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## **The Demersal Fish Community on the West Spitsbergen Shelf**

Biodiversity, species composition, distribution and temporal changes in relation to climate

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Master's thesis in Biology, BIO-3950, May 2020



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# Acknowledgements

First and foremost, I would like to thank my supervisors for support and constructive feedback throughout this process. A special thanks to André for always being available to answer questions, arranging weekly meetings, and following up on my work and progress while guiding me in the right direction. I would also like to thank Sigrid Lind, for providing temperature data as well as essential inspiration and input on the final study design.

Additionally, I would like to show my gratitude to the Institute of Marine Research, for providing the data, and together with NIFA, for spending time and effort in collecting this insightful time series enabling me to conduct this exciting study 30 years later. Also, for allowing me to join the Barents Sea Ecosystem Survey around Svalbard, giving me insightful knowledge about the data collecting process, as well as experience and memories for a lifetime.

Finally, to my fellow students at UiT and UNIS, a big thanks for the inspiration, moral support, and for making these two years unforgettable. A special thanks to Vegard, for always helping me out whatever the problem might have been, motivational or R-studio related, and for lending me the rights to his beautiful picture on the front page.



## Abstract

The Arctic is warming faster than the global average, and increasing ocean temperatures, decreasing ice cover, and alterations of the oceanographic conditions are setting the stage for extensive distribution shifts in Arctic marine fish communities. The Barents Sea is the largest and deepest shelf sea in the Arctic and one of the best monitored regions there. Its fish community is dominated by Arctic and boreal species, geographically separated by the polar front; the area where warm and saline Atlantic Water meets the cold and fresh Arctic Water. Similar hydrographical features characterize the west coast of the Svalbard archipelago, situated on the north-western edge of the Barents Sea. Whereas cold and relatively fresh Arctic water circulates from the east entering the Svalbard fjord systems creating Arctic conditions on the continental shelf, the continental slope is influenced by a branch of the warm and saline North Atlantic Current (NAC) flowing from the south, thus creating a more boreal environment in the deeper areas offshore. Additionally, the temperature and volume flux of the NAC is affected by decadal fluctuations of the North Atlantic Oscillation index, resulting in periods of cold and warm climate regimes. This study explores a historical time series of trawl stations from 1980 to 2007, aiming to understand the spatial and temporal variability of the demersal fish communities on the West Spitsbergen Shelf (WSS). Abundance data of 42 fish species are used to investigate the species composition, richness, and diversity across three different subregions, from 74°N (near Bjørnøya) to 78°N (near Isfjorden). Based on bathymetry and oceanography, each subregion is further split into two areas characterized as under Arctic or Atlantic influence. The results indicate a separation in the fish community between Arctic and Atlantic on the WSS. This Arctic-Atlantic separation is most evident in the first decade of the survey but seems to be weakening towards the end of the studied period. Additionally, the fish species composition on the shelf appears to be affected by the decadal variability of the NAC, converging towards a more similar composition during warm periods and diverging during colder periods. Although species richness and diversity show sharp interannual fluctuations throughout the time series, an increase in diversity was detected in one of the Arctic areas. In contrast, its Atlantic counterpart showed the opposite trend. These results might indicate that the fishes on the continental slope are moving further in on the shelf, adding richness and diversity to these areas while changing the species composition towards a more Atlantic community.

**Keywords** Arctic, demersal fish community, distribution shift, polar front, West Spitsbergen Shelf, North Atlantic Current, time series analysis, species diversity, species composition, climate variability



## List of abbreviations

ACF – Autocorrelation function

ArW – Arctic Water

AtW – Atlantic Water

COG – Centre of Gravity

ESC – East Spitsbergen Current

NAC – North Atlantic Current

NAO – North Atlantic Oscillation

SCC – South Cape Current

nMDS – Nonmetric Multidimensional scaling

WSC – West Spitsbergen Current

WSS – West Spitsbergen Shelf



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# 1 Introduction

The effects of climate change are accelerating in the Arctic ocean and its surrounding seas (ACIA 2005; Meredith et al. 2019). With increasing surface temperatures (Steele et al. 2008), changing atmospheric circulation and hydrographical conditions (Zhang et al. 2008; Lind et al. 2018), and a rapidly retreating and thinning summer sea ice cover (Kwok and Rothrock 2009), the Arctic marine ecosystems are experiencing a progressively changing environment. These oceanic climate alterations reverberate up the marine food web, resulting in changes on all trophic levels, from phytoplankton to sea birds and polar bears (e.g., CAFF 2013; Kortsch et al. 2015).

The Barents Sea region is the largest and deepest shelf sea in the Arctic and, together with the Fram Strait, serves as the most extensive gateway for both heat and boreal species to the central Arctic Ocean (Spielhagen et al. 2011; Pfirman et al. 2013). It is a highly productive ocean, characterized by seasonal ice cover and dominated by two distinct water masses: Atlantic Water (AtW) and Arctic Water (ArW) (Figure 1) (Loeng 1991). The former is typically identified with temperature  $> 3^{\circ}\text{C}$  and salinity usually  $> 35$ , and the latter, which is both colder and fresher, identified with temperature  $< 0^{\circ}\text{C}$ , and salinity usually between 34.3 – 34.8 (Loeng 1991). The area where AtW and ArW meet, the polar front, is a region with seasonally intense phytoplankton blooms and a resulting hotspot for production in the Barents Sea (Sakshaug and Slagstad 1992; Wassmann et al. 1999). This transition zone has been an exciting study area for climate research, oceanography, and marine ecology. Additionally, the Barents Sea serves as a nursery for the world's largest population of Atlantic cod (Kjesbu et al. 2014), as well as several other commercially important species, resulting in a thorough monitoring and surveying of both environmental and biological conditions. As a result, significant changes in the ecosystems and species' range shifts have been detected, many of which directly or indirectly related to the increasing sea temperatures and decreasing ice cover (e.g., Aschan et al. 2009; Fossheim et al. 2015; Kortsch et al. 2015).

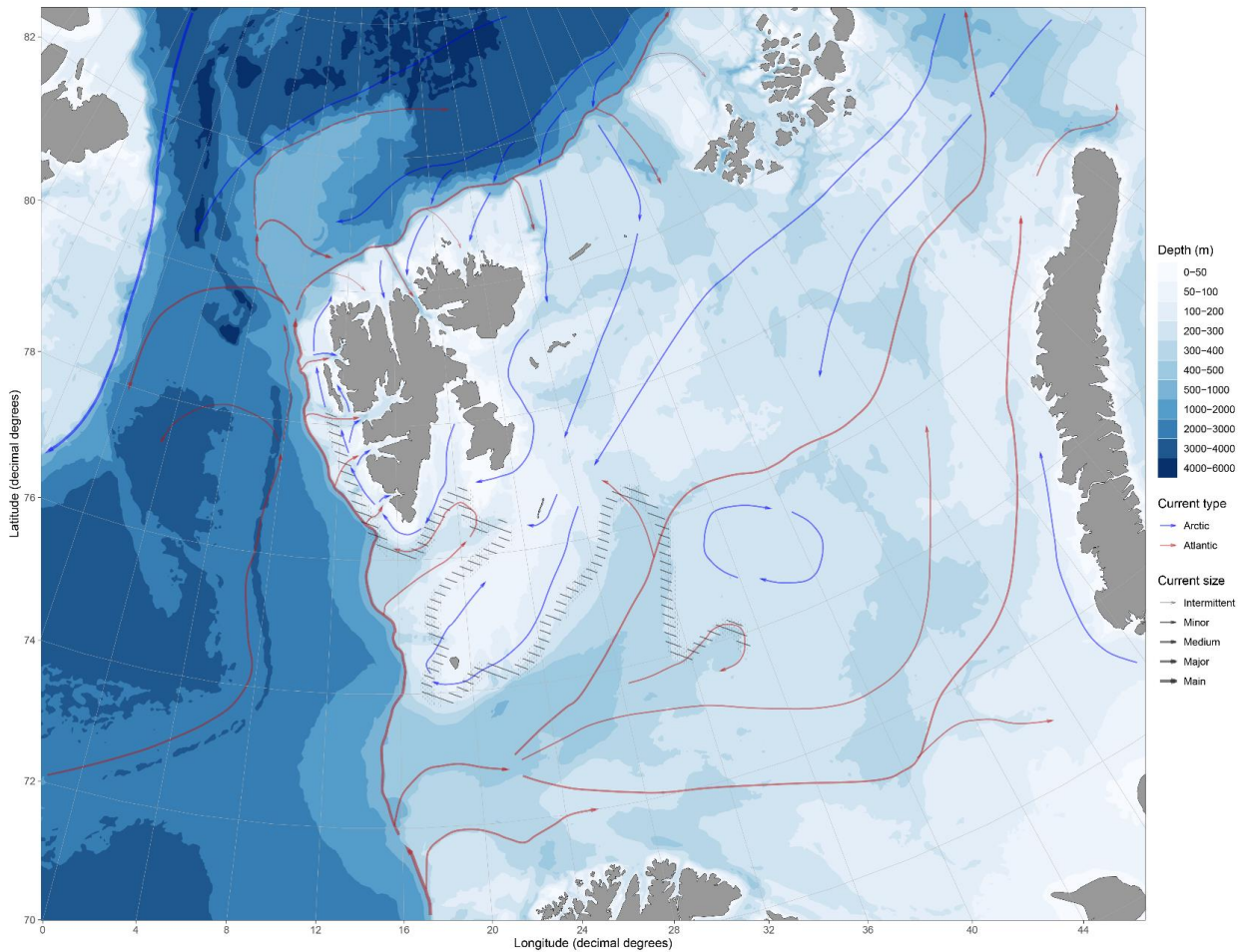


Figure 1: Overview map of the Barents Sea, with bathymetry and ocean currents. Position of polar front indicated by dashed line, adapted from Loeng (1991).

In addition to increasing temperatures due to climate change, the Barents Sea is characterized by natural climatic oscillations that span over decades. Generally, the ocean climate fluctuates between a cold and a warm state, characterized by low and high temperatures, decreased and increased AtW inflow, and extended and reduced ice cover, respectively (Ådlandsvik and Loeng 1991). Changing properties and volume flux of AtW from the North Atlantic Current (NAC) have been identified as the probable explanatory factor regulating the climate variability in the Barents Sea as well as variations in the position of the polar front (Loeng 1991). The decadal alterations between warm and cold states are generally associated with large scale atmospheric oscillations, specifically the North Atlantic Oscillation (NAO) index (Ådlandsvik and Loeng 1991). The NAO index is based on the difference between the subpolar low pressure over Iceland, and the subtropical high pressure over the Azores (Hurrell

et al. 2001). Decadal fluctuations between negative (NAO-) and positive (NAO+) phases have been associated with variability in both ocean climate and ecology of the Barents Sea. For instance, Ottersen and Stenseth (2001) suggested that positive NAO affects the survival and growth of cod larva in the Barents Sea, both directly and indirectly. The general temperature increase resulting from both higher influx of AtW and higher air temperatures will favour better development conditions for the cod larva. Additionally, the increasing strength of the NAC and influx of AtW will result in higher advection of boreal zooplankton, thereby increasing the abundance of the cod larva's main prey. This interaction highlights one relationship between large scale atmospheric circulations and demersal fish communities. It illustrates the importance of investigating the dynamics of the climate to understand the ecology of the Euro-Arctic shelf seas (see Figure 2).

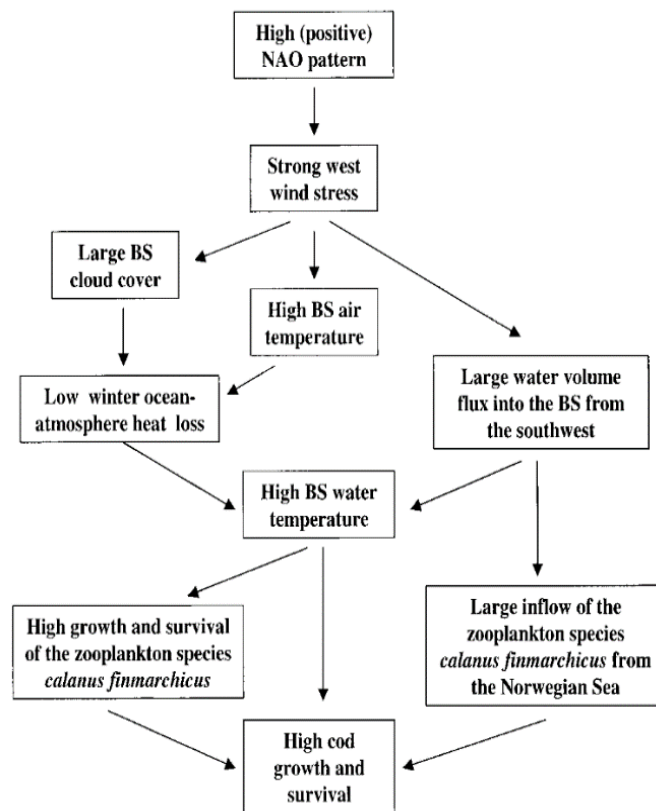


Figure 2: Suggested relationship between a positive NAO index and oceanography and recruitment of Atlantic cod in the Barents Sea. Figure from Ottersen and Stenseth (2001).

Although the Barents Sea has been thoroughly surveyed and monitored, Arctic fish communities are generally understudied compared to those in lower latitudes, and the number of species in the Arctic Ocean is likely underestimated (CAFF 2013). Nonetheless, the general

pattern of species richness and diversity is known to be lower in the Arctic regions compared to that of the warmer Atlantic-influenced Arctic gateways, such as the southwestern Barents Sea and the Fram Strait (CAFF 2013). Following Mecklenburg et al. (2011) definition of the Arctic and its marine fish species, the community consists of 242 different taxa within 45 families, most of which are known to be bottom-dwelling (Christiansen 2012). As marine fish are ectotherms and highly sensitive to ambient temperatures, the zoogeographic distribution is predominantly determined by hydrography and climate (Sunday et al. 2012). The distribution of a species is limited to areas that follow their thermal tolerance range – the temperature range where the species can inhabit and survive. Hence, this range translates into where the species are most frequently found, and Andriyashev and Chernova (1995) compiled a list with description for the species found in the Arctic Ocean and its surrounding seas, with their respective geographic affinity (Table 1). This list describes where the species live and reproduce by placing them in six categories: Arctic, predominantly Arctic, Arctic-Boreal, Boreal, predominantly Boreal, or widely distributed. The polar front in the Barents Sea represents a hydrographical barrier separating two fish communities, Arctic and Boreal, which are spatially confined to their sides with temperatures corresponding to their thermal tolerance window (Johannesen et al. 2012a). Thus, Andriyashev and Chernovas list serves as a useful tool when studying community assemblages and distribution shifts in Arctic fish communities.

*Table 1: List of zoogeographic affinities with descriptions adapted from Andriyashev and Chernova (1995).*

<b>Geographic affinity</b>	<b>Abbreviation</b>	<b>Description</b>
Arctic	A	Species which continuously live and reproduce in Arctic waters
Predominantly Arctic	PA	Species which are usually found in Arctic waters, but which also occur in adjacent boreal waters
Arctic Boreal	AB	Species distributed in Arctic and boreal waters
Boreal	B	Species characteristic of boreal waters but only rarely and temporarily occurring in the bordering regions of the Arctic



Table 1 continued

<b>Geographic affinity</b>	<b>Abbreviation</b>	<b>Description</b>
Predominantly boreal	PB	Species characteristic of boreal waters but common also in the boundary region of the Arctic
Widely distributed	WD	Species common not only in the boreal and subtropical zones but also in warm waters on the southern hemisphere

In addition to distribution patterns, the thermal range can be seen in context with species fitness, with specific temperature spans where the species function optimally and have their fitness maximized (Sinclair et al. 2016). The range typically changes throughout the life cycle, with eggs/larva and spawning adults presumably holding the narrowest tolerance window (e.g., Pörtner and Peck 2010). Successful recruitment of a species is therefore vulnerable to changes in ambient temperatures, which limits their potential habitat.

While the boreal community tends to consist of larger, motile predatory species, the Arctic community consists of smaller, more stationary species, with a higher affinity to the benthic compartment (Frainer et al. 2017). The different functional traits, as well as life-history traits, influence the rate of range expansion and distribution shifts in response to climate change (Perry et al. 2005; Sunday et al. 2015). Species with broader thermal tolerance windows, high fertility, and more generalist niches will have a higher potential for expanding their range of distribution in response to warming. It is, therefore, reasonable to assume that the Arctic will experience a temporary increase in both species richness and diversity as a result of newly introduced boreal species. Thus, the functional ecology and life-history traits of the fish communities are essential to consider when explaining current distribution as well as predicting responses to future environmental changes.

The Svalbard Archipelago is located in the north-west of the Barents Sea, surrounded by the deep Fram Strait in the west, the deep Arctic basin in the north, and the shallow continental shelf in the southeast. Spitsbergen is the largest of the Svalbard islands, predominantly covered by glaciers and characterized by extensive fjord systems. The fjords and coastal zone are complex areas, highly influenced by freshwater runoff and glacier sedimentations from numerous marine-terminating glaciers, rivers, and deltas (e.g., Saloranta and Svendsen 2001;

Svendsen et al. 2002; Zajaczkowski and Włodarska-Kowalczyk 2007). The continental shelf area off the west coast, the West Spitsbergen Shelf (WSS), is a hydrographical frontal zone where the cold and relatively fresh Arctic coastal current, the South Cape Current (SCC) meets a branch of the warm and saline NAC, the West Spitsbergen Current (WSC) (Saloranta and Svendsen 2001). These different hydrographical conditions, comparable to those found in the Barents Sea frontal zone, are likely to affect the distribution of Arctic and Boreal species on the WSS. Additionally, the variability in the NAC in relation to the NAO index has the potential to alter the hydrographical conditions of the WSC, generating temporal variations in the demersal species composition on the WSS. However, the knowledge about how the fish community around Svalbard has changed over time is scarce, especially in relation to climate variability. To be able to discriminate between the effect of decadal/multi-decadal climate oscillations and global warming, biological and environmental time series spanning over several decades are necessary. Additionally, baseline knowledge about the initial state of the fish community is required to detect recent changes in the system. Thus, more extended time series and baseline knowledge are needed in the pursuit to understand the dynamics between climate change and fish communities in the Arctic.

This study aims to get a better understanding of the distribution and temporal changes of the demersal fish community on the WSS by exploring a historical time series of trawl stations spanning over almost three decades, from 1980 to 2007. Additionally, current knowledge about climate variability, hydrography, and fish ecology in the Arctic seas are used to understand how the Svalbard fish community responds to climate oscillations as well as future warming. Here, the research questions addressed are:

1. Is there a differentiation of Atlantic and Arctic fish communities on the WSS reflecting the contrasting hydrographical conditions, spanning from the continental slope in the west to the continental shelf in the east?
2. What is the temporal pattern of important metrics of fish community structure, such as fish species richness, diversity, and abundance? Moreover, is the temporal pattern the same between the two communities?
3. Has fish species composition changed over time, and if so, how are these changes related to the variability in the WSC?

The general expectation is that the communities on the continental shelf (eastern) and on the continental slope (western) will differ in species composition, richness, and diversity. I expect that the western communities will exhibit a higher species richness and diversity, due to the more boreal climate regime on the continental slope. Additionally, I expect that over the survey period, the Arctic-influenced eastern areas will have experienced an increase in species richness and diversity as a result of newly introduced Atlantic species due to the increased presence of Atlantic Water on the continental shelf. I also expect to see some variation in species composition in relation to climatic oscillations, specifically the North Atlantic Oscillation index.

## **2 Material and methods**

### **2.1 Data sampling**

The data was collected during the annual shrimp survey set to investigate the population of the deep-sea prawn (*Pandalus borealis*) in the Barents Sea and Svalbard area. The survey was conducted by The Institute of Marine Research (IMR) from 1980 to 1991 and the Norwegian Institute of Fisheries and Aquaculture (NIFA) from 1992 to 2003. After 2004, the data was collected as part of IMR's annual Ecosystem Survey. All surveys have been conducted between June and September, using four different vessels; two research vessels and two motor trawlers.

A Campelen 1800 survey trawl was used all years, with various modifications (Aschan and Sunnanå 1997). The distance trawled decreased during the survey period; in the '80s, the trawl was towed at 3 knots for one hour, which corresponds to three nautical miles. After 1991, the trawl time was reduced to 20 minutes, covering one nautical mile. All by-catch of fish was registered, identified to the lowest possible taxonomic level, counted, and weighed. The mean bottom depth at each haul was registered.

### **2.2 Study area**

The original dataset covers large parts of the Norwegian Barents Sea, including the Svalbard region and the West Spitsbergen Shelf (WSS), counting over 7000 trawl stations. For the purpose of this study, the data was limited to the stations within the range of 74 – 82°N and 1 – 30°E. This range covers the WSS, from Bjørnøya in the south at 74°N to the northern tip of

Spitsbergen around 80°N. With this spatial limitation, the overlap with previous studies done on this data is reduced, as these focus on the central Barents Sea (e.g., Fossheim et al. 2006; Aschan et al. 2013). Stations shallower than 50 meters and deeper than 500 were removed from the analysis to exclude the “extreme” and avoid the effects of substantial depth variation on the analysis.

Within the chosen range, three subregions were selected based on their (i) bathymetry, (ii) oceanographic features, and (iii) sampling effort. The subregions chosen for the spatial and temporal analyses are as follow; Isfjorden trough, Storfjorden trough, and the small trench north of Bjørnøya, named “Kveite Hålla” (Figure 3). For simplicity, these will now be referred to as “Isfjorden,” “Storfjorden,” and “Bjørnøya.”

The bathymetry enabled these three subregions to be split into two areas; one west, on the continental slope, and one east, on the continental shelf. The two areas were located approximately on the same latitudinal degree. By placing one area on the continental slope and one on the continental shelf within the same subregion, one can study the spatial and temporal differences between Atlantic-influenced and Arctic-influenced fish communities due to the different oceanographic conditions. All three western areas within the subregions are located where a branch of the North Atlantic Current (NAC), the West Spitsbergen Current (WSC), brings warm and saline Atlantic water (AtW) from the south (Figure 1). In Storfjorden Through, a small branch of AtW circulates before it continues north with the WSC. The three eastern areas are located further in on the continental shelf; around Bjørnøya, the Bear Island Current with cold Arctic water (ArW) circulates before it joins the Arctic East Spitsbergen Current (ESC) and forms the South Cape Current (SCC), which flows northwards along the West Coast of Svalbard between the WSC and land (Figure 1). The west is therefore dominated by warm and saline AtW, whereas the east is characterized predominantly by cold and fresher ArW.

Due to the random sampling design, both the location and number of stations surveyed varied from year to year. To be able to study the temporal change, as well as community composition, the areas were defined with a radius of 15 km (~ 8 nm) to include enough stations throughout the time series. By doing so, the areas contain one or more stations approximately every sampling year, enabling a nearly complete time series to be achieved (see Table A 1 in Appendix A). The only exception was 1985 when there were no stations

within the initial range limitation, and therefore not in the chosen subregions. According to the survey report by Tveranger and Øynes (1985), the area west of Svalbard was sampled as in previous years, but the corresponding data could not be found.

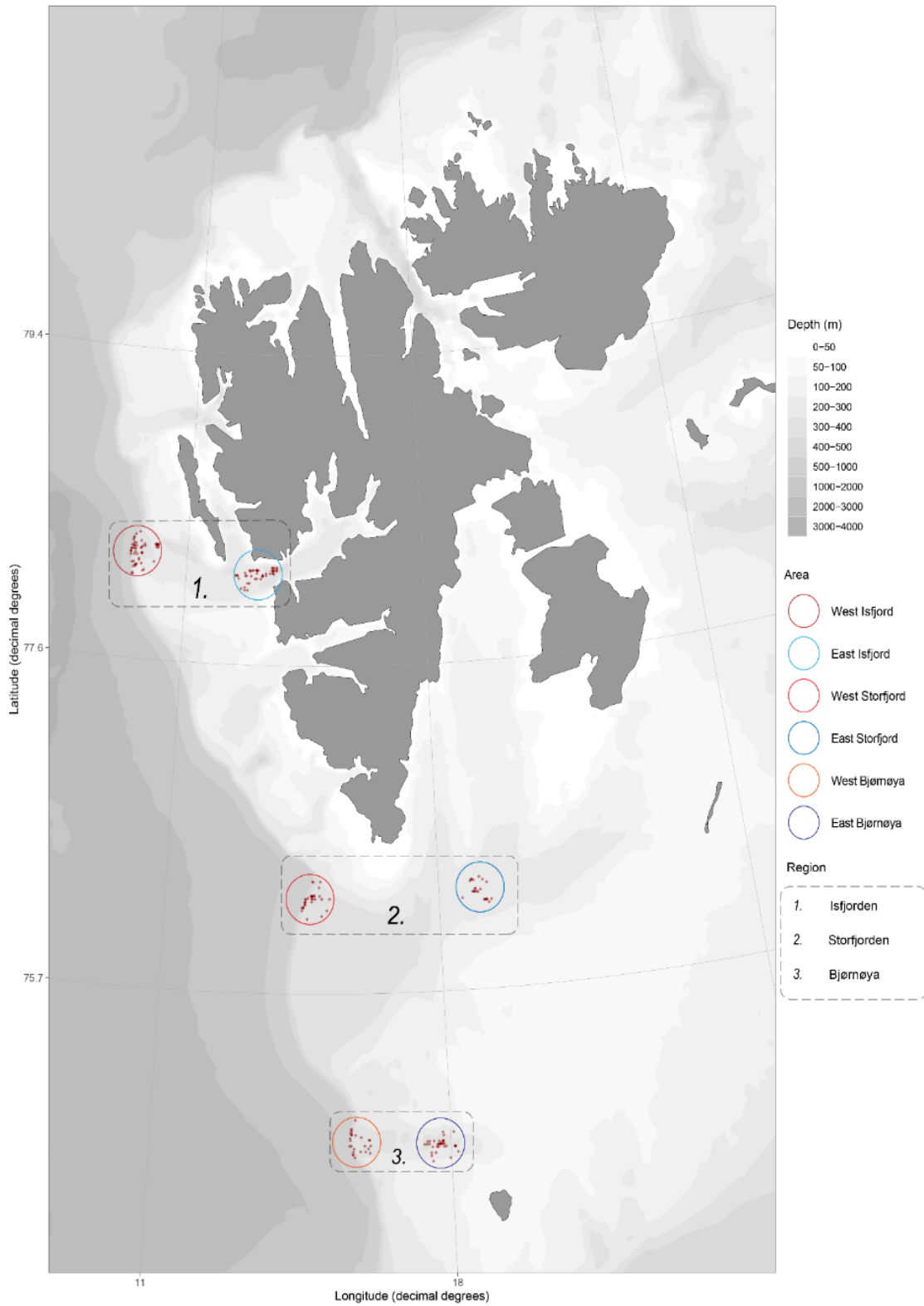


Figure 3: All trawl stations plotted as red diamonds. Dashed lines representing the three subregions, with coloured circles for the areas within the regions.

To ensure that the temporal analysis of biodiversity was not affected by significant variations in sampling depth, the location of the areas was optimized for a homogenous depth distribution throughout the survey. However, the relatively large radius of the areas resulted in some variation in sampling depth throughout the survey (Figure 4).

The area selection and depth range limitation resulted in 254 trawl stations with comparable sampling effort across the areas (Table 2). For information about the annual sampling effort, see Table A 1 in Appendix A.

Table 2: Centre coordinates of the area location and sampling effort for the east and west areas within the three subregions Isfjorden, Storfjorden and Bjørnøya.

Area	Area centre coordinates (decimal degrees)	Sampling effort (all years pooled)
East Isfjord	78.12489 13.13416	53
West Isfjord	78.22000 09.54000	62
East Storfjord	76.28932 19.04617	27
West Storfjord	76.24923 14.70520	37
East Bjørnøya	74.82000 17.75000	48
West Bjørnøya	74.84000 15.81000	27

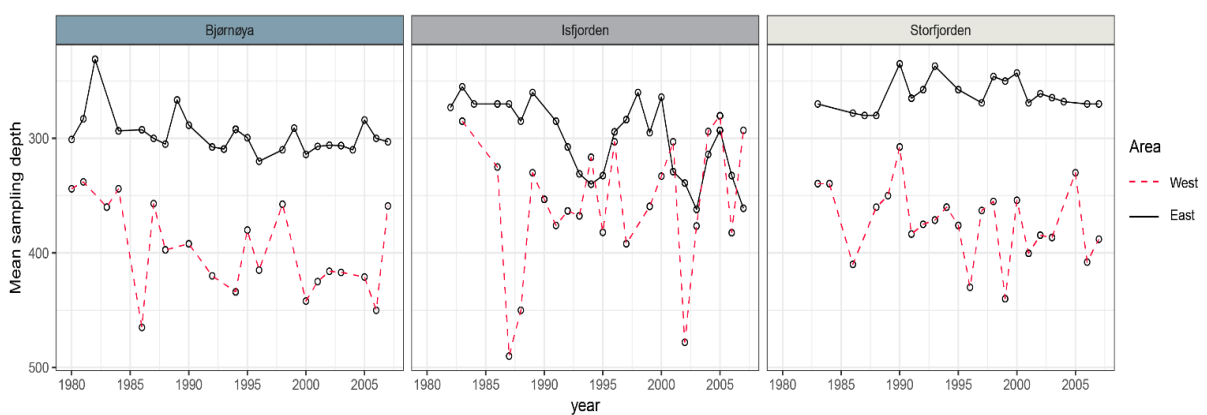


Figure 4: Mean sampling depth throughout the survey period for the three subregions. East and west plotted together with east as solid black line and west with red dashed line.

## 2.3 Species selection

Over the survey period, species identification effort and taxonomic knowledge has improved as well as the focus and registration of less conspicuous, non-commercial species. The change in the species list across the years has the potential to bias the temporal analyses. To account for some of this bias, species that can be challenging to distinguish from one another have been merged at family level. This merging includes snailfishes (*Liparis spp.*), rays (*Rajidae spp.*), and eelpouts (*Lycodes spp.*). Snailfishes contain *Liparis bathyarticus* and other species in the same family not identified down to species level. Rays contain *Raja clavata*, *Dipturus batis*, and other species in the family not identified to species level. Eelpouts include *Lycodes esmarkii*, *L. eudipleurostictus*, and other species in the family not identified to species level. Several other species were only identified to family or genus on the surveys, such as the redfishes, lumpsuckers, sculpins, and some of the wolffishes. The specific species which can be found in these families in Svalbard waters are listed in Pallerud et al. (2004).

All species were allocated a habitat-type according to the classification in fishbase.org. Species with habitat type pelagic, pelagic-oceanic, pelagic-neritic, or bathypelagic were removed from the analyses as these do not reflect the species composition and diversity of the demersal fish community. Additionally, species that were absent from the data the first decade of sampling (1980 – 1990) were removed from the analyses to limit the effect of the increasing taxonomic knowledge and focus on non-commercial species on the analysis of community composition, richness, and diversity.

One species abbreviation, Le\_fi, was not identified to its correct species name until the week before the submission of the thesis but was still included in the table below (marked with an x), and the data analyses. Snakeblenny (*Lumpanus lampraeformis*) was presumably wrongly named in some of the surveys as fries' goby (*Lesueurigobius friesii*), which is a species that does not occur in the Barents Sea (Wienerroither et al. 2011). Le\_fi and Lu\_la are therefore considered as the same species in the data analysis. As the former had zero abundance across the distinct subregions (see Table A 2 in Appendix A), the problematic identification did not affect the results and only serves as one example of the difficulties and uncertainties with changing staff and routines through a long-time survey.



After removing and lumping species, the total number of fish species was reduced from 79 to 42, see Table 3. The species abundance data was standardized by trawl time to ensure that changing sampling effort did not bias the results.

Table 3: Species list with family, abbreviation, species and common name for all species included in the analysis. Zoogeographic affinity obtained from Andriyashev and Chernova (1995).

<b>Family</b>	<b>Abbreviation</b>	<b>Species name</b>	<b>Common name</b>	<b>Geographic affinity</b>
<b>Agonidae</b>	Le_de	<i>Leptagonus decagonus</i>	Atlantic poacher	AB
<b>Anarhichadidae</b>	An_de	<i>Anarhichas denticulatus</i>	Northern wolffish	PB
	An_lu	<i>Anarhichas lupus</i>	Atlantic wolffish	PB
	An_mi	<i>Anarhichas minor</i>	Spotted wolffish	PB
	An_spp	<i>Anarhichas spp.</i>	Wolffishes	PB
<b>Chimaeridae</b>	Ch_mo	<i>Chimaera monstrosa</i>	Rabbit fish	B
<b>Cottidae</b>	Ar_at	<i>Artediellus atlanticus</i>	Atlantic hookear sculpin	PB
	Co_spp	<i>Cottidae sp.</i>	Sculpins	AB
	My_spp	<i>Myoxocephalus scorpius</i>	Shorthorn sculpin	PB
	Tr_spp	<i>Triglops spp.</i>	Sculpins	AB
<b>Cyclopteridae</b>	Cy_lu	<i>Cyclopterus lumpus</i>	Lumpfish	PB
	Cy_spp	<i>Cyclopterus spp.</i>	Lumpsuckers	AB
	Eu_sp	<i>Eumicrotremus spinosus</i>	Atlantic spiny lumpsucker	PA
<b>Gadidae</b>	Bo_sa	<i>Boreogadus saida</i>	Polar cod	A

Table 3 continued

<b>Family</b>	<b>Abbreviation</b>	<b>Species name</b>	<b>Common name</b>	<b>Geographic affinity</b>
<b>Gadidae</b>	Me_ae	<i>Melanogrammus aeglefinus</i>	Haddock	PB
	Po_vi	<i>Pollachius virens</i>	Saithe	PB
	Ga_mo	<i>Gadus morhua</i>	Atlantic cod	PB
	Tr_es	<i>Trisopterus esmarkii</i>	Norway pout	B
<b>Liparidae</b>	Ca_sp	<i>Careproctus spp.</i>	Tadpoles	A
	Li_spp	<i>Liparis spp.</i>	Snail fishes	AB
<b>Lotidae</b>	Mo_mo	<i>Molva molva</i>	Ling	B
	Br_br	<i>Brosme brosme</i>	Cusk	PB
	Mo_di	<i>Molva dypterygia</i>	Blue ling	B
	Rh_ci	<i>Enchelyopus cimbrius</i>	Fourbeard rockling	B
	Ga_ar	<i>Gaidropsarus argentatus</i>	Arctic rockling	A
	Ga_vu	<i>Gaidropsarus spp.</i>		
<b>Macrouridae</b>	Ma_be	<i>Macrourus berglax</i>	Roughhead grenadier	B
<b>Pleuronectidae</b>	Gl_cy	<i>Glyptocephalus cynoglossus</i>	Witch flounder	PB
	Hi_hi	<i>Hippoglossus hippoglossus</i>	Atlantic halibut	PB
	Pl_pl	<i>Pleuronectes platessa</i>	European plaice	PB
	Re_hi	<i>Reinhardtius hippoglossoides</i>	Greenland halibut	PB

Table 3 continued

Family	Abbreviation	Species name	Common name	Geographic affinity
<b>Pleuronectidae</b>	Hi_pl	<i>Hippoglossoides platessoides</i>	Long rough dab	PB
	Li_li	<i>Limanda limanda</i>	Common dab	PB
<b>Rajidae</b>	Ra_spp	<i>Rajidae spp.</i>	Rays	
<b>Sebastidae</b>	Se_spp	<i>Sebastes spp.</i>	Redfishes	PB
<b>Stichaeidae</b>	Le_ma	<i>Leptoclinus maculatus</i>	Daubed shanny	PB
	Lu_la	<i>Lumpenus lampretaeformis</i>	Snakeblenny	PB
	Le_fi	<i>X (Lumpenus lampretaeformis)</i>	Snakeblenny	PB
	St_spp	<i>Stichaeidae spp.</i>		
<b>Somniosidae</b>	So_mi	<i>Somniosus microcephalus</i>	Greenland shark	PB
<b>Zoarcidae</b>	Gy_re	<i>Gymnelus retrodorsalis</i>	Aurora unernak	A
	Ly_spp	<i>Lycodes spp.</i>	Eelpouts	AB

## 2.4 Data analysis

All data exploration, visualization, and analysis were run with the R software (R Core Team 2018). The package “vegan” (Oksanen et al. 2019) was used for calculating biodiversity indices, species accumulation curves, and multidimensional scaling. All maps of the Barents Sea and the Svalbard region were produced using the package “PlotSvalbard” (Vihtakari 2019).

### 2.4.1 Biodiversity, species distribution, and sampling effort

To characterize the fish communities, I estimated basic properties and indices describing community structure: fish abundance, species richness, diversity, and evenness. Fish abundance and fish species richness are the sum of all fish individuals and fish species, respectively, at each trawl station. Fish diversity was calculated for each trawl station and was estimated based on Shannon 's diversity index ( $H'$ ), which is defined as:

$$H = - \sum_{i=1}^S p_i \log_b p_i$$

where  $p_i$  is the proportion of species  $i$ , and  $S$  is the number of species, and  $b$  is the base of the logarithm.

Evenness was calculated by dividing the Shannon Index by the natural logarithm of species richness  $S$ . However, as Shannon diversity and evenness were highly correlated (see Figure B 1 in Appendix B), I decided to use only the former for the community analysis.

Further, to have a first overview of the species distribution around Svalbard throughout the survey, I calculated the centre of gravity (COG) of each of the 42 species. These calculations were done using all the 4079 trawl stations within the initial area range. The COG serves to illustrate the average position where each species was most commonly found throughout the surveys. The COG is calculated for all species by using the following formula:

$$\overline{Latitude} = \frac{\sum_{i=1}^n (Latitude_i \times c_i)}{\sum_{i=1}^n c_i}$$

Where  $n$  is the number of samples,  $c_i$  is the abundance of the species in sample  $i$ , and  $Latitude_i$  is the latitude of sample  $i$ . The same formula is used to calculate the average longitude. All individual species coordinate was then plotted on a map.

The next step was assessing if sampling effort in each of the six areas was adequate to capture the entire species richness in the community. This assessment was done by producing rarefaction curves for each area with all sampling years pooled, which serves to illustrate how many trawl stations are necessary to capture the entire species richness in the area.

### **2.4.1.1 Species composition within the subregions Isfjorden, Storfjorden and Bjørnøya.**

To investigate how species composition differed within subregions, a non-metric multidimensional scaling (nMDS) was performed using a Bray-Curtis dissimilarity matrix of the abundance data for each subregion separately, with all sampling years included. The Bray-Curtis dissimilarity between sampling sites can be calculated with the following formula:

$$BC_{ij} = 1 - \frac{2C_{ij}}{S_i + S_j}$$

Where  $i$  and  $j$  are the two sites being compared,  $S_i$  and  $S_j$  are the abundances of specimens counted on site  $i$  and  $j$ , and  $C_{ij}$  is the sum of only the lesser counts for each species found in both sites.

## **2.4.2 Temporal change in biodiversity and species composition**

### **2.4.2.1 Biodiversity and abundance as a function of time**

To investigate if there was any clear temporal trend throughout the survey period, I fitted a linear regression model to the data for all six areas, with species richness, Shannon diversity, and abundance as a function of time. To control for temporal autocorrelation in the data and thereby dependency in the residuals, I used an autocorrelation function (ACF) on the linear regression model. The ACF assumes equal spacing/time between the observations/lags. To meet this assumption in the ACF, NA's were added to the time series when sampling points were missing. Residuals for all indices were then plotted and controlled. The 95% confidence interval was estimated by  $\pm \frac{2}{\sqrt{T}}$ , where  $T$  is the number of data points, or time units, used in the ACF. To investigate if there was any observable interannual seasonality in data, the standardized residuals for the linear regression model were plotted.

Afterward, an interaction term was added to the model to see if there was any clear difference in the temporal trend between the east and west area within the same subregion. This model included depth as a covariate to account for the differences in sampling depth between east and west. For the areas exhibiting clear temporal trends, separate plots were produced (Figure 12).

In the context of these linear models and null hypothesis significant testing, I have chosen to use a cautionary language approach. With this, I try to follow Dushoff et al. (2019) suggestion of replacing the phrase “statistically significant” ( $p < 0.05$ ) with “clear” whenever describing the results of the null-hypothesis tests. This change in semantics puts less emphasis on results being above or below the  $p < 0.05$  threshold and instead indicates whether particular relationships were more or less clear given the statistical model used.

#### **2.4.2.2 Species composition as a function of time**

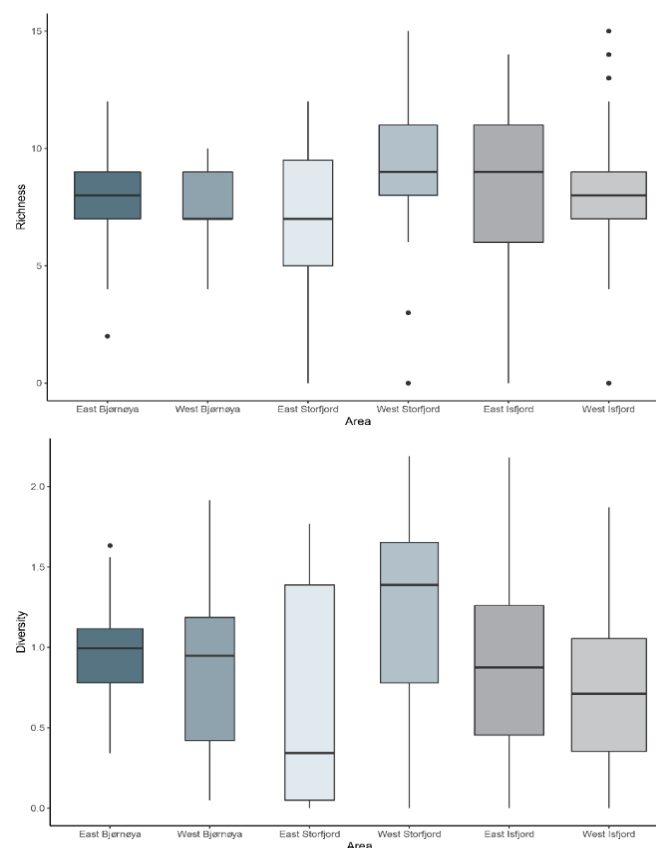
To understand how the fish communities from each area related to each other, and how they changed over time in relation to climate variability, I first lumped the abundance data within 5-year groups: 1980 – 1984, 1986 – 1990, 1991 – 1995, 1996 – 2000, 2001 – 2005 and 2006 – 2007. Due to this 5-year grouping, the last group contains only two sampling years. This grouping was done to be able to investigate how the decadal NAO cycles affect species composition, as this separates the two amplitudes (NAO+/NAO-) of the cycle in its 5-year group. Then, a non-metric multidimensional scaling (nMDS) was performed using a Bray-Curtis dissimilarity matrix of the abundance data for each 5-year group, yielding six nMDS maps with stations and species scores plotted using weighted averages (Figure 13).

## 3 Results

### 3.1 Species distribution, biodiversity, and sampling effort

#### 3.1.1 Distribution of species richness and diversity within the six areas

The 42 fish species present in the initial data set are never found altogether in a single trawl station. When pooling all sampling years together, the median fish richness across all areas is eight species (Figure 5, upper panel), with little variation among areas. East Isfjord, which is the area with the largest sample size (see Table 2 for sampling effort), exhibits the most extensive spread in species richness. The Bjørnøya subregion displays the most similar species richness, while Storfjorden displays the most considerable difference within areas. For diversity (Figure 5, lower panel), the spread is more homogeneous across all areas, and the most considerable difference within subregions is again found in Storfjorden. The median across all areas is 0.89. For the variation in mean richness and diversity across time, see section 3.3.



*Figure 5: Box plot displaying the distribution in species richness (upper) and Shannon-wiener diversity (lower) data, for all six areas. The widths of the boxes are proportional to the square root of the sample size.*

### 3.1.2 Abundance – dominating species within each area

The identity of the ten most abundant fish species is very similar for the six areas when all sampling years are combined. Polar cod (*Bo\_sa*), American plaice (*Hi\_pl*), redfishes (*Se\_spp*), and Atlantic cod (*Ga\_mo*) are found highly dominant in all areas, while just a few species are specific for only one area. These area-specific species are *Cottidae spp* (*Co\_sp*) and lumpfish (*Cy\_lu*) in West Isfjord, spotted wolffish (*An\_mi*) and *Triglops spp* (*Tr\_spp*) in West Storfjord, and northern wolffish (*An\_de*) and Atlantic poacher (*Le\_de*) in West Bjørnøya, while daubed shanny (*Le\_ma*) is among the ten most abundant species only in East Storfjord and East Isfjord.

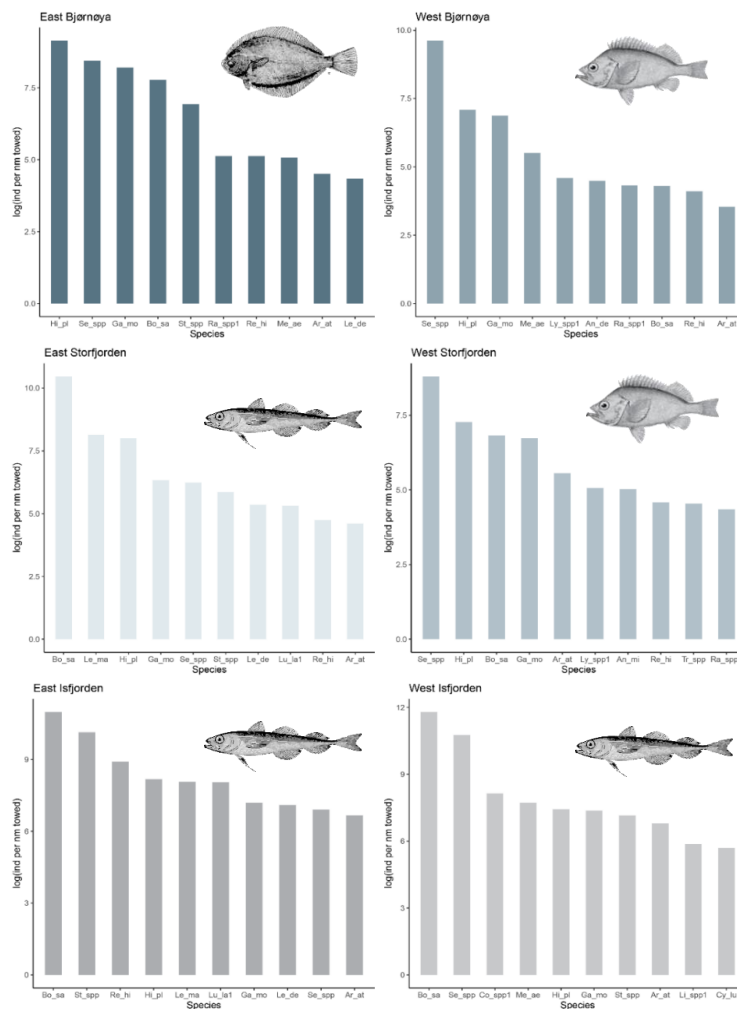


Figure 6: Bar plot displaying the log-transformed abundance of the 10 most abundant species in each area. The dominant species in each area, either *Hippoglossoides platessides*, *Boreogadus saida* or *Sebastes spp.* (here represented with *Sebastes norvegicus*) is illustrated by a picture in the upper right corner of the relevant panel. Pictures adapted from [www.fishbase.se](http://www.fishbase.se).



### **3.1.3 Centre of gravity - species distribution around Svalbard**

The centre of gravity plot serves to illustrate the average position of every species found throughout the survey. From these calculations, the boreal species Norway pout (Tr\_es), ling (Mo\_mo), cusk (Br\_br), and blue ling (Mo\_di) are distributed in the west, along the continental slope. Haddock (Ma\_ae) and Atlantic cod (Ga\_mo), which are both predominantly boreal, have a southeast COG, on the continental shelf. The arctic genus tadpoles (Ca\_sp) and species aurora unernak (Gy\_re) have an extremely eastern COG, together with the Arctic-boreal Atlantic poacher (Le\_de) and sculpins (Tr\_spp). The Arctic species Atlantic spiny lumpsucker (Eu\_sp) has the northernmost distribution, while the predominantly boreal common dab (Li\_li) has the southernmost distribution. Most of the species are found between 74 – 79 degrees latitude, in the area between Isfjorden and Van Mijenfjorden.

Center of gravity

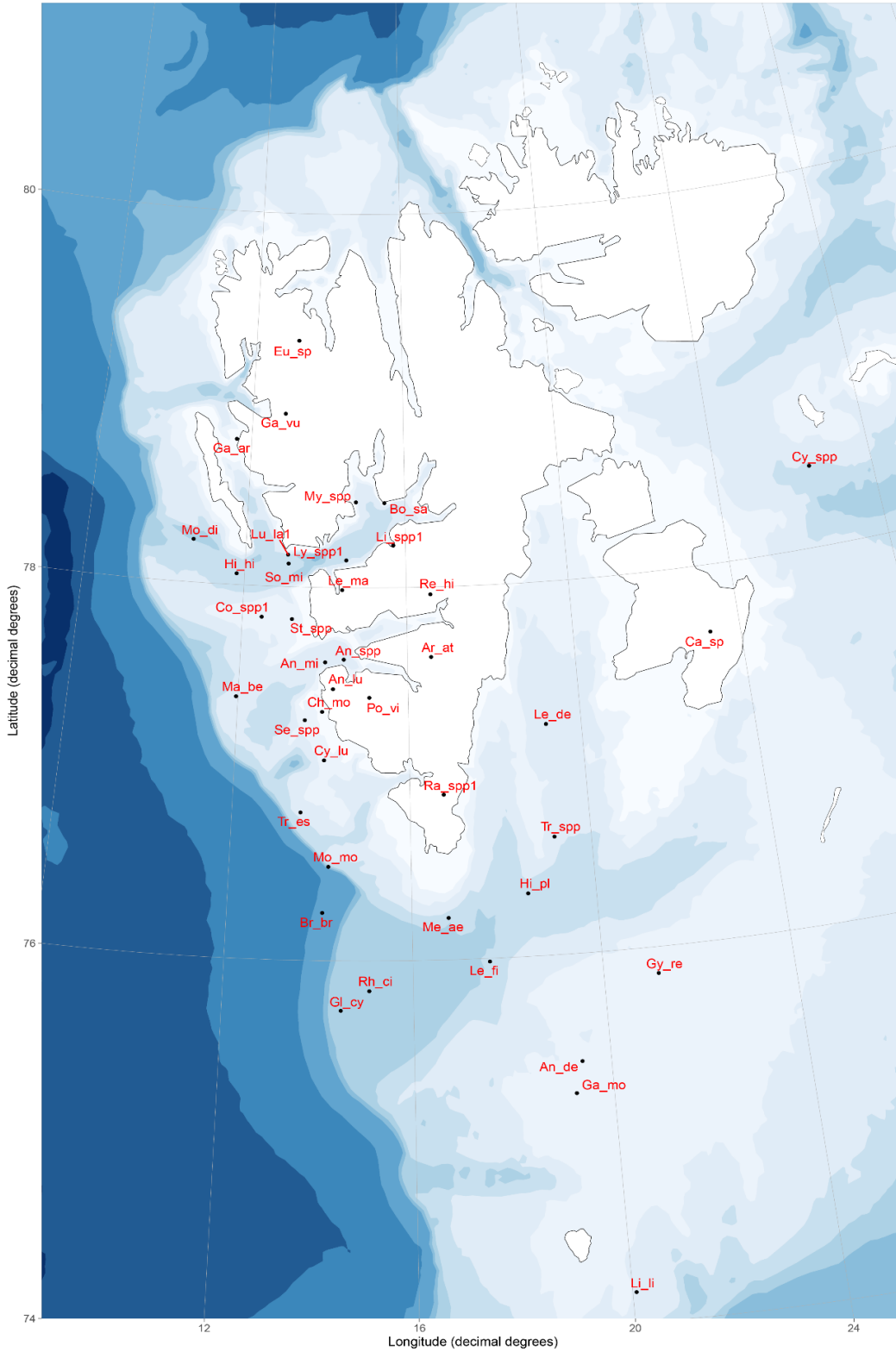


Figure 7: Centre of gravity (COG) plot with species abbreviations (Table 3) indicating the average location for all species throughout the survey period. Due to the large archipelago in the middle of the study area, some of the species' average location is plotted on land.

### 3.1.4 Investigation of species richness in relation to sampling effort

The rarefaction curves indicate a sharp increase in number of species in the first couple of stations, as new species are found in each haul. Then, as the number of new species found in each haul declines, the slope of the curves flattens out. The graph reaches a plateau when there are few or no new species added with increasing effort, meaning that the area is well sampled (Figure 8). All the individual curves reach a plateau except for West Bjørnøya (W\_Bj), where the curve ends with a reasonably steep slope, indicating that the sampling has been inadequate to capture the entire richness of the community. The rarefaction curves thereby reveal the implications of differing sampling effort across areas. However, the analysis indicates that even though East Storfjord (E\_St) has been sampled the same amount as W\_Bj, the sampling effort seems to be adequate for the former area as the curve is reaching a plateau. All the eastern areas display a shallower slope, and they reach a plateau around 20 sampled sites. In contrast, the western areas have steeper slopes. These are still increasing after 20 sampled sites, indicating that these areas are more species-rich and require a higher sampling effort to capture the entire community.

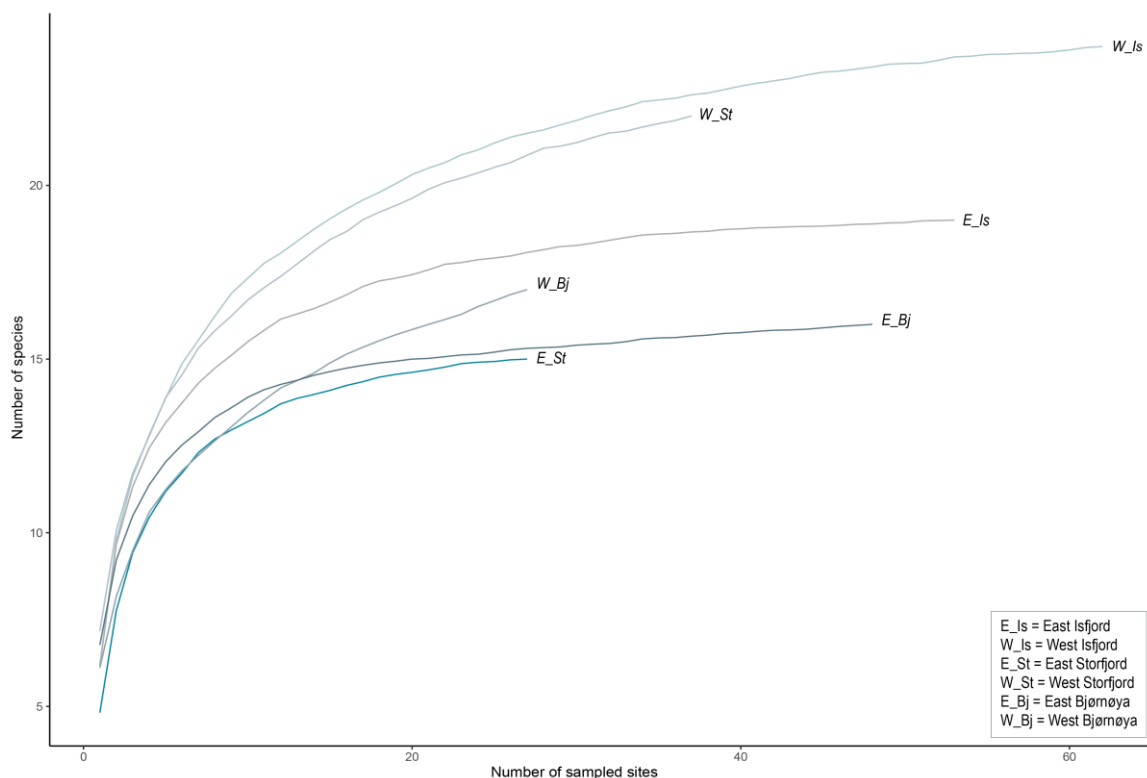


Figure 8: Species rarefaction curves displaying the mean of the cumulative number of species of repeated re-sampling for each area with increasing sampling effort. Each line represents one area.

### **3.2 Spatial analysis of species composition within subregions**

The non-metric multidimensional scaling analysis yielded three nMDS maps with stations and species scores plotted using weighted averages (Figure 9) and indicated differences in species composition within the subregions. In Bjørnøya, the eastern stations are clustered together, characterized by species such as the tadpoles, polar cod, Atlantic hookear sculpin, and snakeblenny. The western stations show lower similarities within the area, as indicated by their more extensive spread in the nMDS. In Isfjorden, there is a higher overlap between the two areas, which seems to be caused by western stations from one specific sampling year, 2005 (Table A 1 in Appendix A). The eastern cluster is characterized by species such as snail fishes, polar cod, sculpins, wolffishes, and saithe while in the western areas Norway pout, aurora unernak, and cusk are found. In Storfjorden, the separation between the east and west is very distinct. A cluster of 11 eastern stations is exhibiting high dissimilarity in species composition from their western counterparts and characterized by the Arctic species polar cod, tadpoles, and snailfishes.

### Nonmetric multidimensional scaling plot for each region

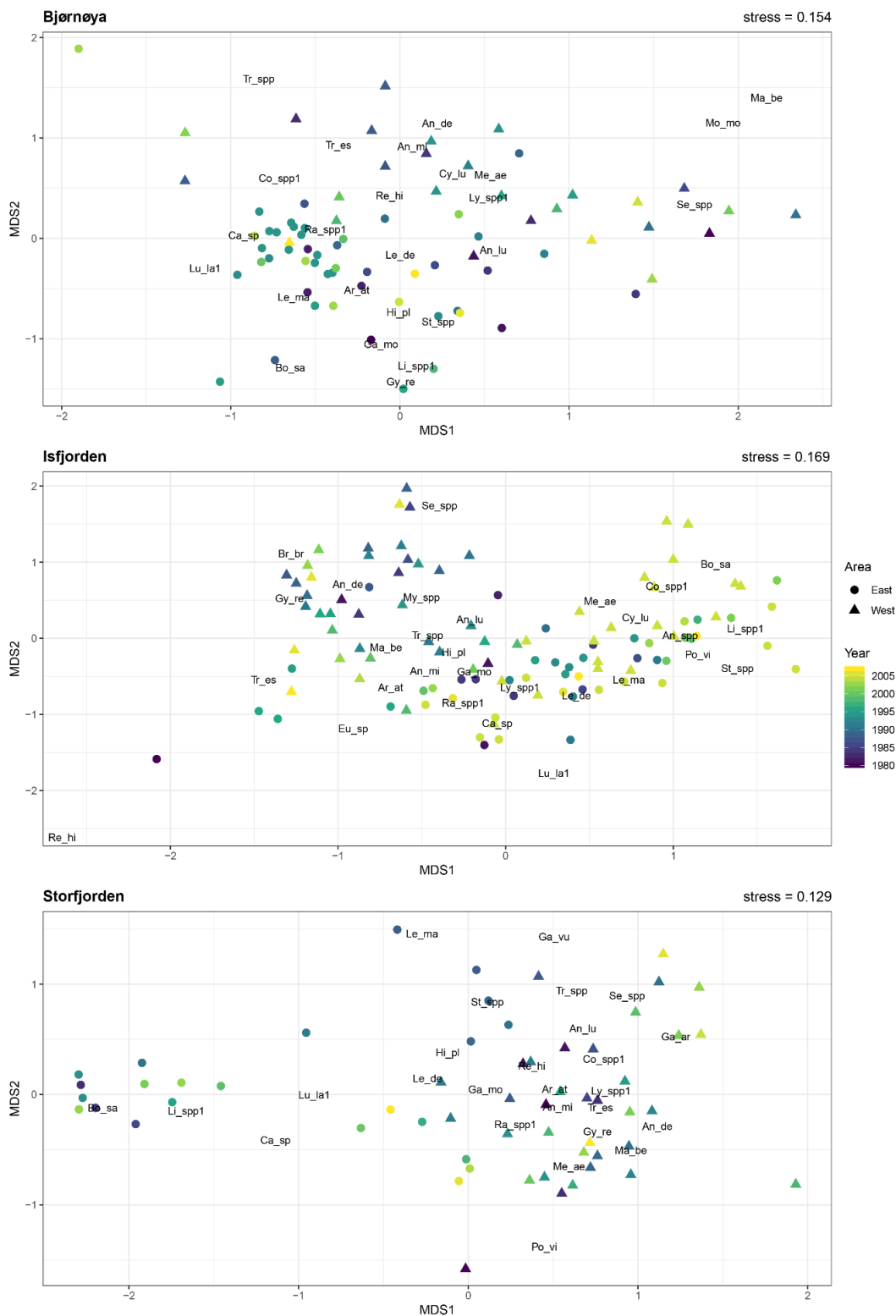


Figure 9: A nonmetric multidimensional scaling map (based on Bray-Curtis dissimilarities) of all stations within each subregion. The nMDS maps for the three subregions are displayed in separate panels. Bjørnøya (upper panel), Isfjorden (middle panel) and Storfjorden (lower panel). The stations are coloured by sampling year and shaped by area; east areas as circles and west as triangles. The stress for each MDS is displayed in the upper right corner of its respective plot.

### 3.3 Temporal analysis of biodiversity and abundance

The temporal autocorrelation analyses revealed no clear temporal dependency in the residuals for species richness and abundance (Figure B 2 & Figure B 4). For diversity, however, West Bjørnøya showed signs of minor autocorrelation on lag 5, East Storfjord on lag 6, and East Isfjord on lag 2 (Figure B 3)

For all indices in the linear model, the residuals show an oscillation around 0, with some indications of a cyclic pattern in relation to NAO phases (Figure 10). Over 95 % of the observations of species richness and diversity lie within two standard deviations from the mean (between 2 and -2), indicating that the residuals are normally distributed. For abundance, there are several observations above 2, meaning that there are some outliers in the data, resulting in a non-normal distribution of the data.

For Shannon diversity, species richness, and abundance, there is a strong interannual variation with fluctuations from year to year (Figure 11). The difference in mean values between east and west for all indices is largest in Storfjorden, where the west area exhibits a higher mean richness and diversity in the first decade of sampling and east a higher abundance. Bjørnøya is the subregion with the most stable species richness over time, as well as the most similar indices for the areas within the subregions.

Storfjorden was the only subregion exhibiting a clear interaction between the east and west, suggesting opposite trends for the two areas (Table 5). While West Storfjord exhibited a negative trend, with a decrease of 0.027 ( $p = 0.025$ ) in Shannon diversity per year, East Storfjorden showed an increase of 0.037 ( $p = 0.013$ ). Additionally, East Bjørnøya displayed a negative trend, with a decrease of 0.014 ( $p = 0.012$ ), though no clear interaction was detected within the subregion. The three areas are plotted with the suggested trend line from the linear model in Figure 12.

Table 4: Analysis of Variance table for the linear model of species richness.

<b>Response: Richness</b>	<b>Bjørnøya</b>					<b>Storfjorden</b>					<b>Isfjorden</b>				
	Df	Sum of Squares	Mean Square	F	p	Df	Sum of Squares	Mean Square	F	p	Df	Sum of Squares	Mean Square	F	p
<i>Depth</i>	1	2.510	2.5100	1.4786	<b>.23131</b>	1	12.454	12.454	3.1292	<b>.0853</b>	1	1.481	1.4811	.3266	<b>.5708</b>
<i>Year</i>	1	5.460	5.4596	3.2160	<b>.08068</b>	1	0.369	0.369	0.0927	<b>.7624</b>	1	2.720	2.7203	.5999	<b>.4431</b>
<i>Area</i>	1	1.546	1.5456	.9105	<b>.34587</b>	1	67.567	67.567	16.9764	<b>.0002</b>	1	3.202	3.2023	.7062	<b>.4056</b>
<i>Year*Area</i>	1	.340	.3450	.2006	<b>.65675</b>	1	18.473	18.473	4.6414	<b>.0379</b>	1	9.844	9.8442	2.1708	<b>.1483</b>
<i>Residuals</i>	39	66.207	1.6975			36	145.282	3.980			41	185.926	4.5348		

Table 5: Analysis of Variance table for the linear model of Shannon diversity.

<b>Response: Shannon diversity</b>	<b>Bjørnøya</b>					<b>Storfjorden</b>					<b>Isfjorden</b>				
	Df	Sum of Squares	Mean Square	F	p	Df	Sum of Squares	Mean Square	F	p	Df	Sum of Squares	Mean Square	F	p
<i>Depth</i>	1	.5173	.51736	4.2144	<b>.04684</b>	1	1.0616	1.0616	5.5699	<b>.02811</b>	1	1.6729	1.67295	8.1506	<b>.00672</b>
<i>Year</i>	1	.1637	.16369	1.3337	<b>.25518</b>	1	0.0025	0.0025	0.0131	<b>.90942</b>	1	.0857	.08570	.4175	<b>.52176</b>
<i>Area</i>	1	.0008	.00081	.0066	<b>.93564</b>	1	1.3724	1.3724	7.2007	<b>.01094</b>	1	.6829	.68292	3.3272	<b>.07543</b>
<i>Year*Area</i>	1	.1506	.15064	1.2273	<b>.27471</b>	1	1.7327	1.7328	9.0912	<b>.00468</b>	1	.0447	.04474	.2180	<b>.6430</b>
<i>Residuals</i>	39	4.7868	.12274			36	6.8614	0.1906			41	8.4155	.20526		

Table 6: Analysis of Variance table for linear model of species abundance.

<b>Response: Abundance</b>	<b>Bjørnøya</b>					<b>Storfjorden</b>					<b>Isfjorden</b>				
	Df	Sum of Squares	Mean Square	F	p	Df	Sum of Squares	Mean Square	F	p	Df	Sum of Squares	Mean Square	F	p
<i>Depth</i>	1	434936	434936	1.0117	<b>.3207</b>	1	15631220	15631220	14.4316	<b>.00053</b>	1	74896	74896	.0174	<b>.8956</b>
<i>Year</i>	1	177534	177564	.4130	<b>.5242</b>	1	525024	525024	0.4847	<b>.49075</b>	1	123188	123188	.0287	<b>.8664</b>
<i>Area</i>	1	172536	172536	.4013	<b>.5301</b>	1	3270324	3270324	3.0193	<b>.09082</b>	1	10870387	10870387	2.5308	<b>.1193</b>
<i>Year*Area</i>	1	271703	271703	.6320	<b>.4314</b>	1	1678918	1678918	1.5501	<b>.22116</b>	1	85375	85375	0.0199	<b>.8886</b>
<i>Residuals</i>	39	16766577	429912			36	38992520	1083126			41	176106622	4295283		



Standardized residuals for species richness, diversity and abundance as a function of time

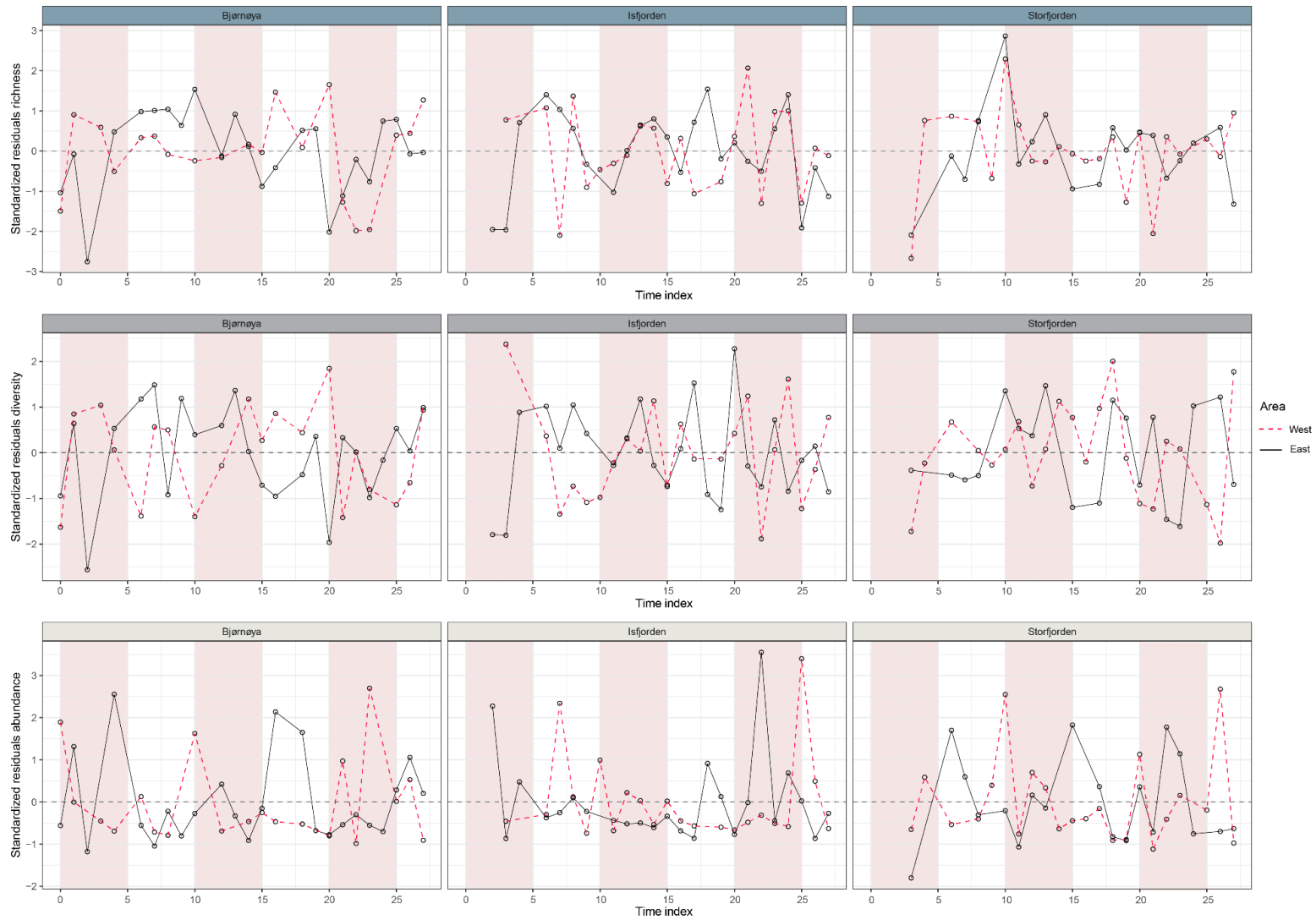


Figure 10: Standardized residuals for species richness (upper), Shannon diversity (middle) and abundance (lower) as a function of time. East and west area plotted together, with east as solid black line and west as a red dashed line. The periods with positive NAO winter index indicated with pink background.

Mean species richness, diversity and abundance for the three regions over the survey period

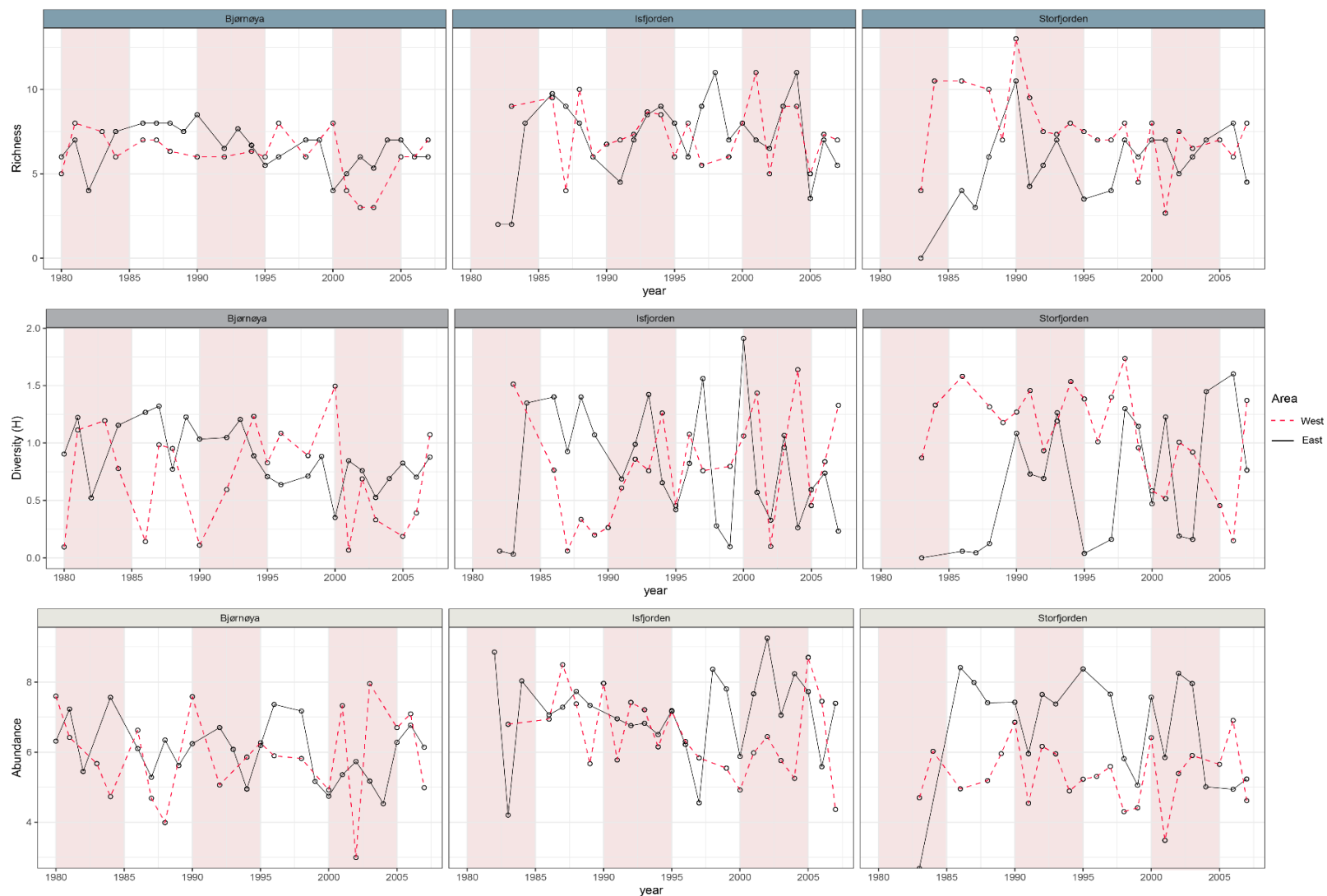


Figure 11: Mean species richness (upper), mean diversity (middle) and mean log-transformed abundance (lower) for all three regions over the entire sampling period. East and west area are displayed on the same plot, east with a black solid line and west with a dashed red line. The periods with positive NAO winter index indicated with pink background.

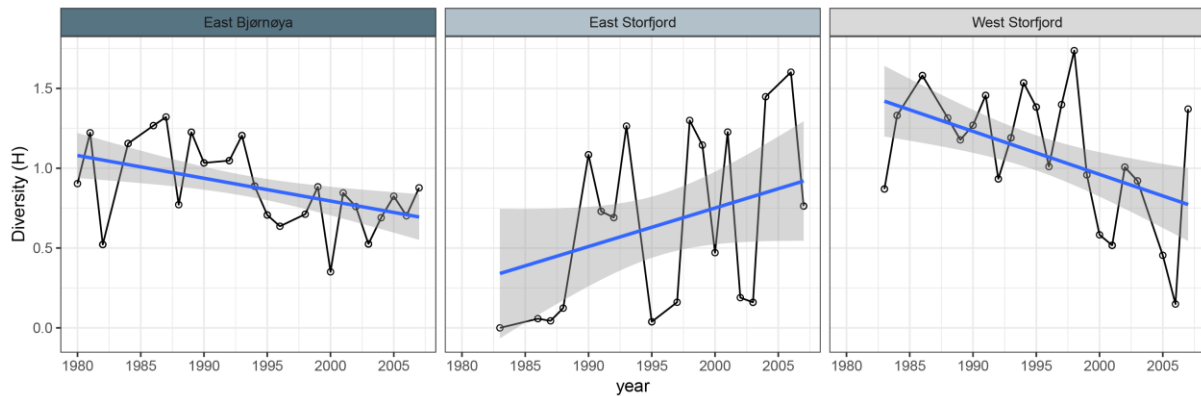


Figure 12: Diversity over the survey period plotted for the three areas where a clear temporal trend was detected. Trend line with confidence interval displayed on the plot.

### 3.4 Temporal analysis of species composition

The nMDS analyses containing all subregions within 5-year intervals (except the last two years, 2006 and 2007, which formed one group) indicate higher similarity in species composition between the eastern areas when compared to the western ones (Figure 13).

All periods, except for 1980-1984 and 2006-2007 show a clear cluster of the eastern stations (East Storfjord and East Isfjord) separated from a cluster of western stations (West Storfjord and West Isfjord) – meaning that the stations within these two groups are more similar to each other in species composition than the stations in the other group. The Bjørnøya subregion is the most ambivalent of the three subregions, showing a “not-so-clear” east-west grouping across the periods.

In Figure 13, the species names are plotted to indicate which species drive the difference in species composition between the stations. When a station is located close to a species name on the plot, this species dominates in this location. The most common species in the east are Arctic species such as the polar cod, tadpoles, and other snailfishes. In the west areas, Atlantic species such as cusk, ling, and redfishes dominate.

#### 1980 – 1984:

This is the first five years of sampling and the period with the poorest area coverage. East Storfjord is not represented, and the number of stations are few. This period shows no apparent clustering, but rather a grouped assemblage of all stations in the centre of the nMDS, with both areas overlapping.

*1986 – 1990:*

In this period, the nMDS yields a clear separation of the east and west areas. East Storfjorden and East Isfjorden are separated from their western counterparts, which cluster together on the right side of the nMDS. Arctic species such as snailfishes and polar cod are represented in the eastern areas, while more boreal species such as cusk, ling, and the redfishes dominate in the western areas. East Bjørnøya is occupying the centre of the plot, while West Bjørnøya clusters with the other west stations to the right.

*1991 – 1995:*

Here there is a similar separation between east and west as the previous period, but with more overlap and less distance between the two groups. East Bjørnøya and three stations from East Storfjord are clustering with the west stations. The grouping is not as clear as the previous period. However, a couple of the East Storfjord and East Isfjord stations still share a more similar species composition than their western counterparts, as they are separated from the rest of the stations.

*1996 – 2000:*

In this period, the east and west areas are more separated than the previous period, with no overlap between east and west. The west areas are clustering to the upper left, while the east is more spread out to the lower right. Polar cod is still a common species in the eastern areas, but here together with the more boreal species saithe.

*2001 – 2005:*

In 2005, Isfjorden was sampled 37 times, as showed by the high number of stations on the nMDS map. Here there is no clear separation between east and west areas, but rather a clustering of both with the eastern areas slightly higher up on the plot than the western areas. Sculpins (AB) characterize stations on the top of the plot, whereas redfishes (PB) characterize stations at the bottom.

*2006 – 2007:*

This nMDS contains only two sampling years. Here we see a similar pattern as in 1986 – 1990, with a clear separation between east and west. Isfjorden east and west are in opposites corners of the plot, with polar cod as dominating species in the east and redfishes in the west.

### Nonmetric multidimensional scaling plot for five-year periods

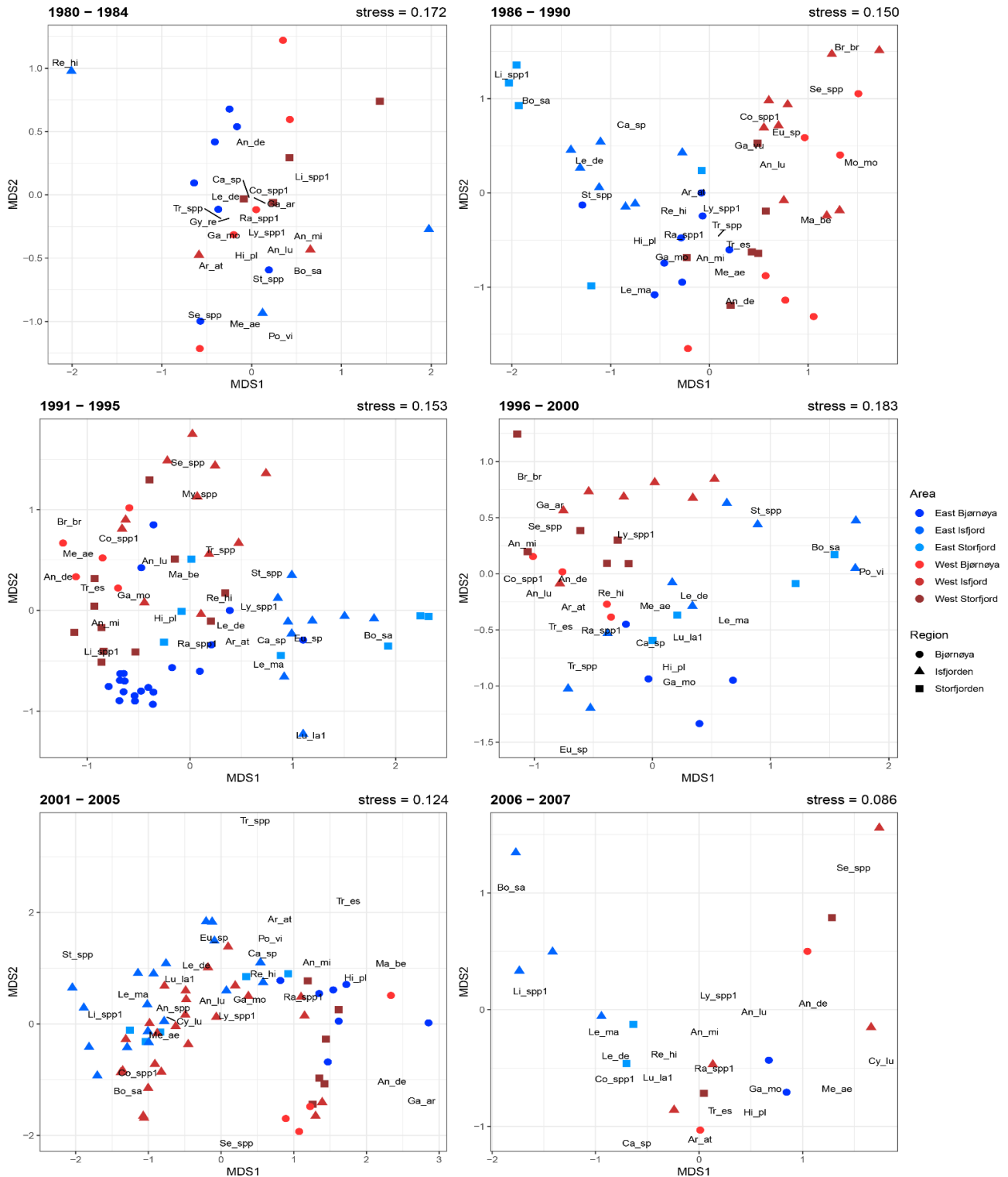


Figure 13: A nonmetric multidimensional scaling map (based on Bray-Curtis dissimilarities) of all sampling stations within six time periods. Stations are shaped by region: circles for Bjørnøya, triangles for Isfjorden and squares for Storfjorden, and coloured by area. Eastern areas displayed in blue, and western areas in red. The stress for each MDS is displayed in the upper right corner of its respective plot.

## 4 Discussion

### 4.1 Biodiversity, species distribution, and composition

Generally, the polar front follows the bathymetry of the Barents Sea and is situated near the continental slope on the West Spitsbergen Shelf (WSS) (Saloranta and Svendsen 2001). Because of its implications to the biota, it is reasonable to assume that the fish species composition follows the bathymetry. The centre of gravity (COG) is the first indication that the east and west areas are representative for Arctic and Atlantic fish communities, respectively, as the boreal species are found near the shelf break. In contrast, the Arctic species are positioned further in on the shelf. However, the high sampling effort at 78°N around Isfjorden, and the extensive sampling on the west coast compared to the east, has influenced the COG by skewing the distribution towards these areas. Nonetheless, the COG serves to illustrate the species distribution in the data, even though it might not be an accurate representation of the actual species distribution around Svalbard. It is important to note that this was the only data exploration done on the entire dataset, without the subregion limitations.

Answering the first question of my thesis, the analyses of species composition for the three subregions suggested differences between each of the eastern-western pair, despite their relatively close geographical proximity on the WSS. This is in contrast with the high similarity in species composition found among the three eastern communities and among the three western communities, despite those subregions being located further apart from each other than the eastern-western pairs within each subregion. These analyses indicate that the chosen subregions are characterized by two different communities, the slope (western) and shelf (eastern), representing Atlantic and Arctic fish communities, respectively. Comparing these results with how Fossheim et al. (2015) classified the Barents Sea community, the same species responsible for the Arctic-Boreal/Atlantic split in their study are found as drivers for the east/west separation in this study. There, the Arctic communities were dominated by snail fishes (Li\_spp), tadpoles (Ca\_sp), snakeblenny (Lu\_la), and Atlantic spiny lump sucker (Eu\_sp). These Arctic communities are found in east Storfjorden and east Bjørnøya. However, the temporal variability in species composition, as well as the observed temporal fluctuations in species richness and diversity within the areas, suggests that the areas do not contain stable assemblages of Arctic and Atlantic fish communities. Furthermore, the same

species are found highly dominant in all the six areas with few exceptions, indicating that the areas have shared much the same abundant species over the survey period.

## **4.2 Increasing diversity in the Arctic community in Storfjorden and ecosystem robustness**

The Arctic-influenced shelf communities were expected to show an increase in biodiversity over time, following the prediction of a warming Arctic and increasing income of Atlantic species (e.g., CAFF 2013). East Storfjorden was, however, the only area where the temporal trend in diversity followed those expectations as well as exhibiting differing trends within the subregion, answering the second question of my thesis. As Shannon-wiener diversity index takes both species richness and evenness into account, this increase could be due to an elevation in the number of species inhabiting the area, or a decrease in dominance and thereby an increase in evenness, or potentially both. However, the high correlation observed between diversity and evenness (Figure B 1 in Appendix B) indicates that these two indices can be considered as “equal.” The high correlation between the two indices is probably due to the generally low species richness in the areas, making diversity highly dependent on species abundance, thereby mirroring the evenness of the community. Thus, it is reasonable to conclude that both diversity and evenness have increased in East Storfjorden.

Even though not statistically clear, the trend in species richness for East Storfjord has been positive. Recent studies have shown that there has been a northeast movement of boreal species in this subregion (Fossheim et al. 2015), as well as increasing richness in Arctic waters related to temperature increase (Mueter and Litzow 2008). However, while high species richness and diversity have been coined as essential factors for maintaining healthy ecosystem functioning (e.g., Costanza and Mageau 1999), the recent increase driven by the boreal newcomers has the potential to alter the ecosystem structure of the native Arctic fish communities. As previously mentioned, Arctic fish communities are comprised of smaller, bottom-dwelling, specialist species compared to the larger, more motile, generalists inhabiting boreal waters (Frainer et al. 2017). The introduction of the latter could potentially increase the predation pressure as well as competition if these two communities continue to overlap in time and space. Moreover, it has been shown that increasing species richness does not necessarily imply an increase in trait richness (Törnroos et al. 2019), referring to the number

of different “*morphological, physiological, behavioral, or life-history characteristics*” in the fish community. Additionally, another study on the same topic has shown similar trends with homogenizing ecological traits over time in response to warming (McLean et al. 2019). Trait diversity has been pinpointed as essential for an ecosystem to resist change and recover from disturbance - termed ecosystem robustness or resilience (Levin and Lubchenco 2008). An ecosystem with a high diversity and heterogeneity in functional traits has a higher potential to withstand environmental change. The extinction of a single species performing a functional role would not be critical to the health of the system due to the diversity of other species that can reinstate the specific role – termed functional redundancy (Levin and Lubchenco 2008).

As these studies have indicated, the observed increase in richness and diversity in the eastern parts of Storfjorden could potentially lead to a decrease in functional redundancy, as the specialist Arctic community shifts towards a more generalist boreal community with fewer unique functional traits. However, one might argue that the homogenization of traits – meaning more species performing the same function in the system – could lead to an increased functional redundancy in the system as several species could potentially replace species lost in the system. Moreover, the large fluctuations observed in both diversity and richness might indicate that the system is somewhat robust to changes and has a capacity to stay “on track” despite significant annual changes in the community. However, using only taxonomic richness and diversity is not enough to reveal such changes over time, and further analyses, including those on functional diversity, must be conducted to examine the temporal change in traits for the demersal fish community in Storfjorden. Nonetheless, the Arctic regions in the Barents Sea have experienced an increase in functional diversity in relation to ocean warming, and this increase has been linked to introduction of boreal species (Wiedmann et al. 2014; Frainer et al. 2017). Thus, it is reasonable to assume that similar changes have taken place in the Arctic communities on the WSS.

In my analyses, I excluded the species which were absent from the dataset during the first decade, for methodological reasons (see section 2.3), which might have some important implications to the results. This reduction of species could potentially weaken the increase in richness and diversity that we would expect to see in the Arctic areas, as a result of removing new species that entered the areas after the first decade of sampling. Examples of such “invading” species are the snake pipefish and the Atlantic mackerel (Fleischer et al. 2007;



Berge et al. 2015), see section 4.3.3. However, by removing these species from the analysis, one accounts for the bias that arrives from the increasing species identification effort throughout the survey period. This reduction ensures, to some degree, that all the species in the data analysis were successfully sampled whenever present, and correctly identified throughout the survey. It is also important to note that the merging of species to family level has the potential to affect the species richness as well as the Shannon-Wiener index for the areas.

### **4.3 Temporal changes in diversity and community composition concerning climate variability**

#### **4.3.1 The effects of the decadal NAO cycles and variability in the WSC**

Previous studies have shown that the North Atlantic Oscillation (NAO) and ocean temperature combined explain over half of the variability in cod recruitment in the Barents Sea region (Ottersen and Stenseth 2001). Additionally, the interannual variability in the NAO index has been related to variability in the benthic macrofaunal community in Kongsfjorden, Svalbard (Beuchel et al. 2006). This relationship is further supported by the correlation between the WSC temperature and the NAO index (Saloranta and Haugan 2001). All these relationships make it reasonable to assume that the NAO index will have both a direct and an indirect effect on the demersal fish community on the WSS.

When considering the east and west areas within each of the three subregions as different communities (Arctic and Atlantic) influenced by the South Cape Current (SCC) and the West Spitsbergen Current (WSC), respectively, the effect of positive and negative NAO-indexes would presumably be different for the two communities. When the NAO is positive, the temperature and strength of the WSC will be more substantial, weakening the influence of the SCC on the continental shelf as the area of Atlantic Water (AtW) increases (Johannesen et al. 2012b). This increased presence of AtW on the continental shelf could potentially homogenize the two areas within the subregion and make the communities more similar. On the other hand, when the NAO is negative, the SCC will have a stronger influence as the area of Arctic water increases, potentially enhancing the difference between the two communities within the same subregion. Indeed, the residual analyses of the time series indicate that the NAO-index may homogenize species richness and diversity on the continental slope and the

continental shelf of both Isfjorden and Storfjorden. Mean species richness is more similar for the two areas in the positive NAO phases, especially in the period 90-95 and 00-05. The same pattern seems to be the case for diversity. Additionally, the difference between the two areas is most evident during the negative NAO phases.

The spatiotemporal analysis of species composition indicated some interesting patterns. By lumping the data together in these periods, the effect of both amplitudes of the decadal NAO cycle on the species composition could be studied, showing that the positive and negative phases of the cycle have contrasting effects on species composition. In the first period, when the NAO-index was positive, and the annual mean summer temperatures were high (Figure 14), the eastern and western areas showed no clear Arctic-Atlantic community separation. The positive NAO-index is not only followed by higher than average temperatures of AtW, but also higher influx (Ådlandsvik and Loeng 1991). With this in mind, the eastern areas would most likely have been warmer and more suitable for Atlantic species, yielding a homogenous species composition within subregions. In the following period, 1986 – 1990, it seems like the picture has changed. The fish communities within the subregions are separate, with Arctic species dominating the eastern areas and Atlantic in the west. This was a cooling period, with negative NAO's and colder annual mean temperatures. With a weaker WSC, the polar front would be positioned further out on the continental shelf, resulting in a separation between Atlantic and Arctic fish communities on the WSS.

In the early '90s, a warming period occurred. Looking at the community composition in this period, the stations showed a more similar composition within subregions and across areas, and the apparent separation found in the previous period is no longer there. Still, East Storfjorden has three Arctic stations clustered separated from the rest, with polar cod as dominant species. This separation could be due to sampling location, as Storfjord exhibits the most substantial distance between the east and west area. In the following period, a cooling happened from 96 – 98 with temperatures below the long-term mean, followed by a slow increase towards the millennium (Ingvaldsen et al. 2003). Here, the communities show a stronger separation between east and west than the previous period, but not as clear as the 86 - 90 period. As we move into the 21st century, the NAO is in a positive phase again, with corresponding warm temperatures. The communities from both east and west areas overlap more than any other period, with strong similarities in species composition. In 2004, a trawl

transect from the inner part of Isfjorden towards the continental slope was done, yielding a very high number of stations in this subregion (see Table A 1 in Appendix A). In the last two sampling years, the NAO was back in a negative phase again, and the communities showed a clear Arctic-Atlantic separation.

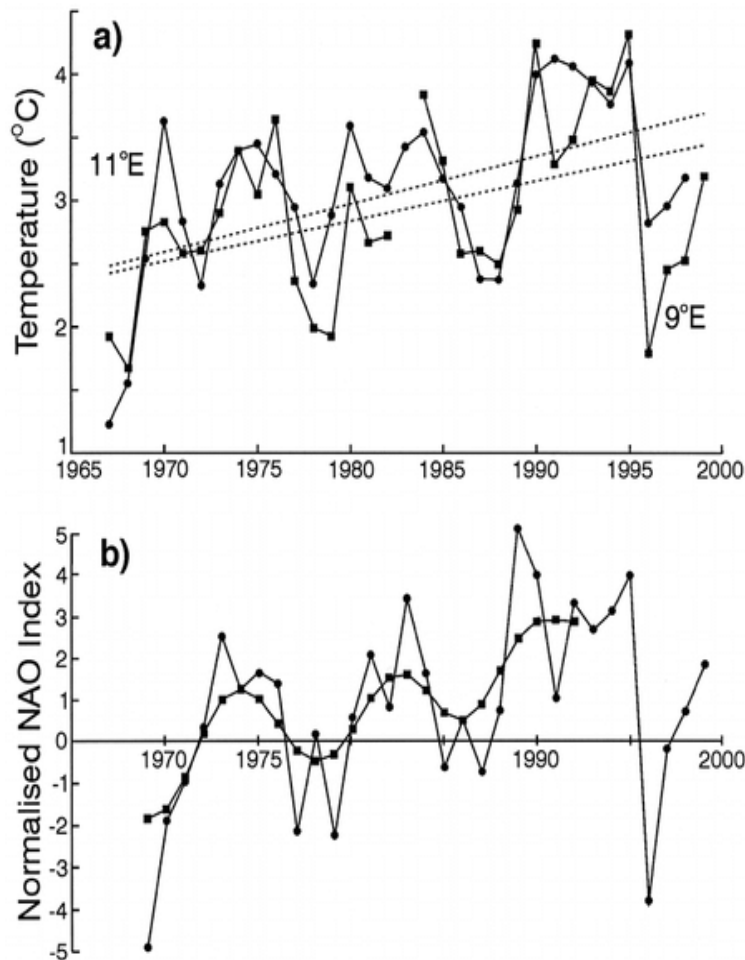


Figure 14: Mean temperature (°C) of the WSC in August – September, at 9° and 11°E on the Sørkapp section (a), and the normalized winter NAO index (b). Figure from Dickson et al. (2000).

The patterns that are appearing in these nMDS-plots are coherent with previous research showing that positive NAOs and increasing temperatures result in species expanding their ranges further north-east (Fossheim et al. 2015). This range expansion is likely the explanation why the subregions have a more homogenized species composition in the warm periods (80-84, 91-95, 01-05), as the Atlantic community shifts further in on the continental

slope, compared to the colder periods (86-90, 96-00, 06-07), when the polar fronts act as a more substantial barrier between the two communities.

These analyses indicate that the species composition on the WSS is affected by large-scale decadal atmospheric oscillations and thereby answering the final question of my thesis. In addition, they emphasise the importance of temperature variability for species distribution and community composition.

#### **4.3.2 Increasing temperature of Atlantic Water and sea ice loss due to global climate change**

Although the climate variability of the North Atlantic Current (NAC) due to the NAO is expected to persist in the future, and the effect of the two phases is evident in the fish communities on the WSS, there is strong evidence pointing towards a recent increase in average temperatures and the influx of AtW, independent of any of the decadal or multi-decadal oscillations (Spielhagen et al. 2011). If these positive trends in the NAC should continue to persist in the future, it is reasonable to assume that the observed differentiation of the fish community in these subregions would cease to exist. The polar front is a highly significant barrier separating the Atlantic and Arctic faunal communities in the Barents Sea region (Fossheim et al. 2006). The observed increase in Atlantic influence in the Fram Strait and the Barents Sea, with a consequential reduction in sea ice, has the potential to weaken or even break this hydrographical barrier (Lind et al. 2018).

In addition to increased temperature and inflow of AtW, the reduction of sea ice in the fjords and on the shelf around Svalbard is likely to affect the distribution of demersal fish due to changing bottom temperature conditions. When sea ice is formed on the shelves during winter, cold and dense brine sinks to the seafloor, creating a pool of cold bottom water (Haarpaintner et al. 2001). This cold pool formation is of high importance for the temperature conditions on the seafloor during summer, as the latter has shown to be strongly correlated with the extent of the sea ice the previous winter (Wyllie-Echeverria and Wooster 1998). The retreat of the sea ice due to climate change, and hence the reduction of the cold bottom water, has been linked to changes in the community structure and distribution shifts of the demersal fish communities, with increasing species richness, trophic level, and biomass of subarctic species (Mueter and Litzow 2008). Accordingly, the observed reduction of sea ice around and

in the fjords of Svalbard (Onarheim et al. 2014; Muckenhuber et al. 2016) could, in all likelihood, affect the distribution of Arctic and Atlantic species on the WSS.

### **4.3.3 “Atlantification” of the West Spitsbergen Shelf?**

As the ocean climate is changing, marine species shift their range of distribution accordingly (e.g., Baudron et al. 2020; Pecl et al. 2017). Previously uninhabitable areas become accessible to new species as their thermal tolerance range expands in response to warming. Examples of such newly introduced species in the Svalbard region are the Atlantic mackerel and the snake pipefish. These two previously purely Atlantic species appear in this survey data in 2004 and 2005, respectively, years before they were first reported in the waters around Svalbard (Fleischer et al. 2007; Berge et al. 2015). However, it is not only the northward range shifts of boreal species that are indicators of a more substantial Atlantic influence around Svalbard but also changes in species composition, fertility, and the Arctic-Atlantic community ratio. Such changes have been observed in the benthic community, the zooplankton, and the polar bears around the Svalbard archipelago (Derocher 2005; Berge et al. 2005, 2009; Hop et al. 2006). These reasonably newly discovered changes have all been linked, directly or indirectly, to the atlantification of the waters around Svalbard.

In addition to the increased Atlantic influence, the Svalbard region has experienced extreme values for both winter temperature and precipitation in the last decade, and these projections are anticipated to escalate further towards the year 2100 (Førland et al. 2011). Considering these observed changes in both the biological and the physical environment, it is reasonable to hypothesize that the future community composition of the demersal fishes on the shelves and in the fjords of the WSS will be occupied predominantly by boreal and Atlantic species. Exceptions might be found in semi-enclosed fjord systems where the exchange of advected AtW is limited, and the sea ice formation persists as a result of the domination of locally produced ArW. Examples of such systems on the West Coast of Svalbard is Van Mijenfjorden. Investigations of the sea ice conditions suggest a reasonably stable ice domain in the fjord from the '80s, with relatively small interannual changes in relation to air temperature and AtW influence (Høyland 2009). Furthermore, the temporal stability of the benthic community structure in the fjord revealed by Renaud et al. (2007), suggests that these ecosystems are, to a greater extent, influenced by local environmental variations rather than

large scale circulation changes. In areas like Van Mijenfjorden, the native Arctic fish communities might have a chance to persist longer in an ever more atlantified region.

#### **4.4 Internal validity and data limitations**

The species identification and taxonomic knowledge on the surveys dating back to the early '80s might be somewhat questionable, especially since The Institute of Marine Research deemed the species identification for many of the taxa unreliable before 2007 (Bergstad et al. 2018). Additionally, the management of the surveys, the technical staff, routines, survey design, and sampling gear has been modified and changed multiple times throughout the survey period (Aschan and Sunnanå 1997). Both factors introduce uncertainties to the analysis and interpretations of the results and set limitations to the applicability of the data. It is also important to note that the original purpose of the surveys was to investigate trends and stock size of deep-water shrimp, not the demersal fish community, so the station stratification is designed to maximize the shrimp catch. However, there is much information to be found by using the available data on by-catch in this historical time series, if one keeps in mind the uncertainties and limitations of the data.

The non-standardized, random sampling stratification in the first decade of the survey created some difficulties for the replicates in the time series. The ideal sampling would be to have stations sampled annually in the same spot. These could then easily be treated as annual replicates for the time series analysis, without the issue of depth variation or missing stations. The area selection done in this thesis was made to reduce some of this variation. By choosing fixed areas with similar depth ranges for the analysis, with a reasonably stable depth distribution, the noise from the unstandardized sampling location was, to some degree, reduced. However, as displayed in Figure 4, the nature of the bathymetry and sampling in the Isfjorden subregion did not allow for stable depth distribution throughout the survey. Sharp fluctuations in the west and the slight decrease in the east are contributing to uncertainty in the temporal and spatial analysis.

In addition to issues regarding species identification and non-standardized sampling stratification, some spatial differences between the subregions may arise from environmental factors other than those focused on in this study. In contrast to the western areas, which, to an extended degree, are under a similar environmental influence, the eastern areas have higher

individual differences regarding environmental conditions. For instance, the significant freshwater input, sedimentation and heterogeneous bottom topography in East Isfjorden which are not found in any of the other subregions. These features are potentially yielding differences in species composition and biodiversity not induced by the main water masses or warming temperatures, which are difficult to control for.

The species accumulation curves suggest that to capture the entire richness of the areas, more than 20 trawl stations are necessary. For the temporal analysis of biodiversity, however, the sampling effort within each area varied on average between one and four stations per year (see Table A 1 in Appendix A), indicating that the data are not adequate for exploring the annual diversity of the community. However, as mentioned, by increasing area range and thereby including more stations, the variation in sampling depth increases. It is, therefore, a trade-off between having an adequate amount of sampling stations and limiting the amount of variation in depth. Furthermore, since all the areas (except West Bjørnøya) showed to be sufficiently sampled across all years, the length of the time series should be able to reveal overall trends for the community.

All these factors combined compose difficulties which enlighten the importance of standardized sampling methods and design when collecting data for time-series analysis. Additionally, it highlights the difficulties of creating a study design 30 years after the initial data collection began.

## **4.5 Perspectives for future research**

As emphasized in the previous section, standardized sampling methods and design are vital for collecting comparable data for time series analysis. The joint Norwegian-Russian Barents Sea ecosystem survey (BESS), which took over the initial shrimp survey, implemented such standardized methods and quality control of species identification after 2004. In addition to sampling of all compartments of the ecosystem, as well as the physical environment, at every station. This expansion of the survey has enabled more extensive research on the ecological effects of climate variability in the Barents Sea region considerably. However, the BESS has so far been conducted for 16 years, which could be considered inadequate to discriminate between the effect of decadal/multi-decadal oscillations and anthropogenic climate change. As Wassmann (2011) pointed out: *“To discriminate between the ecological effects of multi-*

*annual to decadal oscillations in climate and those of the more one-directional anthropogenic climate change, we need time series of climatic drivers and potential biological responses spanning several decades”* (p.13), highlighting the importance of more extended time series. The continuing of this ecological and environmental time series is, therefore, of high importance for understanding how the biological system is responding to a warming ocean.

## **5 Concluding remarks**

The main aim of this thesis was to have a better understanding of the species composition and diversity of the fish community on the West Spitsbergen Shelf and how these could change in relation to climate variability, and how the fish species composition differs spatially along the continental shelf. The results presented here show that the distribution of species with different geographical affinities reflects, to some degree, the distribution of the main water masses on the shelf. The distribution, as well as biodiversity, of fish species, is, to a large extent, affected by larger atmospheric oscillations driving fluctuations in the ocean climate. While biodiversity showed sharp inter-annual fluctuations in all areas, the demersal fish community inhabiting the Atlantic influenced subregions exhibited, as expected, a higher species richness than the areas under Arctic influence. However, there was only one Arctic area that followed the expectation regarding an increasing temporal trend in diversity.

There is still much unrevealed information in this time series. The addition of functional traits to the analysis could potentially reveal how the documented taxonomic changes affect the overall ecology and health of the system. Additionally, the study presented here could be further prolonged using the 16 years of available data from the BESS, creating a community analysis stretching over four decades, but this is unfortunately outside the scope of this thesis. However, the historical time series and analysis presented here indicate how the demersal fish community around Svalbard responds to climate variability, thereby giving valuable insight into the consequences of a warming Arctic. To predict the future, one must understand the past.







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# Appendix

## Appendix A

Appendix A contains an overview of the sampling effort in the six areas over the entire survey period and the abundance matrix for all species used in all the data analyses, except for the Centre of Gravity calculations.

Table A 1: Number of trawl stations within each area from 1980 to 2007

Sampling year	West Isfjord	East Isfjord	West Storfjord	East Storfjord	West Bjørnøya	East Bjørnøya
1980					1	1
1981					1	1
1982		1				3
1983	2	1	2	1	2	
1984		1	2		1	2
1985						
1986	2	4	2	1	1	2
1987	1	1		1	1	1
1988	1	1	1	1	3	1
1989	1	1	1			2
1990	4		2	2	2	2
1991	1	2	2	4		
1992	3	2	2	2	1	2
1993	3	2	3	1		3
1994	2	2	2		3	13
1995	2	2	2	2	1	2
1996	1	3	1		1	1
1997	2	3	1	1		

<b>1998</b>		1	1	1	2	1
<b>1999</b>	3	1	2	1		1
<b>2000</b>	1	1	1	1	1	1
<b>2001</b>	1	2	3	1	1	1
<b>2002</b>	1	2	2	1	1	1
<b>2003</b>	2	2	2	2	1	3
<b>2004</b>	1	1		1		1
<b>2005</b>	<b>24</b>	<b>13</b>	1		1	1
<b>2006</b>	3	2	1	1	1	1
<b>2007</b>	1	2	1	2	1	1





























## Appendix B

Appendix B contains figures displaying species evenness over time compared with Shannon Diversity and correlograms for the temporal autocorrelation analysis.

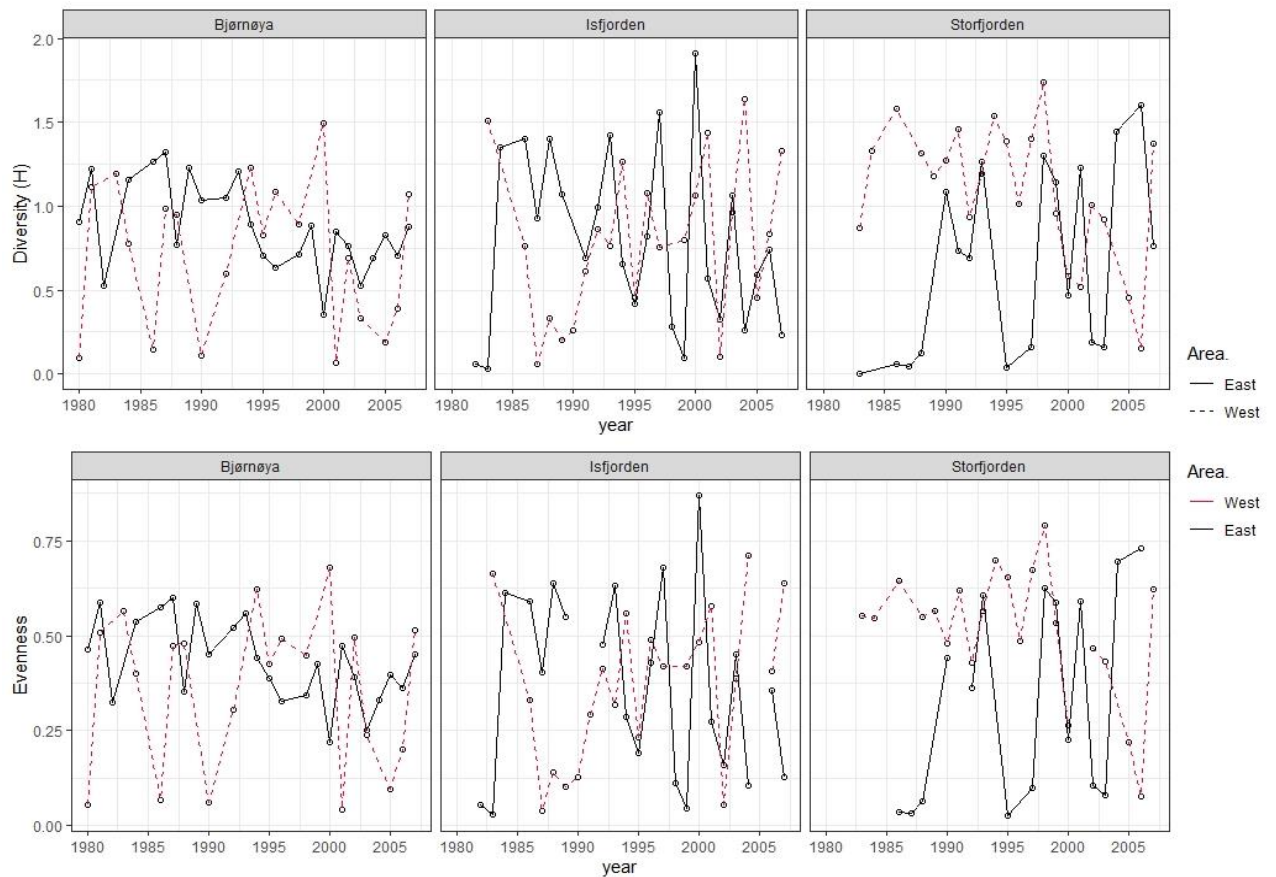


Figure B 1: The mean Shannon diversity (upper) and evenness (lower) plotted over time for the respective areas.



Temporal autocorrelation species richness

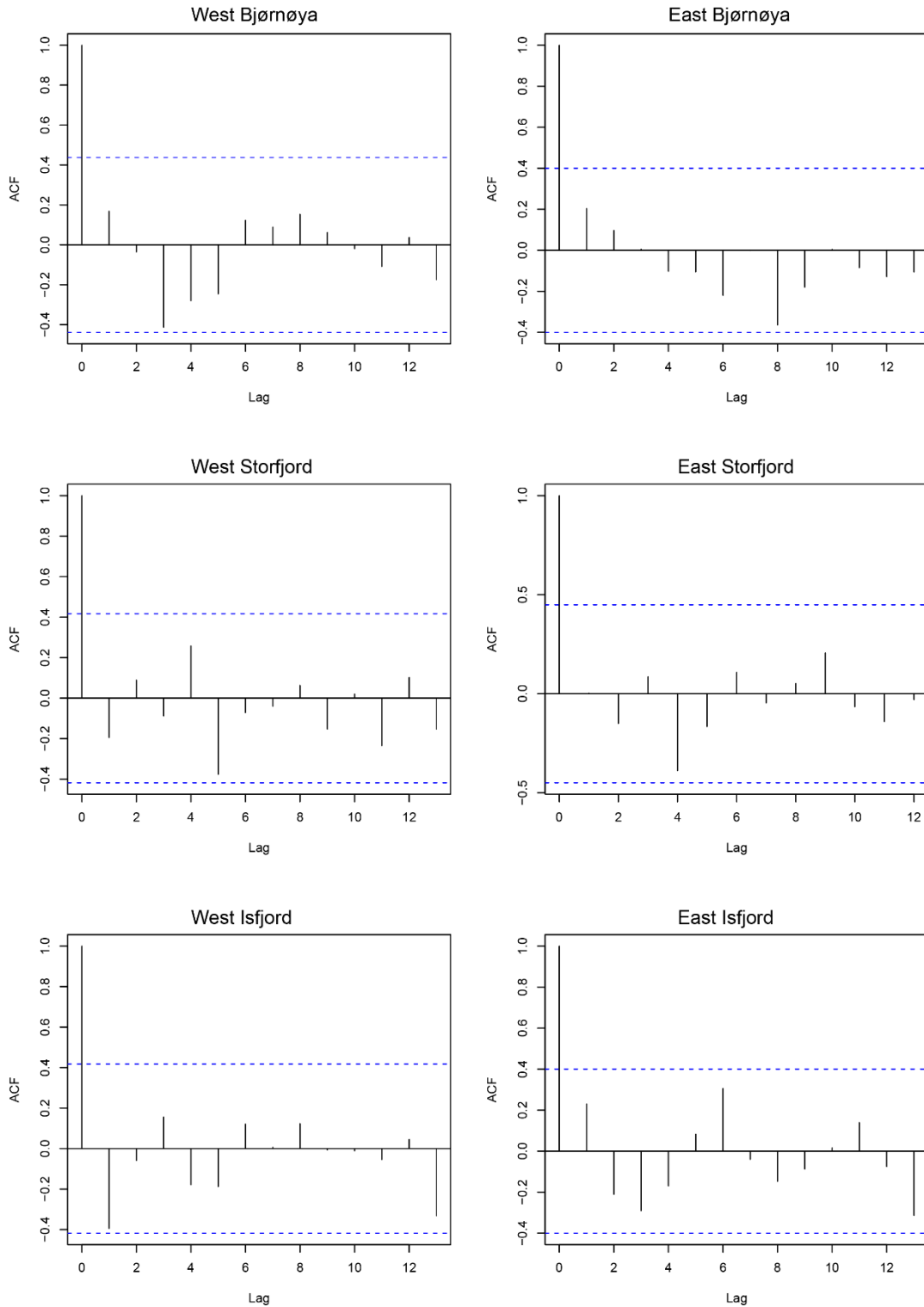


Figure B 2: Correlogram of the observed species richness for each area sampled. The Y-scale displays the correlation coefficient, ranging from 1 (= 100% correlation) and 0 (0% correlation). The lags are evenly spaced in yearly intervals. Dashed blue lines represent 95% confidence interval.

### Temporal autocorrelation species diversity

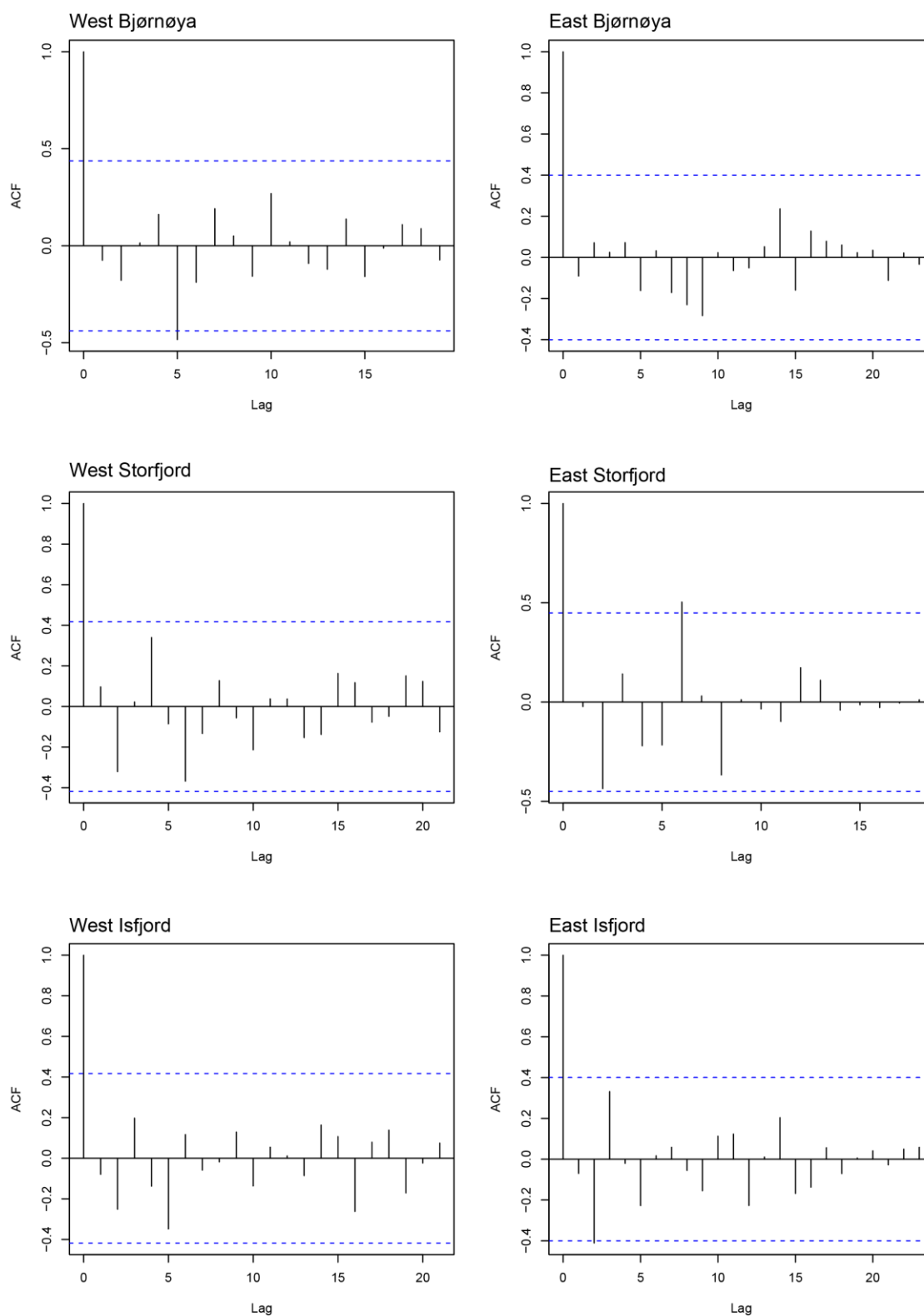


Figure B 3: Correlogram of the observed Shannon Diversity ( $H$ ) for each area sampled. The Y-scale displays the correlation coefficient, ranging from 1 (= 100% correlation) and 0 (0% correlation). The lags are evenly spaced in yearly intervals. Dashed blue lines represent 95% confidence interval.

### Temporal autocorrelation total abundance

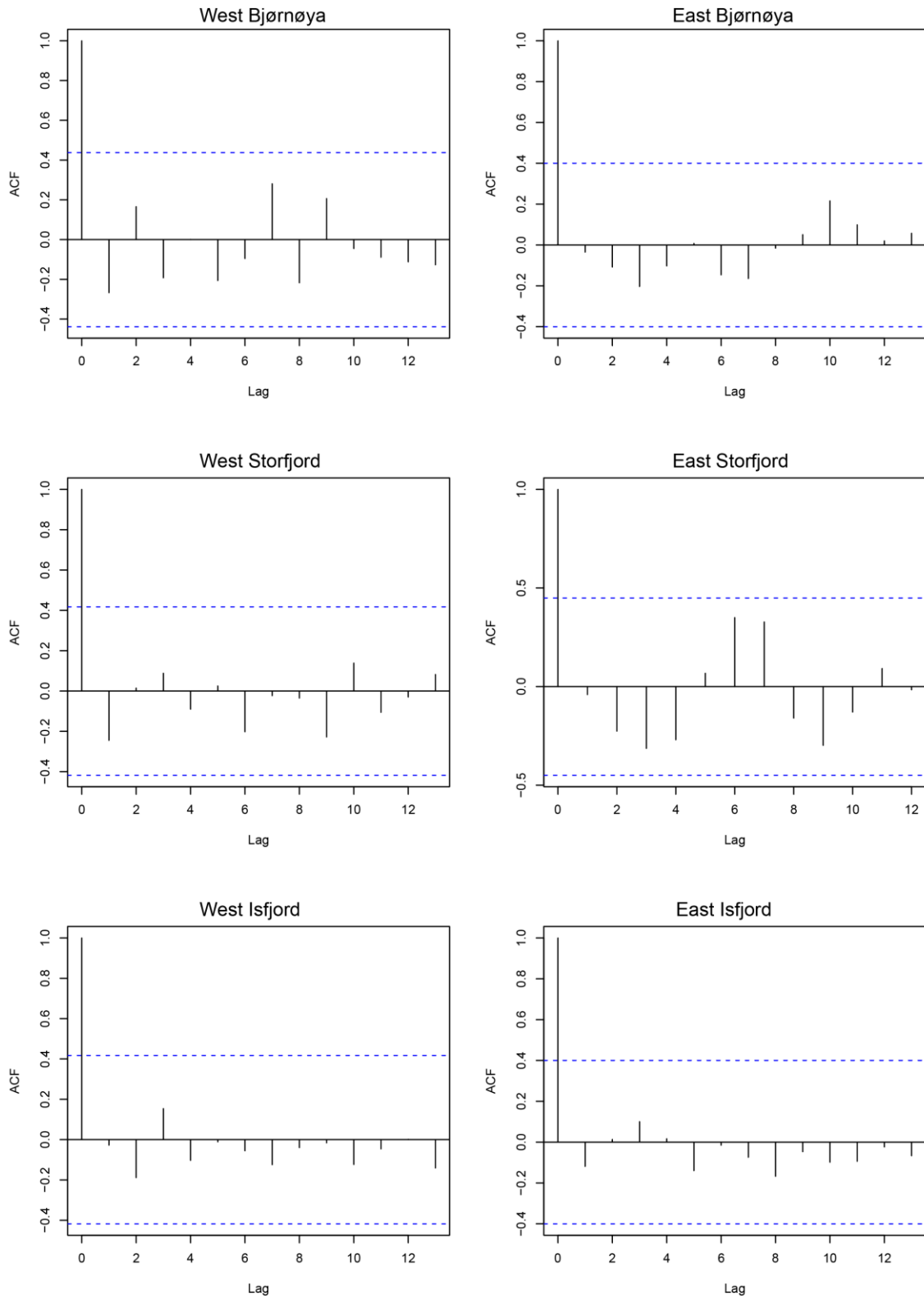


Figure B 4: Correlogram of the observed species abundance for each area sampled. The Y-scale displays the correlation coefficient, ranging from 1 (= 100% correlation) and 0 (0% correlation). The lags are evenly spaced in yearly intervals. Dashed blue lines represent 95% confidence interval.



