Species composition, distribution and ecology of the demersal fish community along the Norwegian coast north of Stad under varying environmental conditions

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Abstract

In the last decades, temperatures of the Atlantic current that enters the Norwegian Coastal Current (NCC) has been above the yearly average, with 2007 as the warmest registration on record (Skagseth 2012). The climatic changes in recent years are likely to have large-scale ecological consequences for the marine demersal fish-populations, especially in arctic latitudes. Many studies have been conducted in areas of the Barents Sea related to the community structure of marine fish, while little is still known about these changes in areas bordering the Norwegian Sea.

This study uses catch and CTD data collected in both coastal areas/inner fjords and open ocean bank areas between Stad (62 ^{o}N) and Varanger (71.3 ^{o}N) by The Institute of Marine Research (IMR) from 1995, 2005 and 2017. This thesis investigates the changes found in distribution, composition and species richness in areas of the Norwegian coast for 86 marine demersal fish from 33 different families in the last 20 years and represent an essential knowledge baseline about both commercial and non-commercial species in this area that has previously been an area of little focus.

The data show that there has been marked northward shifts in spatial distribution for the majority of species. Many increased clearly in abundance at high latitudes in the warmer years, hinting at more favourable conditions due to climate change, which are leading species to become more established in these areas. Such trends are most pronounced for large, boreal generalist such as cod (*Gadus morhua*), Norway redfish (*Sesbastes viviparus*) and whiting (*Merlangius merlangus*).

A large number of demersal species have been registered in 2005 and 2017 that were not present along the Norwegian coast in 1995. There has also been an observed shift for many species to move further from the coast, and into open ocean areas in more recent years. The trends observed are overall consistent with the recorded increases in temperatures of the same years, supporting a claim of a large-scale climate related changes in distribution and abundance. Finally, the data revealed that species composition has changed significantly on a south-north gradient between the years. Species composition from 1995 to 2017 was also

found being significantly ($p<0.05$) related to the changes (i.e. increase) in temperature, fishing depth and the eight subareas investigated along the Norwegian coast.

Table of content

Introduction 8

1.1 Warming of the Arctic Ocean 8

1.2 The study area 9

1.3 Ecology of demersal fish populations & possible ecological consequences 13

1.4 Research questions and aims 14

Materials and Methods 16

2.1 Data sampling 16

2.1.1 The Institute of Marine Research's coastal survey 16

2.1.2 Trawl equipment and standard procedures for catches 18

2.2 Stratification of the study area 20

2.3 Preparation of data 21

2.3.1 Species selection 21

2.4 Data analysis 25

2.4.1 Spatial distribution 26

2.4.2 Species richness and diversity 27

2.4.3 Species composition by multivariate analysis 28

Results 30

3.1 Overview of the study area from 1995 to 2005 & 2017 30

3.2 Investigation of species richness and sampling effort 33

3.3 Species composition 36

3.4 Spatial distribution 39

3.5 Records of new species 49

Discussion 51

4.1 Changes in distribution; borealization of northern Norway 51

4.2 Changes in species richness and composition; southern and Arctic invaders to the Norwegian coast 55

4.3 Ecological consequences 60

4.4 Changes in distribution, composition and species richness; not temperature related? ... 62

4.5 Concluding remarks 63

Reference list 65

Appendix 71

Appendix 1.A 71

Appendix 1.B 75

Appendix 1.C.. 76
Appendix 1.D.. 77

Introduction

Climatic changes in recent years are likely to have consequences for marine ecosystems, as variations in water temperature are known to influence the habitat structure (Kortsch et al. 2015) and the communities of organisms (Aschan et al. 2013) along the Norwegian coast. Most fish have an optimum temperature range that has implications for physical and ecological processes such as growth, reproduction, trophic interactions and distribution (Beittinger et al. 1979). Thus, increasing temperatures are likely to result in unfavourable conditions for many cold-water species, leading to a northward shift with a speed related to the climatic changes.

The distribution patterns of marine organisms inhabiting the Norwegian coastal/fjords and open ocean waters may change with a changing environment. The main objectives of this master thesis is to study the demersal fish community between Stad (62 ^{o}N) and Varanger, Norway (71.3 ^{o}N), and investigate whether there are indications of changes in species composition, diversity and distribution between 1995 and 2017 in the areas bordering the Norwegian Sea.

1.1 Warming of the Arctic Ocean

Over the past decades, a general trend (with regional exceptions) of increasing sea temperatures can be observed (IPCC 2007). It is stated that the Arctic is experiencing a surface-layer warming of twice the global average (Fossheim et al. 2015) and that in the Arctic basin, surface temperatures have increased by 1^{o}C over the past 20 years (Stenevik & Sundby 2007). Main drivers for these physical changes were found to be related to the increased penetration of warm Atlantic water, that increased sea water temperature and the reduced cover of sea ice (Wassmann et al. 2011)

The temperature in the Arctic is expected to increase at twice the global average (Aschan et al. 2013), and is said to be experiencing the most dramatic warming on the planet (Lind et al. 2018). The largest of the seas that make up the Arctic ocean is the Barents Sea, which is a boundary area between arctic and boreal species (Johannesen et al. 2012), as it contains both a favourable ecological area that receives inflow of warm Atlantic water, and an area in the north with an Arctic climate. And while the Arctic has experienced a dramatic warming in the past decade, it is in the Barents Sea where the largest observed increase in ocean heat content is observed (Lind et al. 2018). The Barents Sea is a well-researched area, especially regarding commercially valuable species (Byrkjedal et al. 2007). Several studies conducted in the Barents Sea revealed changes in large scale patterns of benthos and fish (Johannesen et al. 2017), the rapid borealization of fish communities in the Arctic (Johannesen et al. 2012, Fossheim et al. 2015) and changes in fish community structures (Aschan et al. 2013).

Despite the many studies conducted in the Barents Sea, not much is known regarding the status of the ecosystem and demersal fish community in areas bordering the Norwegian Sea, which includes coastal/fjordic and open ocean environments south of the Barents Sea. Hence, with the observed and expected rise in temperature and relative heat content in the Norwegian Sea in the coming years (Mork 2012), it is important to investigate whether changes in species composition, distribution and ecology may have occurred in this area over the last two decades.

1.2 The study area

The Nordic seas, which is a major part of the northern loop of the global thermohaline circulation, include the Norwegian Sea, which is a marginal sea in the Arctic Ocean and covers over 1.1 million km^2. It connects with the Northeast Atlantic Ocean in the southwest, the Icelandic waters and the Greenland Sea in the west and borders the North Sea in the south (ICES 2017). Here, inflow of warm Atlantic water in the east is cooled down into water masses that supply the lower North Atlantic Deep Water with cooler and denser water (Mork 2016). It functions as a transport of warm and saline water from the Atlantic to the Barents Sea (Figure 1.1), and is together with the Barents Sea a transition zone for warm and saline water.

Since the mid 1990’s the Atlantic current that enters the Norwegian Sea has been warmer, with temperatures above the annual average since the early 2000’s, and with 2007 as the warmest on record (Orvik & Skagseth 2005, Mork 2012, ICES 2017). It is therefore expected that the thermohaline circulation will be weakened in the future due to warmer and fresher water in the subpolar seas (Dickson et al. 2002).

The estimated trend of the Relative Heat Content (RHC) in the Norwegian Sea was also greater than for the global average, as IPCC’s long-term global estimate of increase in RHC was 0.3W m^{-2} from 1951-2010 (Skagseth 2012). It was however shown that during the 1960’s to the 1990’s the Norwegian Sea experienced a cooling, while a warming of 3.2W m^{-2} from 1995 to 2010 was measured, which is ten-times higher than the global estimate (Mork et al. 2014). These changes were shown to derive mainly from the inflow of warm Atlantic water which has increased in temperatures by 0.5^{o}C since the 1970’s (Mork 2012).

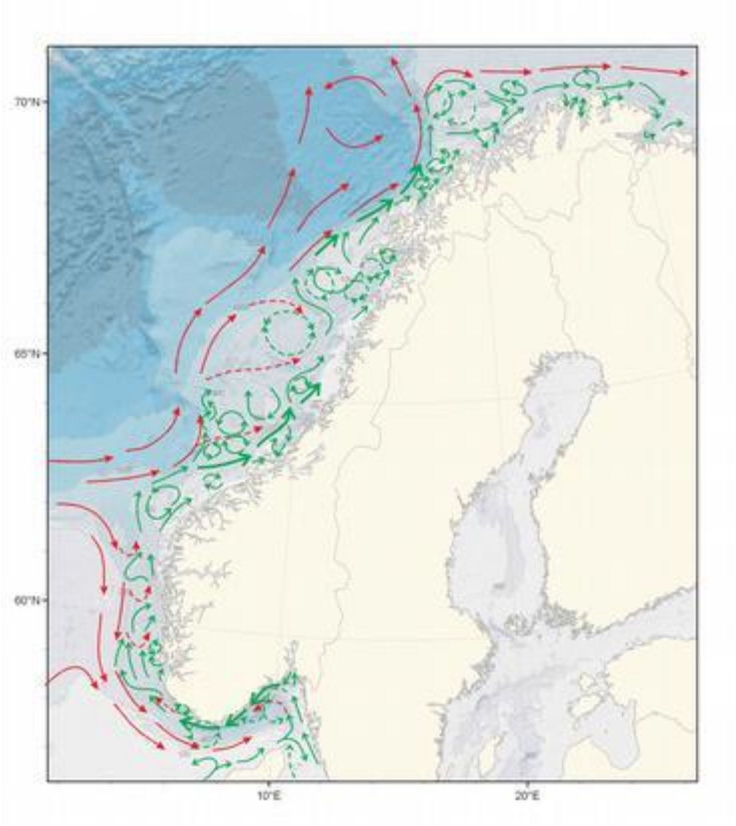

Figure 1.1*: Schematic map of the main current systems along the Norwegian coast. The NCC (Norwegian coastal current) is show with green arrows, while the red arrows denote Atlantic water. Source: IMR (taken from Asplin 2014)*

In the area where the temperature increase in the last two decades has been largest along the Norwegian coast, between Stad and Varanger (62 – 71.3 ^{o}N), there is a wide range of different marine habitats which is fragmented by many islands and inner fjords. There are large variations between different fjords and the different open bank areas in distinct regions of the coast. It is the Norwegian Coastal Current (NCC) that runs northwards along the coast from its origin in Skagerrak, between Denmark and Sweden, and contains Norwegian Coastal Water (NCW) (Mankettikkara 2013). The NCW is continuously mixed with the inflowing warm and saline Atlantic water, creating an area with favourable ecological conditions for marine organisms.

The marine areas of Norway are divided into three main areas from north to south; the Barents Sea-Lofoten, the Norwegian Sea and the North Sea-Skagerrak (Figure 1.2), based on ecosystem-based management plans for Norway’s Exclusive Economic Zones (EEZ).
In the northern part of the study area, from the Lofoten area to the Barents Sea, the many different fjords and outer coastal areas display large ecological diversity, these are also areas with a high level of fisheries activity (Misund & Olsen 2013). These northern fjords are said to be geophysically highly diverse (Mankettikkara 2013), and have lower average sea temperatures than areas further south. Regional temperature differences are also found between inner fjords, which in winters may in some fjords be close to freezing. The areas furthest north, around the Barents Sea are relatively shallow, with large shallow bank areas.

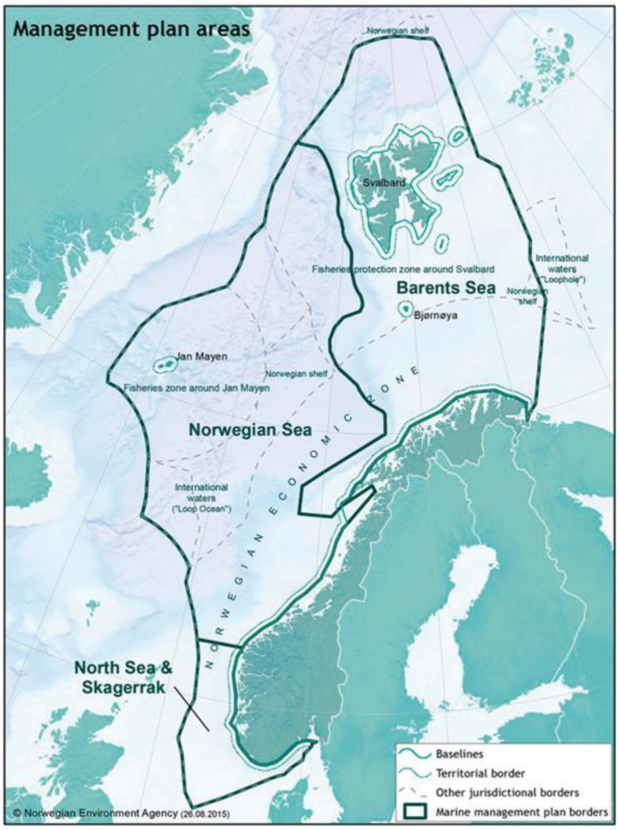

***Figure 1.2** Division of the Norwegian coastline into three main areas based on the Norwegian ecosystem-based management plan. The three areas are The North Sea-Skagerrak, The Norwegian Sea and the Barents Sea-Lofoten, Source: the Norwegian Environment Agency/Norwegian Mapping Authority (Regjeringen.no 2015)*

The large environmental gradients along the Norwegian coastline create conditions for several species with widely different biogeographical origins and affinities (Table 1.1). It is therefore important to have a baseline of knowledge about the community’s state prior to the warming period in order to quantify and characterize possible changes in the ecosystem in the later years (Bergstad et al. 2018). As this is an area where there has been observed some of the most rapid increases in ocean-temperatures in the past decades, knowledge about the distribution, abundance and trophic interactions of demersal fish must be obtained in order to study future impacts of further warming on these communities. Based on heat content levels registered, the heat content north of Stad was lower in 1995 compared to 2005 (Skagseth 2012). This makes a comparison of the marine demersal ecosystem in this area between a cold (1995) and a warmer period (2005) possible, with an additional, more recent year as a control (2017), which one could assume that with the continuing increase in temperature the recent years in the Atlantic is also warmer than 1995.

Table 1.1 *List of terminology taken from Andriyashev & Chernova, 1995, with abbreviations* (Bergstad et al. 2018) *used in characterizing the species geographical affinity*

Geographic Area	Abbreviation	Description
Arctic	A	Species that continuously live and reproduce in Arctic waters.
Predominantly Arctic	MA	Species that are usually found in Arctic waters but which also occur in adjacent boreal waters.
Arctic boreal	AB	Species distributed in Arctic and boreal waters.
Predominantly boreal	MB	Species characteristic of boreal waters but also common in boundary regions of the Arctic (e.g. the Barents Sea)
Boreal	B	Species characteristic of boreal waters and rarely occur in bordering regions of the Arctic.
Southern boreal	SB	Primarily refers to Atlantic boreal species, which are not only found in boreal regions, but also further south.
Widely distributed	WD	Species that are common in boreal and subtropical zones, and also in warm waters from the southern hemisphere.

1.3 Ecology of demersal fish populations & possible ecological consequences

This study examined changes in distribution, species richness and composition on 86 marine, mainly demersal fish from 33 different families, and includes both commercial and non-commercial species. The large amount of different families and taxa makes up a group that vary largely in life strategies, biogeographical affinities, overall distributional patterns and thus potentially express large differences in ecological responses in relation to the climatic changes.

Demersal fish are divided into benthic and benthopelagic species, which respectively rest on the seafloor or live in the water column just above the bottom. Many demersal fish are opportunistic feeders (Gallo et al. 2016), feeding on both pelagic and benthic organisms as many areas including the Arctic, production of benthic food is slow compared to the pelagic zones (Bergstad 2009). Temperature has been shown to be a key factor influencing both directly, through change in species composition and availability of prey, as well as indirectly by affecting reproduction and growth.

The Intergovernmental Panel on Climate Changes states that there is uncertainty regarding the predicted effects climate change would have on the structure and productivity of marine communities and ecosystems. Changes in complex marine ecosystems are difficult to predict, and uncertainty arises since biological models are not yet sufficiently realistic to provide reliable predictions (Stenevik & Sundby 2007). However, several studies have shown that the responses to increased water temperatures on marine ecosystems includes changes in the distribution (Perry et al. 2005), abundance (Fossheim et al. 2015) and have revealed major changes in species composition (Southward et al. 2004).

Even though the notion that temperature changes affect the distribution of fish species is widely accepted, it is also a difficult subject due to the complexity of community-level responses, that are influenced by several conditions differently (Tonn 1990). This means that single-species studies, which previously have been a large area of focus especially on commercial important species, may not give a suitable indication on the possible changes in the ecosystem and may conceal climate change effects (Aschan et al. 2013). However in general, a reduction of native species in ecosystems like the Arctic, which have been found to be less resilient to climatic changes, is more likely than in ecosystems with a high diversity (Frank et al. 2007).

The climatic changes are predicted to potentially result in wide spread local extinctions, perhaps most severe for species constrained by their ability to disperse to new areas (Perry et al. 2005), as suitable habitats can be limited or unavailable. The likely change in distribution for many species towards the poles, would result in new species being introduced to the Norwegian coast, and could affect already existing trophic systems in this area. Long-term ecological consequences are likely to be found in demersal fish either directly (through physiological processes), or indirectly where the increase in competition will affect growth, reproduction and survival. Species and populations' differences in response-rates are suggested to result in an overall reorganization at regional scales, which could trigger cascading effects (Poloscanska et al. 2013). It has also been suggested that marine organisms are going to respond to these changes with magnitudes even greater than the changes occurring for terrestrial organisms (Poloczanska et al. 2013).

1.4 Research questions and aims

This thesis will explore whether the composition of demersal fish along the Norwegian coast has significantly changed from 1995 to 2005 and 2017, and whether the species composition is significantly affected by variables such as temperature, depth and latitude, or the eight different subareas (stratified based on latitude and coastal or ocean categorization). A description of the community's habitat in the Norwegian Sea, including temperature will be presented, together with a discussion of likely ecological consequences following possible changes.

As well as looking at species composition, this thesis will also focus on comparing species distribution and diversity, which are likely to be strongly influenced by different climatic patterns between the cold and warmer periods. Catch data from bottom-trawls and bottom temperatures from CTD's (Conductivity, Temperature and Depth) collected by the Institute of Marine Research (IMR) are the basis for this thesis and will help in trying to answer the following questions:

1) Have species had a northern shift in distribution from 1995 to 2005 and 2017? And is there an observed difference in distributions between inner coastal/fjords to open bank areas?

2) Has there been an increase in species richness and diversity since 1995 in the eight subareas and is this related to the increasing temperatures of the Norwegian Sea?

3) Does species composition change from 1995 to 2005 and 2017, and is the species composition significantly related to the measured temperature, depth and latitude?

This thesis will include comparisons of the open bank areas with areas in inner coastal fjords within four areas divided based on latitude along the coast between Stad and Varanger, making up a total of eight different subareas. This study will be a first addition to an important baseline of knowledge about the demersal fish community around the Norwegian coast, which together with other marine fish communities in high latitudes are already prone to a natural high variability in climate.

Materials and Methods

2.1 Data sampling

2.1.1 The Institute of Marine Research's coastal survey

The Institute of Marine Research (IMR) has since 1985 conducted an annual acoustic survey with the objective of obtaining abundance indices of commercially important fish species, including saithe (*Pollachius virens*). The annual coverage (in October and November) of coastal areas and fjords, as well as open ocean banks, between Stad (62 ^{o}N) and Varanger (71.3 ^{o}N) has since 1995 included measurements of coastal cod (*Gadus morhua*) and is, together with catches of over 80 other taxa of demersal fish, the foundation for the dataset used in this thesis.

The coastal survey has since 2003 been standardized in relation to trawl time, equipment and survey design. This was when IMR's coastal cruise, the annual survey on abundance of saithe and the most important parts from the sprat and herring-cruises were combined to one survey (Aglen et al. 2005). The survey consists of a stratified grid for acoustic measurements, divided into four subareas (A: 69°30'-71°30'N, B: 67°00'-69°30'N, C: 63°30'-67°00'N and D: 62°00'63°30'N) (Figure 2.1) (Mehl et al. 2017.), with fixed bottom trawl stations and additional bottom and pelagic stations on acoustic registrations within each of the strata.

Bottom trawl catch data and environmental data collected on hydrographic stations in 1995, 2005 and 2017 are the basis for this thesis. The study area's state in a colder period is here assumed to be represented by the data from 1995, while the two warmer years are 2005 and 2017. This is based on temperatures measured by hydrographic stations taken together with the trawl-stations on the survey, and in 2005 these recordings were above the average for 1997-2004 (Aglen et al. 2005). The data from the warm period (2005) make it possible to compare variability in the community to the colder period (1995), with an additional warm year as a control (2017). As the survey is conducted in October/November each year no seasonal variability is considered.

During the surveys, hydrographic stations were conducted semi-regularly, where CTD-measurements were taken on some of the fixed bottom trawl stations or with a set distance of 30 nautical miles between each station (Aglen et al. 2005, Mehl et al. 2017). The CTD-measurements were used to obtain information about ocean temperature and salinity levels.

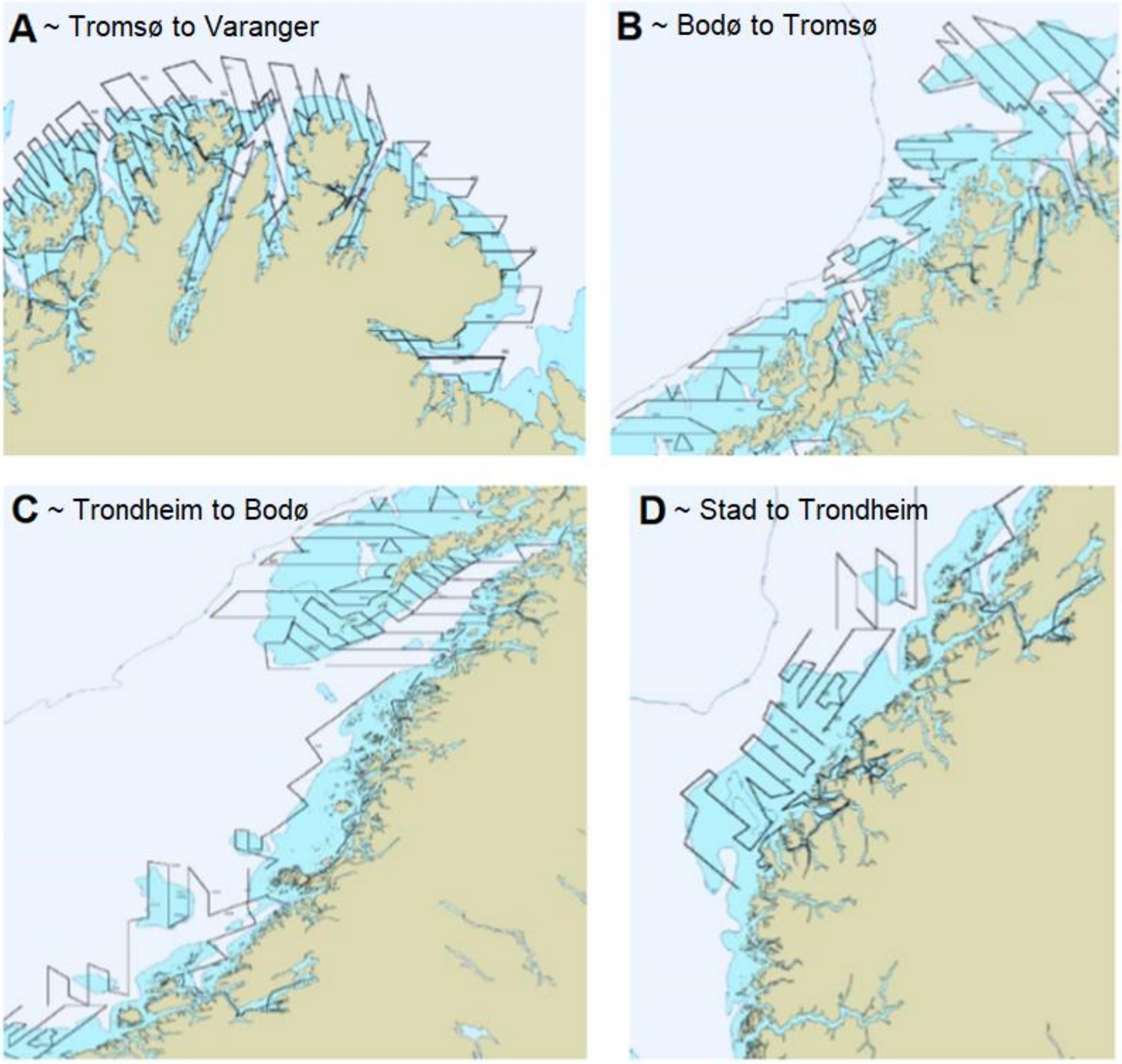

Figure 2.1 *Standard transect in the four study areas (A – top left,* 69°30’-71°30’N*), (B – Top right,* 67°00’-69°30’N*), (C – bottom left,* 63°30’-67°00’N*), (D- bottom right,* 62°00’63°30’N*) along the Norwegian coastline, used in IMR’s annual coastal survey, here from 2017. Taken from IMR’s annual coastal survey report (Mehl et al. 2017)*

2.1.2 Trawl equipment and standard procedures for catches

i) *Year 1995*

In 1995, IMR's coastal survey on saithe started to include measurements of coastal cod to obtain length, weight and age information. Similar to 2005 and 2017, the survey in 1995 also included stations in both inner fjords and open ocean (bank) areas. However, no trawls were conducted in the open banks for area D (i.e. 62^{o} to 63.5 ^{o}N) (Table 2.1).
Trawl gear consisted of the Campelen 1800 standard shrimp trawl (Figure 2.2) with rock hopper gear and 35 mm mesh size in the cod end, together with Scanmar sensors that provided the ship with information about the opening of the trawl, door spread and bottom contact.

ii) *Years 2005 & 2017*

The equipment, stations and survey design are very similar for 2005 and 2017 (Table 2.1), as the survey was standardized in 2003. Additional stations were added in 2017, which was done as it was considered necessary to gather more information on deep water shrimps and redfish (Mehl et al. 2017).

The Campelen 1800 standard shrimp trawl with rock hopper gear, 20 mm mesh size in the cod end and 80mm (stretched) in the front part is the standard fishing gear used together with Scanmar sensors. Standard trawl duration is 30 minutes at a speed of 3 knots. Data were collected with several vessels, in 2005 with RV Johan Hjort and RV Helmer Hansen (also RV Jan Mayen), and in 2017 with RV Johan Hjort and RV Kristine Bonnevie.

Trawl catches are sorted and weighed by species according to standard procedures (Mjanger & Senneset 2017). Length measurements (e.g. total length; from snout to end of the caudal fin) are done for most species, either of all sorted individuals or of a subsample from large catches. Additional information such as otoliths, sex and gonad maturity stage are collected for a few selected species. All the biological data is stored together with trawl station information in a database onboard. Such biological data are however not an area of focus in this thesis.

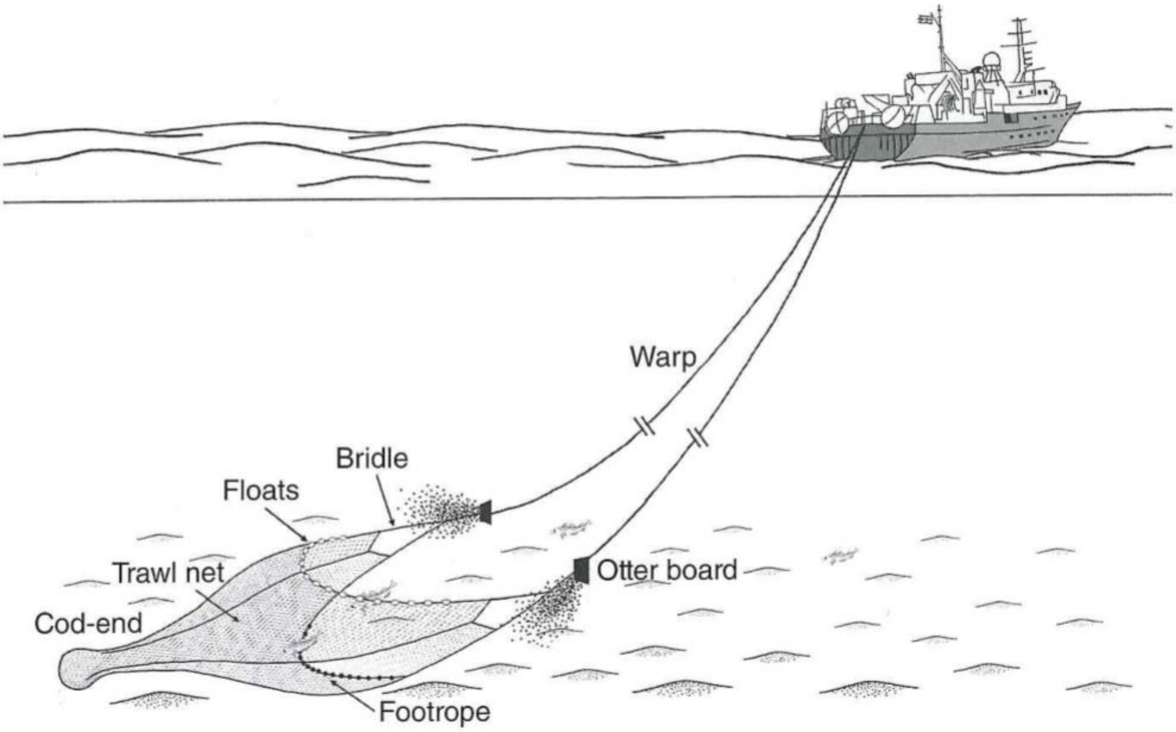

Figure 2.2 *Illustration of a bottom trawl with its components, illustration by R. Jakobsen (Salvanes et al. 2018).*

Table. 2.1 *Total number of bottom trawl stations in the dataset from 1995, 2005 and 2017 from IMR's annual coastal survey between Stad and Varanger. Distance is given in nautical miles (nm) and stations are separated by distance to the nearest shoreline (stations >8nm from the shoreline is defined as ocean zone, and <8nm is defined as coastal zone) and by latitude: Area A (69.5º to 71.3º N), Area B (67º to 69.5ºN), Area C (63.5º to 67ºN) and Area D (62º to 63.5ºN)*

	Area	Number of coastal stations (<8nm)	Number of ocean stations (>8nm)	
1995	A	51	5	
	B	24	4	
	C	23	8	
	D	14	0	
			Sum	129
	Area	Number of coastal stations (<8nm)	Number of ocean stations (>8nm)	
2005	A	58	5	
	B	24	9	
	C	13	5	
	D	3	1	
			Sum	118
	Area	Number of coastal stations (<8nm)	Number of ocean stations (>8nm)	
2017	A	79	12	
	B	32	12	
	C	24	7	
	D	10	6	
			Sum	182

2.2 Stratification of the study area

The study area along the Norwegian coastline between Stad and Varanger was divided into eight subareas based on latitude and a fixed nautical mile (nm) distance from the mainland's shoreline. The latitude gradient from 62ºN to 71.3ºN were divided into four areas; Area A (69.5º to 71.3º N), Area B (67º to 69.5ºN), Area C (63.5º to 67ºN) and Area D (62º to 63.5ºN) (Figure 2.3).

In order to compare results from inner fjords and open bank areas, each area was further divided based on a nautical mile distance to coast. Every trawl station in closer proximity to the mainland's shoreline than eight nm were categorized as coastal (Co), while remaining stations (> 8 nm) were categorized as ocean (Oc). Subareas with fewer than three stations per year (Table 2.1) are excluded from further discussion as so few stations cannot be regarded to represent the complexity and diversity of an entire area. This includes only open ocean subareas in area D for both 2005 and 1995 (Table 2.1), which thus are not included in the discussion as reliable results.

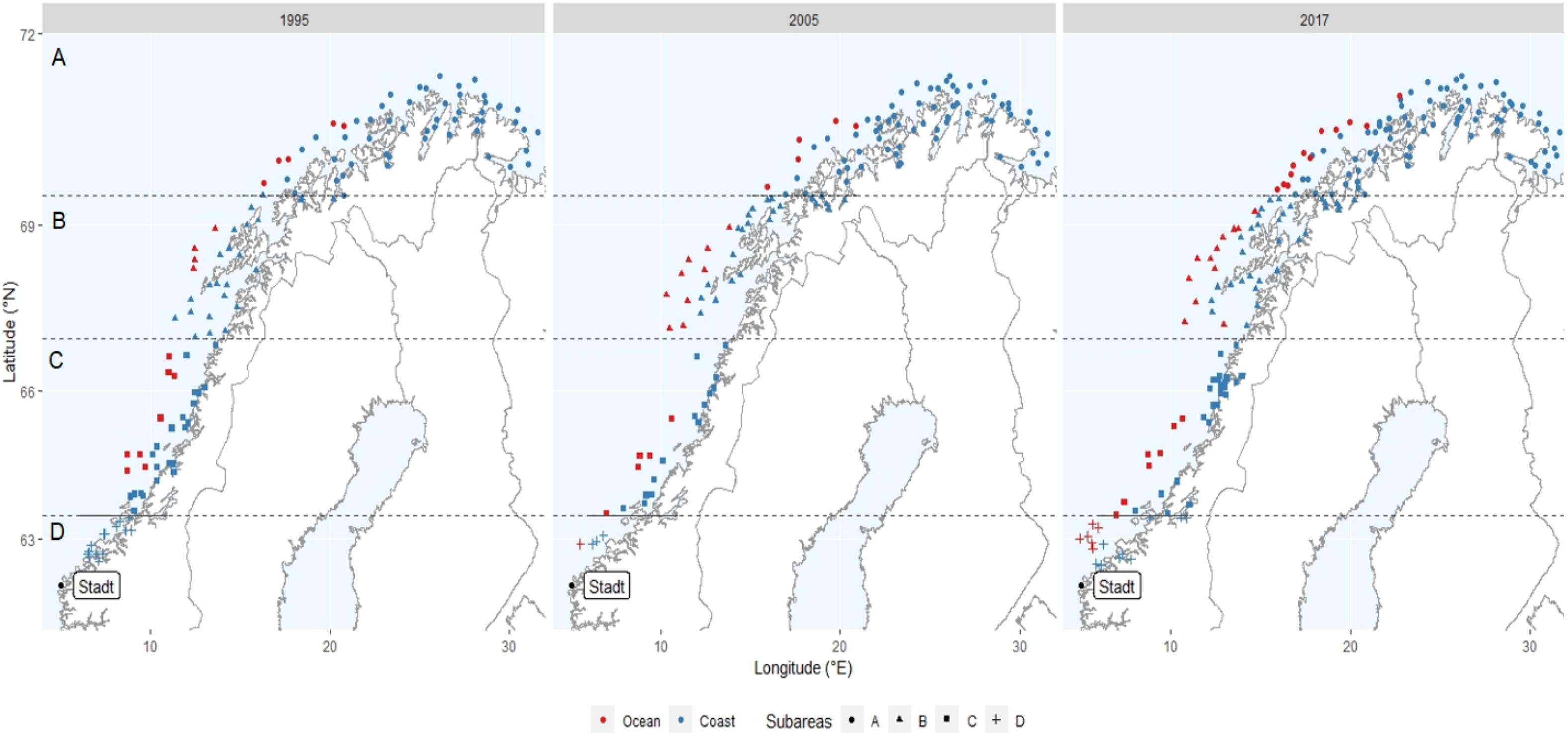

Figure 2.3 All bottom trawl stations from IMR's annual coastal survey, separated by latitude (dashed line) Area A (69.5º to 71.3º N), Area B (67º to 69.5ºN), Area C (63.5º to 67ºN) and Area D (62º to 63.5ºN), and with coastal or ocean categorization for the years 1995, 2005 and 2017

2.3 Preparation of data

The raw data-files for the years 1995, 2005 and 2017 were extracted from the IMR database and converted using R (version 3.5.0) into a common spreadsheet. Only valid bottom trawls were selected for the final dataset (i.e. interrupted or not acceptable hauls, due to reasons such as tearing of the net are not seen as valid). The stations distance to the mainland's shoreline were estimated using ArcMap (version 10.5) at IMR. The CTD data were not included in the files from IMR's database. These were extracted from the Norwegian marine data-centre (Norsk marint datasenter - NMD), and consists of the bottom temperature, depth and the position of the hydrographic station. CTD measurements not conducted at the bottom trawl stations were considered representative for the station based on two criteria; the hydrographic station must be within a 5 nm distance to the nearest trawl station and with no more than 50 m in vertical depth differences between the CTD and the bottom trawl. Stations not meeting these criteria were excluded from the constrained correspondence analysis (CCA). This was done as the CCA is the only analysis that directly compares trawl stations and the relating temperature, and as temperatures fluctuate rapidly over both horizontal and vertical distances in the ocean, this was seen as the best solution to avoid drawing false conclusions. They are however still included in the overall investigation of the area's temperature-conditions.

In order to adjust for differences in sampling effort (trawl duration) in the different areas and years, all catches presented are standardised catches per unit of effort (CPUE), with effort being trawled distance in nm.

2.3.1 Species selection

The species included in the final dataset are based on modifications from a report on the demersal fish community in the Barents Sea (Artamonova 2012). The full species list (Table 2.3) includes 86 taxa from 33 different families.

1. Species not classified as fish were all excluded from the data set.
2. Only catches that were identified to complete species name were qualified; taxa that were only identified to family or genus are not included.
3. Epipelagic, nerito-pelagic and bathypelagic taxa (Chernova et al. 1995) were also removed from the data set, with the exception of *Argentina silus*, *Argentina sphyraena, Pollachius virens, Pollachius pollachius, Trisopterus esmarkii* and *Galeus melastomus*, that were included.

4 Species with fewer than eight individuals caught per year and/or found at fewer than three stations per year are included in the full species list (Table 2.3), but are not included in any analyses. This reduced dataset still includes more than 50 taxa for 2017, over 35 for 2005 and over 30 for 1995.

Table 2.3 *Species list with species common name, biogeographical affinity according to (Chernova et al. 1995) and (Mecklenburg et al. 2011). With additional sources on species not found in Chernova and Mecklenburg; (Magnussen & Magnussen 2009), (Bañón & Serrano 2010), (Ellis et al. 2004), (Aboim et al. 2005), (Coelho & Erzini 2008), (Sanchez et al. 1998), (Halliday 1969), (Møller & Jørgensen 2000), (Byrkjedal & Høines 2007). Zoogeographical affinity definition; Arctic (A), Mainly Arctic (MA), Arctic Boreal (AB), Boreal (B), Mainly Boreal (MB), Southern Boreal (SB) and Widely Distributed (WD). Years the species were caught are also listed.*

Family	**Species**	**Common name**	**Zoogeographical affinity**	**Year(s) caught**
Liparidae	*Careproctus derjugini*	Derjuginis' snailfish	AB	2017
	Liparis liparis	Common seasnail	B	*2017
	Liparis bathyarcticus	-	MA	*2005
	Careproctus reinhardti	Sea tadpole	MA	2005
Ammodytidae	*Hyperoplus lanceolatus*	Great sandeel	B	2017
	Ammodytes marinus	Lesser sandeel	B	*2017
Lotidae	*Gaidropsarus argentatus*	Silver rockling	AB	*(2017, 2005)
	Molva molva	Common ling	B	2017, 2005, 1995
	Enchelyopus cimbrius	Fourbeard rockling	AB	2017, 2005, 1995
	Brosme brosme	Cusk/tusk	B	2017, 2005, 1995
	Molva dypterygia	Blue ling	B	2017, *1995
Cottidae	*Icelus bicornis*	Twohorn sculpin	MA	*2005
	Artediellus atlanticus	Atlantic hookear sculpin	AB	2017, 2005, *1995
	Triglops pingelii	Ribbed sculpin	AB	*2017, 2005
	Triglops murrayi	Moustache sculpin	B	2017, 2005,*1995
Zoarcidae	*Lycodes esmarkii*	Greater eelpout	MB	*(2017, 1995)
	Lycodes rossi	Threespot eelpout	A	2017
	Lycenchelys sarsii	Sars' eelpout	A	*2017
	Lycenchelys muraena	Moray wolf eel	AB	2017
	Lycodes vahlii	Vahl's eelpout	MB	2017, 2005
	Lycodes seminudus	Longear eelpout	A	*2005
	Lycodes squamiventer	Scalebelly eelpout	A	2017
Gadidae	*Boreogadus saida*	Polar cod	A	*2005
	Trisopterus esmarkii	Norway pout	B	2017, 2005, 1995
	Gadus morhua	Cod	MB	2017, 2005, 1995

	Trisopterus minutus	Poor cod	MB	2017, 2005, 1995
	Pollachius pollachius	Atlantic pollock	B	2017, 2005, 1995
	Pollachius virens	Saithe	B	2017, 2005, 1995
	Melanogrammus aeglefinus	Haddock	MB	2017, 2005, 1995
	Merlangius merlangus	Whiting	SB	2017, 2005, 1995
	Gaidropsarus argenteus	Silvery pout	SB	2017, 2005, 1995
Arhynchobatidae	*Bathyraja spinicauda*	Spinetail ray	MB	2017
Pleuronectidae	*Microstomus kitt*	Lemon sole	B	2017, 2005, 1995
	Platichthys flesus	European flounder	MB	*1995
	Reinhardtius hippoglossoides	Greenland halibut	AB	*(2017, 2005)1995
	Hippoglossus hippoglossus	Atlantic halibut	MB	2017, 2005 1995
	Hippoglossoides platessoides	American plaice	AB	2017, 2005, 1995
	Pleuronectes platessa	European plaice	MB	2017, 2005, 1995
	Limanda limanda	Common dab	MB	2017, 2005, 1995
	Glyptocephalus cynoglossus	Witch flounder/Grey sole	MB	2017, 2005, 1995
Macrouridae	*Coryphaenoides rupestris*	Rock grenadier	B	2017, *2005, 1995
	Macrourus berglax	Roughhead grenadier	MB	*2017
Carapidae	*Echiodon drummondii*	Pearlfish	B	*2017
Stichaeidae	*Anisarchus medius*	Stout eelblenny	MA	*2017
	Lumpenus lampretaeformis	Snake blenny	A	2017, 2005*, 1995
	Leptoclinus maculatus	Daubed shanny	A	2017,*(2005, 1995)
Rajidae	*Dipturus batis*	Blue skate/Common skate	B	*1995
	Rajella fyllae	Round ray	MB	2017,2005, *1995
	Leucoraja fullonica	Shagreen ray	MB	*2005
	Dipturus oxyrinchus	Longnosed skate	B	2017, *2005, 1995
	Raja clavata	Thornback skate	B	*1995
	Rajella lintea	Sailray	B	*2017
	Amblyraja radiata	Thorny skate	B	2017, 2005, 1995
	Dipturus nidarosiensis	Norwegian skate	B	2017
	Leucoraja circularis	Sandy ray	B	*(2017, 2005)
Agonidae	*Leptagonus decagonus*	Atlantic poacher	AB	*2017
Argentinidae	*Argentina silus*	Greater argentine	B	2017, 2005, 1995
	Argentina sphyraena	Lesser argentine	SB	2017, 2005
Lophiidae	*Lophius piscatorius*	Anglerfish	SB	2017, 2005, 1995
Anarhichadidae	*Anarhichas lupus*	Atlantic wolffish	MB	2017, 2005, 1995
Sebastidae	*Sebastes viviparus*	Norway redfish	B	2017, 2005, 1995
	Sebastes norvegicus	Rose fish	AB	2017, 2005, 1995
	Sebastes mentella	Deepwater redfish	MB	2017, 2005, 1995
	Helicolenus dactylopterus	Blackbelly rosefish	B	2017, 2005

Psychrolutidae	*Cottunculus microps*	Polar sculpin	MA	2017, *2005
Paralepididae	*Paralepis coregonoides*	Sharpchin barracudina	WD	*2005
	Arctozenus risso	Spotted barracudina	WD	2017,*2005,1995
Etmopteridae	*Etmopterus spinax*	Velvet belly lanternshark	B	2017, 2005, 1995
Callionymidae	*Callionymus lyra*	Common dragonet	B	*2017
	Callionymus maculatus	Spottet dragonet	B	2017,*2005
Pholidae	*Pholis gunnellus*	Rock gunnel	MB	*2017
Bothidae	*Arnoglossus laterna*	Mediterranean scaldfish	MB	*2017
Cyclopteridae	*Cyclopterus lumpus*	Lumpfish	MB	2017,2005,1995
Moronidae	*Dicentrarchus labrax*	European bass	SB	2017
Anguillidae	*Anguilla anguilla*	European eel	SB	*2017
Scyliorhinidae	*Galeus melastomus*	Blackmouth catshark	SB	2017, 2005, 1995
Merlucciidae	*Merluccius merluccius*	European hake	B	2017, 2005, 1995
Phycidae	*Urophycis tenuis*	White hake	SB	*2017
	Gaidropsarus vulgaris	Three-bearded rockling	SB	*(2005, 1995)
	Phycis blennoides	Greater forkbeard	SB	2017, 2005, 1995
Scophthalmidae	*Lepidorhombus whiffiagonis*	Megrim	B	2017, 2005 1995
	Phrynorhombus norvegicus	Norwegian topknot	B	*(2017, 2005)
	Lepidorhombus boscii	Four-spot megrim	SB	*(2017,2005,1995)
Chimaeridae	*Chimaera monstrosa*	Rabbit fish	B	2017, 2005, 1995
Triglidae	*Eutrigla gurnardus*	Grey gurnard	SB	2017, 2005, 1995
Squalidae	*Squalus acanthias*	Spiny dogfish	WD	2017, 2005, 1995

*Species with fewer than eight individuals present and/or present at fewer than three sites in that year

2.4 Data analysis

All data preparation, analyses and graphical visualisations were done using R (version 3.5.0) in R Studio. A simple exploratory graphical data analysis was first conducted in order to investigate the patterns and distributions of the data, together with discovering possible outliers and to determine if any data transformations were necessary. Histograms were made for total catch (CPUE) and of some of the most abundant species (Appendix 1.A). As the data were highly skewed with a few very large catches dominating, it was apparent that a data transformation was necessary. A logarithmic transformation was chosen as the data set contains count-data ($\log_e$+1 to account for all the zero's in the dataset) to make the data less skewed.

2.4.1 Spatial distribution

The investigation of the spatial distribution of species in 1995, 2005 and 2017 was done by comparing species centre of distribution from the cold period to the warm periods.
The centre of distribution (COD) is defined as the average latitude where each specie is located for each year. It is calculated using the number of stations (n) the species is caught, and the abundance of that species (x) (CPUE – number of individuals) in each station (j) as weight (equation 1). This was done for the coastal stations (Co) and ocean stations (Oc) in order to observe possible shifts in species distribution in both areas.

$$Average\ latitude\ (COD) = \frac{\sum_{j=1}^{n} Latitude_j x_j}{\sum_{j=1}^{n} x_j} \qquad (1)$$

Where latitude $_j$ refers to the latitude of station j and x $_j$ the CPUE of station J.
COD could not be calculated for all species as many taxa were not caught in all three years. Only species that were present above the set threshold (i.e.; present at ≥3 or more stations or caught ≥8 individuals per year) in the cold period (1995), and at least in either 2005 and/or 2017 were selected. Only species that present a marked shift in distribution since 1995 are included in figures.

Species may be present along the entire Norwegian coastline, thus pinpointing a distributional centre could be misleading. Each species distribution is therefore also presented graphically using maps for those showing marked trends in latitude shifts or from coastal to open bank areas, to avoid drawing false conclusions for species having a wide distribution.

2.4.2 Species richness and diversity

Data exploration was first done to give insight into whether the different years and subareas are comparable in relation to the number of species and number of sites sampled, as there is almost always an association between the number of observations and the number of species registered. In order to quantify whether the number of stations sampled in all three years have resulted in the same expected number of species for all subareas, rarefaction curves were made. This is a common technique in ecology to assess species-richness based on sampling effort, given a number of sampled individuals. Rarefaction conducts a repeated random re-sampling in a pool of individuals, and then plots the average number of species represented by an increasing number of individuals (King et al. 2005). This results in a curve which increases rapid at first (where the most common species are), then reaches a plateau when only the most rare species remain. Species richness can only be compared between areas if they have reached this plateau (King et al. 2005).

Rarefaction assumes that the number of times a species appears is a reflection of sampling-effort (effort is defined as the number of individuals sampled). Hence, it does not take into account species-abundance, only species-richness (Gotelli et al. 2011), and is overall a reflection of how completely the areas have been sampled. This was done for each year, presenting rarefaction curves for each of the eight subareas. The R package “vegan” (Oksanen et al. 2018) was used to make rarefaction curves.

Investigation of the eight subareas species diversity was done using the Shannon-Wiener index (equation 2). It is one of the most common indices used to measure ecological diversity in a community, and is based on two main components. 1) The number of species present (richness) and 2) their relative abundance (evenness) (Kerkhoff 2010). Shannon’s index (H’) uses the proportion of individuals (p_i) in a species (i) and sums it over the total number of species in the community (S), which is then multiplied by -1 to obtain a positive value.

$$H' = -\sum_{i=1}^{S} p_i \ln p_i \qquad (2)$$

2.4.3 Species composition by multivariate analysis

The reduced data set still includes over 50 taxa and several environmental variables, hence multivariate analyses (MVA) are necessary. Such methods will make it possible to comprehend and interpret such large ecological data, show the effects of several variables and help present the structures in the data set. Ordination was chosen as a way to summarise complex multivariate data in a convenient, low-dimensional way, and thus be able to investigate whether there has been a change in species composition between 1995, 2005 and 2017.

A constrained correspondence analysis (CCA) was implemented, with a χ^2 distance as a default for the model, and was chosen based on the unimodal responses of the species along a continuous gradient, which was investigated using the R package "vegan" (Oksanen et al. 2018)**.** A Decorana analysis was first conducted to investigate the axis length of the first dimension (DCA1), in order to avoid some common faults in linear correlation techniques like PCA; curvature of straight gradients and how it is only valid over a short gradient (Palmer no date). As the analysis showed an axis length of more than 2.5, linear models were excluded (Appendix 1.D).

A CCA uses weighted principal components, which results in a species optimum score, a site optimum score and an environmental optimum score, as it simultaneously ordinates both species, sites and environmental variables in order to find weighted sum of environmental variables that fit the species best. This type of analysing allows for species composition to be investigated, and makes it possible investigate at the amount of variance in the species that is explained by the three years.

An ordination was conducted to gain insight in the species composition, with several constraints influencing the model. The three years were included in the model transformed to factors, together with the eight subareas (A, B, C, D and coastal/ocean division). Temperature, depth and latitude were the other variables of interest set prior to the analysis. The continuous variables (temperature, depth and latitude) were fitted as vectors onto the ordination, presented as arrows onto the ordination space, which are showing the direction of increase. Not all constraints are presented (not included; area A, B, C and D, or area Co and Oc) in the ordination graphics in order to avoid unnecessary clutter.

In order for the analysis not to be dominated by rare species, the threshold for species to be present at minimum three sites to be included was chosen also in this analysis. The CCA and ordination graphics are limited to the first two dimensions after investigations on the necessity of including further dimensions were done using a simple graphical method in screeplot**,** which displays the proportion of the variance that is explained by each dimension in the CCA (Appendix 1.D). As most of the variance was explained in the first two dimensions, adding further dimensions was deemed unnecessary. Ordination graphics are made using the R-package “ggvegan” (Simpson 2017).

For the statistical testing of the constrained ordination results, a Monte Carlo permutation test was used via anova.cca, which tests the statistical significance of species-environment relationships, under the null-hypothesis that species are unrelated to the set constraints. The test randomly permutes (i.e. it builds a sampling distribution by resampling the observed data) the environmental data (set to 999 permutations), then if the species relate better to the observed data than the random data above a threshold of 95% ($p<0.05$) of the time, the species are said to be significantly related to the environmental variables (Oksanen 2005). Finally, the envfit function was used to obtain the p-value of each variable with the overall species composition, to see which constraints significantly influence the species composition.

Results

3.1 Overview of the study area from 1995 to 2005 & 2017

Average bottom temperatures have increased in all of the seven comparable subareas since 1995 (Figure 3.1.1;, Appendix 1.B). In 1995, the average temperature measured between Stad and Varanger was 6.62 °C, in 2005 this temperature had increased by 1.6 °C to 7.8 °C and was at 7.74 °C in 2017. The areas in higher latitudes had generally lower temperatures than those closer to Stad, while the coastal/ocean temperature differences were minimal, with the exception in the area around Tromsø to Varanger (area A: 69.5 to 71.3° N). The increase in temperatures were most dramatic for area D (62 to 63.5° N), which is located furthest south.

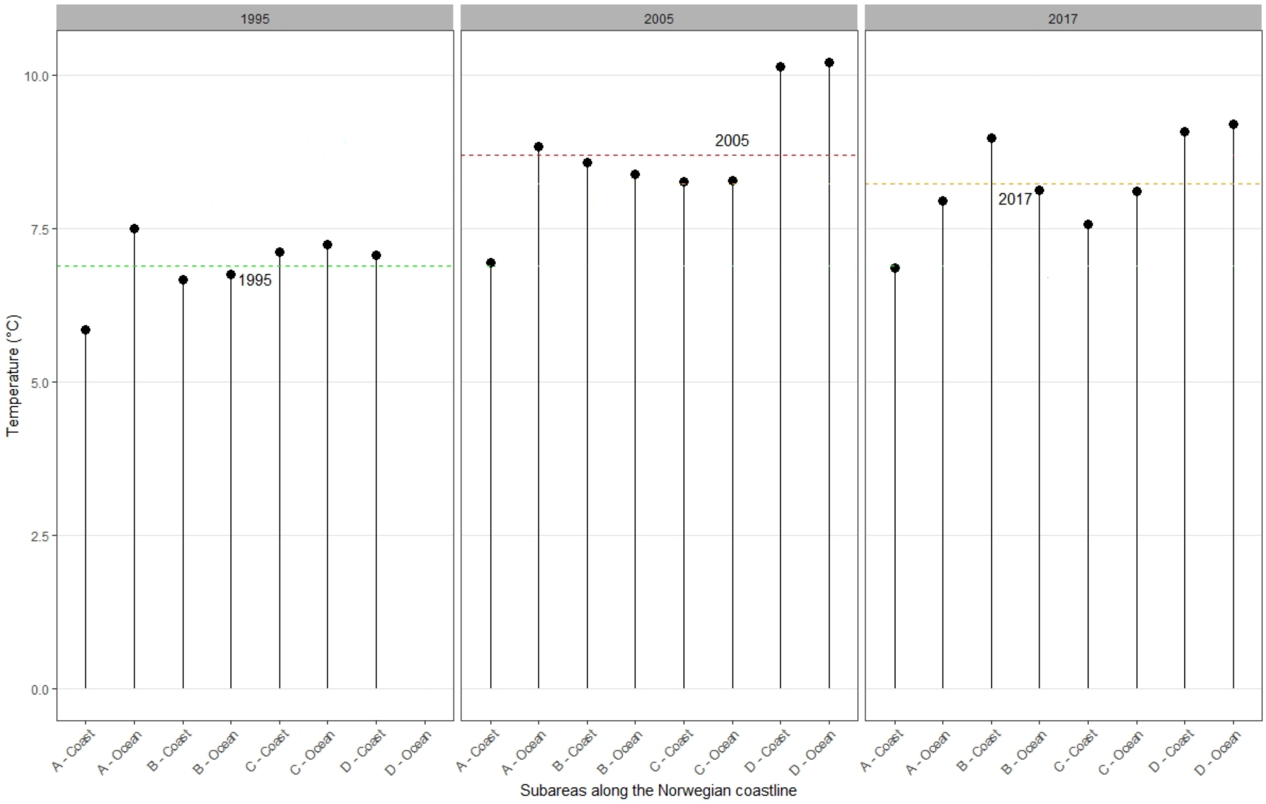

Figure 3.1.1 *Average temperatures (°C) measured for the eight subareas; Area A (69.5° to 71.3° N), Area B (67° to 69.5°N), Area C (63.5° to 67°N) and Area D (62° to 63.5°N), and with coastal (Co) or ocean (Oc) categorization, along the Norwegian coastline from 62-72°N, with the mean temperature for each year (dashed line).*

There is a trend of increasing abundance for most species from 1995 to 2017. Species such as Norway pout (*Trisopterus esmarkii*), haddock (*Melanogrammus aeglefinus*), saithe and greater argentine (*Argentina silus*) are some of the species with largest CPUE, while species such as lesser argentine (*Argentina sphyraena*), moustache sculpin (*Trigplos murrayi*) and Atlantic hookear sculpin (*Artediellus atlanticus*) have shown clear increases in most areas from 1995 to the warmer years (Figure 3.1.2). Overall, the ocean subareas show the clearest increase in abundance.

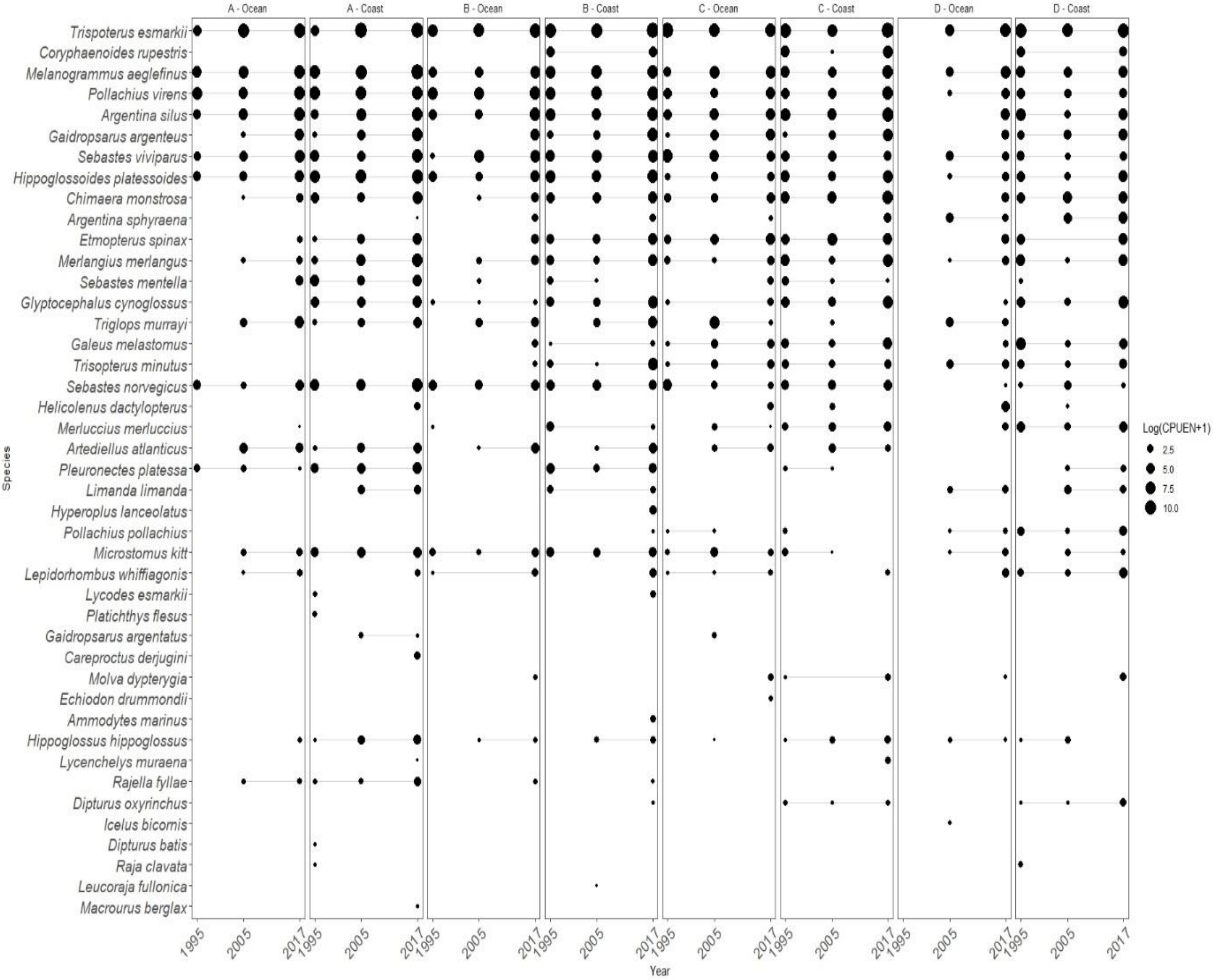

Figure 3.1.2 *Overview of the 86 taxa recorded on IMR's annual coastal survey in 1995, 2005 and 2017. Filled circles refer to Catch Per Unit of Effort on log$_e$ scale (log(CPUE+1)), with catch being number of individuals and the effort used is trawled distance per nm. There is one panel for each of the eight study areas between Stad and Varanger; Area A: 69.5º to 71.3º N, Area B: 67º to 69.5ºN, Area C: 63.5º to 67ºN and Area D: 62º to 63.5ºN, for coastal and ocean areas. Horizontal lines connect species that were caught in more than one year.*

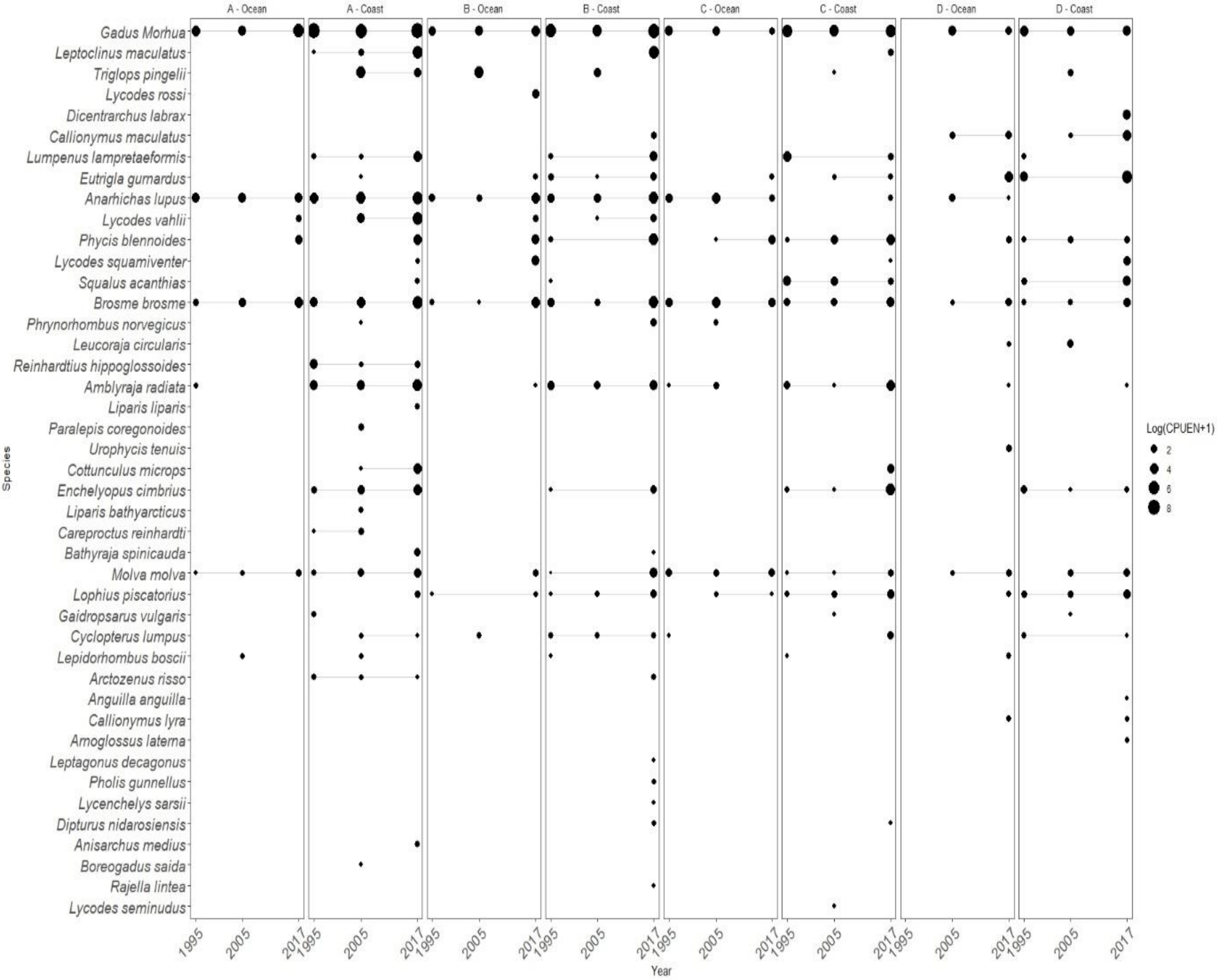

Figure 3.1.2 continued

3.2 Investigation of species richness and sampling effort

3.2.1 Rarefaction curves

The open bank areas (Oc) in the two areas furthest north; area A and B (i.e. between Varanger and Bodø), and the coastal (Co) areas in area A, C and D appear under-sampled as the curves are still steeply increasing (Figure 3.2.1). Areas C - Oc and B - Co (i.e. between Trondheim and Tromsø) are the only areas that indicate a flattening of the curve and thus sufficient sampling. Overall, area C - Oc shows a clear lower species-count than all coastal areas.

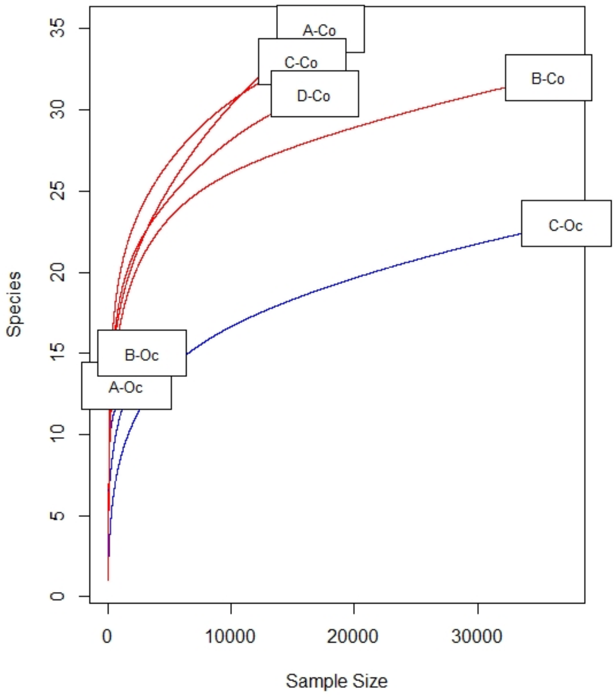

Figure 3.2.1 *Rarefaction-curve to assess species richness in relation to sampling effort in 1995 for subareas along the Norwegian coastline from Stad to Varanger; Area A (69.5 to 71.3 º N), Area B (67 to 69.5 ºN), Area C (63.5 to 67 ºN) and Area D (62 to 63.5 ºN), and coastal (Co) and ocean (Oc) categorization. Sample size is number of individuals.*

In 2005, only areas A and B which are furthest north appear sufficiently sampled as rarefaction curves for area A – Co and B – Co appear to reach a horizontal asymptote (Figure 3.2.2), and area A -Oc and B - Oc are showing a somewhat less steep increase. All other areas are still increasing. Species count and sample sizes has increased from 1995 to 2005, and coastal areas are still appearing more species rich than open ocean areas.

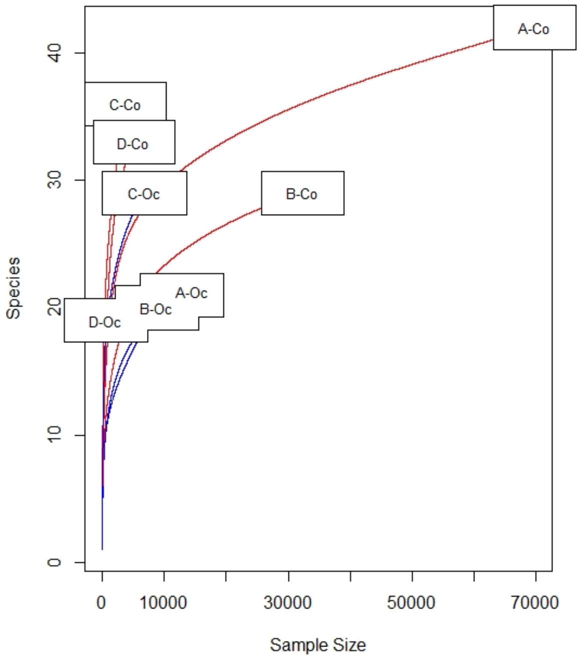

Figure 3.2.2 *Rarefaction-curve to assess species richness in relation to sampling effort in 2005 for the eight sampled subareas along the Norwegian coastline from Stad to Varanger; Area A (69.5 to 71.3 º N), Area B (67 to 69.5 ºN), Area C (63.5 to 67 ºN) and Area D (62 to 63.5 ºN), and coastal (Co) and ocean (Oc) categorization. Sample size is number of individuals.*

Sample size had increased further in 2017, and now a majority of the areas seem to reach a horizontal asymptote (Figure 3.2.3), thus indicating a sufficient number of stations. Only the areas furthest south, area C and D (i.e. between Bodø and Stad) are still increasing. Overall, the number of species found between Stad and Varanger increased from 1995 to 2005 and 2017, and the coastal areas are more species-rich than open bank areas (Figures 3.2.1-3.2.3).

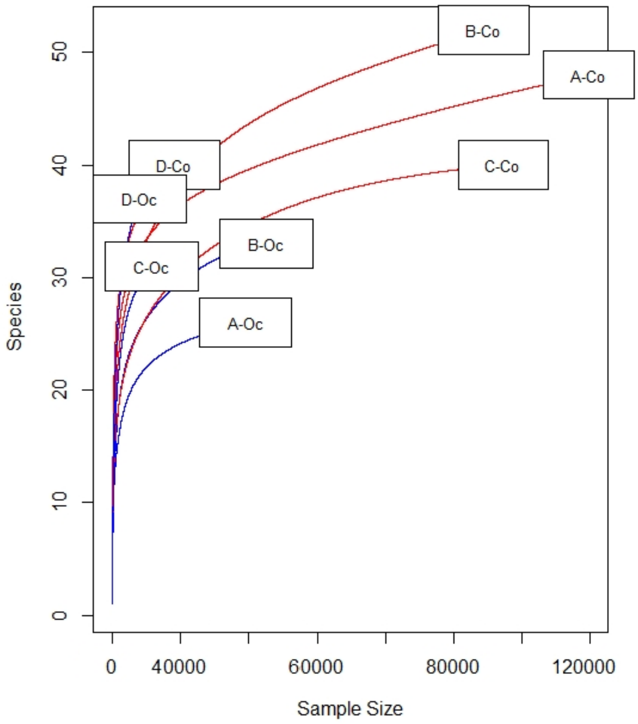

Figure 3.2.3 *Rarefaction-curve to assess species richness in relation to sampling effort in 2017 for the eight sampled subareas along the Norwegian coastline from Stad to Varanger; Area A (69.5 to 71.3 °N), Area B (67 to 69.5 °N), Area C (63.5 to 67 °N) and Area D (62 to 63.5 °N), and coastal (Co) and ocean (Oc) categorization. Sample size is number of individuals.*

3.2.2 The Shannon-Wieiner diversity index

No apparent trend in values from the diversity index is found for the areas along the Norwegian coast (Table 3.2). In the cold year 1995, most coastal areas had a higher diversity value than those of open bank areas, except for area B (67 to 69.5^{o} N). There is also an increase in diversity with increasing latitudes in this year. In the warmer years 2005 and 2017 the coastal/ocean trend is similar to 1995, with the only exception being the coastal zone in area C (63.5 to 67^{o} N), which now has a lower Shannon index than that of the open bank in 2017. Overall, the coastal subareas are more diverse than those further from the mainland, and the most diverse areas are found at the coast of area A (between Tromsø and Varanger) and area C (between Trondheim and Bodø).

Table 3.2 *Shannon's diversity index for all species registered in 1995, 2005 and 2017 for the eight subareas outside the Norwegian coastline from Stad to Varanger; Area A (69.5 to 71.3 ºN), Area B (67 to 69.5 ºN), Area C (63.5 to 67 ºN) and Area D (62 to 63.5 ºN), and coastal and ocean categorization.*

Year	A - Ocean	A - Coast	B - Ocean	B - Coast	C - Ocean	C - Coast	D - Ocean	D - Coast
1995	1.569	1.765	1.329	0.958	0.601	1.197	-	0.971
2005	0.797	1.393	1.197	1.195	1.499	1.934	-	0.801
2017	1.434	1.988	1.223	1.482	1.433	1.155	1.307	1.755

3.3 Species composition

The ordination graphic from the constrained correspondence analysis (CCA) presents as expected a negative correlation between temperature and latitude and between temperature and depth (Figure 3.3). Species near each other are likely to be found in similar environments/habitats, and their position in relation to the vectors in the ordination space reflects their affinity for those variables. Similarly, stations found close to each other are similar in species composition and abiotic conditions such as temperature, depth and latitude/longitude. Species and stations found close to the centre are seen as average for all years, or the model are explaining them poorly in the first two dimensions.

Arctic (A), Mainly Arctic (MA) and Arctic Boreal (AB) species like vahl's eelpout (*Lycodes vahlii*) and rose fish (*Sebastes norvegicus*) are frequent along the latitude gradient (Figure 3.4). Other arctic species such as moray wolf eel (*Lycenchelys muraena*), polar sculpin (*Cottunculus microps*), greenland halibut (*Reinhardtius hippoglossus*) and sea tadpole (*Careproctus reinhardti*) are more frequent along the depth gradient (Figure 3.5). Species along the temperature vector are associated with higher temperatures, and no arctic-species are found here. Southern-Boreal (SB) species such as grey gurnard (*Eutrigla gurnardus*), lesser argentine, megrim (*Lepidorhombus whiffiagonis*) and anglerfish (*Lophius piscatorius*) are common at this temperature gradient, together with several Boreal (B) and Mainly Boreal (MB) species.

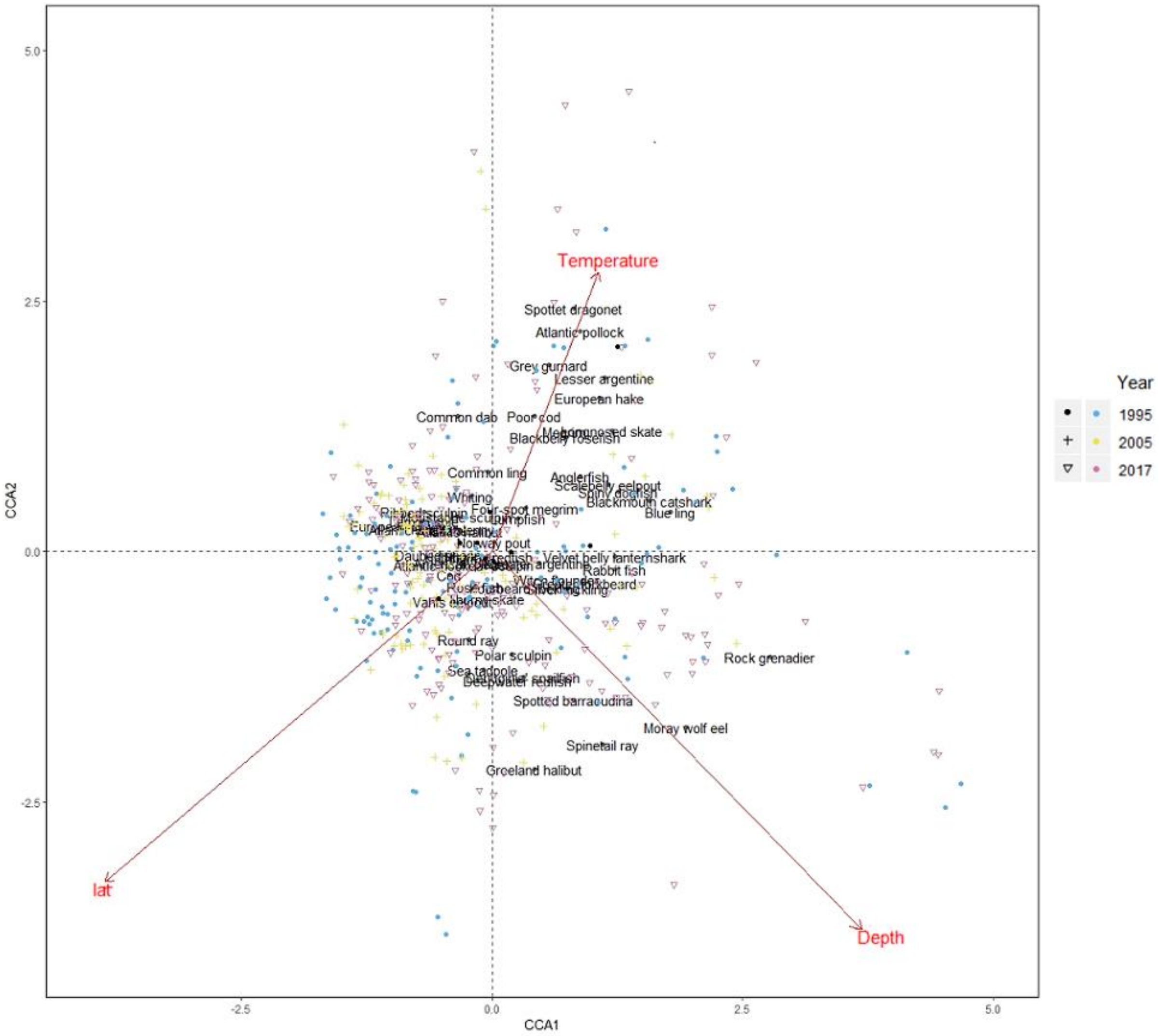

Figure 3.3 – *Ordination plot from the constrained correspondence analysis (CCA) for the years 1995, 2005 and 2017, represented by colour and shape. Presented for the first two canonical axes (CCA1 and CCA2). Arrows represent vectors showing the direction of increase for the continuous constraining variables (temperature, depth and latitude).*

The total (constrained inertia + unconstrained inertia) and constrained inertia reveal that the full model explains ~19% of the variation found in species composition (Table 3.3.1). The permutation test (Monte-Carlo) showed a significant p-value for the full model (Appendix 1.D), indicating that the observed differences in species composition are affected by the differences measured in temperature, latitude, depth, and also varies within the eight subareas of the Norwegian coast from 1995 to 2005 and 2017.

The envfit output (Table 3.3.2) showed significant p-values for all variables included in the CCA, with the lowest p-values found for temperature, depth and latitude (i.e. vectors), and the subareas A, B, C and D. These results reveal that there has been a change in species composition between the cold and the warm years, together with differences occurring between the eight subareas. The very low p-values for subareas A, B, C and D indicates that a change in species composition is more pronounced between these areas than for the coastal/ocean subareas.

Table 3.3.1 *Model output from the constrained correspondence analysis (CCA) for all three years. Eigenvalues for the first three canonical axes for the constrained and unconstrained models are presented, together with the total constrained and unconstrained inertia.*

	Constrained axes			
	CCA1	CCA2	CCA3	
Eigenvalues	0.3011	0.1558	0.0761	
		Total constrained		0.6466
	Unconstrained axes			
	CA1	CA2	CA3	
Eigenvalues	0.2238	0.1828	0.1592	
		Total unconstrained		2.8665

Table 3.3.2 *Model output from the envfit exploration of the constrained correspondence analysis (CCA). Eigenvalues for the first two canonical axes for the constrained model are presented (CCA1 & CCA2) for vectors and centroids (factors) included in the model. P-values for all constraints are also presented (p<0.05*, p<0.01**, p<0.001***). Area A: (69.5 to 71.3 ºN), Area B: (67 to 69.5 ºN), Area C: (63.5 to 67 ºN) and Area D: (62 to 63.5 ºN).*

	CCA1	CCA2	Pr(<r)
Vectors			
Temperature	0.3872	0.9219	0.001***
Depth	0.7229	-0.6909	0.001***
Latitude	-0.7804	-0.6252	0.001***
Factors			
Strata - Ocean	-0.0225	0.3972	0.005**
Strata - Coast	0.0055	-0.0964	
Strata - A	-0.5359	-0.4672	0.001***
Strata - B	-0.1537	0.0864	
Strata - C	0.9770	0.0580	
Strata - D	1.2519	2.0397	
1995	-0.0709	-0.0713	0.011*
2005	-0.3295	0.0830	
2017	0.1835	-0.0074	

3.4 Spatial distribution

3.4.1 Centre of distribution (COD)

Twenty-three out of 30 (~ 77%) species in the coastal zone (i.e. caught within an eight nm distance from the shoreline) showed a northern shift in distribution from 1995 to 2005, and 22 of 37 (~ 60%) species from 1995 to 2017 (Appendix 1.C). The species experiencing the most pronounced shifts in latitudinal distribution (Figure 3.4.1), are mainly Southern Boreal (SB) species such as whiting (*Merlangius merlangus*), silvery pout (*Gaidropsarus argenteus*), greater forkbeard (*Phycis blennoides*), blackmouth catshark (*Galeus melastomus*) and grey gurnard. Several Boreal (B) species also show pronounced northward shifts in distribution, such as for megrim, velvet belly lanternshark (*Etmopterus spinax*), lemon sole (*Microstomus kitt*) and greater argentine.

Nine of 37 (24%) species were found at a higher latitude in the cold year 1995 than in the two warmer years, and 20 of 37 (54%) species were observed at the lowest latitudinal mean in 1995 (Appendix 1.C).

Ten out of 14 (~71%) species in the open bank areas (i.e. caught further out than eight nm from the shoreline) have had a southern shift in distribution from 1995 to 2005, and from 1995 to 2017, 11 of 14 species moved further north (~78%). There is a clear increase in the number of taxa found above the set threshold in these open ocean areas from 1995 to 2017. This is apparent by the number of species that were present enough to have their COD calculated in the warmer years in these areas.

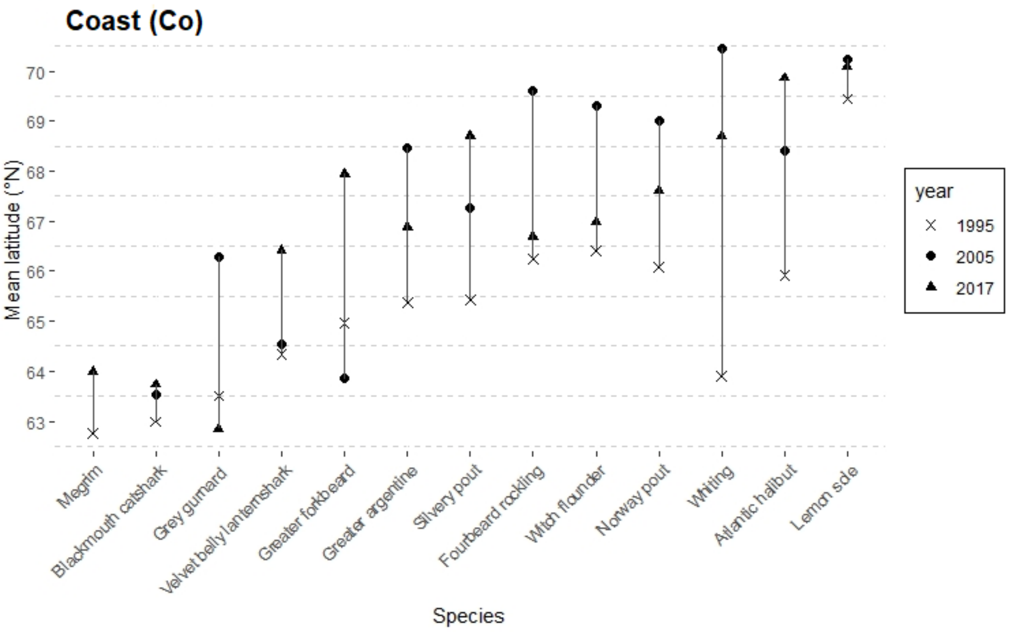

Figure 3.4.1 *Change in centre of distribution (COD) measured as mean latitude for species with noticeable shifts in COD between 1995 and 2017 in the coastal zone (caught within an eight nm distance from the coastline), along the Norwegian coastline*

There were 15 taxa registered in the ocean subarea in 1995 (above the set threshold set for presence of species), and by 2017, the number of taxa had increased to 26. While patterns in distribution for most species show opposite changes between 1995 and 2005 than for 1995 and 2017, some species, like Norway pout. Norway redfish (*Sebastes viviparus*), whiting, tusk (*Brosme brosme*) and velvet belly lanternshark does display clear northwards shifts in distribution in the oceanic zone for both years (Figure 3.4.2).

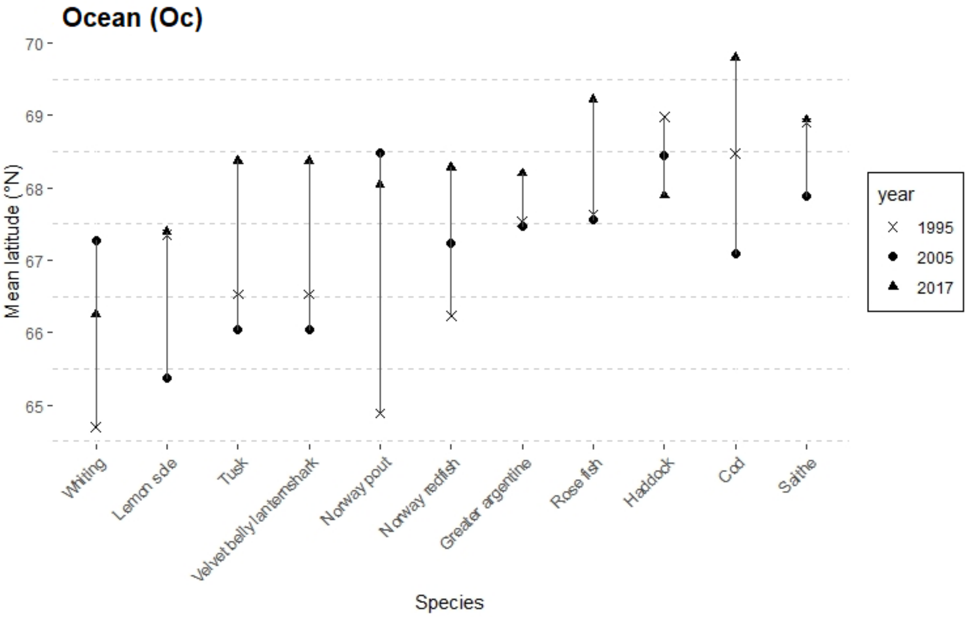

Figure 3.4.2 *Change in centre of distribution (COD) measured as mean latitude for species with noticeable shifts in COD between 1995 and 2017 in the ocean zone (caught more than eight nm from the coastline), along the Norwegian coastline*

3.4.2 Graphical mapping of spatial distribution for selected species

The boreal species greater argentine shows a clear increase in overall abundance and a noticeable increase in catches in northern latitudes around Varanger (Figure 3.4.3). There has also been an increase in catches of greater argentine in the open bank areas from 1995 to 2017.

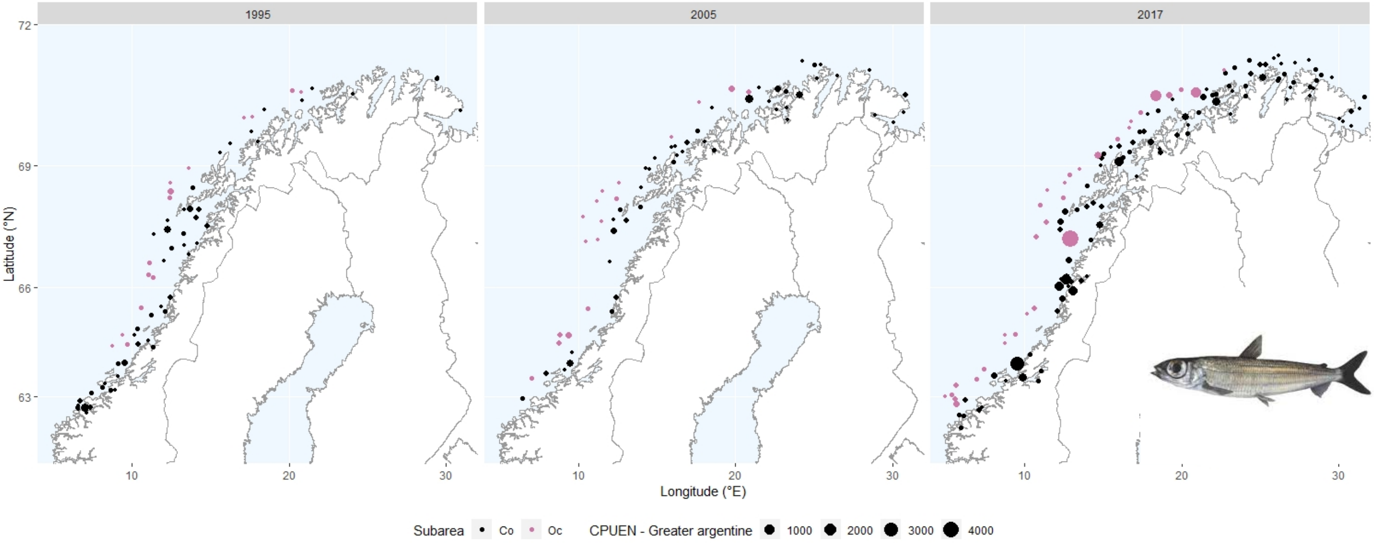

Figure 3.4.3 *Distribution of greater argentine (A. silus) along the Norwegian Coastline from 62-71.3 °N in 1995, 2005 and 2017. Abundance is displayed as the size of the circle and given in CPUE (number of individuals). Catches are categorized as coastal (black) or open ocean (pink). Photo greater argentine: Fiskeridirektoratet*

Norway pout shows a prominent increase in abundance from the cold year to the warmer years (Figure 3.4.4). In the areas furthest north the abundance has clearly increased, there has also been a noticeable decrease in area D (62 to 63.5 °N) from 1995 to 2017, particularly in the open ocean areas. While Norway pout abundance is highest in coastal areas in all three years, abundance in open ocean areas have increased by 2005 and 2017, especially in area A and B, around Varanger and Lofoten.

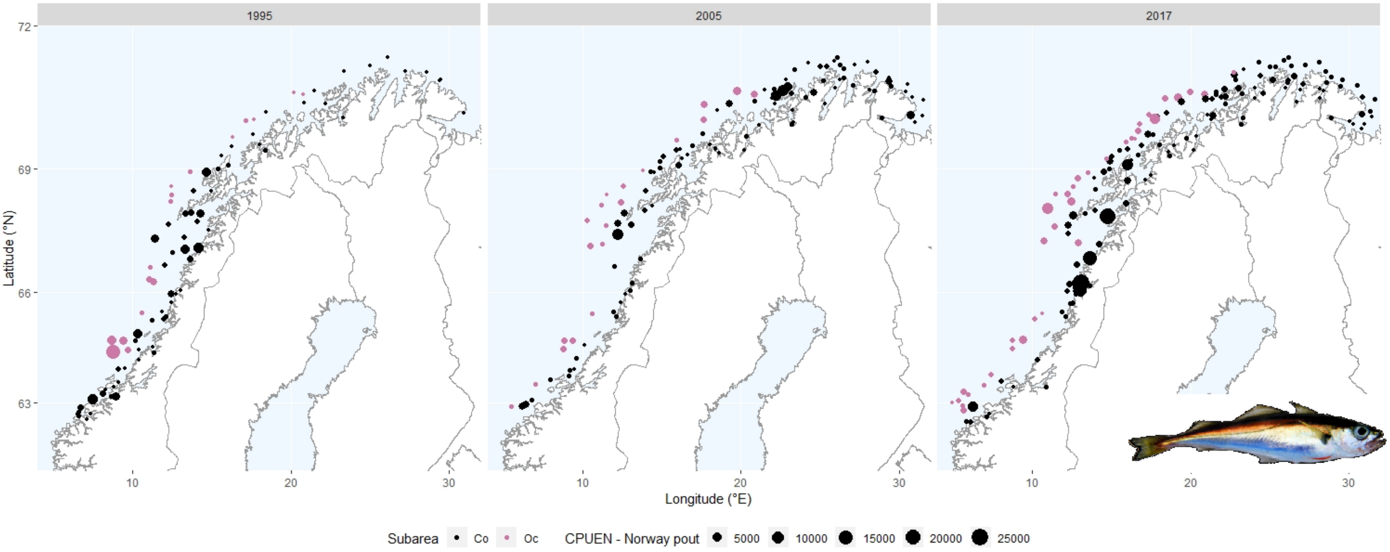

Figure 3.4.4 *Distribution of Norway pout (T. esmarkii) along the Norwegian Coastline from 62-71.3 ºN in 1995, 2005 and 2017. Abundance is displayed as the size of the circle and given in CPUE (number of individuals). Catches are categorized as coastal (black) or open ocean (pink). Photo Norway pout: Norges Sildesalgslag*

Silvery pout, classified as a southern boreal species, was caught in small amounts in 1995 compared to 2017, and was mainly found in the southern areas C and D (i.e. between Bodø and Stad) of the study area (Figure 3.4.5). An increase in catches is noticeable in 2005, and by 2017 there has been an overall increase along the entire coast, with a very prominent northward shift in distribution. Silvery pout was only found at one station in the ocean area in 1995, but in 2017 it was more widely distributed and common here as well (Figure 3.4.5).

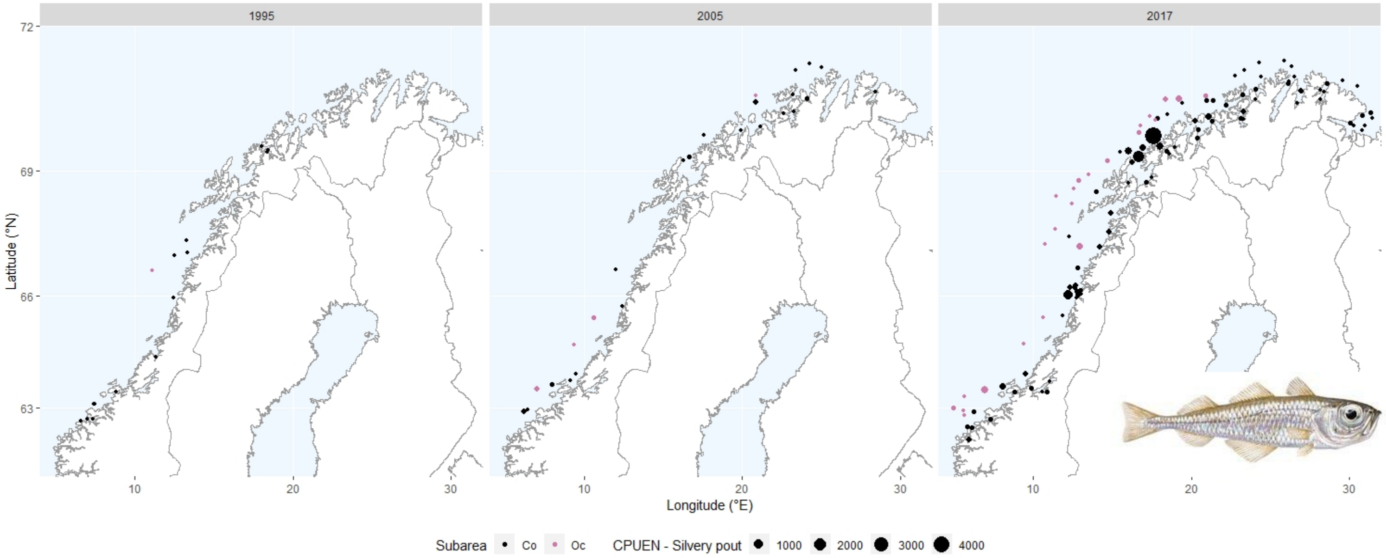

Figure 3.4.5 *Distribution of silvery pout (G. argenteus) along the Norwegian Coastline from 62-71.3 ºN in 1995, 2005 and 2017. Abundance is displayed as the size of the circle and given in CPUE (number of individuals). Catches are categorized as coastal (black) or open ocean (pink). Photo silvery pout: Alchetron.com*

Witch flounder (*Glyptocephalus cynoglossus*) showed a clear increase in abundance from 1995 to 2017 (Figure 3.4.6). There is a trend of smaller witch flounder catches in areas B and C (i.e. from Trondheim to Bodø) from 1995 to 2005, which was not the case in 2017. No clear shifts were found between inner coastal to open ocean areas, and witch flounder was still distributed evenly along the Norwegian coastline in 2017.

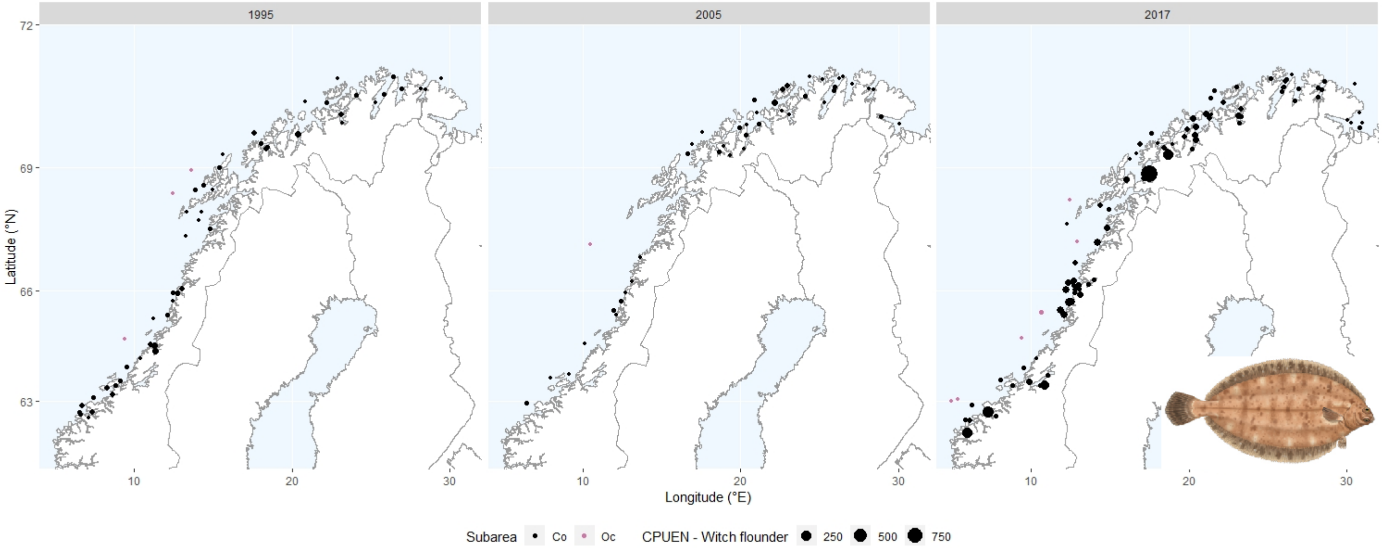

Figure 3.4.6 *Distribution of witch flounder (G. cynoglossus) along the Norwegian Coastline from 62-71.3 ºN in 1995, 2005 and 2017. Abundance is displayed as the size of the circle and given in CPUE (number of individuals). Catches are categorized as coastal (black) or open ocean (pink). Photo witch flounder: Cornwall good seafood-guide*

Greater forkbeard displayed a noticeable difference in abundance the last 20 years. It is now more common in northern areas A and B (71.3 – 67 ºN), where it was not present in 1995 (Figure 3.4.7). There increase in abundance from 1995 to 2017 is clear, while from 1995 to 2005 it is barely noticeable.

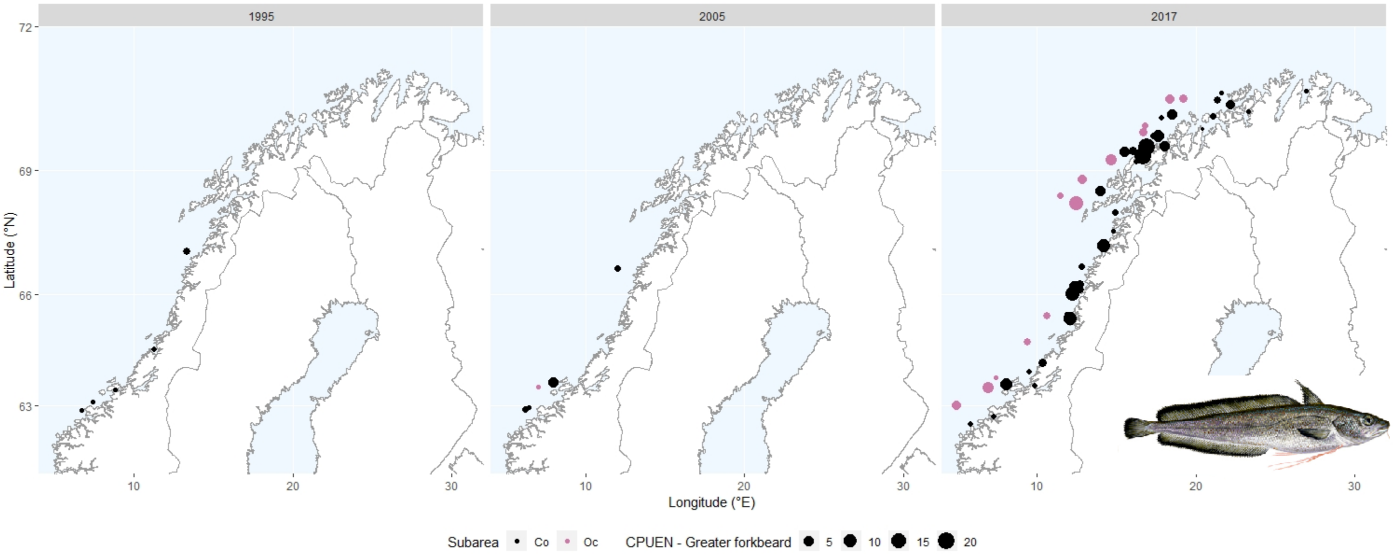

Figure 3.4.7 Distribution of greater forkbeard (P. blennoides) along the Norwegian Coastline from 62-71.3 °N in 1995, 2005 and 2017. Abundance is displayed as the size of the circle and given in CPUE (number of individuals). Catches are categorized as coastal (black) or open ocean (pink). Photo greater forkbeard: oceandragon.ie

Lemon sole was only found to have a 0.65 °N northward shift in the coastal zone from 1995 to 2017 (Figure 3.4.1), but still displays an expansion in distribution from coastal to open bank areas (Figure 3.4.8). Along most of the coastline, there has been an increase in abundance of lemon sole further offshore from 1995 to 2005 and 2017. Lemon sole found along the coast displayed a similar distribution pattern in 2005 and 2017 as in 1995, though with an increase in abundance in the northern area.

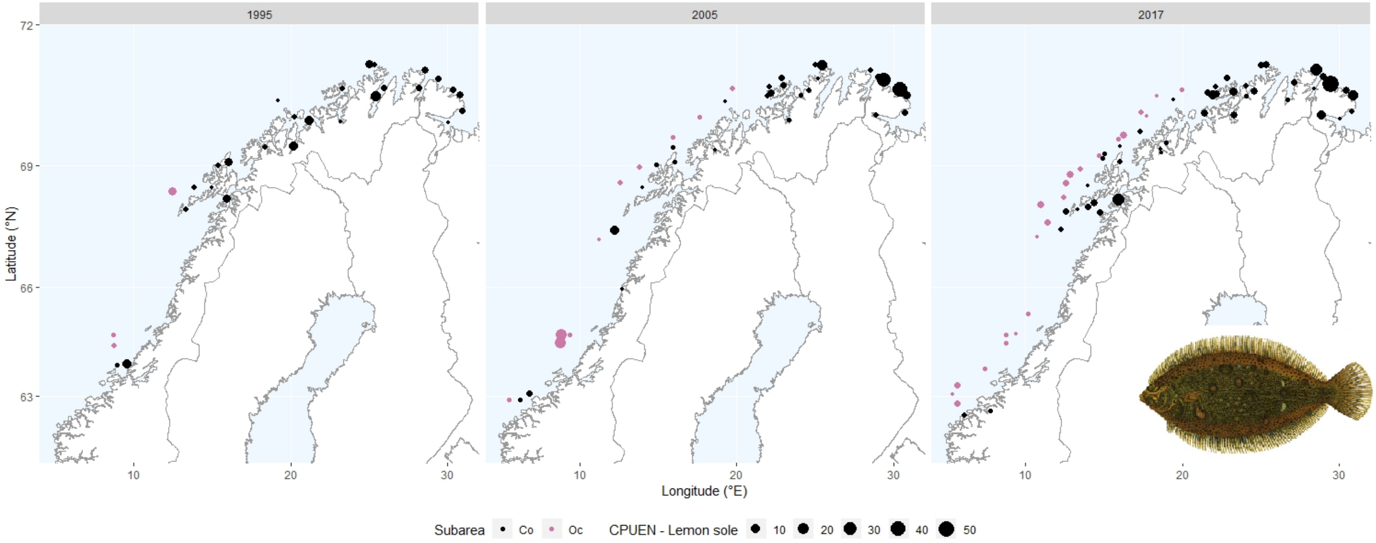

***Figure 3.4.8** Distribution of lemon sole (M. kitt) along the Norwegian Coastline from 62-71.3 °N in 1995, 2005 and 2017. Abundance is displayed as the size of the circle and given in CPUE (number of individuals). Catches are categorized as coastal (black) or open ocean (pink). Photo lemon sole: Fishsource.org*

Common ling (*Molva molva*) was caught in relatively small numbers in all three years (Figure 3.4.9). The species has still clearly increased in abundance since 1995 along the study area, mainly in the coastal zone and in the areas A and B, which are located furthest north (i.e. between Bodø and Varanger), with several catches around Lofoten in 2017.

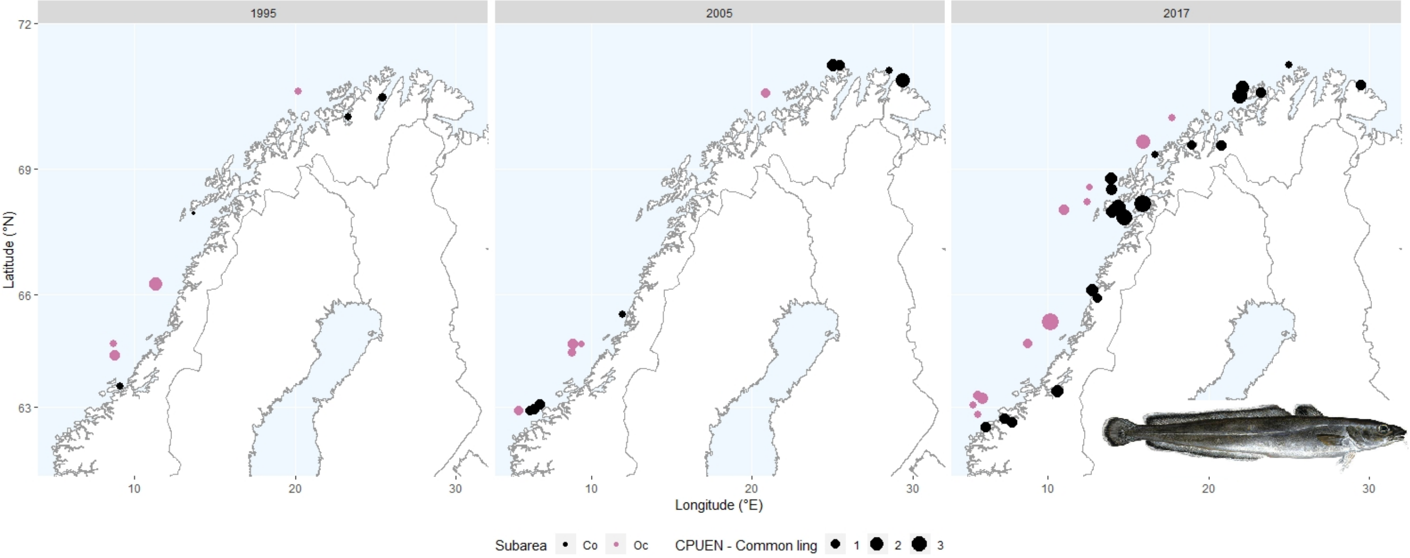

Figure 3.4.9 *Distribution of common ling (M. molva) along the Norwegian Coastline from 62-71.3 °N in 1995, 2005 and 2017. Abundance is displayed as the size of the circle and given in CPUE (number of individuals). Catches are categorized as coastal (black) or open ocean (pink). Photo common ling: snl.no (Store norske leksikon)*

From 1995 to 2005, the centre of distribution of grey gurnard shifted from 63.5 to 66.28° N in the coastal zone (Figure 3.4.1), though such a shift is not as apparent in Figure 3.4.10, which show a decrease in abundance in the area outside of Stad (i.e. area D) from 1995 to 2005 and an increase of catches again in 2017. Catches in the ocean zone and increased catches of grey gurnard around the Lofoten area are found in 2017 (Figure 3.4.10).

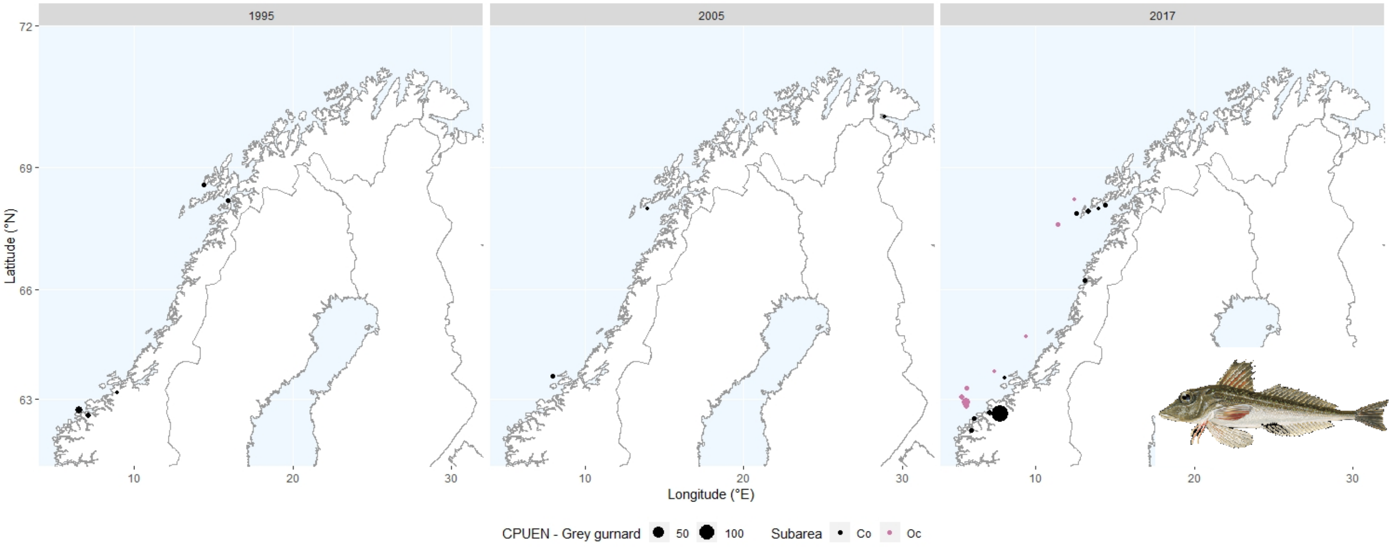

Figure 3.4.10 *Distribution of grey gurnard (E. gurnardus) along the Norwegian Coastline from 62-71.3 °N in 1995, 2005 and 2017. Abundance is displayed as the size of the circle and given in CPUE (number of individuals). Catches are categorized as coastal (black) or open ocean (pink). Photo grey gurnard: Hooked.no*

Atlantic halibut (*Hippoglossus hippoglossus*) displays a clear pattern of a northward shift from 1995 (Figure 3.4.11). In 1995, there were few observations of Atlantic halibut. Abundance in the north increased to 2005, with no clear change in the southern parts of the study area. In 2017 the species has been caught more in the ocean areas, and there has been an overall clear increase in abundance in the areas furthest north.

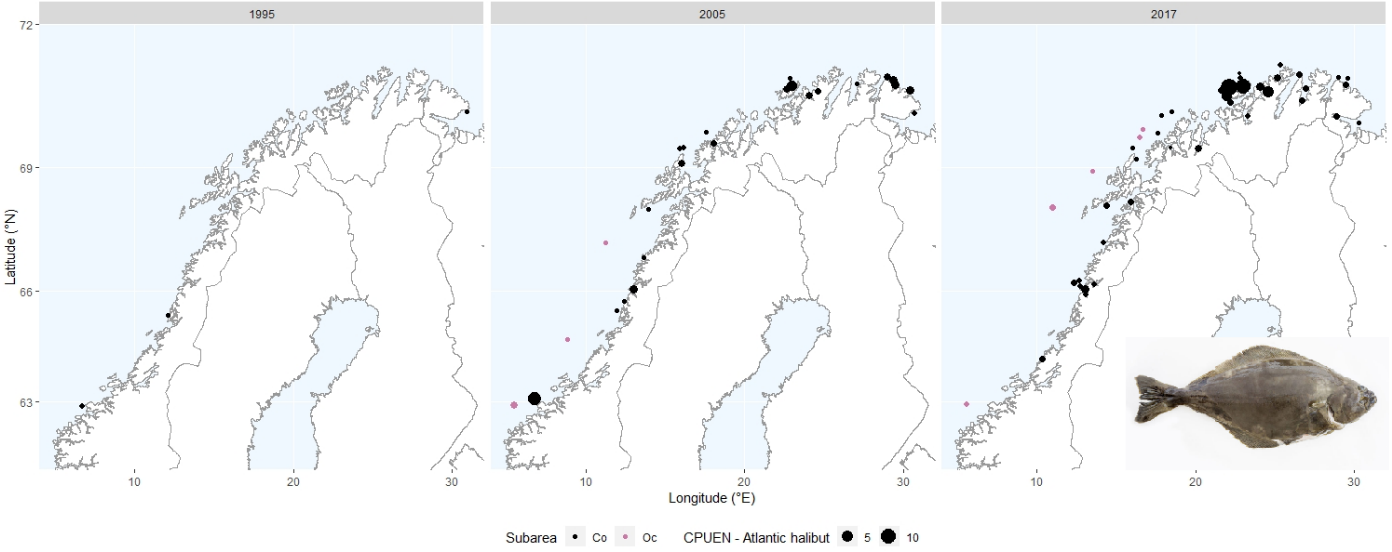

Figure 3.4.11 *Distribution of Atlantic halibut (H. hippoglossus) along the Norwegian Coastline from 62-71.3 °N in 1995, 2005 and 2017. Abundance is displayed as the size of the circle and given in CPUE (number of individuals). Catches are categorized as coastal (black) or open ocean (pink). Photo Atlantic halibut: Eivind Senneset, nifes.hi.no*

Whiting displays a clear change in spatial distribution, with a large northwards shift in COD (Figure 3.4.12). In 1995, most of the whiting were caught in the coastal zone in area C and D. Already by 2005, abundance had decreased here and the species was more frequently caught in areas further north. This pattern became even more apparent in 2017. There are also now several catches of whiting in open ocean areas, even at high latitudes.

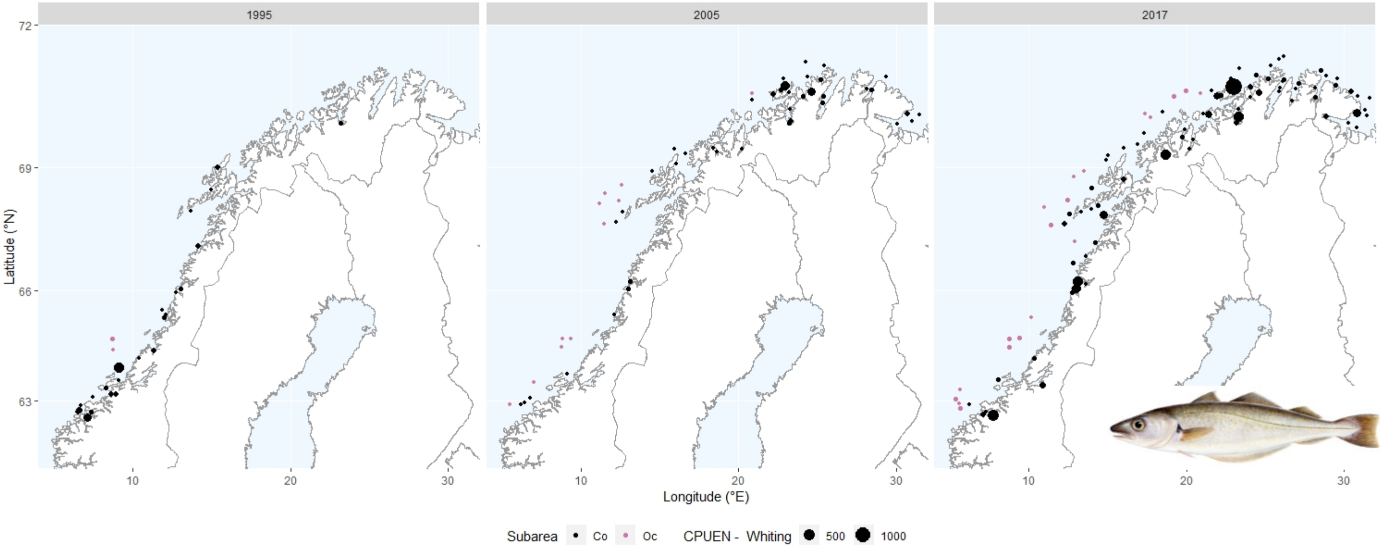

Figure 3.4.12 *Distribution of whiting (M. merlangus) along the Norwegian Coastline from 62-71.3 ^{o}N in 1995, 2005 and 2017. Abundance is displayed as the size of the circle and given in CPUE (number of individuals). Catches are categorized as coastal (black) or open ocean (pink). Photo whiting: Marz seafood*

In 1995, megrim was not found at latitudes above 69 ^{o}N, and was uncommon above ~64 ^{o}N (Figure 3.4.13). Abundance of megrim has clearly increased from 1995 to 2017, while there was little observed change from 1995 to 2005. Megrim is now found at higher latitudes, and displays a clear change in spatial distribution, even with the increase in abundance outside of Stad in area D.

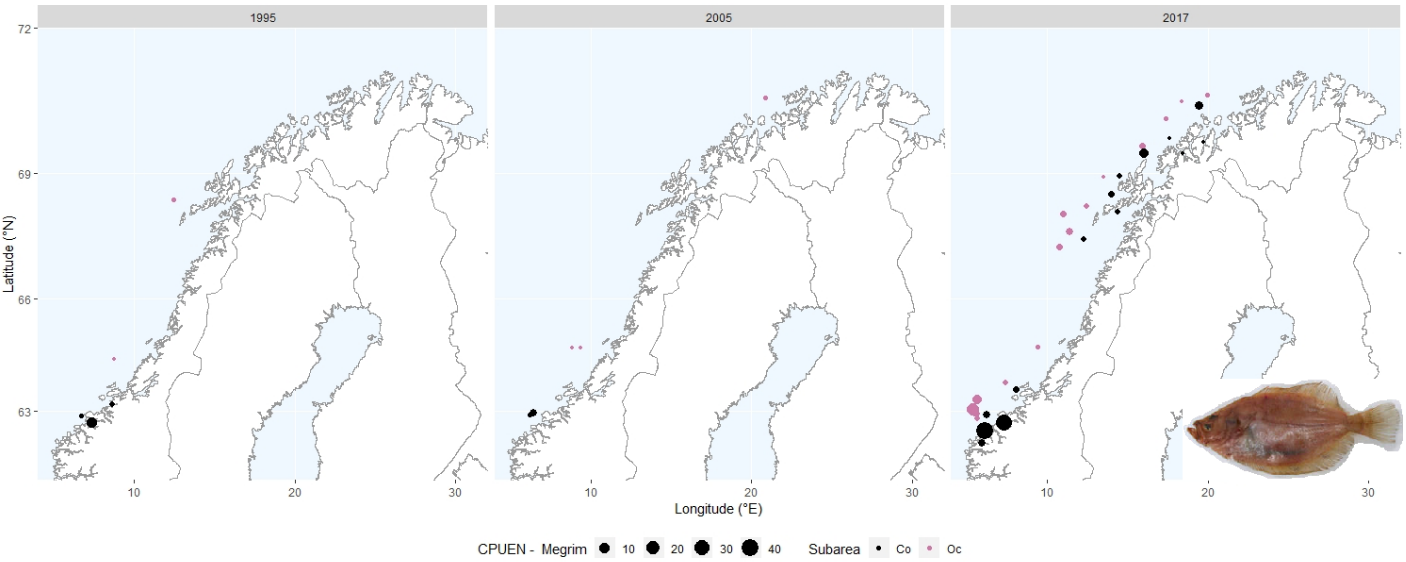

Figure 3.4.13 *Distribution of megrim (L. whiffagonis) along the Norwegian Coastline from 62-71.3 ºN in 1995, 2005 and 2017. Abundance is displayed as the size of the circle and given in CPUE (number of individuals). Catches are categorized as coastal (black) or open ocean (pink). Photo megrim: marrfish.co.uk*

Fourbeard rockling (*Enchelyopus cimbrius*) displays a northward shift in spatial distribution (Figure 3.4.14). Already from 1995 to 2005 there was an increase in catches of fourbeard rockling in area A, which increased further by 2017. No shift from inner coastal to open ocean areas can be distinguished, as all catches were registered in the coastal zone.

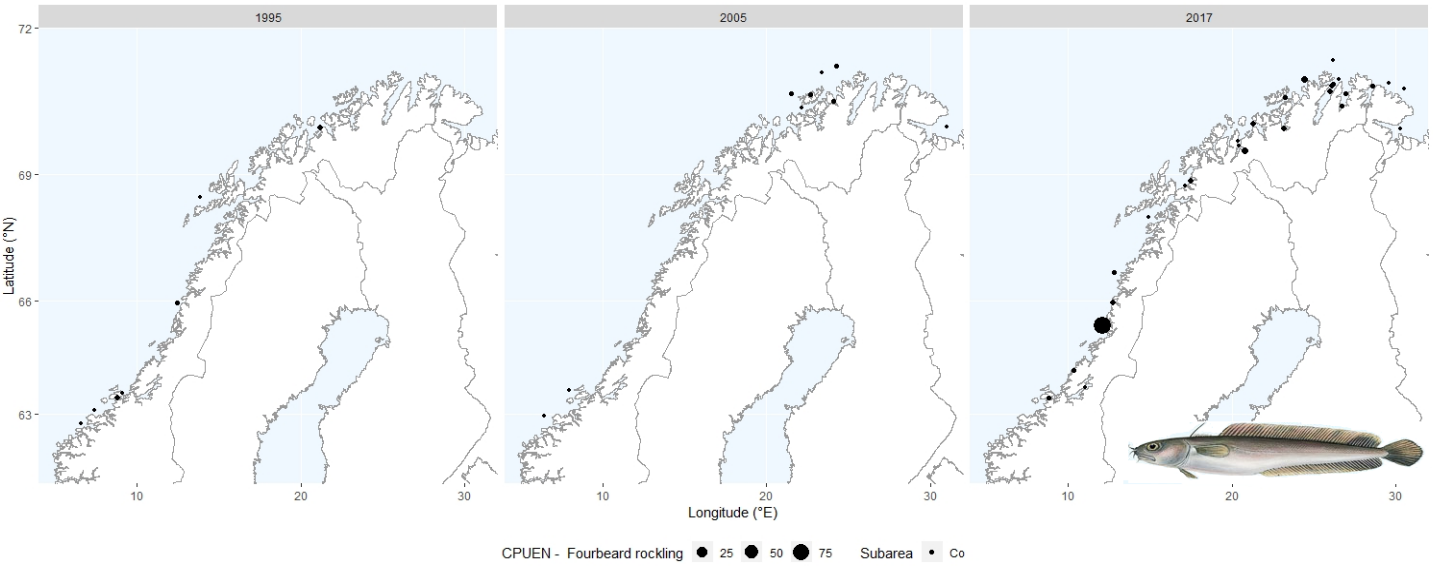

Figure 3.4.14 *Distribution of fourbeard rockling (E. cimbrius) along the Norwegian Coastline from 62-71.3 ºN in 1995, 2005 and 2017. Abundance is displayed as the size of the circle and given in CPUE (number of individuals). Catches are categorized as coastal (black). Photo fourbeard rockling: scandfish.com*

Clear patterns of a spatial distributional shift towards higher latitudes are also observed for velvet belly lanternshark (Figure 3.4.15). Larger catches are registered in the warmer years, together with catches at latitudes above 69 °N in both 2005 and 2017. Velvet belly lanternshark was found in open ocean areas further north in 2017.

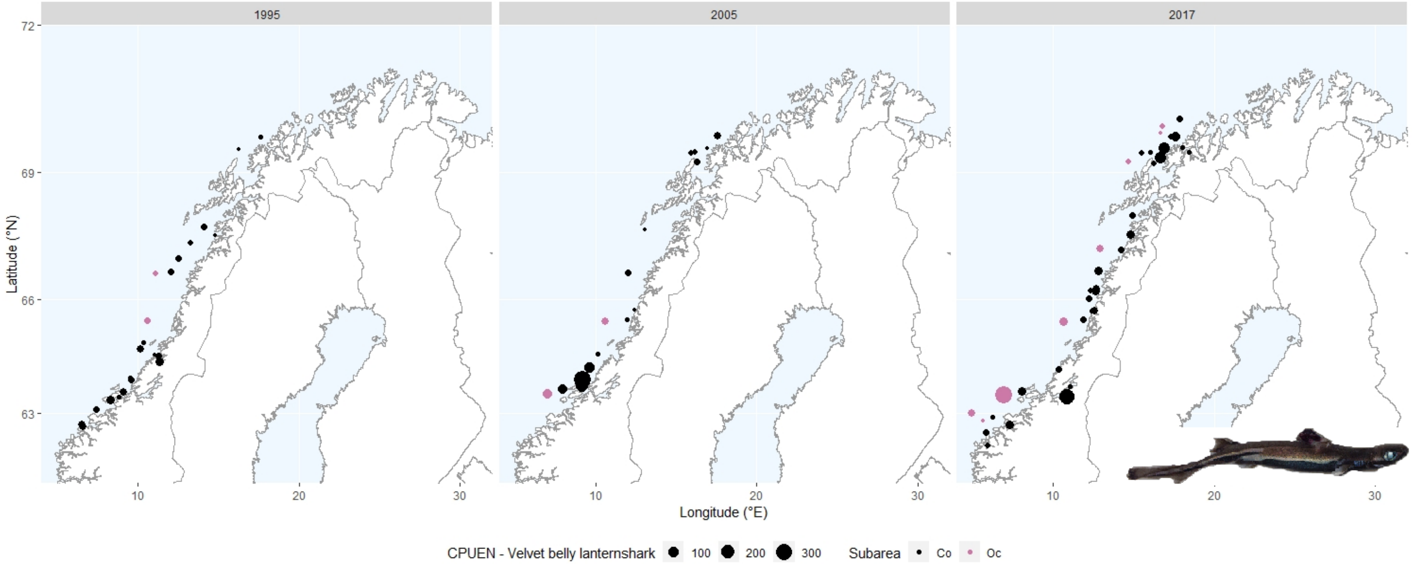

Figure 3.4.15 *Distribution of velvet belly lanternshark (E. spinax) along the Norwegian Coastline from 62-71.3 °N in 1995, 2005 and 2017. Abundance is displayed as the size of the circle and given in CPUE (number of individuals). Catches are categorized as coastal (black) or open ocean (pink). Photo velvet belly lanternshark: Christoph Noever, (uib.no 2014)*

3.5 Records of new species

Several taxa that were not present in the cold year 1995 have now been registered in large amounts in the warmer years 2005 and 2017 (Figure 3.5). Many new species were registered in 2005, but the change is most visible in 2017. The largest increase is found in the northern study areas, where the increase of Arctic-Boreal (AB), Mainly-Arctic (MA) and Arctic (A) species such as ribbed sculpin (*Triglops pingelii*), Atlantic hookear sculpin, polar sculpin and daubed shanny (*Leptoclinus maculatus*) is noticeable. The new taxa in southern areas are mainly of Boreal (B) and Southern-Boreal (SB) classification; blue ling (*Molva dypterygia*), blackbelly rosefish (*Helicolenus dactylopterus*) and lesser argentine.

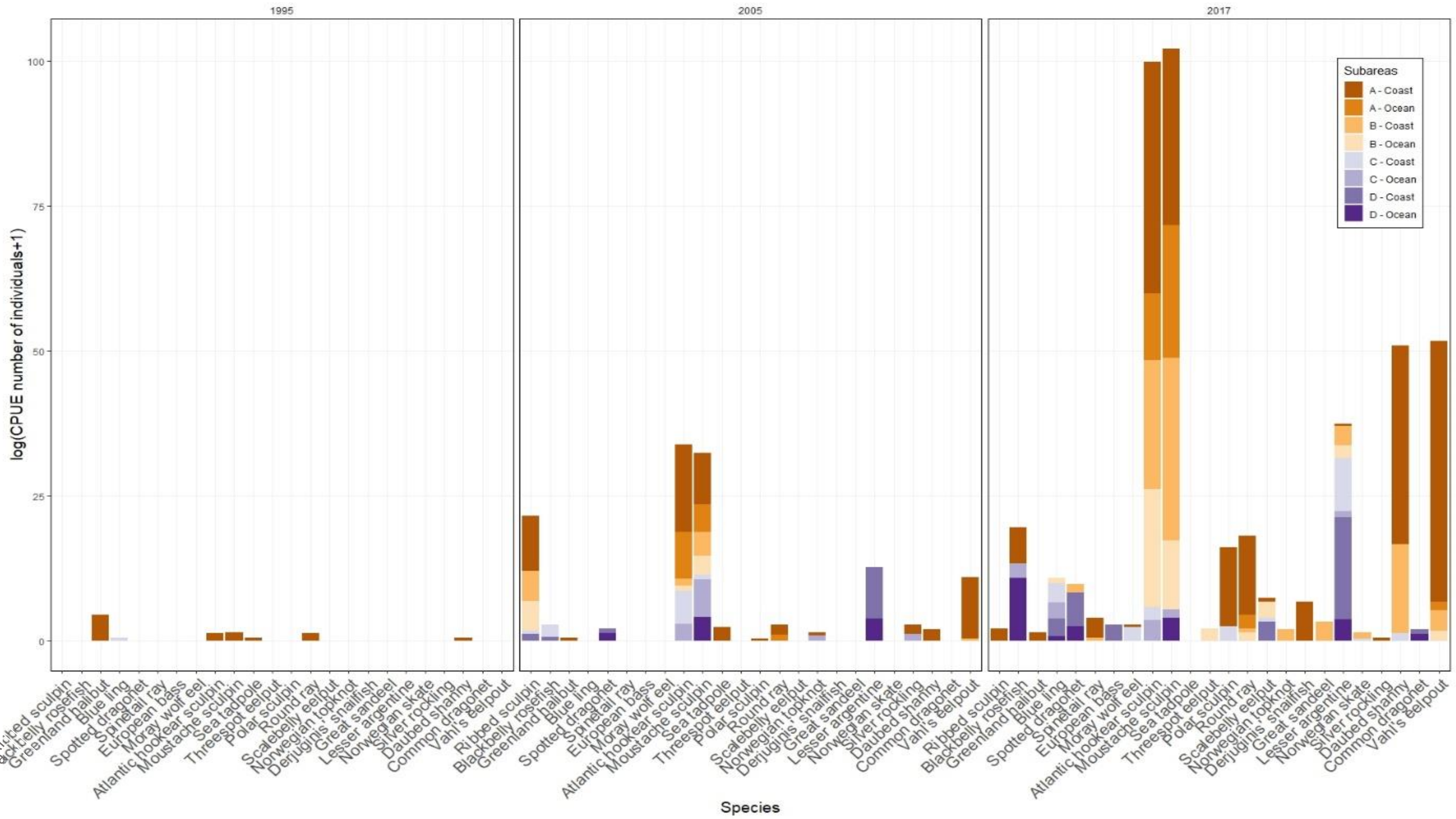

Figure 3.5 *The Catch Per Unit of Effort on log_e scale (log(CPUE+1)), with catch being number of individuals and the effort used is trawled distance per nm for species registered in 2005 and/or 2017 above the set threshold (caught $\geq$ eight individuals or/and at $\geq$ three sites). Represented by colour for the eight subareas; Area A (69.5 to 71.3 ^{o}N), Area B (67 to 69.5 ^{o}N), Area C (63.5 to 67 ^{o}N) and Area D (62 to 63.5 ^{o}N), with coastal or ocean categorization*

Discussion

4.1 Changes in distribution; borealization of northern Norway

A northward shift in distribution that trends with the simultaneous increase in temperatures in the last two decades is apparent for most species studied in this thesis, as 60% of species registered in the coastal zone and 78% in the open banks have experienced such northward shifts from 1995 to 2017. Similar poleward movements have recently been documented in the Arctic (Kortsch et al. 2015), and are well documented in areas of the Barents Sea (Byrkjedal et al. 2007, Aschan et al. 2013, Fossheim et al. 2015). These large-scale shifts in distribution are suggested to be a result of the warming of the Arctic (Fossheim et al. 2015), and with the observed increase of over 1.5 ^{o}C in bottom temperature in the study area bordering the Norwegian Sea since 1995 (Figure 3.1.1), this is a very probable factor driving the northward shift of the demersal fish populations also here.

While it is an undoubtedly complicated task to predict the outcomes and structural changes associated with species distributional shifts, some generalizations can be made. Large, boreal generalists (e.g. cod, saithe, whiting, haddock and redfishes) are expected to respond most rapid to the climatic changes and are likely going to be more established in Arctic regions, as they are able to exploit a diverse range of prey and niches in new regions. This trend has already been observed in the Barents Sea since the 1990's (Fossheim et al. 2014, Fossheim et al. 2015, Kortsch et al. 2015).

The Norwegian Sea contains many of these boreal generalists and the COD (centre of distribution) results in this study show that large boreal species have all shifted in their centre of distribution northward since 1995. This includes species such as whiting, with the largest change in COD from 63.9^{o} to 68.7^{o} N, haddock, moving from 69.6^{o} to 70.3^{o} N, cod, shifting largest in the open banks from 68.4^{o} to 69.8^{o} N and Norway redfish that moved from 68.3^{o} to 70^{o} N (Appendix 1.C). While these results presents interesting trends, it is important to note that most of these species were already present in the areas furthest north in 1995 and any change in COD is very likely due to an increase in their abundance due to more favourable conditions in later years rather than spatial movements. Nevertheless, the increase of the

abundance of these species at higher latitudes is expected to enhance the top-down regulations of already existing food-webs (Kortsch et al. 2015). This is a trend suggested to happen in the North Sea in the near future, where the return of predators that were previously overfished are leading to a decrease in a lower prey-biomass (Gemert et al. 2018). Predators shifting northwards would further leave areas at lower latitudes with a weakened top-down control (i.e. reduced predation pressure) as southern areas with higher temperatures are less favourable for such species. This may have cascading effects similar to what was found in the area of Nova Scotia in the northwest Atlantic. Here, the disappearance of cod as a key predator was followed by a significant increase in benthic crustaceans such as snow crab (*C. opilio*) (Frank et al. 2005).
Similar COD shifts for smaller species such as poor cod (*Trisopterus minutus*) and grey gurnard was also found in this study. These results could potentially be slightly influenced by the small difference in mesh-sizes (largest mesh-size in 1995) used in sampling, that could leave some smaller species, mainly of arctic categorization, such as sculpins, snail-fishes and eelpouts to be underrepresented in 1995. However, the use of sampling-gear has been standardized by IMR since 2003 and the northward movement is still apparent for many species from 2005 to 2017 as well. The northward movement for poor cod and megrim has also previously been documented in areas of the North Sea (Dulvy et al. 2008) which further supports the argument of poleward movement for such species is due to changes in temperature rather than a change in mesh-size.

While the Norwegian Sea is located south of the Arctic Ocean, 22 of 86 taxa in this study are classified as Arctic, mainly Arctic or Arctic boreal. And while large, boreal species are becoming more established in Arctic climates, the already present Arctic species in mainly northern areas A and B (i.e. from Varanger to Bodø) are predicted to be restricted in moving into new areas (Johannesen et al. 2016). Most Arctic fish are small (few of the Arctic species studied here are expected to exceed 30 cm in body size), stationary and with specialized diets, such as ribbed sculpin, a benthivore that feeds on polychaetes and small crustaceans. Their narrow temperature range and specialized diets are making Arctic species overall vulnerable to climatic changes as they have a difficulty in moving into new areas (Fossheim et al. 2014). This mixing of previously separated groups of species could thus potentially lead to the local disappearance of some species due to increased competition and a restructuring of the food web in these areas. Some Arctic species are suggested to decrease as a consequence of increased temperatures and competition are snailfishes (*Liparidae*), Greenland halibut, sculpins (*Cottidae.*) and polar cod (*Boreogadus saida*) (Fossheim et al. 2014). Greenland halibut is the only species that was found along the Norwegian coast in 1995 and not (above the set threshold) in 2005 or 2017, supporting the assumption of a local disappearance. However, shifts into areas outside the study area cannot be ruled out, and as this is a species often caught in deeper waters, it is likely that the survey may not have covered its distribution adequately. Most Arctic species (e.g.moustache sculpin, daubed shanny (*L. maculatus*) and Derjuginis' snailfish (*Careproctus derjugini*)) have however been found in increased abundance in the Norwegian Sea in later years. This is not surprising as the temperature increase was least severe in the area furthest north (e.g. area A), and thus these species have not been exposed to the same changing temperatures as further south.

There are clear changes in distribution northwards for many species found along the Norwegian coast. However, there is also a significant increase in abundance and number of species caught in open bank areas, which might indicate that latitudinal changes for some species are not the only change occurring, but also a shift from the coast to areas further out. These open bank areas are overall deeper than the shallower coastal areas. It is in the subareas furthest south; from Stad (area D; from 62 to 63.5^{o} N) to outside of Bodø (area C; from 63.5 to 67^{o} N) that the change in distribution to the ocean area is most noticeable. This offshore shift from the inner coastal areas could suggest a deepening of habitats for some species (e.g. megrim, lemon sole and Atlantic halibut), as a way to expand into new areas with lower temperatures, as there is a negative correlation between temperature and depth (Figure 3.3). This is currently happening in the North Sea, where one study found that the majority of marine fish (e.g. megrim, grey gurnard and poor cod) exhibited a deepening of habitats in the last 25 years, and cold-water species such as megrim were deepening fastest (Dulvy et al. 2008). Megrim was also found in this study to be one of the species with the most dramatic increase in abundance in the open ocean areas. However, it is more likely that these changes have occurred due to a change in temperature range on the open banks, making it a more suitable habitat without forcing species into deeper waters.

While there has been no clear evidence that the species of the Norwegian coast have deepened their habitats in the last 20 years, it could potentially be a consequence with continued warming in the following decades. And while the northward movement for species and its consequences are previously documented in areas of the North Sea (Perry et al. 2005), the ecological significance of species deepening their habitats is more unclear. It is however suggested that deeper-dwelling fishes are going to be limited in relation to habitat availability in the future, as a study from the North Sea explained that there are smaller areas available of deeper habitats than there are of more shallow areas (Dulvy et al. 2008). It is also suggested that for the species not able to respond to rapid climatic changes in their geographical distribution, the consequences will potentially be fatal as some species may be outcompeted by incoming species, while others may lose prey due to lack in production of plankton or the migration of prey-species to new areas (Fisher et al. 2008).

The distribution results present clear trends with a northward shift and an increase in abundance further from the coast for many species. This trend is likely to continue for certain marine fish given the projected continued increase in temperature in the future. It is however important to note that differences in age structure may result in a different response for some species in the future. As many marine fish are habitat-dependent during different stages of their life-cycles, differences here will likely affect and complicate their future sensitivity to climate change (Heath et al. 2012). The age-structure of the fish researched in this thesis has however not been considered.

One could argue that the thresholds set for calculating species centre of distributions (COD) is too low for assessing a species distribution in such a large area. However, it provides valuable insight, and with a higher threshold, many (mainly uncommercial) species that are previously not well researched on a large scale in these areas would remain unstudied. The threshold is therefore set as it is since it is of interest to obtain a baseline of information also for these species in order to monitor future changes.

Overall, the differences in sampling effort in the warmer years at high latitudes could be a significant influencer, resulting in an underestimation of abundance for species in the areas furthest north in the cold year 1995. The lack of sampling in some open ocean areas far south could also lead to an underestimation of abundance in area C and D, and thus make for a northward skewed COD. However, standardizing catches as CPUE (catch per unit effort, with effort being trawled distance in nm) and including a threshold for the number of stations and individuals in an area for it to be considered, should make both over and underestimations less of a concern. Furthermore, as distributional changes for marine, demersal fish in both the adjacent Barents Sea and the North Sea in the last decades are widely documented, provides strong support to the claim of a northward shift for the demersal fish of the Norwegian coast (Fossheim et al. 2014, Dulvy et al. 2008).

4.2 Changes in species richness and composition; southern and Arctic invaders to the Norwegian coast

Species with southern-boreal affinities have become more numerous in Norwegian waters since 1995, and overall, more new species are registered in the coastal subareas than in the open bank areas. This appearance of new taxa will result in new ecological interactions between incoming and already present species, as most demersal fish are opportunistic feeders (Gallo et al. 2016) and are therefore likely to have to share both habitat and prey in the future. New species could thus potentially have severe consequences for the established marine fauna of the Norwegian coast such as the loss of native habitats, less food (i.e. increased competition) and new predators. The possible outcomes of mixing before separated groups of species in regions of the Arctic is however poorly studied (Wisz et al. 2015), and makes comparisons of the results with similar ecosystems difficult. This means that the specific future consequences of these changes are uncertain, and only general assumptions can be made. Nevertheless, the results present clear trends, and these species will most likely affect the native demersal, fish of the Norwegian coast.

An increase in abundance of warm-water species since 1995, such as blue ling, blackbelly rosefish, European hake (*Merluccius merluccius*) and lesser argentine in the southern parts of the study area (area D and C, e.g. between Stad and Bodø), is apparent (Figure 3.5). Similar trends have been observed in areas of the North Sea, which experienced a large increase in immigration of warm-water species in the last 80 years (Beare et al. 2004). Here, lesser argentine, a predator species that feeds on lower trophic levels (e.g. polychaetes, molluscs and crustaceans), has shown similar increases in abundance in warm periods in the Atlantic (Pinnegar et al. 2002). Lesser argentine was suggested to have a negative effect on high trophic levels, as the decrease in these prey organisms would mean less food for other species at high tropic levels such as cod, haddock and whiting (Votier et al. 2008). An increase in species such as lesser argentine in the future could thus possibly have negative effects on commercial fisheries as it is mainly focused on catching large predators that feed on the same trophic levels (Votier et al. 2008). Furthermore, the introduction of predatory-species such as blue ling and blackbelly rosefish could potentially replace native predators such as whiting and cod who have shifted northwards in their COD since 1995.

Overall, changes in the dynamics of marine food-webs are near impossible to predict as ecological interactions and already existing food-webs are complex and some species may have several hundred connections (i.e. keystone species) (Bond 1994).

There was also an observed increase in the number of species with Arctic classification found in the northern parts of the study area around Varanger and Lofoten (i.e. area A; 69.5 to 71.3 °N and area B; from 67 to 69.5° N), from 1995 to 2005 and 2017 (Figure 3.5). These are mainly small, stationary fishes like sculpins and eelpouts, which are predicted to be most vulnerable in relation to the climatic changes, but have nonetheless become more numerous in these areas even with increasing ocean temperatures in the last 20 years. The registration of new species is visible by 2005, but most pronounced in 2017, suggesting a slight lagged effect. The increase of these Arctic species could be an effect of deficient species identification in 1995 than in the more recent warmer years, as identification is said to be a method under constant development (Artamonova 2012) and could therefore be an area of concern in relation to data quality. To minimize the differences in species identification between 1995 and 2017, several criteria were set, such as not including taxa not fully identified to species and setting a threshold for the presence of the species in a subarea for it to be included. The removal of several species only classified to family or genus should help avoid drawing false conclusions and overall minimize any bias. Nevertheless, not being able to fully identify the whole range of species will put limitations on an accurate and full description of the whole demersal fish community. This is only regarded as a concern for a small group of different taxa of skates, small arctic fishes and redfish as these were the largest not fully identified groups in the original dataset. Overall, with the adjustments implemented, the results should still be viewed as reliable. Further monitoring of these Arctic species in Norwegian waters are however crucial in the future as they could face local extinction as a response to environmental changes.

Arctic marine environments are known for being less diverse than areas with a more temperate climate (Bergstad 2009). The results of the Shannon-Weiner diversity index for the eight subareas of the Norwegian coast support the claim of an ecosystem of low diversity, as there were overall low scores for all eight subareas (Table 3.2). This indicates an ecosystem of both low species richness and evenness. As the index considers both evenness and richness it makes comparing ecosystems that vary largely in species richness difficult, which has been viewed as a weakness (Kerkhoff 2010). However, in light of the analysis of sampling effort (i.e. rarefaction curves), index values could possibly be low due to sampling effort not being sufficient in all eight subareas and thus not capturing the areas full species richness. This would give an underestimation of diversity in the area as the association between the number of stations and the number of species/individuals registered will almost always exist.

Overall, comparing the Shannon index values obtained within areas of sufficient sampling is considered reliable. Rarefaction curves for 2005 showed that almost all areas appeared under-sampled, hence a comparison of values should be restricted to 1995 and 2017 (Figures 3.2.1-3.2.3).

In 1995, coastal areas had a slight higher Shannon-index than for the open ocean areas, with the exception of area B (67 to 69.5^{o} N). There was also registered a much higher number of species in the coast than in the open ocean areas, however area A and B (area A; 69.5 to 71.3 ^{o}N and area B; from 67 to 69.5^{o} N) in the open banks appear severely under-sampled, and area D (e.g. 62 to 63.5^{o} N) is not even sampled in 1995. In 2017, coastal areas continued to show a higher number of species for all four areas, and here the number of species registered have increased by more than 10 since 1995.

Overall, only some coastal areas (mainly area A and B) have been sampled sufficiently to show whether there has been an increase in the number of observed species from the cold to the warmer period. While the northern areas have a higher number of species registered, the north/south differences are however not very clear in the Shannon index values even with these clear differences in number of taxa in the different areas. This could indicate an ecosystem of low evenness for all three years. Low evenness presents an ecosystem that has some very abundant species present while others are rare, and is said to be less diverse than an area of equally partitioned abundance of species.

With the inadequate sampling of area D (e.g. 62^{o} to 63.5^{o} N) and almost all open ocean areas in the cold period 1995 (except for area C) the argument that warmer ocean-conditions will increase the diversity of Norwegian waters is not very strong. Nevertheless, species richness increased noticeably from the cold to the warm period in even the adequately sampled areas, presenting strong evidence of some structural changes occurring. It is therefore necessary to increase sampling (i.e. add more stations), especially in open ocean areas as it is crucial to monitor species richness and diversity in also these remaining areas in the future.

The results of the constrained correspondence analysis (CCA) (Table 3.3.1) and the Monte-Carlo permutation test (Appendix 1.D) revealed significant differences in species composition between 1995, 2005 and 2017. The ordination graphics (Figure 3.3) showed that many species were found at the centre of the plot, and can thus be interpreted as average for the model, it does however not instinctively mean that they have been caught in all three years. A large proportion of species being average could suggest a high degree of homogeneity for all years, it appears however that this is not the case and the dispersion of many species suggest spatial patterns (Bergstad et al. 2018). Such patterns could largely be influenced by the differences found in species COD from 1995 to 2017.

The majority of species with highest frequency along the temperature gradient are of boreal and southern-boreal categorization (Figure 3.3), and it is therefore likely that they have an affinity for higher temperatures (e.g. European hake, lesser argentine, grey gurnard and blackbelly rosefish). With previous distributional results, it was expected that species such as whiting, megrim, grey gurnard and velvet belly lanternshark, which previously in the COD results showed climate-related changes in latitude (Figure 3.4.1 & 3.4.2), would be found along the latitude gradient in the ordination graphics (Figure 3.3). Instead, they appear most frequent along the temperature gradient, which most likely suggests a positive association with temperature rather than a negative correlation with latitude. Some species such as rock grenadier (*Coryphaenoides rupestris*), spinetail ray (*Bathyraja spinicauda*), spotted barracudunia (*Arctozenus risso*) and deep-water redfish are deep-water fishes, and it is therefore not surprising that these are found as a group along this depth gradient.

A significant difference in species composition was found in relation to the eight subareas set, supporting the claim of changes occurring within both the south-north gradient and within the coastal-ocean areas since 1995 (Table 3.3.2). While some of the change may be due to changes in the stations sampled between the years in the different areas, the distributional results presented earlier support a change in composition especially at higher latitudes. This could be due to the increase in both Arctic species registered here (e.g. Atlantic hookear sculpin, moustache sculpin and Vahl's eelpout) and of large, boreal species being more established in the north since 1995 (e.g. whiting, cod and Norway redfish). The results of the analysis on species composition in relation to the eight subareas are showing the lowest P-values ($p<0.001$) for the subareas separated by latitude (areas A, B, C and D), and is thus presenting a stronger evidence against the null-hypothesis (which is that species composition is not related to the different constraints set) than the coastal/ocean subareas ($p<0.05$) (Dahiru 2008).

All continuous variables (i.e. depth, temperature and latitude) constraining the CCA were also recognized to significantly influence the composition of the species (Table 3.3.2), as was expected due to the pronounced effect temperature has shown to have on physiology and ecology of fish (Dulvy et al. 2008). With the negative correlation between temperature and latitude (i.e. as latitude increases, temperature decreases) and between temperature and depth, it is not surprising that these also were found to significantly influence the composition of species, as many species are likely to shift to polar or deeper areas to find more suitable temperatures. However, while the Monte-Carlo permutation test that was used to reveal the effects of the set constraints on species composition was significant, it is worth mentioning that the full model was found to only explain ~19% of the variance in species composition, giving it medium explanatory power. A large proportion of unexplained variance could be something we have not measured or included in the model. However, it does not mean it is necessarily biological, as it could be sampling error or simply just noise. Some aspects of the uncaptured variance could be due to the fact that not all stations are identical between the three years, some due to changes in survey design since 1995 and some due to insufficient CTD-measurements for some stations. Thus, comparing stations in the ordination space in relation to each other or variables such as temperature will be affected by the differences in latitude, possibly making it unbalanced. However, it is not considered a large problem here as they are all conducted in roughly the same region.

While the percentage of variance explained is not very large, limiting the model to only a few variables is still seen as a reasonable choice as environmental factors are difficult to determine successfully, while factors such as years and areas are easier to determine as they are clearly separated units (Fossheim 2000). A minimization of the use of highly correlated variables was also done by not including both latitude and longitude as continuous variables (Gelfand et al. 2019). This was done as a way of distinguishing between the species distributions along these gradients, which might otherwise be identical to each other even though one could be ecologically unimportant.

It is overall a complex task to relate communities to environmental variables such as temperature that vary continuously in time and space. It is also important to mention that although the CCA finds the best linear combination of the set explanatory variables it is not guaranteed to find the true, underlying structure, as it can only find relationships between measured variables and species composition (Gelfand et al. 2019). There might still be important variables that remain unmeasured. However, CCA is still a robust method to use, given that its major assumption is not violated (e.g. that the response model is unimodal). The fact that this assumption is respected, together with the set threshold for species included in the CCA and the transformation of catch data to a logarithmic scale that helped reduce the domination of very rare or very abundant species, makes up a robust statistical model that provides overall reliable results.

4.3 Ecological consequences

As the Norwegian coast inhabits a large species diversity with different ecological niches, environmental changes will affect species differently, as individual species' response to increased temperatures depend on several behavioural and physiological/physical traits such as body size and feeding behaviour (Dulvy et al. 2008, Pörtner et al. 2010), which determines their responses to recent warmings. Ecological consequences are difficult to determine due to species complex interactions with higher and lower trophic levels, thus one can only attempt to make general assumptions.

A review on climate change effects on marine fish and shellfish from the waters outside of the UK and Ireland produced a condensed list about the key points of the different stages marine fish will most likely be affected by climate change (Heath et al. 2012):

1. Time of spawning being significantly influenced by the seasonal production of plankton
2. The dispersal of egg and larvae by water currents, as these are strongly influenced by temperature
3. The physiological and phenotype effects of temperature on growth and maturation
4. Biological and physical alterations of habitats for both juveniles and adults
5. The effect on complex food-web structures (prey/predator-relationships) and top-down/bottom-up regulations.
6. The alterations of migration cues for adult, migratory fish
7. The vulnerability in different life stages in relation to fishing gear

These effects can further be summarized as four large-scale levels of ecological responses in marine fish in relation to environmental changes such as increased temperature (Pörtner et al. 2010). The first level are the physiological changes on organisms in response to changing environmental variables such as temperature. The second level is at the individual-level, as behaviour responses may be observed as the abandonment of old habitats and movement into new, suitable areas in order to avoid unfavourable conditions. The third is observed at the population-level, where the changes are occurring due to the change in balance between mortality-rates, growth-rates and reproduction-rates. Finally, the ecosystem-level of change is seen as changes in the structure of food-web interactions, as shifts due to warming-induced biodiversity will overall affect productivity. Hence, it is likely that the Norwegian coast will experience changes in productivity in the future, as ecosystem-level changes have already been observed in this thesis by increases in overall abundance of both Arctic and boreal species, shifts in distribution and the registration of new species into the already existing marine demersal populations of the Norwegian coast.

According to Stenseth et al. 2002, delayed ecological effects are important to consider in marine systems as size at birth depending on the climate that year will result in cohort effects that are visible at later stages in life. Cohorts with smaller individuals at birth will be less abundant when older as body-size affect individual’s resilience to environmental changes and smaller individuals have a higher level of natural mortality. Thus, many effects of climate on the species of the Norwegian coast may still be concealed. It is important to highlight that climate variations, such as presented here can have contrasting ecological responses on species having different life histories and on biogeographical groups. This has recently been shown in the Barents Sea. One study on life-history variation in marine fish found an increase of species with slower life histories (e.g. boreal species) in the northeast region in warmer years. This area had previously consisted mainly of species with faster life cycles (i.e. Arctic species) which are categorized as fast as they have smaller in body size, a shorter life-span and earlier maturation (Wiedmann et al. 2014).

Overall, many ecological responses of marine fish caused by changes in environmental variables have already been well researched in areas of the Barents Sea. Where there has been observed changes in community structures in relation to the removal of top-predators that reduces the top-down control of the area which resulted in increased abundance of species on lower trophic-levels (Frank et al. 2005) and the reconfiguration of the ecological structure of communities due to borealization of large, generalist that are expanding their habitat into Arctic areas and thus Arctic food-webs (Johannesen et al. 2017). Such responses are all directly or indirectly related to increases in temperature, and are all prompting changes for not only demersal fish, but also the entire marine ecosystem. The possible ecological outcomes of the climatic changes are many and of considerable interest, not only in relation to the economic aspects of fisheries, but also considering the significant losses it could have on biological diversity in the future.

4.4 Changes in distribution, composition and species richness; not temperature related?

Community responses are difficult to study as many mechanisms and responses have to be considered. It is therefore important to question whether these recent observed changes are individual responses, a systematic indicator of change due to climate or if other, previously unconsidered factors are influencing the results. Most publications in the last 20 years on climate change impacts on marine fauna are focused on temperature as a key factor (they are also largely focused on single species) (Harley et al. 2006, Aschan et al. 2013). There is however consensus that this might be oversimplified and it is not reliable to draw conclusions about climate change effects based solely on temperature (Harley et al. 2006) as there may be many other underlying mechanisms.
Factors such as 1) sea level rise that could lead to an upward shift in species distribution, 2) changes in ocean circulation due to extreme winds that would affect upwelling and disturb intertidal systems, and 3) abiotic factors such as pH, salinity and CO_2-levels should all be considered as they lead to different ecological responses (Harley et al. 2006, Denman et al. 2011). Other factors to consider is the earth's naturally varying climate over temporal, seasonal and inter-annual scales that might influence certain results.

The exploitation (i.e. fishing) of the commercial fish that were investigated in this thesis (e.g. cod, saithe and haddock) is another major factor that more than likely has had a large impact on the regional abundance and distribution of the species. Commercial fishing is said to have an impact on species interactions, alter and destroy seabeds (Thrush et al. 2016), making habitats unavailable, have a pronounced effect on fish size and age structure (Hsieh et al. 2010, Garcia et al. 2012) and even affect reproductive properties (Heath et al. 2012) due to its often high degree of selectivity. These aspects are likely affecting the species of the Norwegian coast and thus influencing the results to an unknown extent.

The demersal fish communities along the Norwegian coast are hard to study and it is difficult to present accurate conclusions much due to its large scale and the nearly 90 species that were investigated with large variations in life-history strategies. However, the previous comparisons of marine fish in similar studies of other areas still give a strong indication and present general patterns that these changes are in fact occurring as a large-scale systematic change, much due to the increase in temperature. However, untangling the effects due to temperature, fisheries, unmeasured factors and natural variations in the ocean is a tremendous task. Thus, the results must overall be interpreted with the notion that other factors can also affect species composition, distribution and diversity.

The data collected from IMR’s coastal survey is undoubtedly valuable information, but differences in data quality, species identification and effort can have significant effects on the results and limit their overall reliability. However, adjustments have been made in order to minimize these effects such as standardizing catches as CPUE, setting thresholds for the number of trawl-stations required to be present in a subarea for it to be considered representative, minimizing the biases of CTD measurements by not including those too far from the nearest trawl, together with several criteria for which species were accepted into the final dataset. These considerations should present valid results, and can thus be viewed as a good baseline for further research.

4.5 Concluding remarks

In this thesis, an effort was made to gather more information and provide a baseline of knowledge for both commercial and non-commercial species of demersal, marine fish. By not focusing on single species, a more ecosystem and community-level approach has been used, as it can be said that this provides a more realistic picture of large-scale change.

Overall, some conclusions can be drawn from the present study, with results being most pronounced in relation to changes in distribution and abundance. Majority of species have increased their abundance in areas of higher latitudes and thus becoming more established due to more favourable conditions. There is a clear trend of many large, boreal species shifting northwards as these are more mobile than smaller, arctic species.

A trend for many species to move further from the coast was also shown, most likely as a result of the observed changes in temperature range in these open banks from 1995 to 2017. Overall, species not able to shift into new areas to avoid unfavourable conditions could be at risk of local extinctions in the future due to increased competition and predation, destruction of habitats and direct physiological responses of temperature change.

Species composition was shown to be significantly different between the 1995, 2005 and 2017, and changed with temperature, depth, latitude and within the subareas (e.g. ocean/coast and latitudinal separated areas) stratification of the area. Further, several new species have been registered along the Norwegian coastline since 1995, with mainly species of boreal and southern boreal affinities recorded in the southern part of the study area, and species of Arctic and Arctic boreal affinities in the northern areas.

While there are many interesting results presented, it has also been noted that it is an undoubtedly hard task to capture the spatial dynamics with high precision of an ecosystem and predict future implications. Differences and improvements (largely in the area of species identification) in methods used from 1995 to 2017, exploitation of the stocks due to fisheries, and natural variations in populations over space and time are all more than likely influencing these results to an unknown extent.

This thesis aimed at highlighting both the strengths of the results, which presents clear patterns of several changes, but also acknowledge its limitations, as there are many underlying mechanisms not captured or considered. Continued future monitoring of the demersal fish community along the Norwegian coast is of great importance, as we might continue to observe large-scale changes in spatial distribution-patterns and in species composition and richness in the following decades. Future research should most importantly include increased sampling effort in the offshore areas, especially in the areas between Stad and Bodø, as sampling has been shown to not be sufficiently adequate here.

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Appendix

Appendix 1.A

The catch data (CPUEN – N: number of individuals) were $\log_e$ transformed because of the skewed distribution of total catches (Figure 1.A.1) and histograms for a few of the most abundant species (Figure 1.A.3-1.A.7) are presented as a way of showing the catches distribution. The $\log_e$ (+1) (Figure 1.A.2) of total CPUEN presents an overall less skewed distribution.

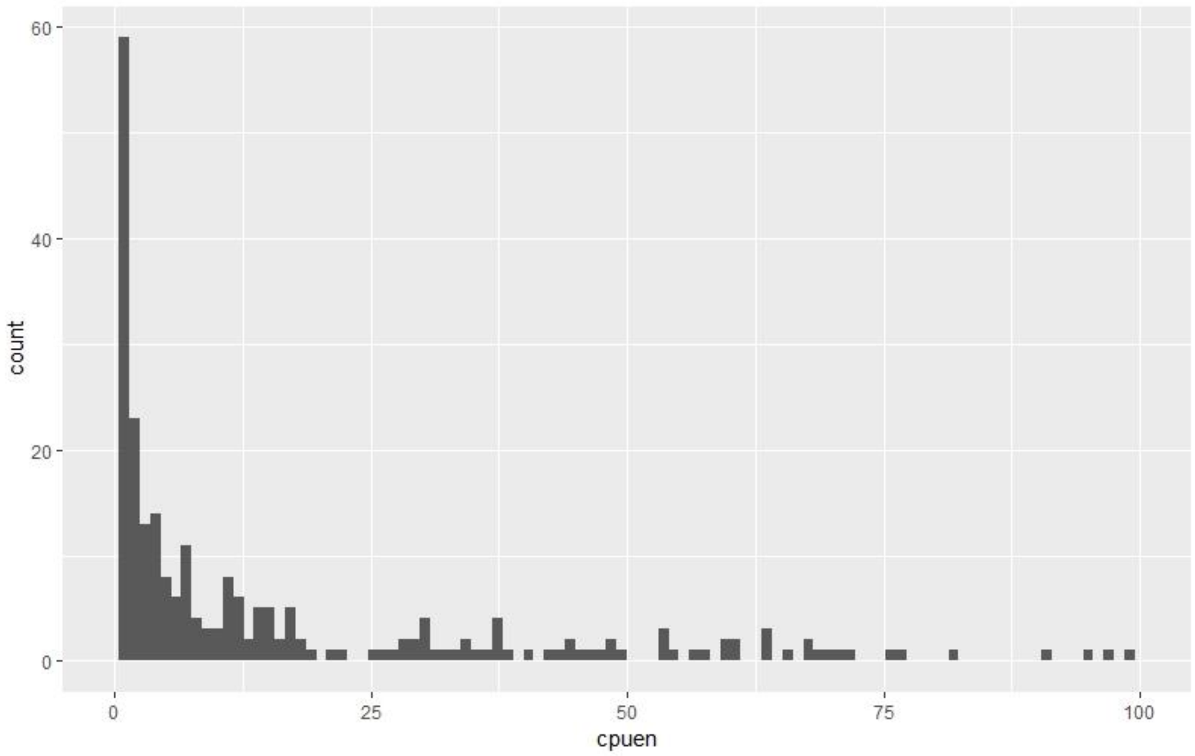

Figure 1.A.1 *Histogram of the CPUEN (N-catch number of individuals) for all fish caught in 1995, 2005 and 2017 on IMR's annual coastal survey along the Norwegian coastline between Stad and Varanger.*

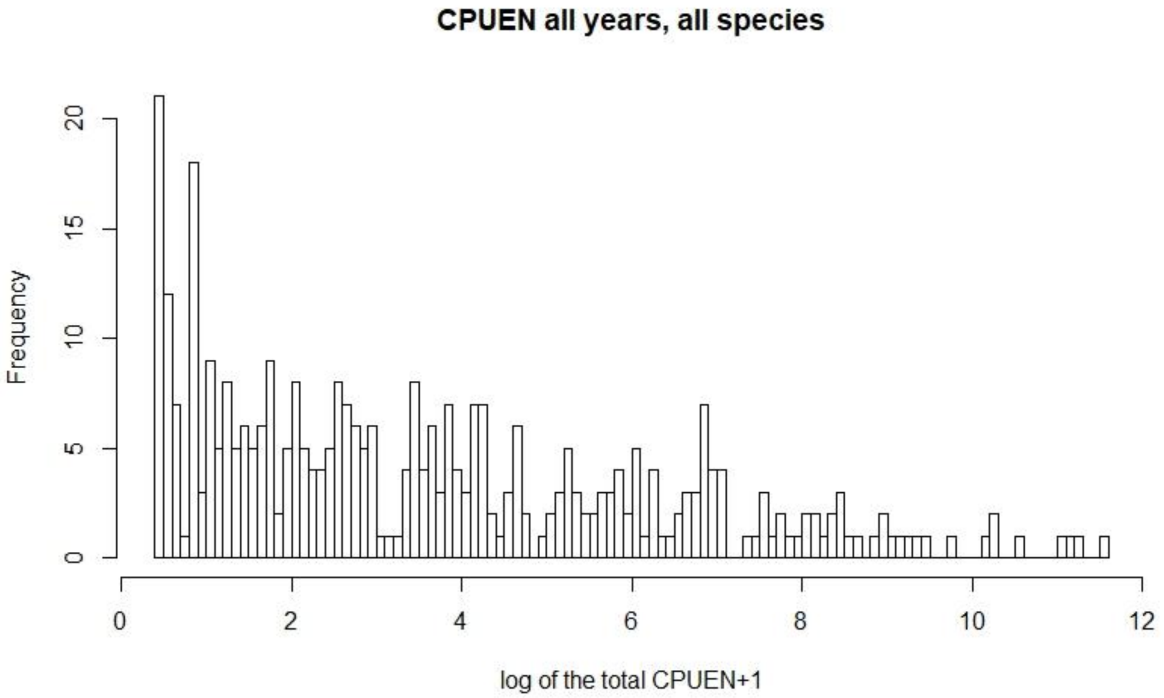

Figure 1.A.2 Histogram of the log(CPUEN (N-catch number of individuals)+1) for the sum of all taxa caught in 1995, 2005 and 2017 on IMR's annual coastal survey along the Norwegian coastline between Stad and Varanger.

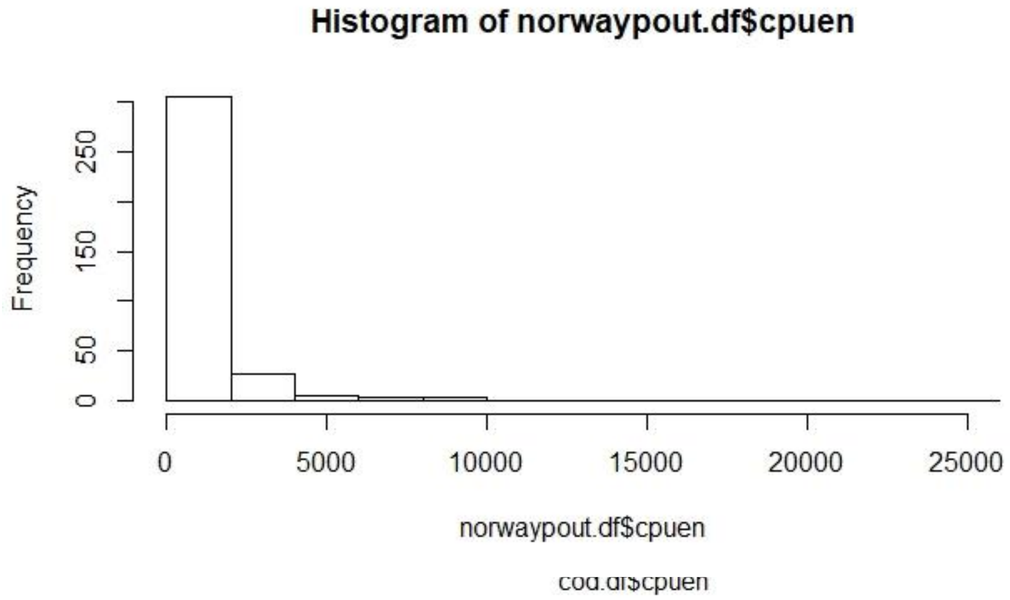

Figure 1.A.3 Histogram of the CPUEN (N-catch number of individuals) of Norway pout (T. esmarkii) caught in 1995, 2005 and 2017 on IMR's annual coastal survey along the Norwegian coastline between Stad and Varanger

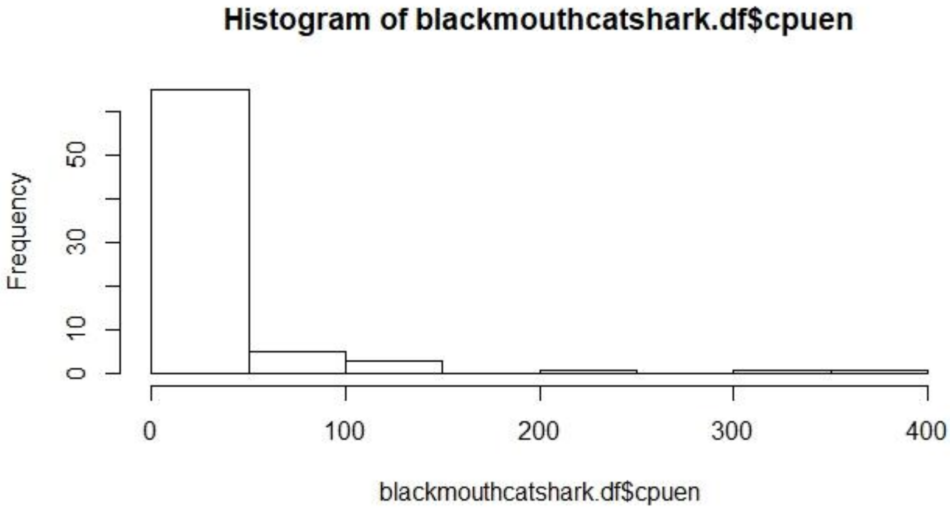

Figure 1.A.4 *Histogram of the CPUEN (N-catch number of individuals) of blackmouth catshark (G. melastomus) caught in 1995, 2005 and 2017 on IMR's annual coastal survey along the Norwegian coastline between Stad and Varanger*

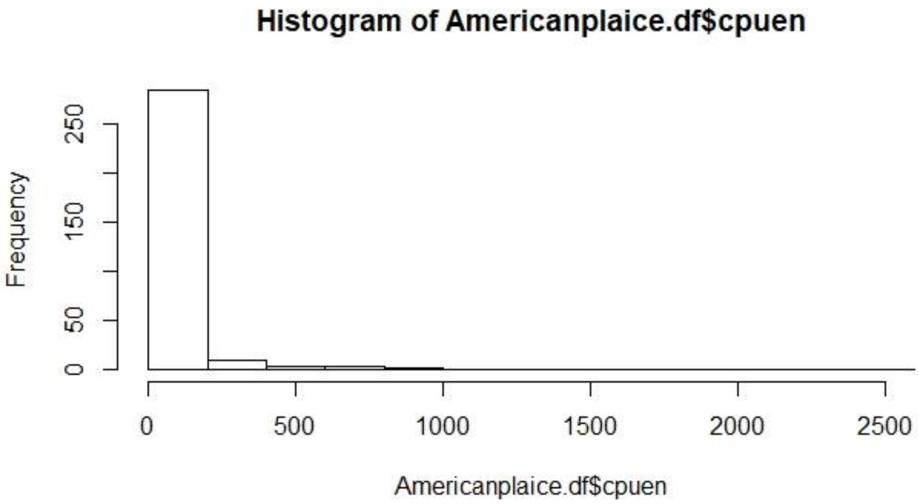

Figure 1.A.5 *Histogram of the CPUEN (N-catch number of individuals) of American plaice (H. platessoides) caught in 1995, 2005 and 2017 on IMR's annual coastal survey along the Norwegian coastline between Stad and Varanger*

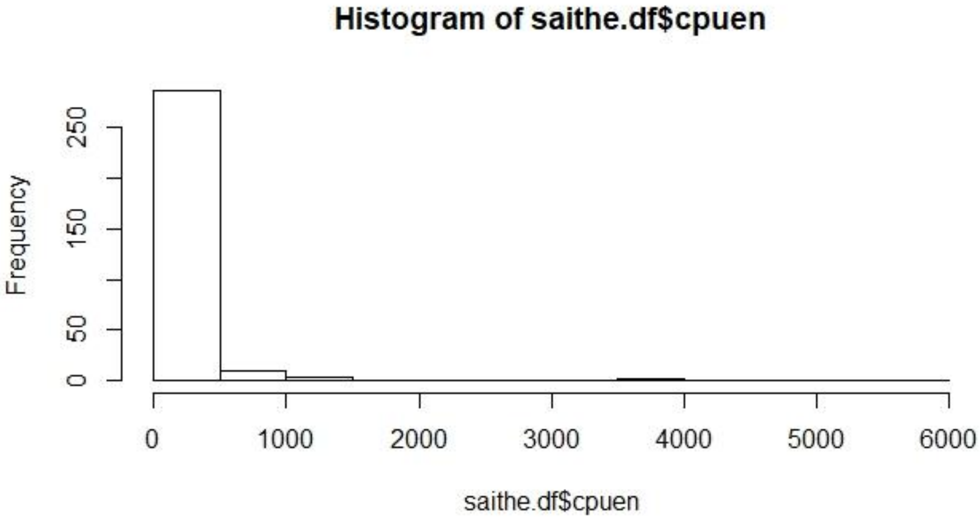

Figure 1.A.6 *Histogram of the CPUEN (N-catch number of individuals) of saithe (P. virens) caught in 1995, 2005 and 2017 on IMR's annual coastal survey along the Norwegian coastline between Stad and Varanger*

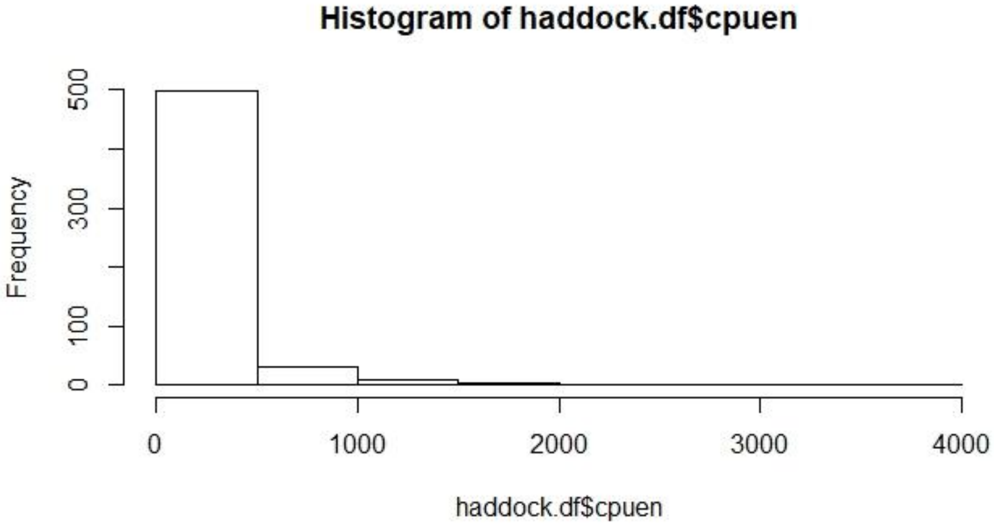

Figure 1.A.7 *Histogram of the CPUEN (N-catch number of individuals) of haddock (M. aeglefinus) caught in 1995, 2005 and 2017 on IMR's annual coastal survey along the Norwegian coastline between Stad and Varanger*

Appendix 1.B

Table 1.B *Mean temperatures (ºC) for the eight different subareas along the Norwegian coast from Stad to Varanger; Area A (69.5 to 71.3 ºN), Area B (67 to 69.5 ºN), Area C (63.5 to 67 ºN) and Area D (62 to 63.5 ºN), and coastal and ocean categorization in 1995, 2005 &2017. Standard error (Sd) is noted in parenthesis. Colour-code on areas with too few stations to be representative.*

Subarea	1995 Mean Temperature (ºC)	2005 Mean Temperature (ºC)	2017 Mean Temperature (ºC)
A - Coast	5.86 (1.5)	6.95 (1.7)	6.86 (1.7)
A - Ocean	7.50 (0.9)	8.83 (0.3)	7.95 (0.9)
B - Coast	6.67 (0.6)	8.58 (1.4)	8.70 (1.6)
B - Ocean	6.76 (0.2)	8.38 (0.6)	8.13 (0.8)
C - Coast	7.11 (0.3)	8.26 (1.0)	7.56 (1.0)
C - Ocean	7.23 (0.2)	8.27 (0.3)	8.10 (0.3)
D - Coast	7.07 (0.0)	10.14 (0.5)	9.07 (1.4)
D - Ocean	-	10.20 (0.0)	9.19 (0.3)
	6.62	7.8	7.74

Appendix 1.C

Table 1.C *Calculated centres of distribution (COD) for all species found above the set threshold (i.e. caught ≥ 8 individuals and/or at ≥ 3 stations in a year). Presented for the three years 1995, 2005 and 2017 in the coastal and ocean zone.*

	Coast			**Ocean**		
	1995	**2005**	**2017**	**1995**	**2005**	**2017**
Species	Mean latitude	Mean latitude	Mean latitude	Mean latitude	Mean latitude	Mean latitude
Grey gurnard	63.50	66.28	62.84			63.31
Blackmouth catshark	62.99	63.53	63.73		64.48	65.48
Lumpfish	65.61		66.41			
Spotted barracudina	70.11		69.17			
Deepwater redfish	70.68	70.49	70.54			68.33
Rabbit fish	65.95	65.55	66.19	65.33	64.81	65.41
Megrim	62.76		63.99		67.37	64.88
Greater forkbeard	64.96	63.87	67.94			67.62
European hake	64.00	63.58	62.88			63.34
Rose fish	69.45	69.29	70.28	67.63	67.57	69.22
Norway redfish	68.37	68.96	70.06	66.23	67.23	68.28
Atlantic wolffish	70.41	70.83	69.96			64.81
Thorny skate	69.33	70.01	69.08			
Silvery pout	65.43	67.28	68.71		64.02	66.99
Cod	69.90	70.30	68.88	68.48	67.10	69.80
Norway pout	66.08	69.02	67.62	64.89	68.48	68.05
Greater argentine	65.38	68.47	66.87	67.54	67.48	68.20
Saithe	69.80	69.02	68.94	68.90	67.89	68.94
Velvet belly lanternshark	64.34	64.53	66.42	66.53	66.05	68.37
Spiny dogfish	64.30		63.95			
Common ling	68.11	67.95	67.89	66.20	65.50	66.18
Poor cod	64.34	65.14	67.59			63.65
Atlantic pollock	63.13		62.53			
Haddock	69.65	70.34	70.00	68.08	68.45	67.89
Whiting	63.90	70.45	68.71	64.70	67.27	66.27
European plaice	68.97	70.43	70.11	70.10		
American plaice	69.26	70.20	69.31	68.85	68.54	69.16
Atlantic halibut	65.91	68.40	69.86		64.07	67.54
Lemon sole	69.45	70.25	70.10	67.36	65.37	67.39
Fourbeard rockling	66.24	69.62	66.68			
Longnosed skate	64.15		63.66			
Snake blenny	66.08	70.42	69.23			
Rock grenadier	65.02		63.82			
Witch flounder	68.52	69.30	66.99			
Common dab	68.60	67.55	68.52			62.92
Anglerfish	64.12	65.16	65.62			64.81
Tusk	68.64	70.11	69.24	66.53	66.05	68.37

Appendix 1.D

Investigation of the choice of a constrained correspondence analysis (CCA) by a Decorana analysis (Table 1.D) and the axis length of the first dimension (DCA1). And an investigation of the number of dimension selected by screeplot (Figure 1.D).

Table 1.D *Decorana analysis output for all three years (1995, 2005 & 2017)*

	DCA1	DCA2	DCA3	DCA4
Eigenvalues	0.6024	0.4779	0.3992	0.4296
Decorana values	0.6440	0.4831	0.3647	0.2605
Axis lenghts	5.3628	2.7730	3.5369	3.2673

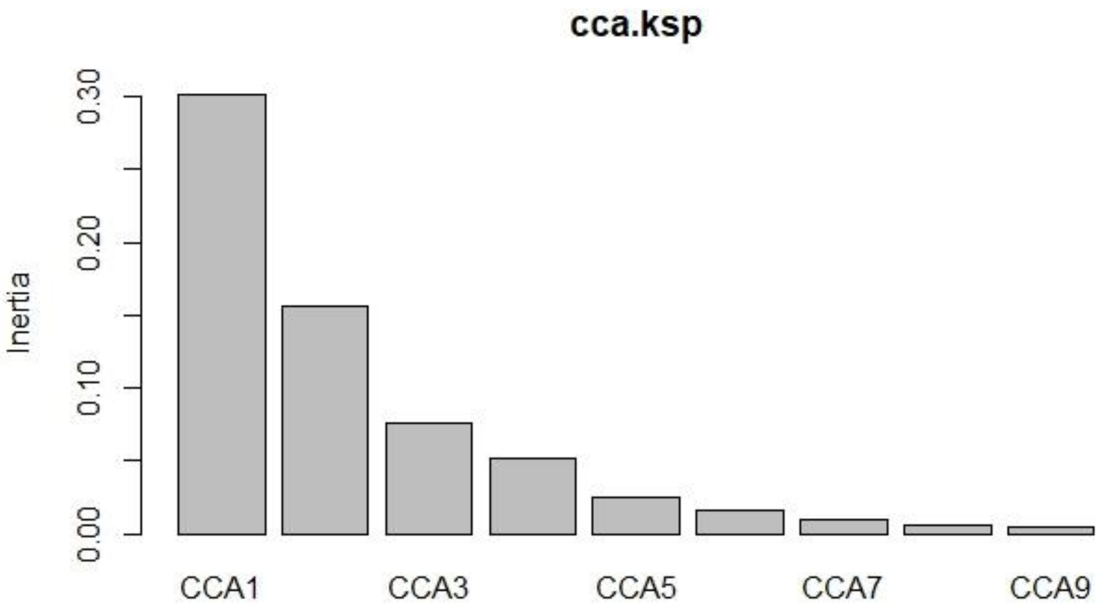

Figure 1.D *Screeplot from constrained correspondence analysis (CCA) for all three years (1995, 2005 & 2017), which presents the dimensions (CCA) and their explained intertia.*

R-script output from Monte-Carlo permutation testing of the full CCA model for the years 1995, 2005 and 2017.

```
> mod1<-anova.cca(cca.ksp, permutations = 999, model='full')
> mod1
Permutation test for cca under full model
Permutation: free
Number of permutations: 999

Model: cca(formula = log(k.vegan + 1) ~ Temperature + Depth + lat + strat2
+ year.x + strat, data = env.ksp)
          Df ChiSquare      F Pr(>F)
Model      9   0.64655 11.118  0.001 ***
Residual 424   2.73958
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```