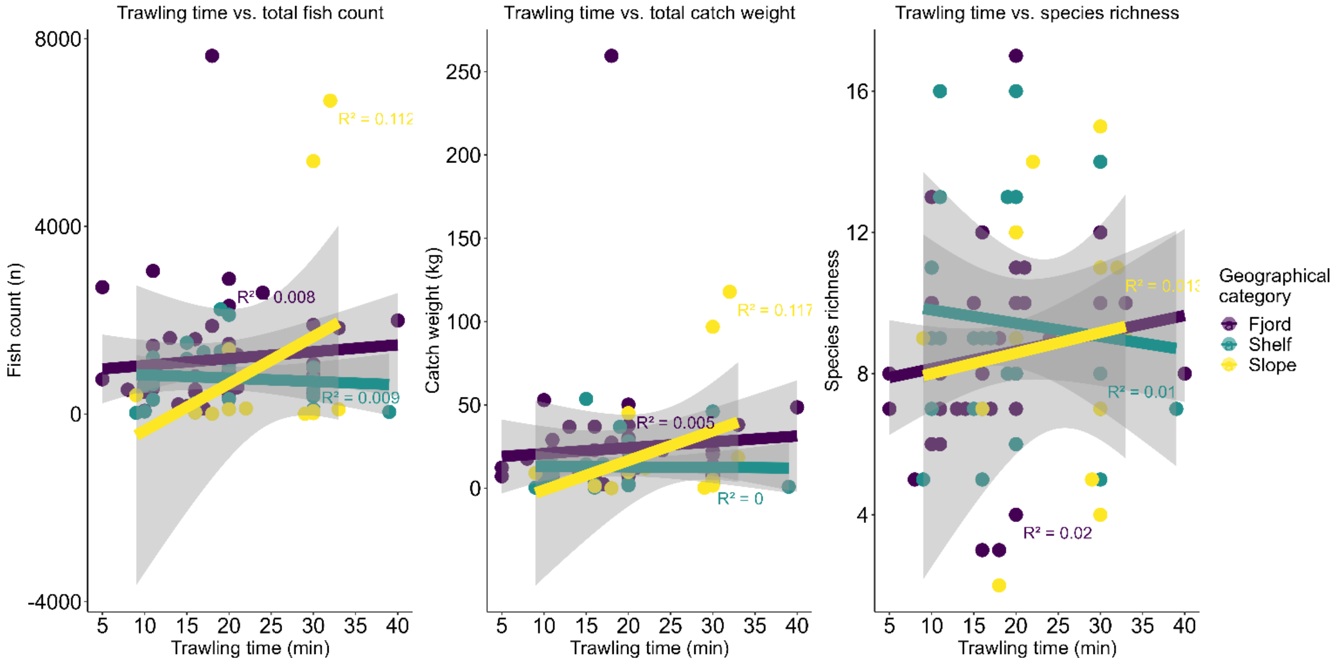
Figure 2*: The red line at 72°N indicates stations omitted when comparing temporal data. a) Station categorization where shapes indicate geographical categorization and colour indicates decade categorizations. b) Revisited stations where shapes indicate decade categorization and colour indicates revisited area name.*

Both species and family richness, as well as Shannon's and Simpson's diversity indices, were used to get an overview of the species and family diversities at the different stations. Species richness is the number of species present and the easiest and most common way to measure biodiversity (Lin et al., 2023). Family richness is the number of fish families present. Species diversity was calculated using the Shannon Index (Shannon, 1948) and Simpson Index (Simpson, 1949) to assess ecological variability. The R package *Vegan* (Oksanen et al., 2023) was used. The Shannon index permits us to understand the broader aspects of biodiversity such as richness and evenness and gives especially more weight for the rare species. The Simpson diversity index gives less weight to rare species but more importance to the abundant species, and thus permits us to understand the impact of dominant species and their impact on the ecosystem.

A Non-metric Multidimensional Scaling (NMDS) (Kruskal, 1964) on the fish community composition per station was done to check whether there were any similarities or dissimilarities between the species composition within the stations. I used Bray-Curti's (Bray & Curtis, 1957) dissimilarity to transform the abundance data. We visualised the results per station and colour-coded the stations based on environmental values (depth, temperature and latitude) to find which ecological factors appear to be the main drivers of species composition in the study area to distinguish habitats from one another. In the marine environment, species richness is linked to depth (Lin et al., 2023). A linear model was used to explain the variability of the first two axes of variation of the fish community composition, NMDS1 and NMDS2, according to environmental variables (geographical category, latitude, temperature, depth and decade). To assess which environmental variables explained most of the observed variability in NMDS1 and NMDS2 the models were statistically assessed with Akaike Information Criterion (AIC) (Akaike, 1974). R Studio version 4.3.2 (RStudio Team, 2024, Version 4.3.2) was used for data analysis. R package *ggOceanmaps* (Vihtakari, 2024) was used to create maps. R package *ggplot2* (Wickham et al., 2023) was used for plotting.

3 Results

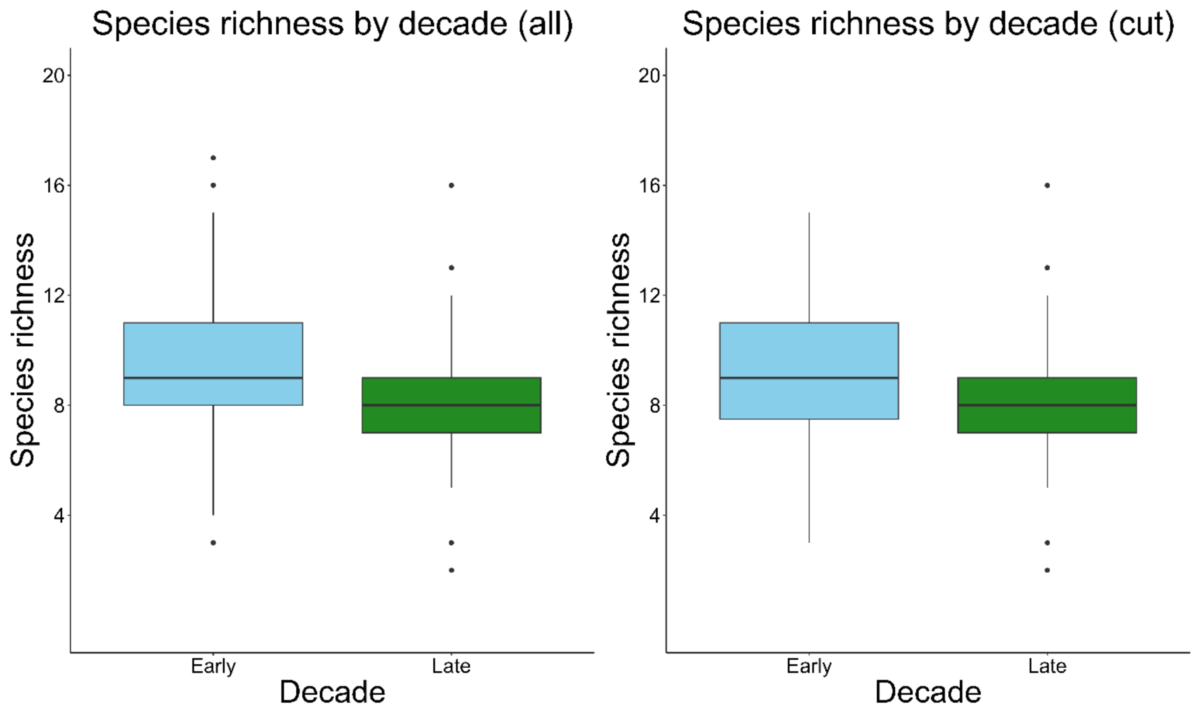
Linear regression was used to check whether trawling time had any influence on fish count, catch weight, and species richness. The overall trend was that there was little to no dependence on trawling time (highest $R^2 = 0.117$). Linear regression of depth over trawling time followed the trend of little influence and can be seen in the appendix Figure 1.



a) b) c)

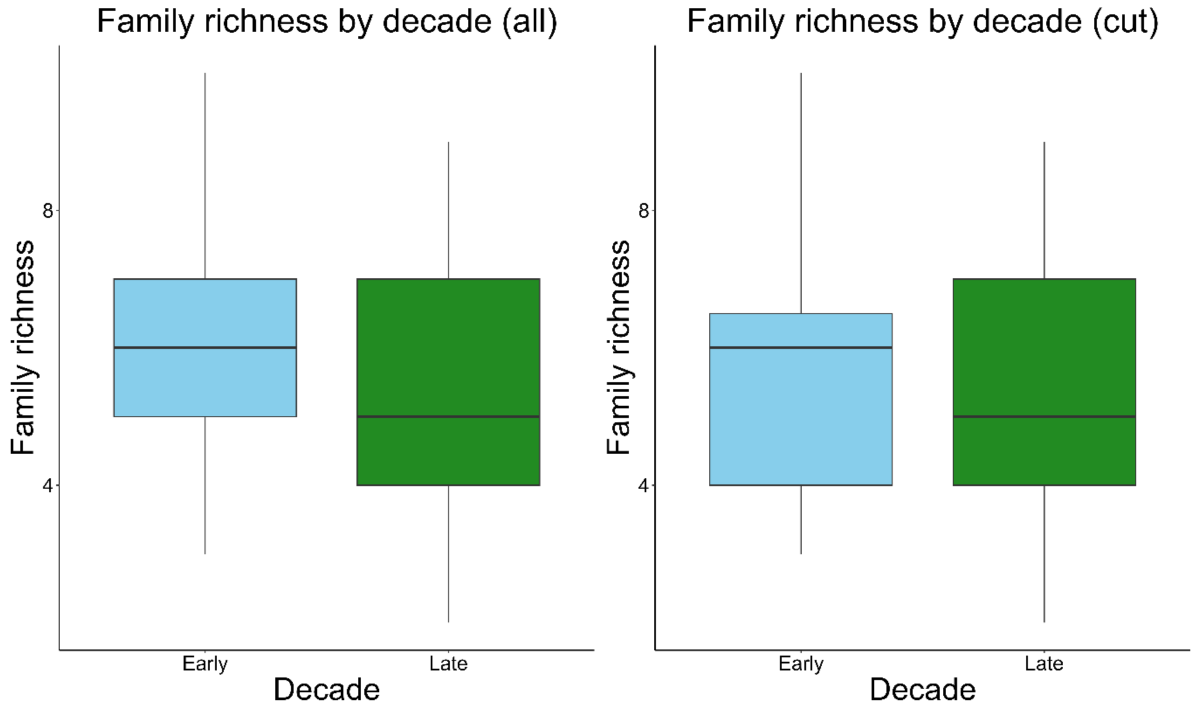
Figure 3: *Plots with trendlines showcasing whether trawling time has any influence on various variables. R^2 values show the statistical measures of the plots. Different colours showcase different geographical categories: fjord, shelf, and slope. a) Fish count over trawling time. b) Catch weight over trawling time. c) Species richness over trawling time.*

The effect of omitting stations below 72°N in average mean ranges for species richness can be observed when comparing (all) stations (Figure 4a) to (cut) stations meaning below 72°N omitted (Figure 4b). The same influences can be seen in family richness (Figure 5). The outliers in the early decade (all) influenced the mean species richness distribution a little, which could affect further analyses like species richness comparisons between time periods.



a) b)

Figure 4*: Average and outliers of species richness showcased in boxplots. a) Species richness differences between early and late decade with all stations. b) Species richness differences between early and late decade with stations below 72°N omitted. Early decade, 2002 – 2010, and late decade, 2013 – 2022.*



a) b)

Figure 5: *Average and outliers of family richness showcased in boxplots. a) Family richness differences between the early and late decades with all stations. b) Family richness differences between early and late decades with stations below 72°N omitted. Early decade, 2002 – 2010 and late decade 2013 – 2022.*

3.1 Early and late time period changes

3.1.1 Family richness and relative abundance

Most family groups in the study area exhibited low species diversity (1 species per family group), with Zoarcidae showing the greatest family richness containing 12 species, followed by Cottidae and Liparidae containing 7 species each (Figure 6). The Gadidae family, despite being the most relatively abundant species (Figure 7), contains only three species in its family.

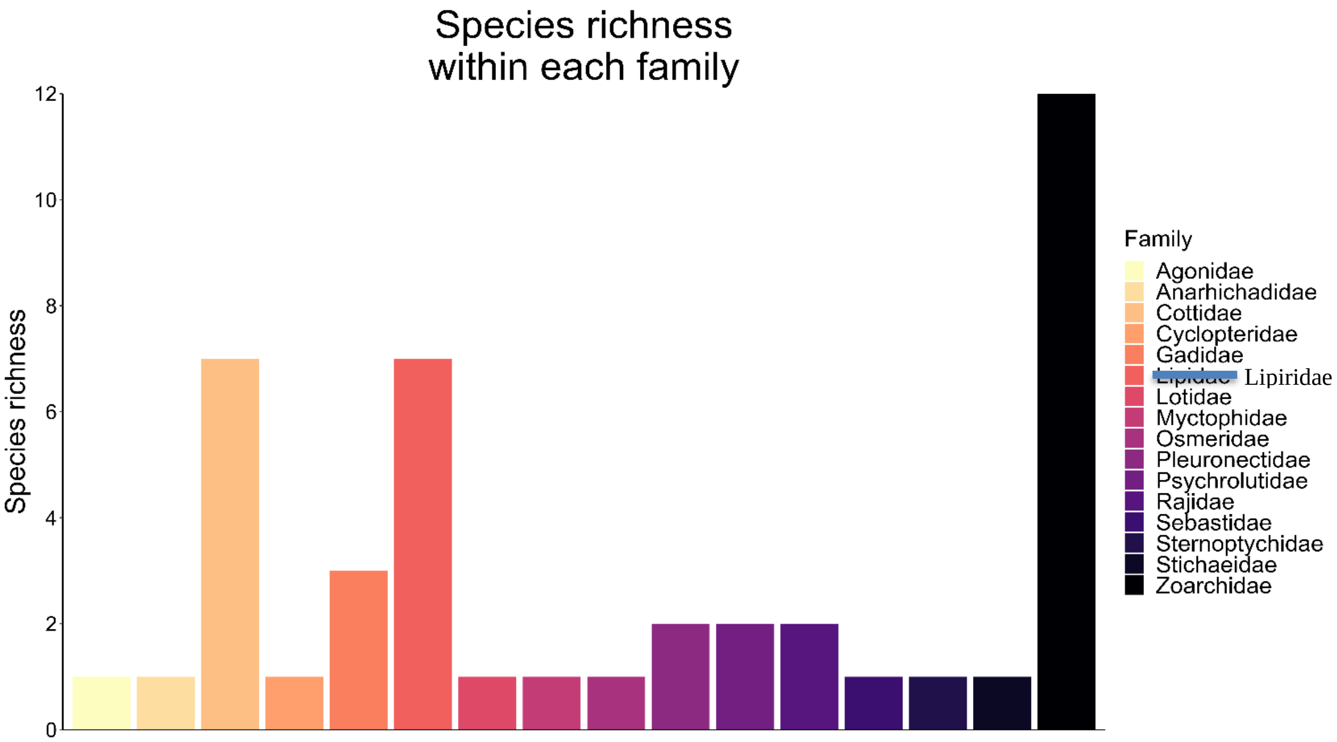
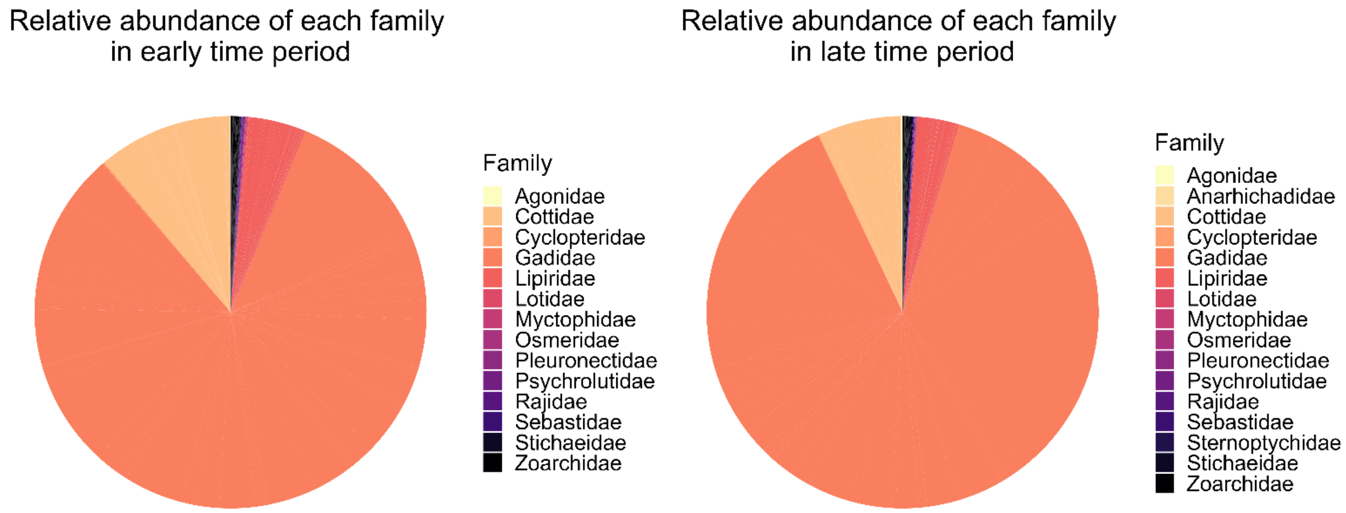


***Figure 6**:Species richness within each family group found in the study area.*

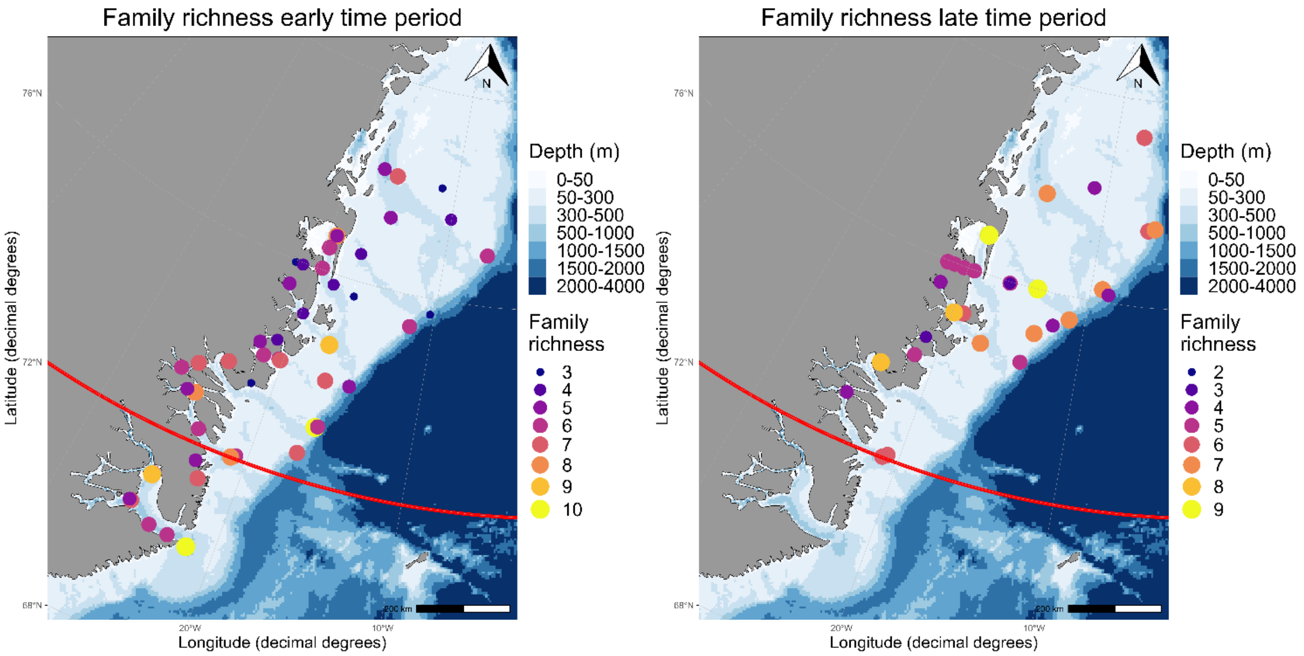
The relative abundance was dominated by Gadidae, the most relatively abundant species. Its relative abundance increased from approximately 80% in the early decade (2002 – 2010) to approximately 85% in the late decade (2013 – 2022). The relative abundance of Cottidae and Lipiridae decreased from approximately 10% and 7% to 7% and 5% respectively in the late decade (Figure 7a and 7b, respectively). Family richness increased from 14 family groups in the early decade to 16 family groups in the late decade with the addition of Anarhichadidae and Sternoptychidae (Figure 7).



a) b)

Figure 7: *Pie charts of the relative abundance of each family group. Stations below 72°N omitted to temporal compare approximately the same study area. a) Early decade, 2002 – 2010. b) Late decade, 2013 – 2022.*

Family richness increased from being dominated by 3–6 family groups to 5–8 family groups. The early decade (2002 – 2010) has more stations with low family richness (smaller and darker dots) compared to the late decade (2013 – 2022) (Figure 8).

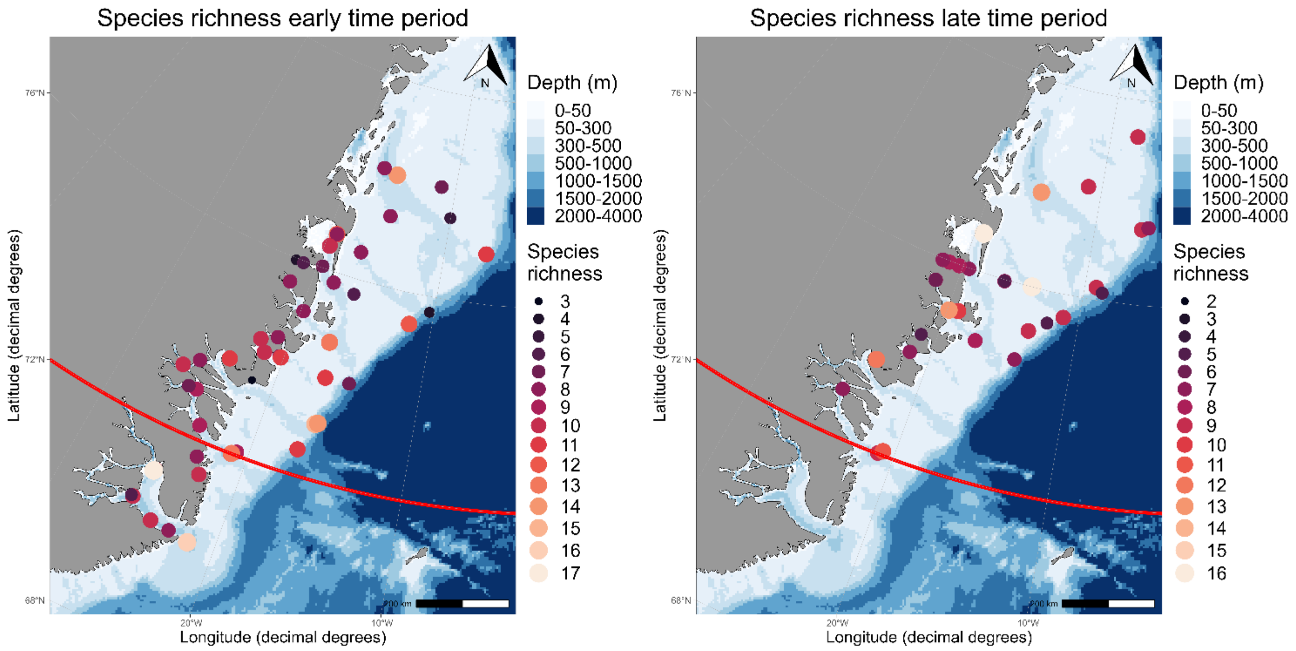


a) b)

Figure 8: *Family richness at different stations where smaller and darker dots indicate fewer family groups compared to lighter and bigger dots. The red line at 72°N indicates stations omitted when comparing temporal data. a) Early decade, 2002 – 2010 b) Late decade, 2013 – 2022.*

3.1.2 Species richness

Species richness increased from being dominated by 3–10 species to 5–10 species. The early decade (2002 – 2010) has more stations with low species richness (smaller and darker dots) compared to the late decade (2013 – 2022) (Figure 9).

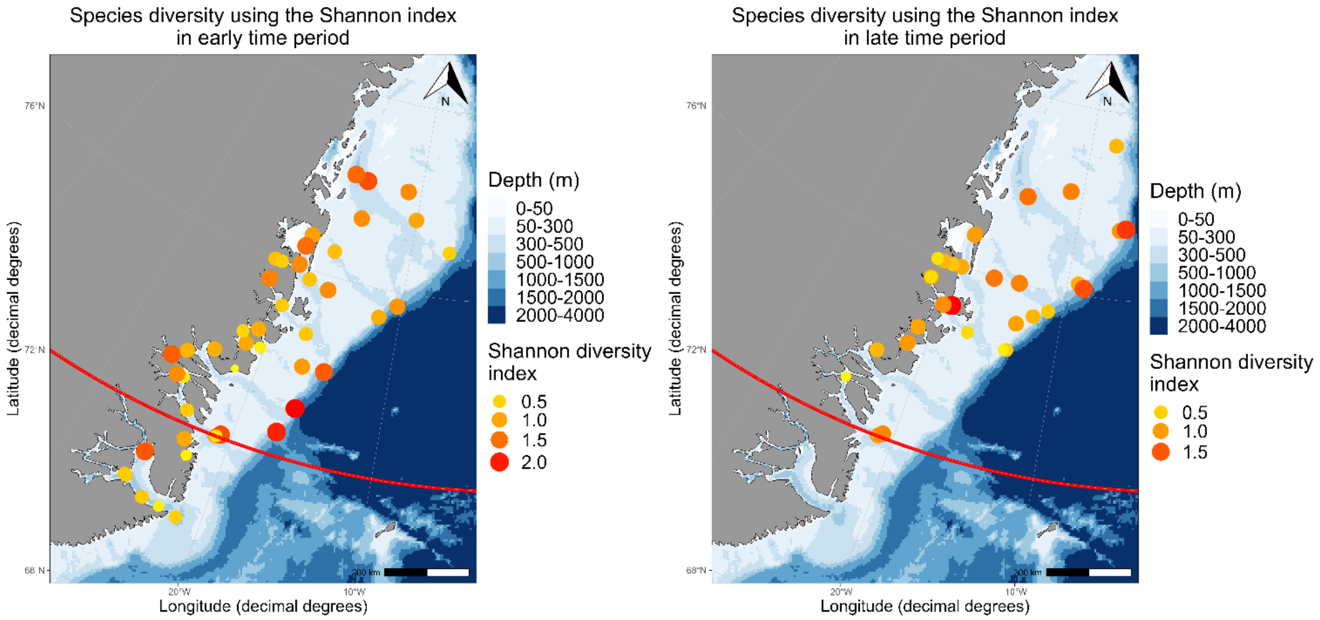


a) b)

Figure 9: Species richness at different stations where smaller and darker dots indicate fewer species compared to lighter and bigger dots. The red line at 72°N indicates stations omitted when comparing temporal data. a) Early decade, 2002 – 2010. b) Late decade, 2013 – 2022.

3.1.3 Species diversity index

There was an increase in species diversity seen between early and late decade (Figures 10a and 10b, respectively). The Shannon index was dominated by low indices of 0.5–1.0 in the early decade whereas in the late decade 1.0–1.5 (Figure 10), which indicates a higher species diversity in the late decade compared to the early decade. The Simpson's diversity indices for the early and late decades, displayed in the Appendix (Figure 3), followed a similar pattern to that of the Shannon diversity index.



a) b)

Figure 10: *Shannon diversity indices on different stations. The lighter and smaller size of dot the smaller the Shannon index value. The red line at 72°N indicates stations omitted when comparing temporal data. a) Early-decade stations 2002 – 2010. b) Late-decade stations 2013 – 2022.*

3.1.4 Zoogeography

The most abundant zoogeography category was Arctic followed by Arctic-Boreal. There was a relative abundance decline of Arctic species from approximately 85% in the early decade (2002 – 2022) to 80% in the late decade (2013 – 2022). There was an increase of Arctic-Boreal species from approximately 10% in the early decade to 15% in the late decade. A new zoogeographic category, *Widely distributed*, appeared in the late decade (Figure 11).

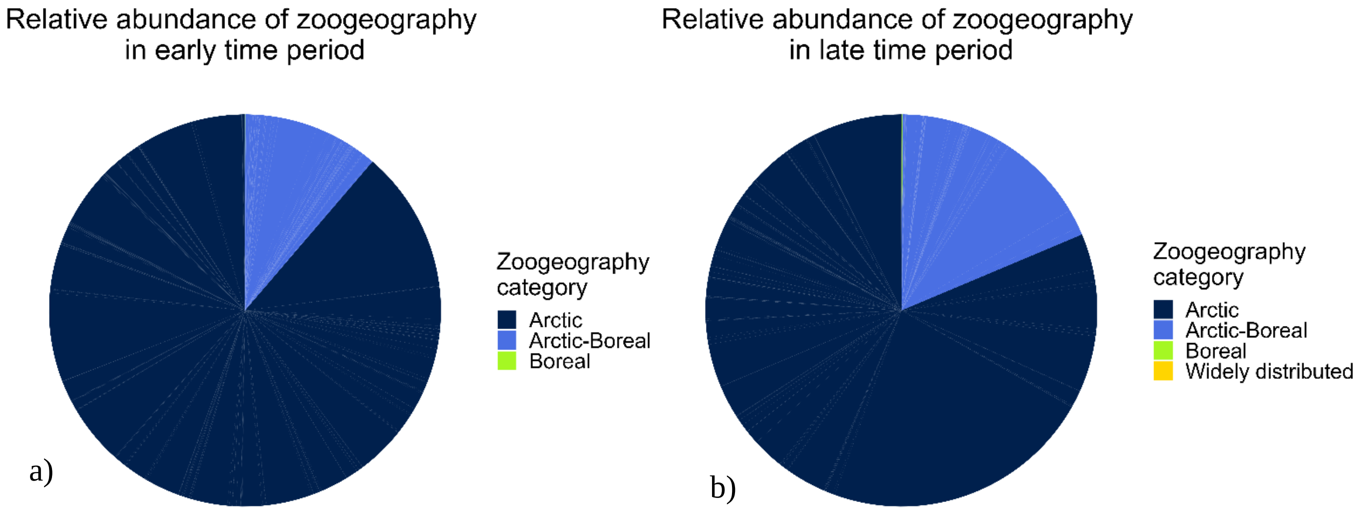
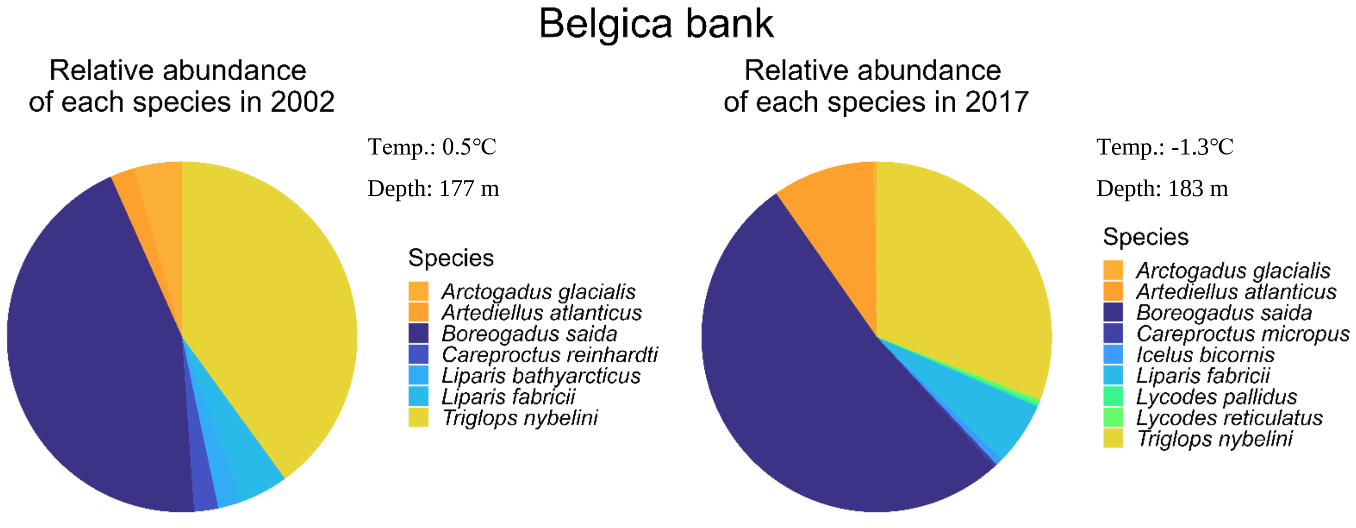


Figure 11:Pie charts of the relative abundance of each zoogeography category: Arctic, Arctic-Boreal, Boreal and Widely distributed. Stations below 72°N omitted. a) Early decade, 2002 – 2010. b) Late decade, 2013 – 2022.

3.2 Temporal changes at revisited locations

Between 2002 and 2017 a small relative abundance increase of *Boreogadus saida* (approximately 45 – 50 %), *Liparis fabricii* (approximately 7 – 10%), and *Artediellus atlanticus* (approximately 5 – 10%) are seen in the Belgica Bank (Figure 12), the most northerly location in this study (Figure 2b). A decrease of *Arctogadus glacialis* (approximately 7 – 1%), *Triglops nybelini* (approximately 40 – 33%), and *Liparis bathyarcticus* (4 – 1%). Species richness has increased even though some species were only seen in 2002 and not in 2017 such as *Carepructus reinhardti* and *Liparis bathyarcticus*. Temperature has decreased from 0.5 °C to -1.3 °C.



a) b)

Figure 12: *Pie charts of the relative abundance of each species at Belgica Bank. a) 2002. b) 2017.*

Dove bugt was one of the most revisited locations and was visited four times, in 2002, 2003, 2017, and 2022. There was a species richness decline from 2002 – 2003 (Figure 13a and 13b, respectively) from 12 species to 8 species. In 2017 the species richness increased where there were 10 species. This increased further in 2022 when there were 16 species caught. An increase of *Lycodes spp.* species have been documented (Figure 13). The temperature changed alongside the differences in species richness with a decrease in temperature from -0.05°C in 2002 to -0.35°C in 2003 (Figure 13a and 13b, respectively). A temperature increase occurred from -0.2°C in 2017 to 0.99°C in 2022 (Figure 13c and 13d, respectively). The overall trend was that the relative abundance of *Boreogadus saida* increased by approximately 60 – 75 % (2002 – 2022, respectively) (Figure 13a and 13d, respectively). The second most abundant species changed from *Triglops nybelini* (2002 and 2003) (Figure 13a and 13b, respectively) to *Arctogadus glacialis* (2017 and 2022) (Figure 13c and 13d, respectively).

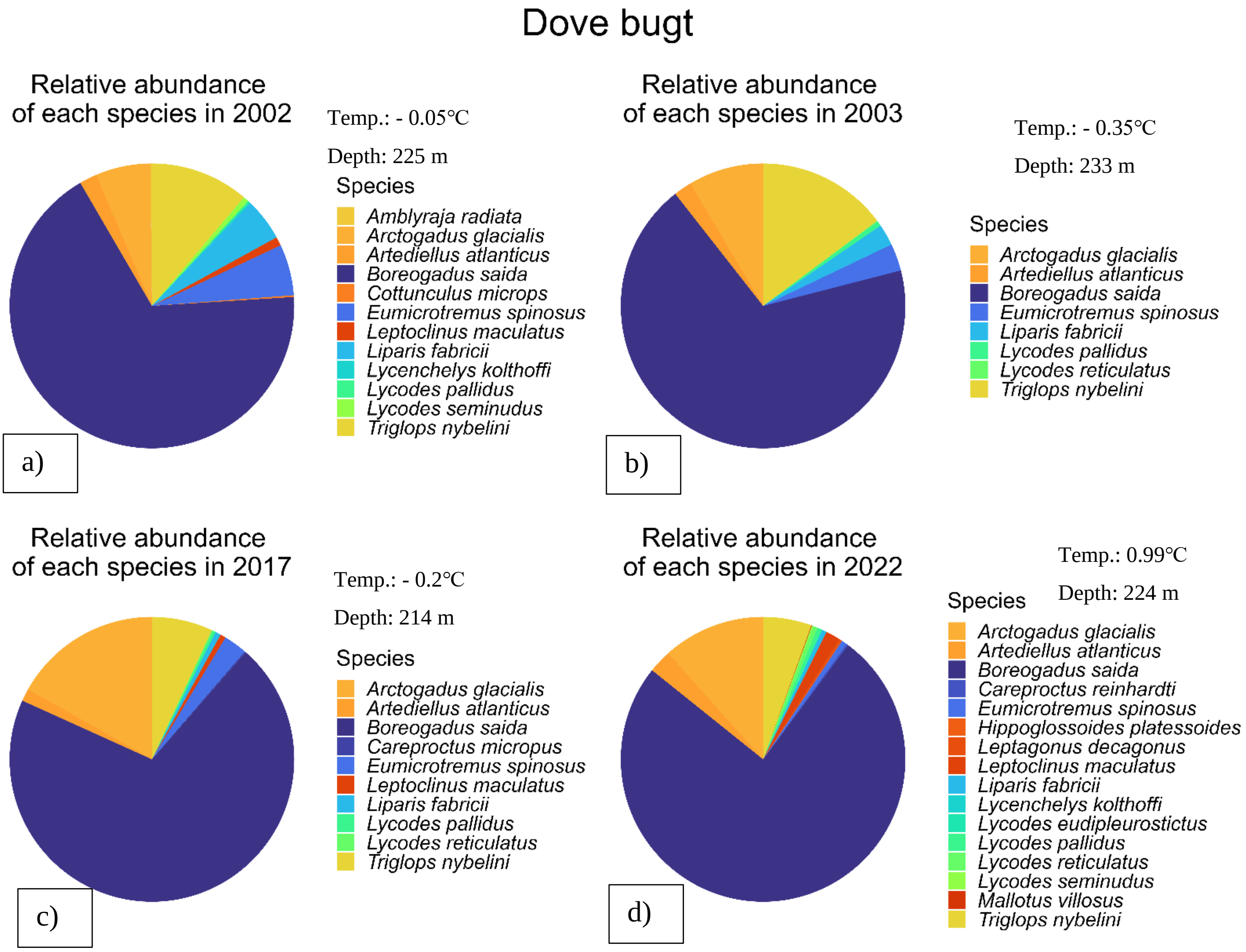
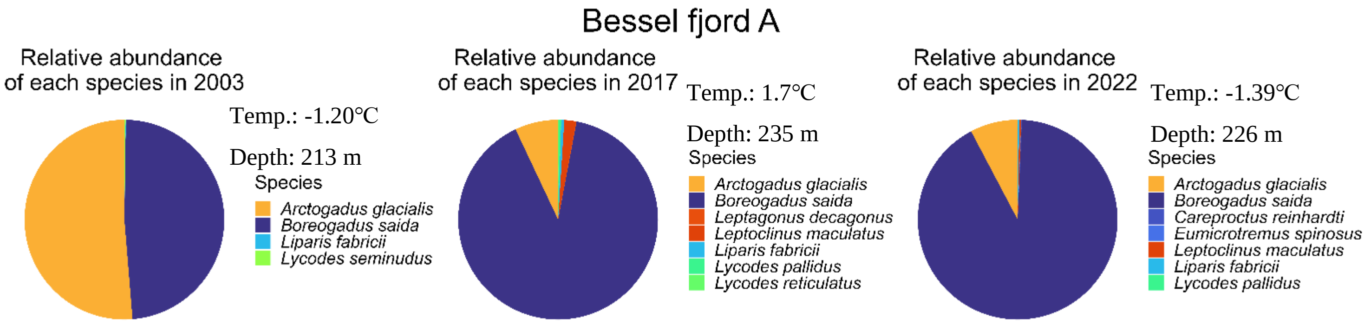


Figure 13: *Pie charts of the relative abundance of each station at Dove bugt. a) 2002. b) 2003. c) 2017. d) 2022.*

Similar temperature trends of warming temperatures between 2003 and 2017 and then cooling between 2017 and 2022 were observed between the inner- and middle part of Bessel fjord (Bessel fjord A and Bessel fjord b, respectively) (Figures 14 and 15, respectively). Their location in the overall study can be seen in Figure 2b. The two locations differed in depth, with the inner part (Bessel fjord A) having depths in the lower 200s (m) and the middle part (Bessel fjord B) having depths in the upper 300s (m) (Figures 14 and 15, respectively).

Species richness in Bessel fjord A (Figure 14) increased from four species in 2003 (Figure 14a) to seven species in 2017 and 2022(Figures 14b and 14c, respectively). Three species

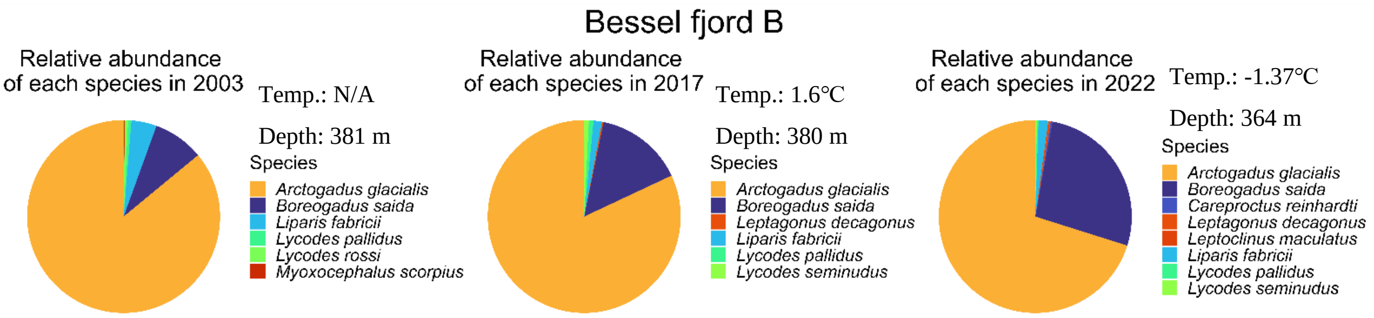
(*Arctogadus glacialis, Boreogadus saida* and *Liparis fabricii*) remain the same in all sample years (Figure 14). The relative abundance of dominance changed from having a ratio of almost 1:1 of *Arctogadus glacialis* and *Boreogadus saida* with a slight dominance of *Arctogadus glacialis* to being a relative abundance domination of *Boreogadus saida* being around 90% of the species present (Figure 14).



a) b) c)

Figure 14: *Pie charts the relative abundance of each species at Bessel fjord A. a) 2003.b) 2017. c) 2022.*

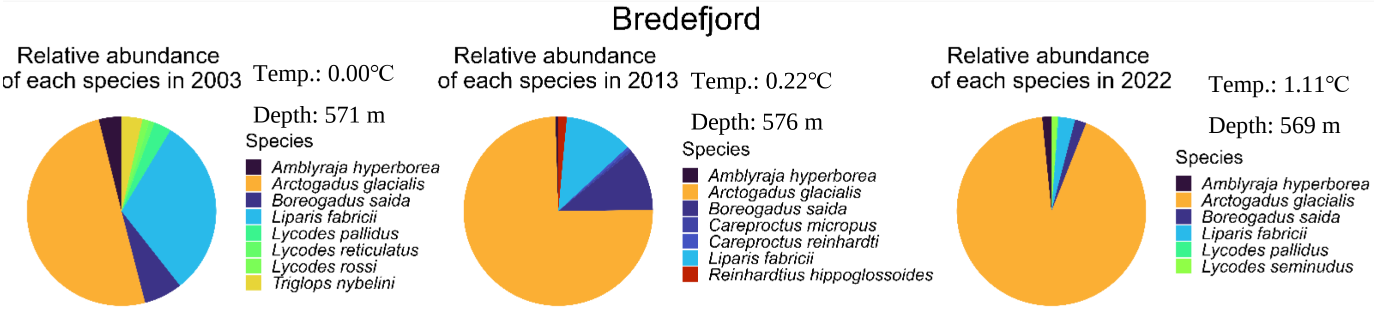
The most abundant species in Bessel fjord B remained *Arctogadus glacialis*, but the relative abundance showed a declining trend (85% in 2003; 80% in 2017; 70% in 2022; Figure 15). Conversely, the relative abundance of *Boreogadus saida* showed an increasing trend (7% in 2003; 15% in 2017; 27% in 2022; Figure 15). The relative abundance of *Liparis fabricii* decreased from approximately 5% in 2003 to approximately 1% in 2017 and 2022 (Figure 15). The species richness between 2003 and 2017 remained the same (being six species), but the specific species present differed with two species between the years (*Lycodes rossi* and *Myoxycephalus Scorpius* being present in 2003, and *Leptagonus decagonus* and *Lycodes seminudus* being present in 2017). In 2022 a species increase to eight species occurred. *Arctogagus glacialis*, *Boreogadus saida*, *Liparis fabricii* and *Lycodes pallidus* have been observed all years (Figure 15).



a) b) c)

***Figure 15**: Pie charts of the relative abundance of each species at Bessel fjord B. a) 2003. b) 2017. c) 2022.*

A temperature increase from 0.00°C in 2003 to 0.22°C in 2013 to 1.11°C was recorded in Bredefjord (Figure 16). A decline of one species per revisit occurred with eight species observed in 2003 and six species in 2022. Relative abundance remained *Arctogadus glacialis*, but the abundance increased from approximately 50% in 2003 to approximately 75% in 2013 to approximately 90% in 2022 (Figure 16). *Liparis fabricii* remained the second most relatively abundant species but showed a decreasing trend with each revisit from approximately 25% in 2003 to 10% in 2013 to approximately 3% in 2022 (Figure 16). The relative abundance of *Boreogadus saida* increased between 2003 and 2013 from approximately 5% to approximately 10% (Figures 16a and 16b, respectively). It decreased like most of the other species in 2022 (Figure 16c). *Amblyraja hyperborea*, *Arctogadus glacialis*, and *Liparis fabricii* appear in all visits. *Lycodes pallidus* was seen in 2003 (Figure 16a), and was absent in 2013 (Figure 16b), but reappeared in 2022 (Figure 16c). The remaining species were only observed once.

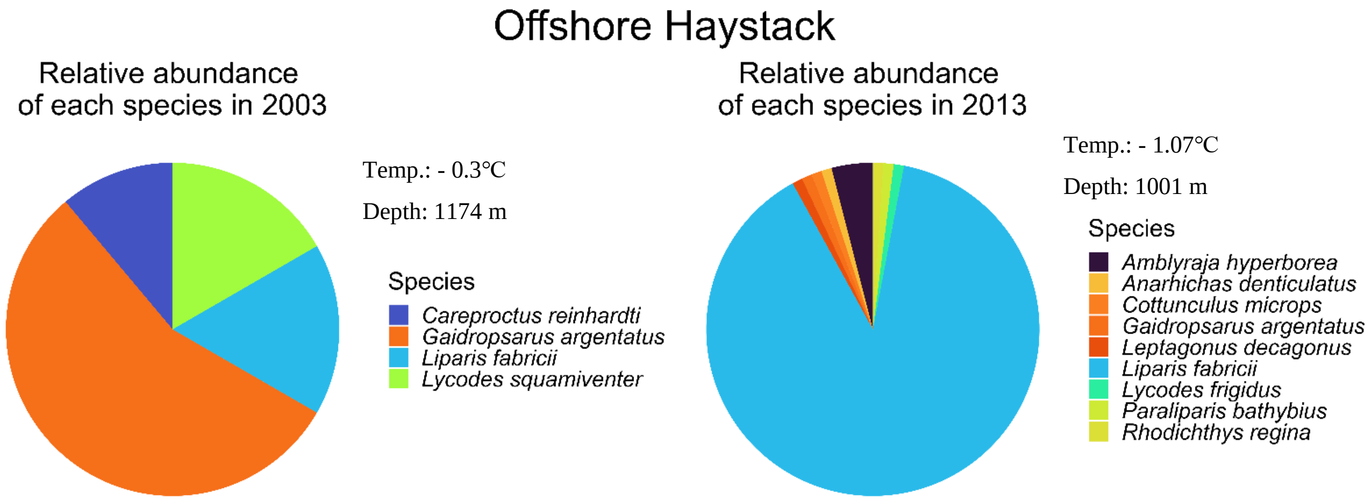


a) b) c)

***Figure 16**: Pie charts the relative abundance of each species at Bredefjord. a) 2003. b) 2013. c) 2022.*

Temperature declines occurred at both slope locations, Offshore Haystack and Offshore Bontekoe Ø (Figures 17 and 18, respectively). A temperature from -0.3°C in 2003 to -1.07°C in 2013 at Offshore Haystack (Figure 17), and a decline from -0.5°C in 2003 to -0.73°C in 2010 (Figure 18). Species richness increased in both places. In Offshore Haystack an increase from four species in 2003 to nine species in 2013 occurred (Figure 17). In Offshore Bontekoe Ø an increase from nine species in 2003 to fourteen species in 2010 occurred (Figure 18).

The relative abundance at Offshore Haystack changed from *Gaidropsarus argentatus* dominating with approximately 60% in 2003 to *Liparis fabricii* dominating approximately 90% in 2013 (Figure 17). The rest of the species showed an approximately equal relative abundance in 2003 of approximately 20% each with *Careproctus reinhardti* having a slighter relative abundance of approximately 15% compared to *Liparis fabricii* and *Lycodes squamiventer* (Figure 17a). The second most abundant species in 2013 was *Amblyraja hyperborea* approximately 5% of the total relative abundance in which the remaining species shared the last 5 % among themselves (Figure 17b). *Gaidropsarus argentatus* and *Liparis fabricii* were the only recurring species (Figure 17).

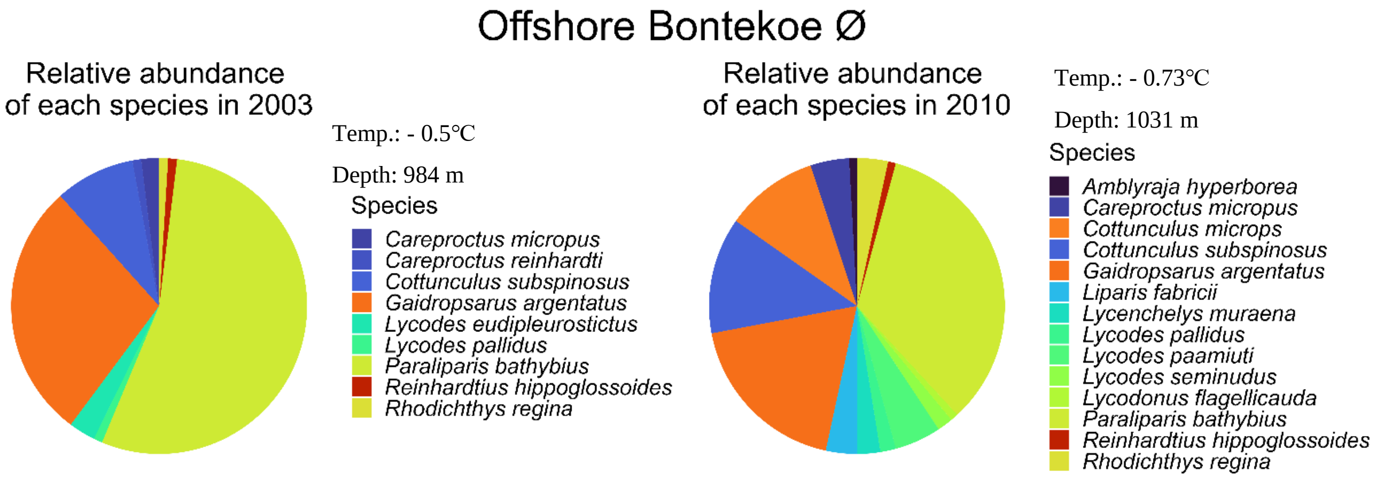


a) b)

Figure 17: *Pie charts the relative abundance of each species at Offshore Haystack. a) 2003. b) 2013.*

The relative abundance at Offshore Bontekoe Ø was dominated by *Paraliparis bathybius* approximately 55% in 2003 to approximately 20% in 2010 (Figure 18). The relative abundance of *Gaidropsarus argentatus* being the second most abundant species had a decline from approximately 30% in 2003 to approximately 20% in 2010. The relative abundance of *Cottunculus subspinosus* increased from approximately 10% in 2003 to approximately 15% in

2010. of *Cottunculus subspinosus*, *Careproctus micropus*, *Reinhardtius hippoglossoides*, *Paraliparis bathybius*, *Gaidropsarus argentatus*, *Lycodes pallidus*, and *Rhodicthys regina* were the seven out of nine species in 2003, which were also seen in 2010 (Figure 18).



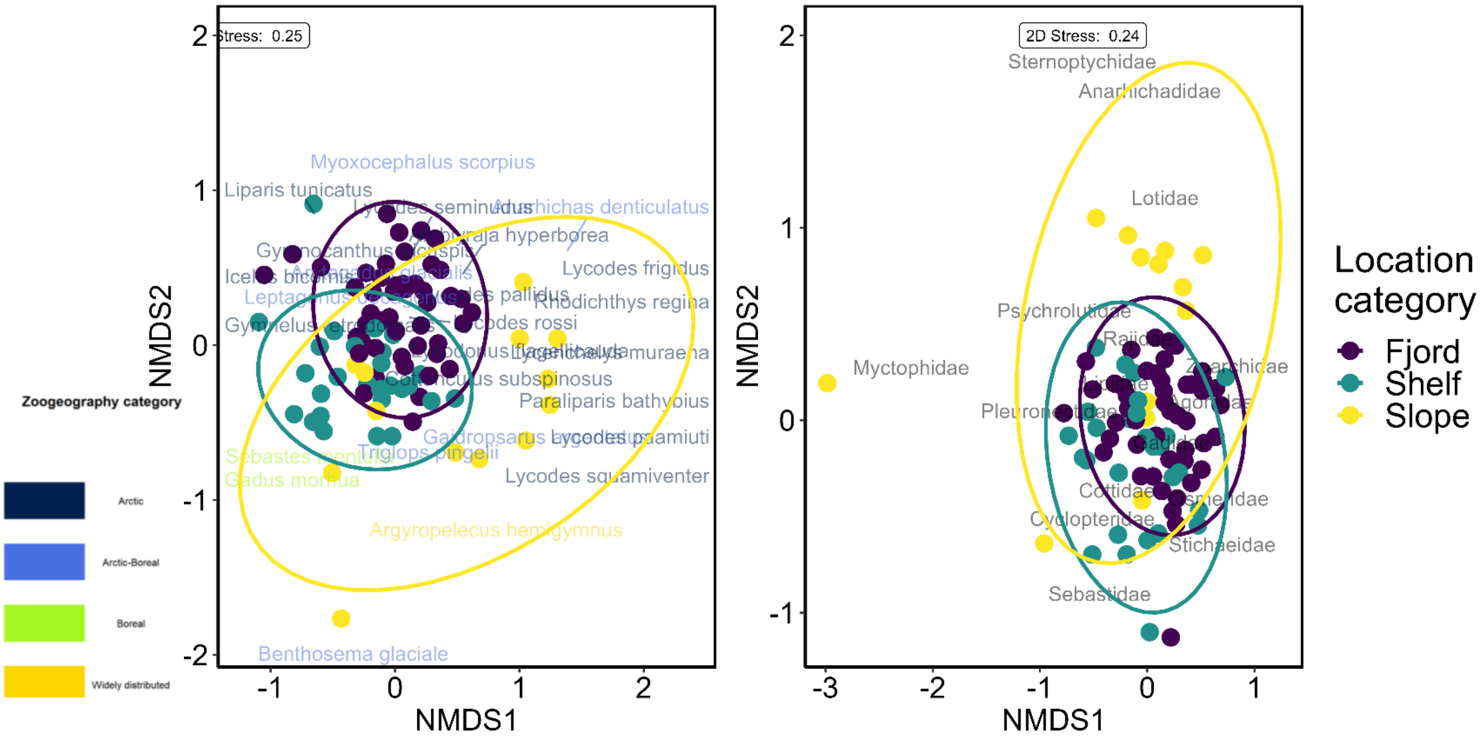
a) b)

Figure 18: *Pie charts of the relative abundance of each species at Offshore Bontekoe Ø. a)2003. b) 2010.*

Additional changes at revisited locations can be found in the appendix: Ardencaple (Figure 4), Davy Sund A (Figure 5), Davy Sund B (Figure 6), Ella Ø East (Figure 7), Godthåb Gulf (Figure 8), Moskusoksefjord (Figure 9), Offshore Hochstetter (Figure 10), Store Belt (Figure 11), and Tyrolerfjord (Figure 12). The overall trend showed that *Boreogadus saida* dominated the relative abundance, followed by *Arctogadus glacialis*, except Tyrolerfjord and Godthåb Gulf, which had an increase of *Arctogadus glacialis.* Most remaining revisited locations also showed an increase in species richness, though there were locations with no change or a small decrease (appendix figures 3 – 12).

3.3 Species and family composition factors

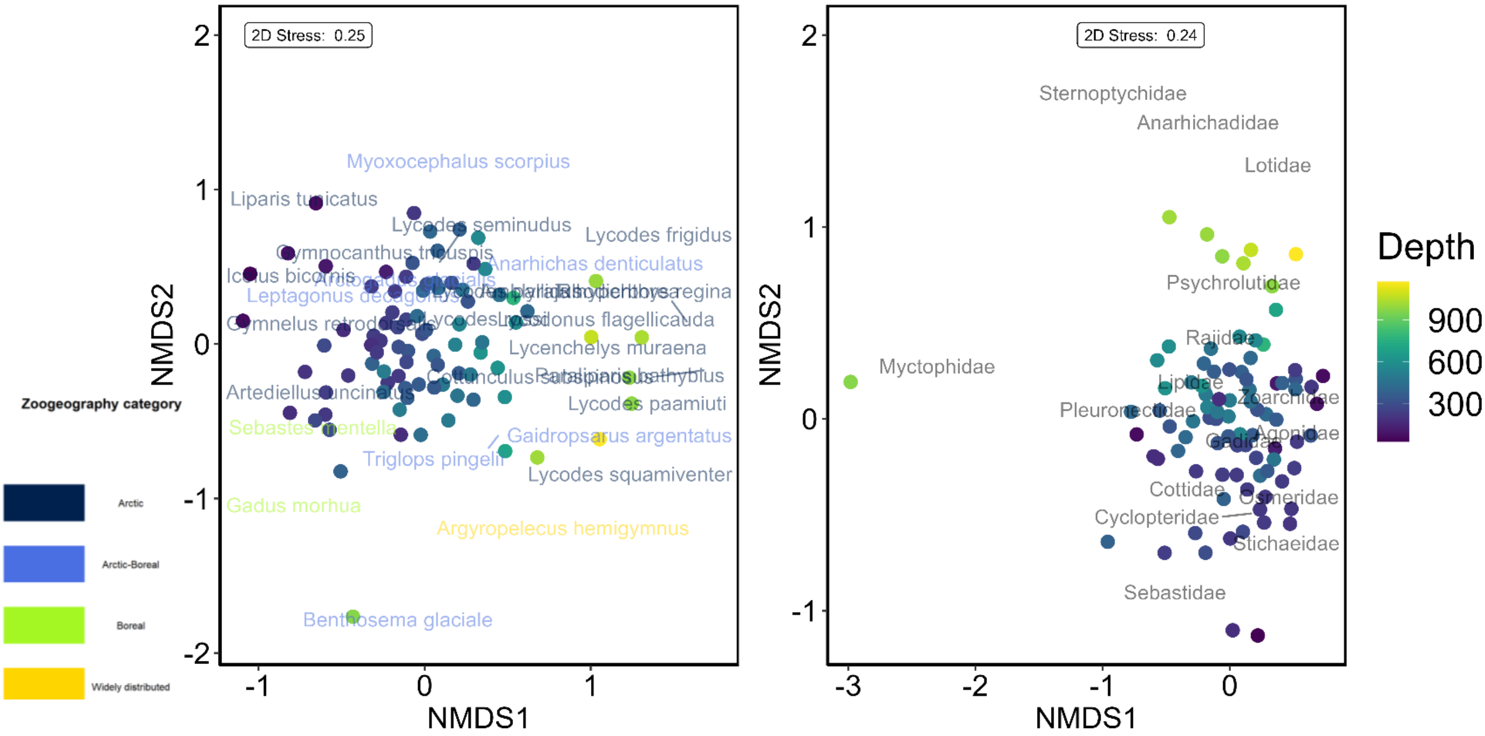
The NMDS plots show the variation in the community composition based on species (Figure 19a) and family (Figure 19b) composition at each sampling station in the study area. There were overlaps where species and family groups could be found in all location categories e.g. Gadidae (Figure 19b), but there were also specific species and family groups that were distinct to a location category e.g. *Paraliparis bathybius* (Figure 19a). Most species in the fjords could be zoogeographically categorized as Arctic or Arctic-Boreal (Figure 19a).



a) b)

Figure 19: *Non-metric multidimensional scaling in three different geographical categorizations distinguished by different colouring: fjord (purple), shelf (teal) and slope (yellow). Each point is a station. Species are coloured into their zoogeographic category. a) Species. b) Family.*

Colour coding the stations based on environmental variables can help us identify which environmental variable(s) might explain the observed variation in community composition. There was a clear pattern in the preferred depth ranges for different species and family groups e.g. *Liparis tunicatus* preferred 300 m or shallower and *Lycodes squamiventer* preferred deeper waters approximately 700 m or deeper. It seems like there was no preferred depth with zoogeography categories (Figure 20a). Depth clearly increased from shallow to deep areas along the NMDS1 axis (Figure 20a). Family categorizations also showed a trend of preferred depths e.g. Osmeridae at approximately 200 – 300 m (Figure 20b).



a) b)

Figure 20: *Non-metric multidimensional scaling with continuous depth scaling.* The zoogeographic classification of each species—Arctic, Arctic-Boreal, Boreal, or Widely distributed—is represented by the colour of the species names. Each point corresponds to a station. *a) Species. b) Family.*

There appears to be a slight pattern that temperature influences species composition by the colouration range following a trend (Figure 21a), but no influence when looking at family groups (Figure 21b).

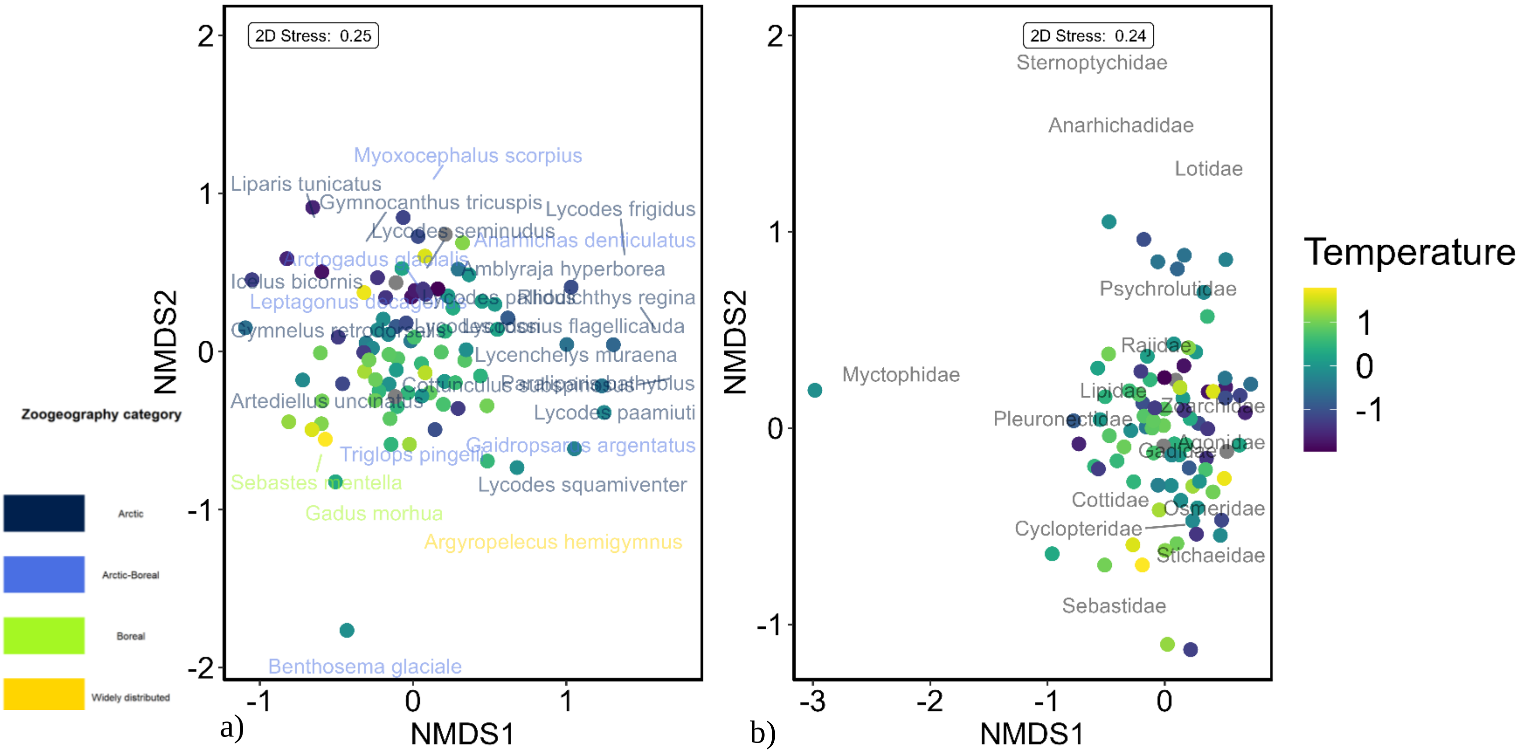


***Figure 21:** Non-metric multidimensional scaling with continuous temperature scaling. The zoogeographic classification of each species—Arctic, Arctic-Boreal, Boreal, or Widely distributed—is indicated by the colour of the species names. Each point represents a station.*
a) Species. b) Family.

There is no clear pattern that the latitude of the sampling station influences species and family group composition (Figure 22).

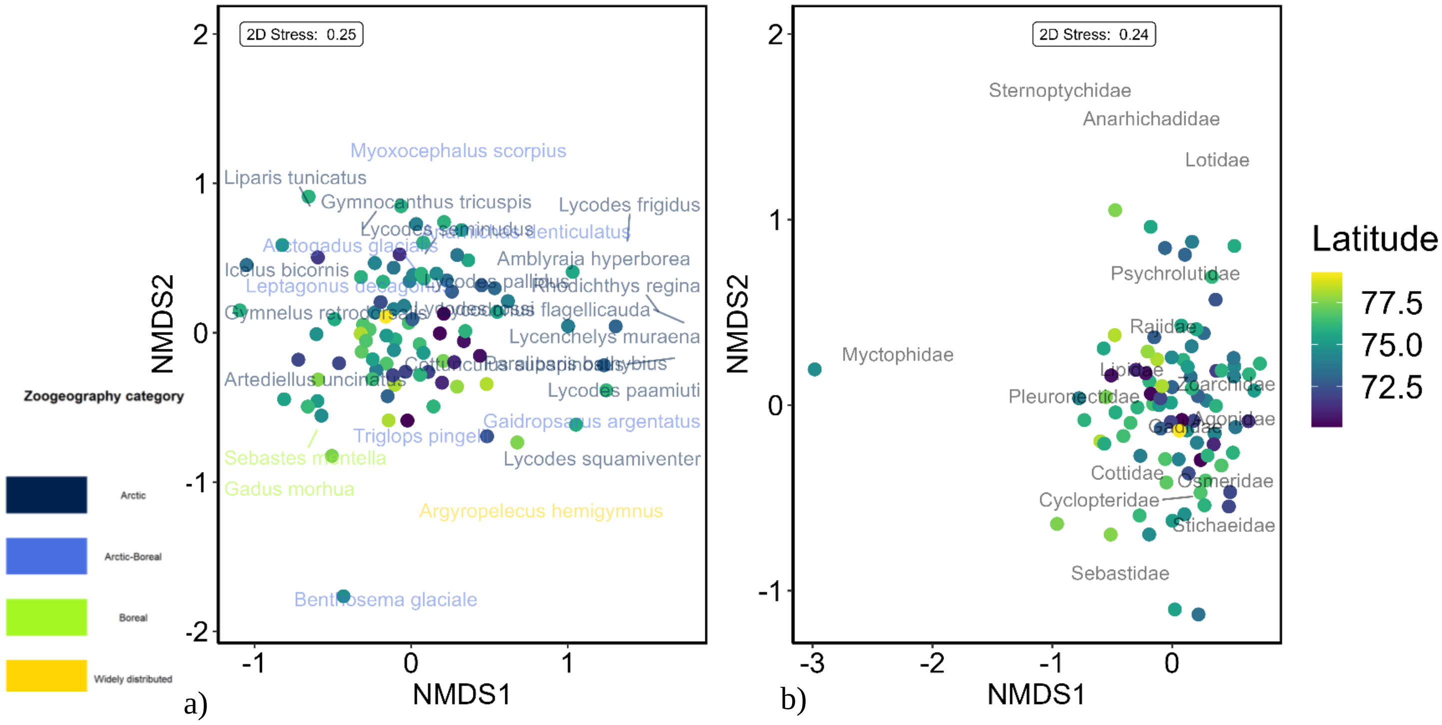
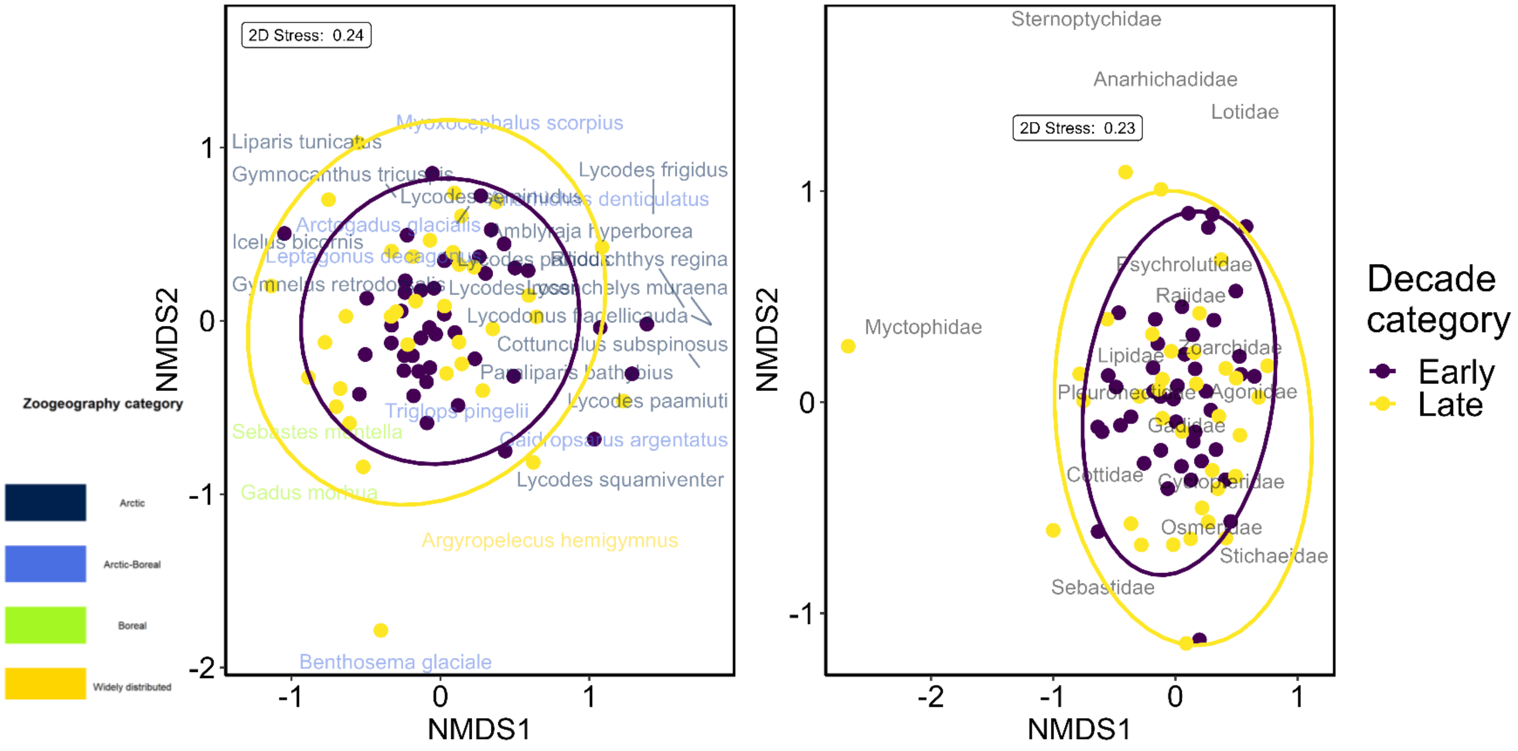


Figure 22: *Non-metric multidimensional scaling with continuous latitude scaling.* The zoogeographic classification of each species—Arctic, Arctic-Boreal, Boreal, or Widely distributed—is represented by the colour of the species names. Each point corresponds to a station. a) *Species. b) Family.*

There seems to be an increase in the observed diversity of community composition between station, for both species and family groups, from the early decade (2002–2010) to the late decade (2013–2022) (larger circle for the late period than the early period, Figure 23).



a) b)

Figure 23: *Non-metric multidimensional scaling of two time periods. The zoogeographic classification of each species—Arctic, Arctic-Boreal, Boreal, or Widely distributed—is indicated by the colour of the species names. Each point represents a station. Stations below 72°N omitted. a) Early decade (2002 – 2010). b) Late decade (2013 – 2022).*

The stress values for all the NMDSes are >0.2 indicating the reliabilities are poor. Regardless of this information, we modelled the variability in NMDS1 and NMDS2 against environmental variables using a linear model. Models were evaluated using AICs for NMDS1 and NMDS2, selecting the best model as the one with the lowest AIC. The best models indicated that temperature, depth and distance-to-coast were indicator variables.

The model testing including all potential explanatory variables of NMDS1 was (Depth + Temp + Latitude + Trawling_min + Coast_distance) and had an AIC value of 19.176 whereas the model with only (Depth + Coast_distance) had a lower AIC value of 16.297. The model testing all NMDS2 parameters (Depth + Temp + Latitude + Trawling_min + Coast_distance) had an AIC value of 62.918 whereas the model with only (Temp + Coast_distance + Depth) had a lower AIC value of 59.920.

4 Discussion

The results from the linear regressions assessing impact of sampling parameters and the effect of omitting station below 72°N “(cut) data” confirmed the reliability of the subsequent analyses.

4.1 Early and late time period changes

There were 28 Arctic-, 14 Arctic-Boreal-, two boreal- and one widely distributed species identified in the study area. General temporal changes in the study area were assessed by looking into family richness, species richness, species diversity, zoogeography category changes, and an NMDS between the early decade (2002 – 2010) and the late decade (2013 – 2022) (Figures 7 – 11 and 23, respectively). All tests led to the conclusion that there is an increase in species richness. These findings correspond to events happening in other parts of the Arctic e.g. a regime shift in Southeast Greenland’s marine ecosystem has recently been observed (Heide-Jørgensen et al., and citations therein, 2022), and whether that could also happen in Northeast Greenland is something which should be studied further. It should be noted that Northeast- and Southeast Greenland are influenced by different waters and currents making them two separate ecosystems, each with their challenges.

4.1.1 Family richness and relative abundance

During Longshan et al.’s, (2014) investigation of the Bering Sea fish community composition, the species sampled were: eight species in Cottidae and Zoarcidae, five species each in the Stichaeidae, Lipiridae, and Pleuronectidae. Similar results were seen in Zhang et al.’s (2022) investigations. The number of species in each family group in this study is similar to the Cottidae and Lipiridae family groups in another study, but different for the remaining family groups. In this study, there are seven Cottidae, 12 Zoarcidae, one Stichaeidae, seven Lipiridae, and two Pleuronectidae.

4.1.2 Species richness

The general species richness increase can be observed when looking at Figure 9, which shows an increase between the early- and late decades. The specific species richness changes can be seen when analysing the temporal changes at revisited locations (Figures 12 – 18) where most locations show a species richness increase. There are also revisited locations, which indicate a species decline or species composition change. These are mostly fjord stations e.g. Bessel fjord A, and Bredefjord (Figures 14 and 16, respectively). Increases in total biomass and species richness have also been observed in the Bering Sea (Mueter & Litzow, 2008). In a study of East Greenland (Emblemsvåg et al., 2020), south of my study area, species richness and total abundance decreased while an increase of bottom temperature increased in the deep sea. The decrease in species richness at some revisited locations could be due to certain species evading capture because of their agility. Observations of certain species are important because they do not move or migrate as easily. Zoarcidae, Cottidae, Liparidae and Stichaeidae are considered non-migratory demersal fish. *Liparis fabricii, Gymnocanthus tricuspis* and *Leptoclinus maculatus* have planktonic larvae, but most Arctic fish species lay few demersal eggs and often exhibit parental care (Christiansen, and citations therein, 2017).

4.1.3 Species diversity

It seems there is a higher species diversity along the slopes followed by shelf and then fjord locations. The highest species richness, hence, diversity, in Southeast Greenland, also found the highest species diversity off the shelf break (Emblemsvåg et al., 2022). It should be noted that species diversity may be influenced by metrics that account for species evenness. When looking at the relative abundance of species in the revisited locations it is noticeable that most locations are dominated largely by *Boreogadus saida*. The species diversity has increased regardless of being influenced by evenness or not. Similar results in a study between the Bering Sea and the Chukchi Sea concluded that the diversity (using the Shannon diversity index as in this study) and species richness is higher in the Bering Sea than in the Chukchi Sea. A trend of high species diversity in the south and low species diversity in the north (Longshan et al., 2014), which is a trend different from my findings where geographical categorization influenced the species diversity and there not being a concrete trend with latitude. This result is also confirmed by the NMDS where latitude was a factor (Figure 22).

4.1.4 Borealization

Whether the decrease in the relative abundance of Arctic species between the early- and late decade is due to an introduction of more Arctic-Boreal species or the increase of the relative abundance of the Arctic-Boreal species cannot be concluded by the pie chart (Figure 11) alone. However, the increases in both species- and family richness (Figure 23) could support an increase in Arctic-Boreal species. It could be assumed an increase in the relative abundance of

Arctic-Boreal species could be due to the temperature rise seen in many locations between the early and late decades, which could be favourable for the Arctic-Boreal species. The abundance of Arctic-boreal species in the Bering Sea was correlated to bottom temperature while Arctic species were not (Mueter & Litzow, 2008). Jan Mayen Island, like Northeast Greenland, is a relatively understudied area. In a study by Wienerroither et al. (2011), species presence was documented primarily through literature sources. Observations also noted an increase and spread of new species in the area, suggesting a possible borealization effect. Fish species have increased in Svalbard, including observations of mackerel, a boreal species, which may indicate an effect of borealization (Berge et al., 2015). Svalbard, like Northeast Greenland, is influenced by the WSC, suggesting that changes observed there may foreshadow future changes in Northeast Greenland. A decline of ice-dependent and cold-tolerant (Arctic) species has occurred in Southeast Greenland where the abundance of *Boreogadus saida* has decreased as temperatures have risen (Heide-Jørgensen et al., and references therein 2022,). In the Barents Sea, the stock of *Boreogadus saida* increased, possibly due to better conditions for growth and survival, likely related to higher temperatures and still within their optimal range (Hop & Gjøsæter, 2013). Another study observed the arrival of new species from warmer regions in Southeast Greenland, where they were previously absent (Heide-Jørgensen et al., and references therein 2022). This study documented a new zoogeographic category (Widely distributed), suggesting potential range expansions for southern species. These findings may indicate similar shifts are underway in Northeast Greenland.

The juvenile boreal species (*Gadus morhua, Sebastes norvegicus,* and *Mallotus villosus*) obtained within my data set have in another study been genetically tested to investigate their origin. The findings were that most of the fish were related to the population from the Barents Sea while 5% of the redfish were assigned to the Icelandic population. The specimens are thought to have travelled with the WSC to cross the Fram Strait and then travel downwards with the RAC. An estimation of up to 50% of the WSC is believed to connect to the RAC. It is hypothesized that further borealization will occur from the Barents Sea (Andrews et al., 2019). The 5% could have travelled with the Northeast Greenland Coastal Counter Current. Borealization is happening in most areas in the Arctic. Warming water is likely the source of distribution changes in the Bering Sea (Mueter & Litzow, 2008). Fish species in the North Sea have shown climate-related latitudinal changes as well as a shift in depth (Perry et al., 2005;

Dulvy et al, 2008). Narayanaswamy et. al (2010) found that 200 species have extended their northerly limits to being in Norwegian waters. In the Finmark region, an increase of 17% in species has been recorded since then. Wiedmann et. al (2014) in their study of the Barens Sea found that the Arctic species *Liparis fabricii* had to cope with the increased presence of boreal species including *Gadus morhua*. This trend suggests that similar changes may occur in Northeast Greenland in the future.

4.2 Regional divergence changes

The borealization trends in the area are primarily occurring on the continental shelf, referred to as the "shelf" in this study. However, other areas exhibit different changes in this study e.g. fjords. Many revisited locations are experiencing a decrease in temperature rather than an increase, and some areas are showing a decline in species richness rather than an expansion.

4.2.1 Fjords

Most fjords showcased a constant species richness or a slight species richness decline. The relative abundance of *Boreogadus saida* increased in most areas, and if not a relative abundance increase of *Boreogadus saida*, it was a relative abundance increase of *Arctogadus glacialis*. The occurrence of *Arctogadus glacialis* is always accompanied by *Boreogadus saida*, but not the other way around. This could be due to *Arctogadus glacialis* being confined to fjords and shelf areas, and absent from deeper waters. The two sympatric Arctic cods do not share feeding habits. *Arctogadus glacialis* is linked with the benthic and *Boreogadus saida* is linked with the pelagic food web (Christiansen et al., and citations therein, 2012; Renaud et al., 2012). The fjord locations that did not decrease or stayed constant are fjords that could potentially be classified as shelf locations e.g. Dove bugt (Figure 13), which technically is a bay, and Ardencaple fjord (Appendix, Figure 4), which is at the entrance of a fjord. When comparing Ardencaple fjord to a revisited location further in the fjord system, Bredefjord (Figure 16), the composition of species differs. There is a depth difference between the two locations, which could be a factor in their differences as well. But it could also be an indicator that one location could be identified as a shelf community and the other location as a true fjord environment. It could also be that the two locations are influenced by different waters as seen in the Ilulissat Icefjord system, the distribution of *Mallotus villosus* and *Boreogadus saida* seem to follow separate water types where *Mallotus villosus* is linked to Atlantic water (Schiøtt et al., 2023).

4.2.2 Shelf

The shelf changes can be concluded to have already been discussed in the borealization section. The indication of borealization has mostly been seen in the shelf, which could be due to the WSC being circulated to the shelf rather than any of the other geographical locations.

4.2.3 Slope

Like the trends observed on the shelf, the revisited slope locations are also showing an increase in species richness accompanied by a decrease in temperature. These changes may be due to species shifting from shallower waters to deeper, cooler areas that now align more closely with their preferred temperature range. In another study an increase in boreal traits has been observed in the deep sea (300–900 m) of Southeast Greenland, likely driven by warming-related changes in habitat characteristics and food availability (Emblemsvåg et al., 2022). In the Barents Sea, an Atlantic deep sub-community did not show a geographical shift but remained in the deeper basin. The Arctic community, found in cold areas, retracted to the northernmost regions conducted in their study area (Fossheim et. al., 2015).

4.3 Composition factors

Temperature and depth were found to be influential factors, as revealed by the NMDS analysis. The AIC analysis supported these findings and additionally identified distance to the coast as a significant factor. Temperature and depth as community structuring factors were also identified in the study by Jørgensen et al. (2015), which examined community assemblages in Southeast Greenland. This study found that temperature influenced fish distribution between the colder Iceland Sea and the warmer Irminger Sea, while within each area, depth was the primary factor determining fish distribution patterns.

4.4 Ecological influences

Changes in fish species composition can impact dependent species, potentially leading to shifts in the entire ecosystem. In a similar study, Yurkowski et al. (2018) found that an increase in *Mallotus villosus* and a decrease in *Boreogadus saida* in Cumberland Sound affected the diets of predators like belugas and ringed seals. Comparable effects could potentially occur in Northeast Greenland.

4.5 Limitations

Data collection has been limited to a single season, which may influence the distribution of some species. Unfortunately, the available data is insufficient to account for this limitation. This issue is commonly encountered across the pan-Arctic region (Wassmann et al., 2011).

4.6 Future research

Understanding the dynamics of an area is crucial before effective management can take place, as recognizing changes requires data to illustrate those shifts. This knowledge is vital for future management, as ecological transitions could have significant economic implications, particularly if new, productive fisheries are established in the area. Hence, continued research is advised.

5 Conclusion

In conclusion, the overall temperature observations reveal an increase on the continental shelf, while the fjords and slope exhibit temperature declines. This pattern suggests that the rise in species richness on the shelf may be attributed to borealization, and the species richness on the slopes due to species shifting to deeper, cooler waters. In contrast, the fjords appear to be impeded from undergoing Atlantification and borealization, likely due to sills that restrict the influx of Atlantic water into the fjord system. The increase in the relative abundance of *Boreogadus saida* in most locations, as well as *Arctogadus glacialis*, may be attributed to optimal temperatures that support their growth and survival.

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Appendix

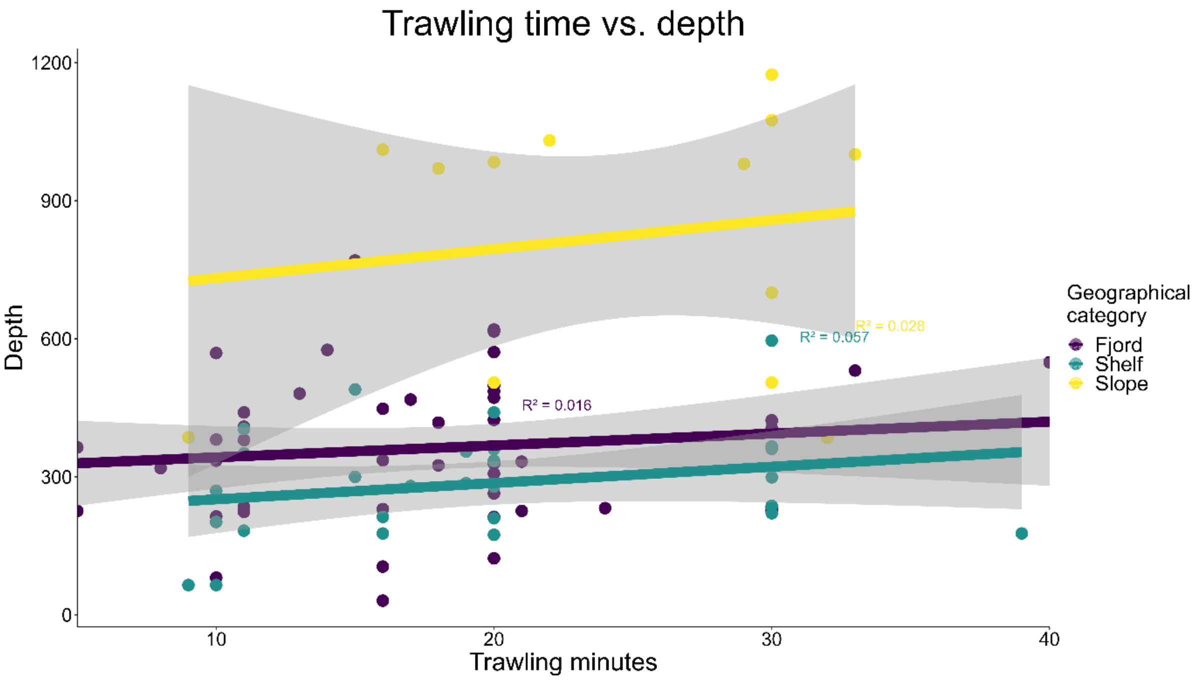
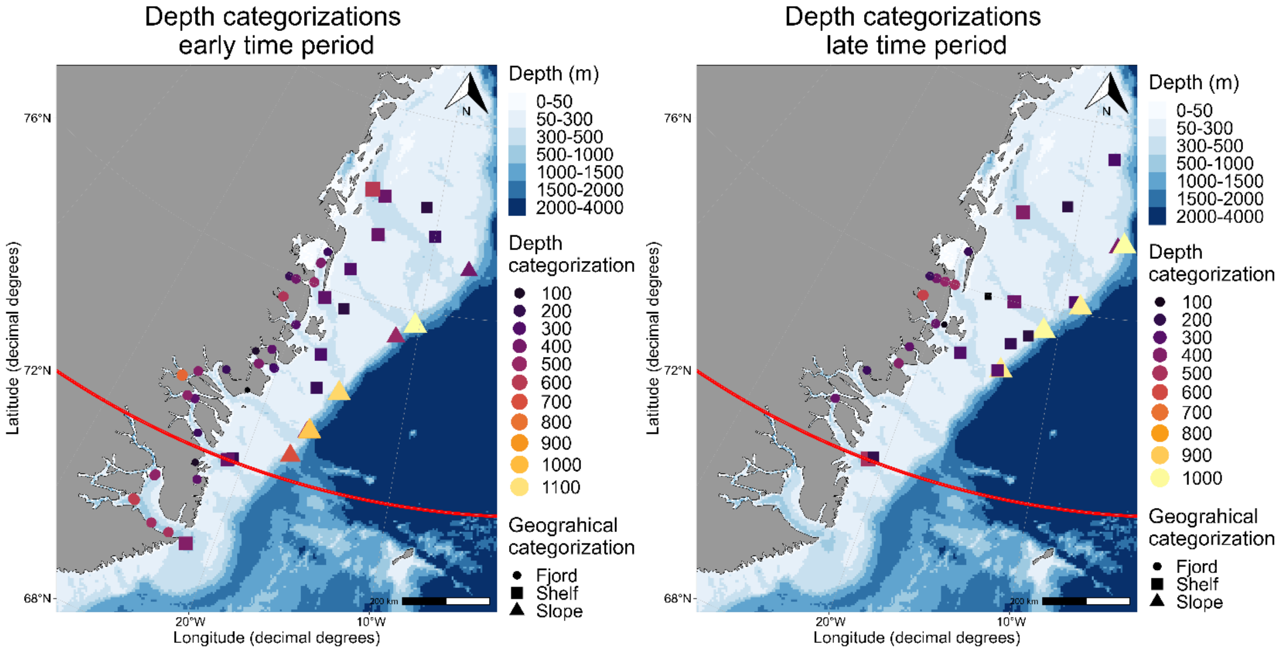
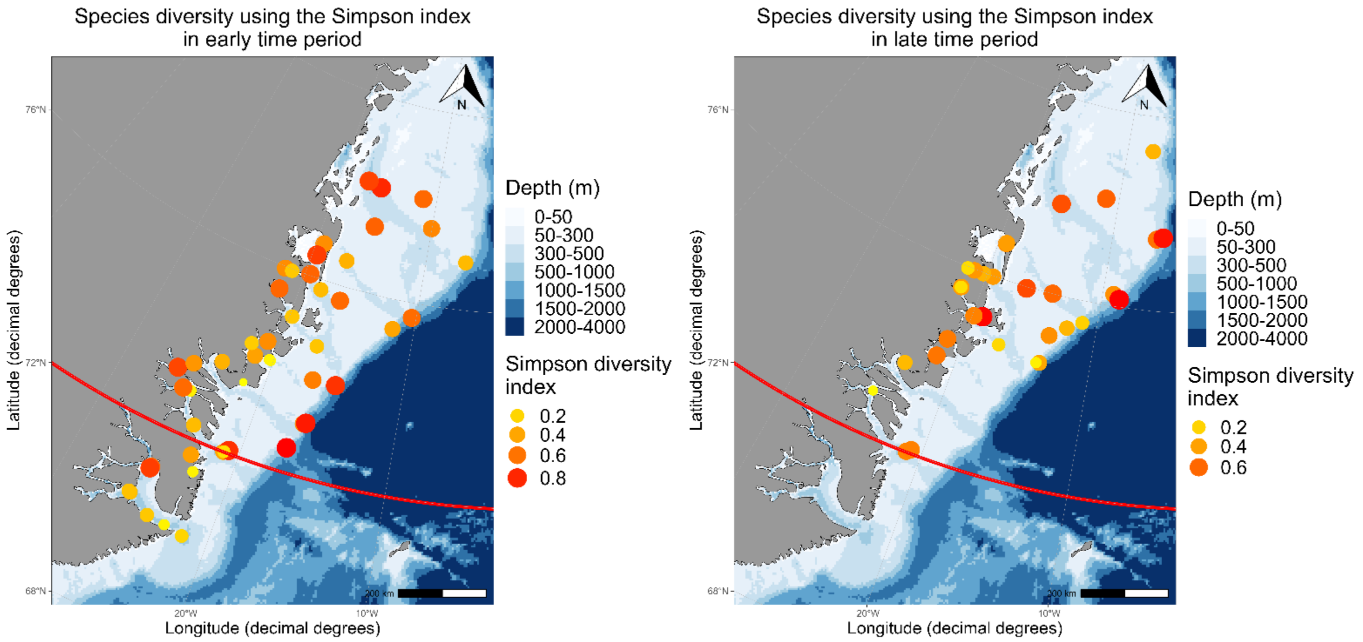


Figure 1: *Depth over trawling time in different geographical categorizations: fjord, shelf and slope. R^2 values and trendlines for each geographical categorization are shown.*



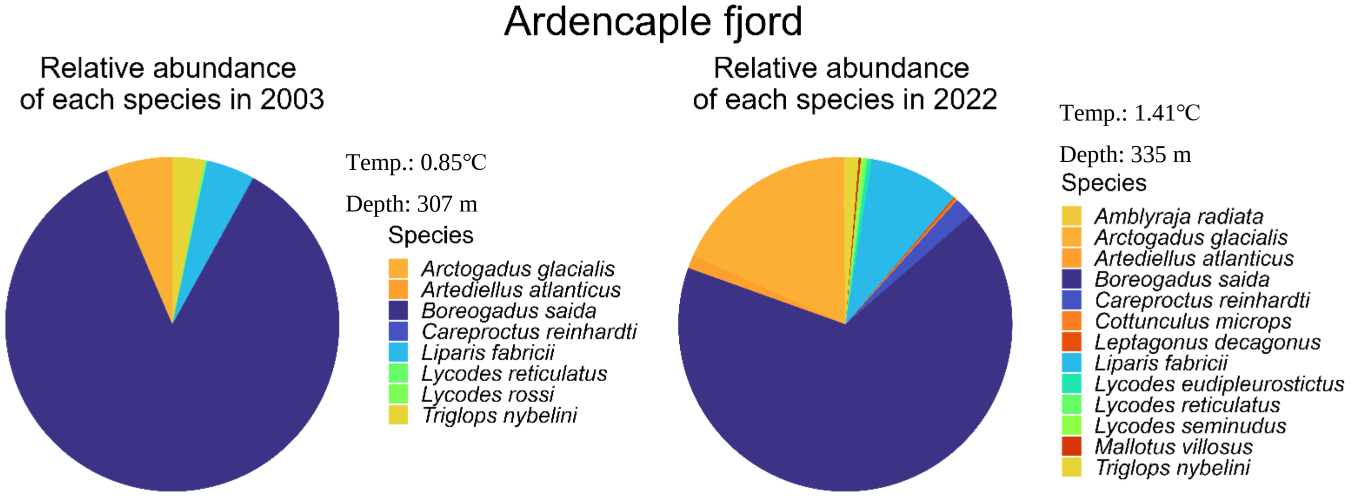
a) b)

***Figure 2**: Depth categorization in different geographical categorizations in early and late decades. Size and colour indicate the closest hundred-meter depth categorization and different shapes indicate geographical categorization. The red line at 72°N indicates stations omitted when comparing temporal data. a) Early decade, 2002 – 2010 b) Late decade, 2013 – 2022.*



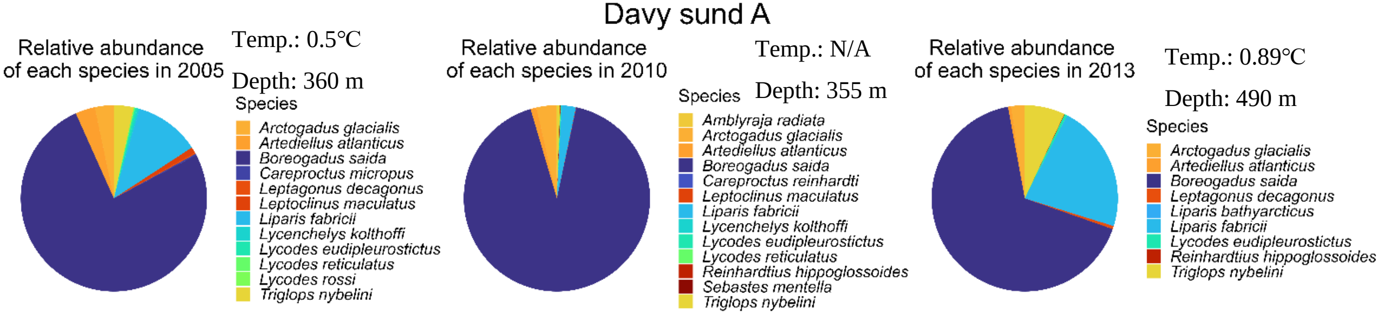
a) b)

Figure 3*: Simpson diversity indices on different stations. The red line at 72°N indicates stations omitted when comparing temporal data. a) Early decade stations 2002 – 2010. b) Late-decade stations 2013 – 2022.*



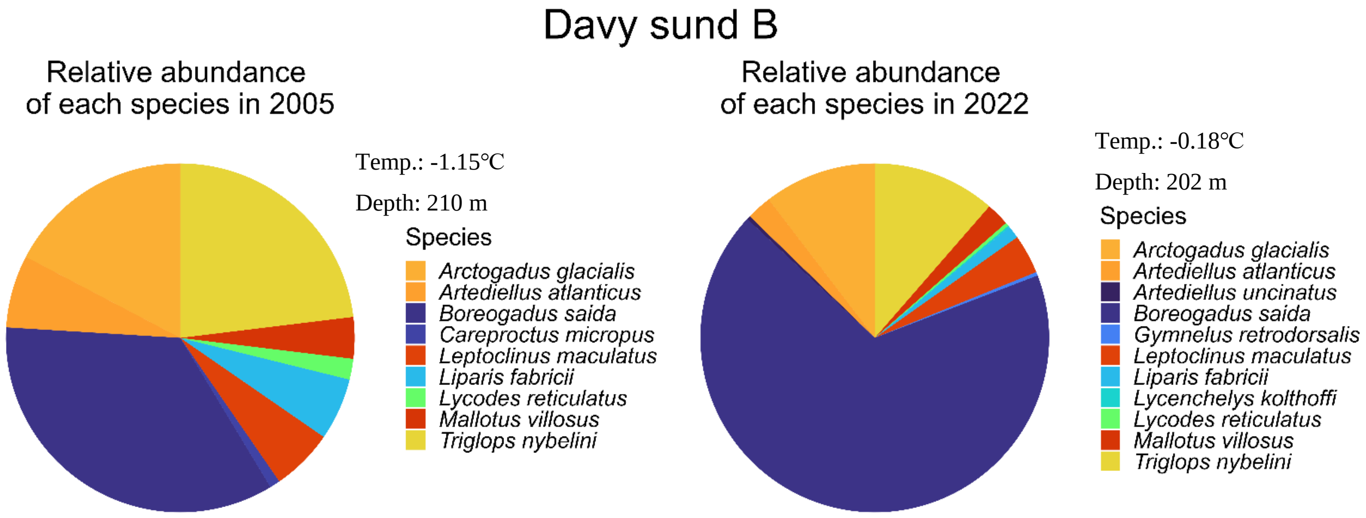
a) b)

Figure 4: *Pie charts the relative abundance of each species at Ardencaple fjord. a) 2003. b)2022.*



a) b) c)

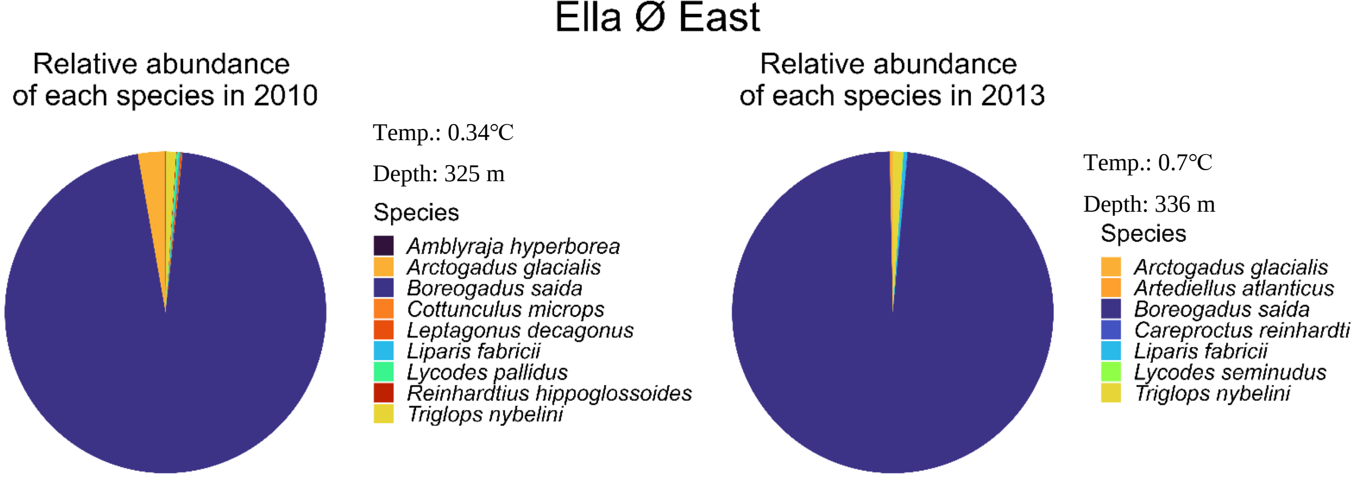
Figure 5*: Pie charts the relative abundance of each species at Davy Sund A. a) 2005. b) 2010. c) 2013.*



a)

b)

Figure 6: *Pie charts the relative abundance of each species Davy Sund B. a) 2005. b) 2022.*



a)

b)

Figure 7: *Pie charts the relative abundance of each species at Ella Ø East. a) 2010. b) 2013.*

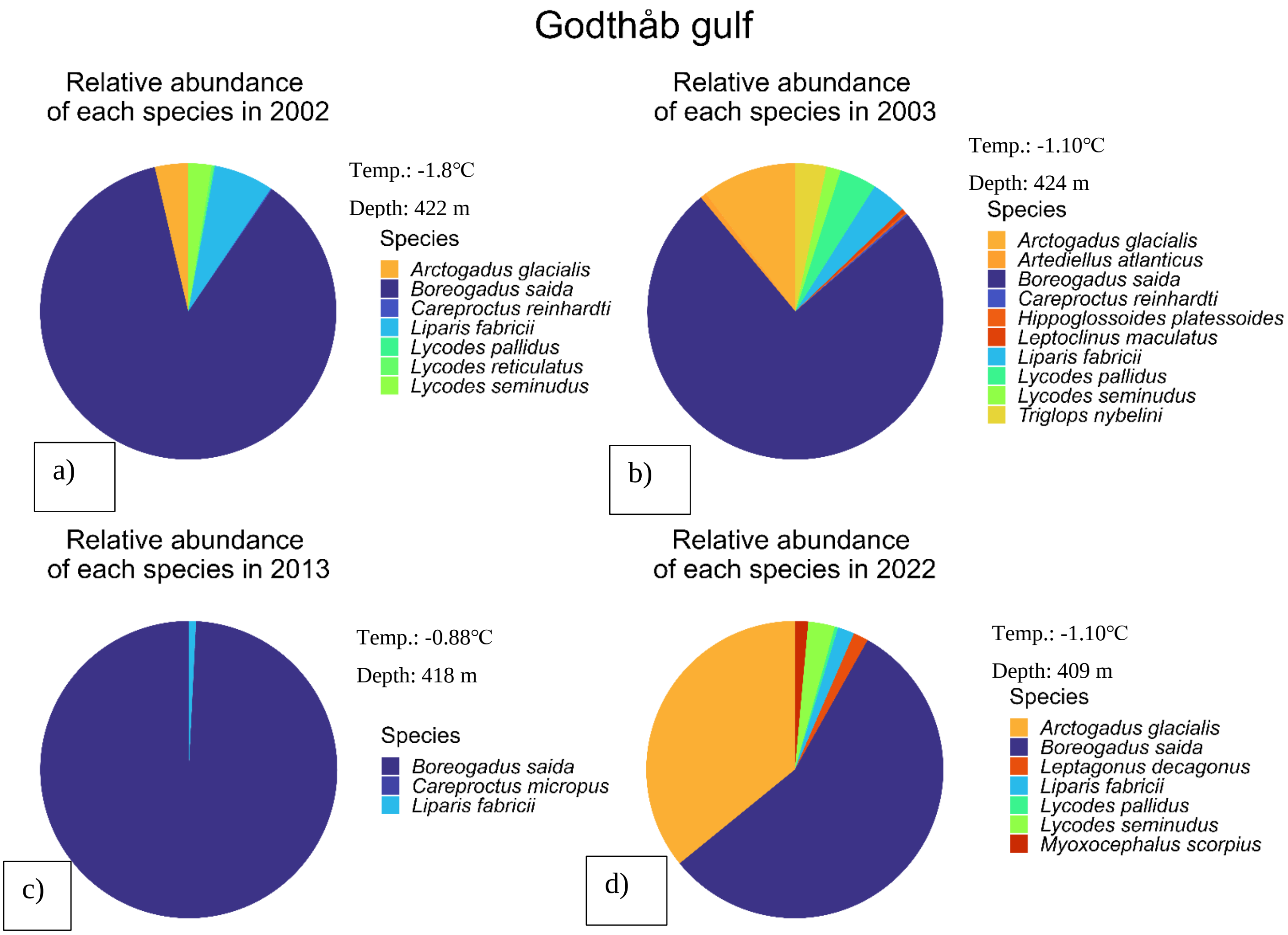


Figure 8: *Pie charts the relative abundance of each species at Godthåb Gulf. a) 2002. b)2003. c) 2013. d) 2022.*

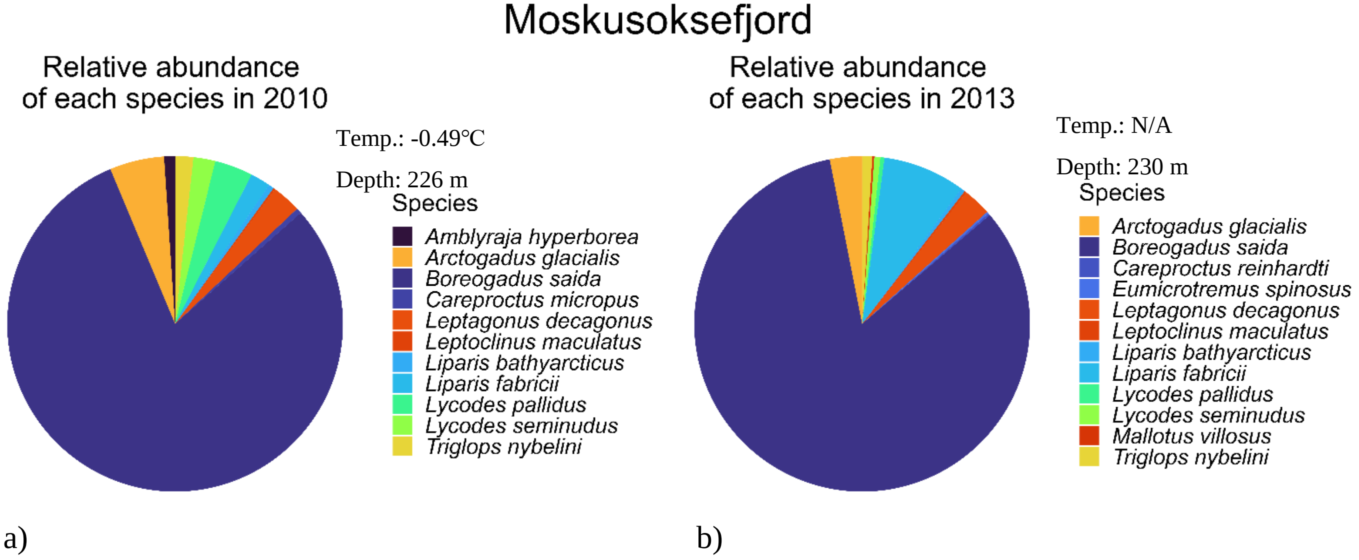
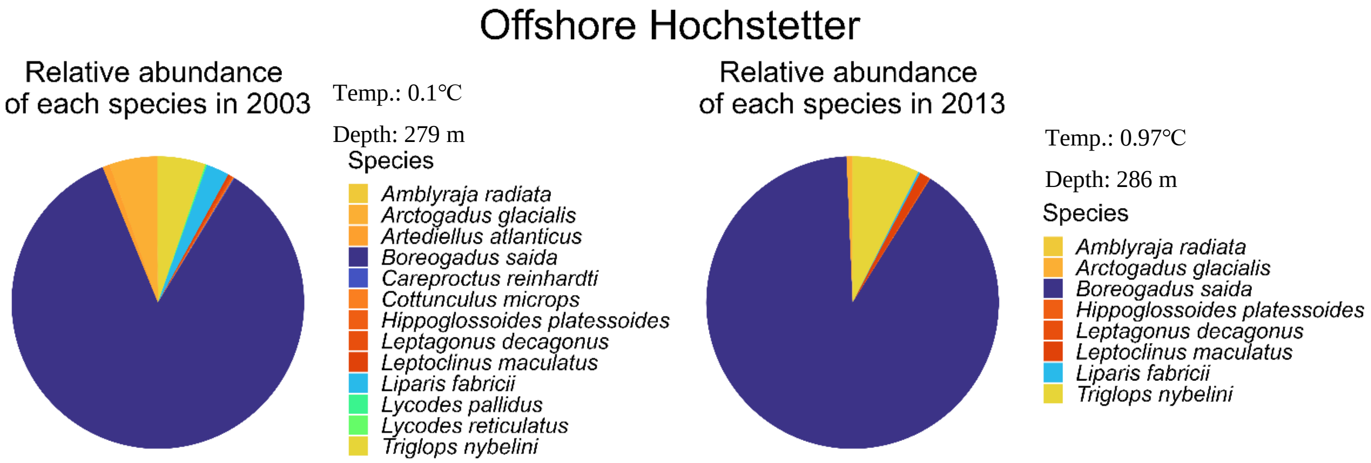
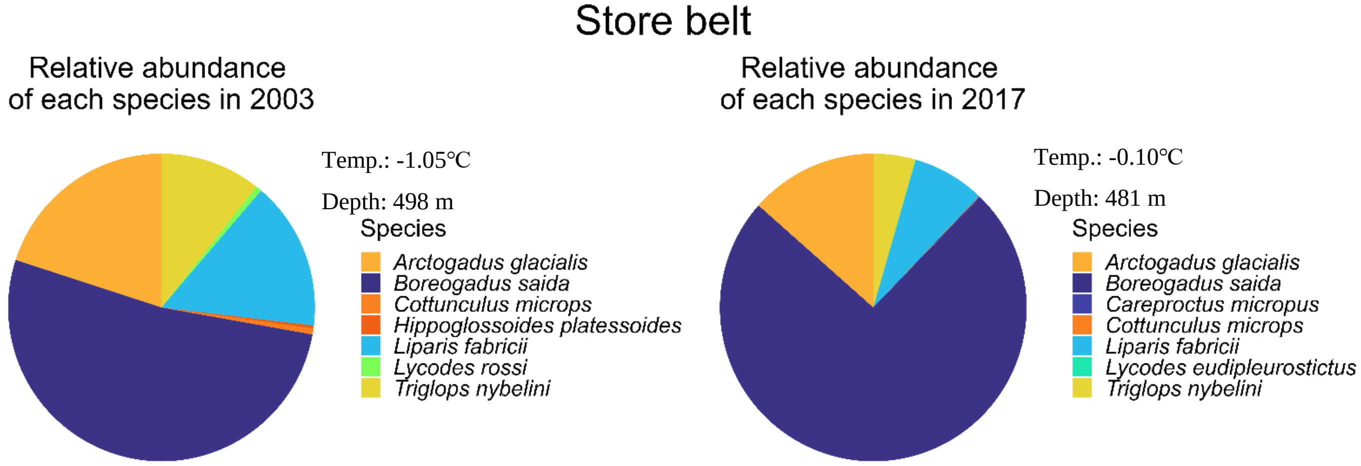


Figure 9: *Pie charts the relative abundance of each species at Moskusoksefjord. a) 2010. b) 2013.*



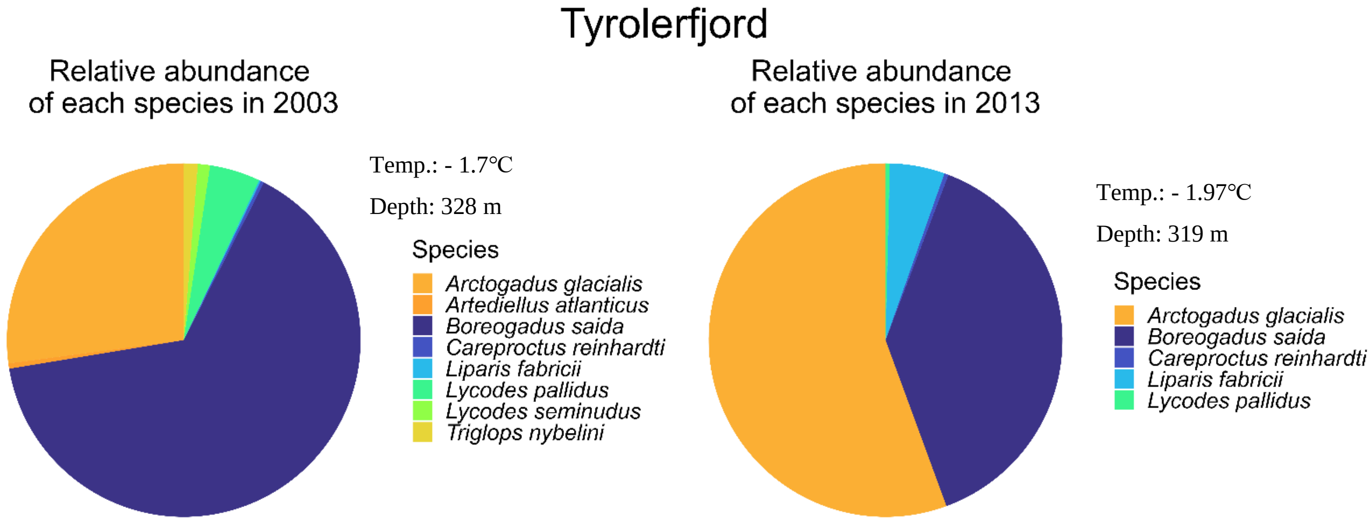
a) b)

Figure 10: *Pie charts the relative abundance of each species at Offshore Hochstetter. a) 2003. b) 2013.*



a) b)

Figure 11: *Pie charts the relative abundance of each species at Store belt. a) 2003. b) 2017.*



a) b)

Figure 12: *Pie charts the relative abundance of each species at Tyrolerfjord. a) 2003. b) 2013.*

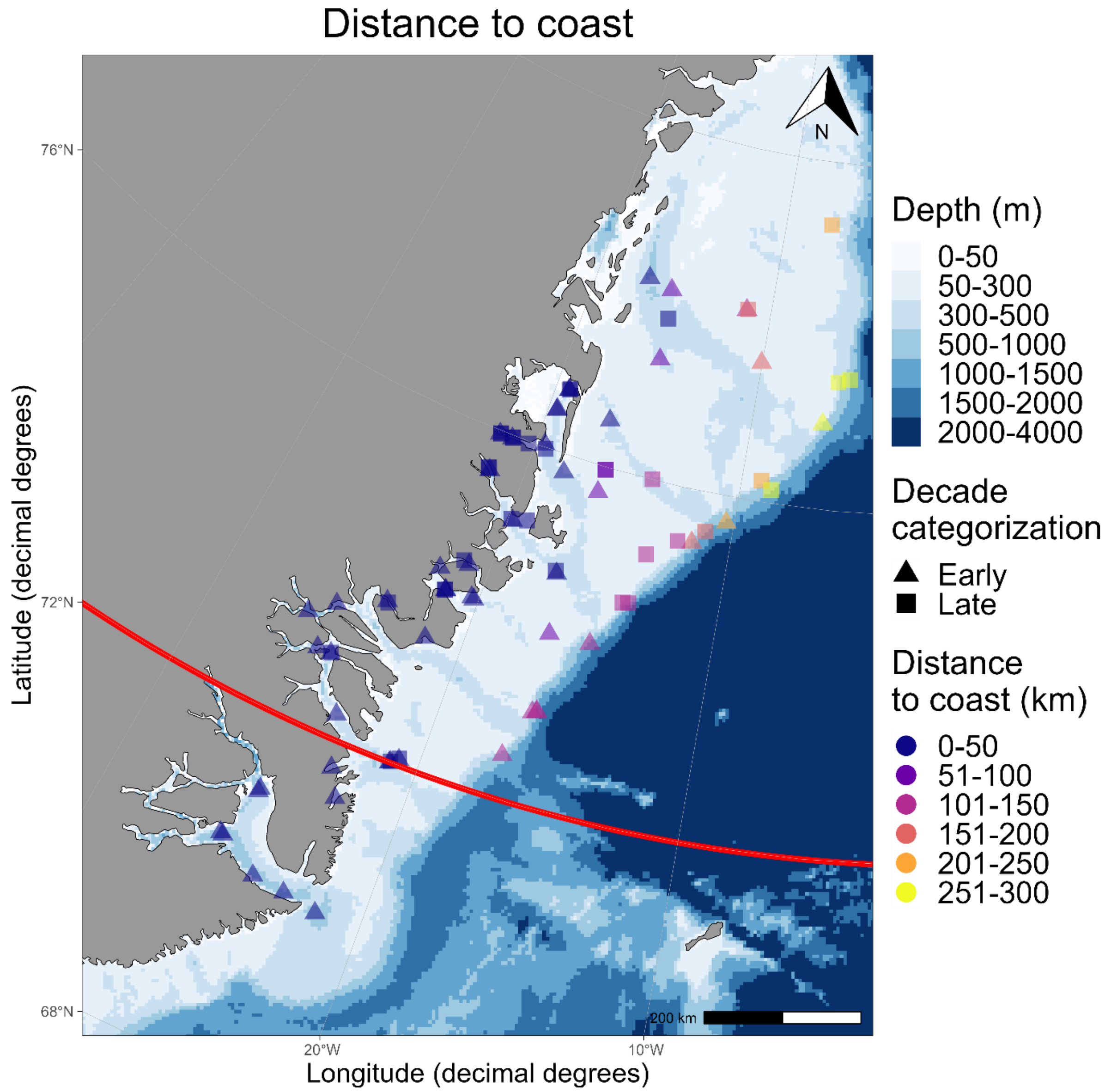


Figure 13: *Distance to coast categorization with 50 km intervals in different colours. Shape indicates whether the station belongs to an early (2002 – 2010) or late (2013 – 2022) decade categorization. The red line at 72°N indicates stations omitted when comparing temporal data.*