

In deep water: Long-term trends in demersal fish diversity in Skagerrak and the Norwegian trench

AINA PAULSEN

SUPERVISOR

Halvor Knutsen Even Moland Guldborg Søvik Patrik Börjesson

University of Agder, 2023

Faculty of Engineering and Science Department of Coastal Ecology

University of Agder, 2023 Faculty of Engineering and Science Department of Coastal Ecology Gimlemoen 25 4604 Kristiansand http://www.uia.no © 2023 Aina Paulsen

Abstract

Throughout history, human activities have had profound impacts on marine ecosystems, with clear evidence of these consequences observable in the Skagerrak region. Oceans have historically been a critical resource for humankind, supplying food for the world's population. However, unsustainable practices such as overfishing and the emission of CO2, which leads to increased sea temperatures, have jeopardized this valuable resource.

The current study investigates changes in biodiversity and population size of various fish species in deep water areas of Skagerrak. The data is obtained from the Norwegian Bottom Trawl Survey for Northern Shrimp (*Pandalus borealis*) in Skagerrak and the Norwegian Deep. Initiated in 1984, this annual survey is conducted by the Norwegian Institute of Marine Research (IMR).

The Shannon index generally revealed large fluctuations in the three shallowest depth strata, down to 400 meters, without a clear trend. Only depth stratum 400-500 meters showed a significant decrease in biodiversity over time (2006-2022). Beyond this depth (500-600m), a weak, non-significant positive trend was noted. Both Norway pout and blue whiting may have influenced the Shannon index values within the 400-500m stratum. Moreover, Norway pout has had an impact on the Shannon index values in other depth strata, except for the 500-600 meters range.

Throughout all depth strata, diversity (*H*) remains generally low due to the dominance of Norway pout in large areas. At depths of 500-600 meters, roundnose grenadiers have more impact in the *H*-value, contributing to low diversity in 2008. Recent expansion of bottom trawling at greater depths is discussed as a possible reason for the putative changes in biodiversity in depth strata 400-500 meters. Population assessments conducted earlier suggest that the most significant declines occurred prior to 2006, leading to an assumption of relatively minor changes in many species' populations from 2006 to 2022. Bottom temperature measurements taken during this period showed no substantial changes that might have significantly influenced the deep-water fish species communities.

Sammendrag på norsk

Menneskelig aktivitet har hatt betydelig innvirkning på det marine miljøet gjennom historien. Havet har vært en viktig ressurs for mennesker i lang tid, og det har blant annet sørget for mat til store deler av verdens befolkning. Dessverre har denne utnyttelsen vært preget av ikkebærekraftige praksiser, som for eksempel overfiske som desimerer de marine ressursene, og utslipp av CO2 som fører til økning i havtemperaturen som gjør at flere arter opplever ufordelaktig miljø. Disse påvirkningene har også blitt observert i Skagerrak-området.

Dette studiet tar sikte på å undersøke endringer i biodiversitet og populasjonsstørrelse av ulike fiskearter i dypere områder av Skagerrak både romlig og temporalt (2006-2022). Dataene ble hentet fra den norske bunntrålundersøkelsen for nordlige reker (*Pandalus borealis*) i Skagerrak og Norskerenna. Undersøkelsen startet i 1984, og gjennomføres årlig av Havforskningsinstituttet (IMR).

Studiet viser en tydelig nedgang i biodiversiteten på dybder mellom 400 og 500 meter i perioden 2006-2022. De grunnere dybdestrata var det store svingninger i *H* verdi, men ingen signifikante trender ble observert. Generelt sett viser alle dybdestrata lav biodiversitet, da øyepål dominerer i store deler av disse områdene. I dybde strata 500-600 meter er det arten skolest som dominerer og påvirker *H*-verdien, men den er også årsaken til lav biodiversitet i 2008. I perioden ble konsistente, signifikante endringer i biodiversiteten kun påvist i dybde strata 400-500 meters dybde. Nylig utvikling av bunntrålfiskerier på større dyp diskuteres som mulig årsak til de påviste endringene av biodiversitet i denne dybdestrata. Tidligere målinger av forskjellige arters bestander tyder på at den største nedgangen skjedde før 2006 og at flere bestander har forblitt lave med få endringer fra 2006-2022. Temperaturmålingene i samme periode antyder at temperaturen ikke har hatt en betydelig innvirkning på fiskebestandene.

Table of content

1 Introduction	9
1.1 How changes in temperature affect fish communities	9
1.2 How the fishing industry affects fish communities	11
1.3 Anthropogenic effects on deep-sea communities	12
1.4 Deep waters in Skagerrak	13
1.5 Aims and objective	14
2 Methods	16
2.1 Norwegian shrimp survey	16
2.2 Survey area	16
2.3 Vessel and trawling	17
2.4 Equipment	18
2.4.1 Bottom trawl	18
2.4.2 Fish lab	19
2.5 Dataset	19
2.6 Diversity indices and statistical data analysis	21
2.6.1 Shannon diversity index	21
2.6.2 Simpson diversity index	22
2.6.3 Heatmap	23
2.6.4 Catch per unit effort (CPUE)	23
2.6.5 Linear regression	24
2.6.6 Model testing	24
2.6.7 Trawling and Temperature data	25
2.7 R-Script	25
3 Results	26
3.1 CPUE of dominating fish species	26
3.1.1 CPUE of Norway pout	26
3.1.2 CPUE of blue whiting	28
3.1.3 CPUE of dominating predatory species	29
3.2 Diversity in the fish communities	31

3.2.1 Biodiversity of all demersal fish species in deep water areas	31
3.2.2 Shannon Equitability index	35
3.3. Species with the greatest impact on the diversity	35
3.3.1 Without roundnose grenadier	35
3.3.2 Without Norway pout	36
3.3.3 Without blue whiting	40
4 Discussion	42
4.1 What changes have occurred in species dominating the systems	42
4.2 How has diversity changed over time?	44
4.3 What caused these changes in diversity and populations	47
4.3.1 Is the alteration in fish communities brought on by overfishing?	48
4.3.2 Is the apparent alteration in fish communities brought on by temperature changes?	52
4.4 Other studies reporting on similar research	53
5 Conclusion	55
6 References	57
7 Appendices	68
Appendix A	68
Appendix B	72
Appendix C	87
Appendix D	89
Appendix E	94

Preface

First, I'd like to express my deepest thanks to my supervisors Even Moland, Guldborg Søvik, Halvor Knutsen og Patrik Börjesson for their incredible support, guidance and feedback throughout the project. I appreciate all the help and could not have wished for any better supervisors than you guys! Your knowledge and positivity have made this project so much fun to work with.

I would also like to express my gratitude to the research team that I worked with in January 2023, when collecting data. Their experience and guidance taught me a lot about deep water fish, prawns, and gave me the opportunity to work like them in their field. Also, thanks to the rest of the crew working at Kritine Bonnevie, within the boat and the trawl team. All you guys are the reason for the amazing time out in the field!

Special thanks to Trude Hauge Thangstad for the amazing figures (map, temperature map), which I could use in this thesis. And Heidi Gabrielsen for some of the pictures used in the method.

And then it is my studybuddies, my girls! Without Annika Lie, Carina Thomassen, Emilie Johnsen, Ingrid Marie Helms and Såve Marie Sveinson, this year wouldn't be the same. We all have been in the same situation, where there has been tears, happiness, craziness, and frustration. Whatever emotions there have been in the office, we have all supported each other! Thank you, girls, I am happy to have experienced this year with you guys!

The last ones I want to give a special thanks to are my closest people! My family has always supported me to follow my dreams and have been my number 1 support throughout the whole process to become a marine biologist! My boyfriend, Ole Petter Nilsen, has been a very important person while doing this thesis. He has been my solid rock when it comes to sharing his experience with how to write a thesis and his knowledge in programming. With his teaching in programming, I can finally say that my programming skills in R are okay!

Kristiansand 22.05.2023

Aina Paulsen

1. Introduction

The term biodiversity refers to the variety of all different kinds of organisms in the natural world. Loss of biodiversity, due to a broad spectrum of human activities, is a major concern both nationally and internationally (Convention on Biological Diversity: http://www.cbd.int/; Living Planet Report 2020: https://livingplanet.panda.org/; Isbell *et al.*, 2017; Mace *et al.*, 2018; Duarte *et al.*, 2020). To address those concerns, the UN General Assembly has adopted 17 Sustainable Development goals for the period up to 2030. Goal 14 refers directly to conserve and sustainably use the oceans, seas, and marine resources. Presently, coastal biodiversity is under stress from over-fishing, aquaculture, habitat destruction, land use and developments, from introduction of exogenous organisms and genes, and from environmental changes, including climate change (Rilov *et al.*, 2019). To protect biodiversity, we need to know how it is structured spatially at different levels and how it varies temporally, what natural processes are responsible for this structuring, and how human activities may erode it.

Climate change and overfishing both decrease species adaptability and increase the risk of population collapse (Allison *et al.*, 2009). Overfishing and climate change are the main causes of changes in marine food webs, leading to the dominance of species from lower trophic levels due to the reduction of top predators (Worm & Myers, 2003; Baum & Worm, 2009). Overfishing and global warming make marine reproduction more vulnerable, hindering efforts to rebuild overfished stocks (Free *et al.*, 2019). Overfishing weakens the resilience of fish stocks and marine ecosystems to climate change and is one of the biggest threats to ocean health (Pauly *et al.*, 2005; Halpern *et al.*, 2015; Gattuso *et al.*, 2018).

1.1 How changes in temperature affect fish communities

Anthropogenic climate change has caused significant changes in natural systems, including the alterations in species distributions and ranges, and composition of species assemblages, leading to a decline in biodiversity (Parmesan *et al.*, 2013). The rising temperatures have been convincingly linked to these changes (Doney *et al.*, 2012, Bellard *et al.*, 2012). However, our knowledge of the impact of climate change on marine systems is relatively limited compared

to terrestrial systems (Rosenzweig *et al.*, 2008, Parmesan and Yohe, 2003). Recent metaanalyses suggest that marine species are shifting their geographic distribution towards the poles at a faster rate compared to their terrestrial counterparts (Poloczanska *et al.*, 2013). This shift is partly due to the slower warming of oceans compared to land, which allows marine species to occupy their potential latitudinal ranges to a greater extent, making them more responsive to temperature changes (Sunday *et al.*, 2012). Different species can enter or leave regions depending on their heat tolerances. They can potentially produce new assemblages and alter the community dynamics of a system or region with their individual dispersal tactics (Blanchard et al., 2005; Fisher et al., 2008; van Hal et al., 2010).

New species can change the taxonomic identity of a biological community, which can further change important ecosystem functions and structure (Dawson *et al.*, 2011). As such, investigating changes in functional characteristics of species within evolving assemblages has become increasingly important (Webb *et al.*, 2010). A functional trait is broadly defined, such as morphological, physiological, behavioral, and ecological or life history-oriented, which influences the organism's performance (Violle *et al.*, 2007). These traits encompass a wide range of characteristics, including diet, body shape and size, and spawning mode (Rogers *et al.*, 2011; Freitas *et al.*, 2023), all of which can provide insight into the mechanisms behind changes in community structure resulting from climate fluctuations (Kjesbu *et al.*, 2023; Freitas *et al.*, 2023). Ecological traits such as habitat can also change community structure given by climate fluctuations, which includes habitat associations and biogeographical affinities (Bates *et al.*, 2014, Barcelo *et al.*, 2016).

Climate change and its impact on nature are among the most pressing issues of our time. This phenomenon has the potential to disrupt biological communities in most parts of the world with direct and indirect effects on distribution, growth, and mortality (Campana *et al.*, 2020). Over the past 30 years there have been a sharp increase in temperature across the Northern European continental shelf (Gonzàlez *et al.*, 2018), and across the Norwegian coast (ICES, 2019; Campana *et al.*, 2020). In the North Sea the last 25 years, the temperature has been rising faster than in the surrounding seas, with nearly 1.6°C at the surface (Möllmann & Diekmann, 2012; Hobday & Pecl, 2014). This region has been identified as a "hot spot" for global warming (Murgier *et al.*, 2020). Temperature has a major impact in species distribution in northern waters. This influences species and their life history directly, through

changes in species composition and prey availability. Also indirectly, by affecting reproduction and growth (Cartes *et al.*, 2013; Tanaka *et al.*, 2021).

Despite these changes, the current and future impact on diversity remains uncertain, mainly due to the great variability in biological responses (Lenoir *et al.*, 2010). Understanding past and present changes related to global warming is important in order to predict future changes.

1.2 How the fishing industry affects fish communities

Fisheries play a significant role in the global decline of fish populations. Over the past decades, there has been a notable expansion in fishing activities (Morato et *al.*, 2006; Issifu *et al.*, 2022), leading to changes in community structure and fish size and age, distributions due to selective harvesting of target species and large individuals, and incidental bycatch of non-target species (Bianchi *et al.*, 2000). Fishing has also resulted in habitat modification, especially bottom trawling, which has triggered changes in biomass, species composition, and size structure (Pauly *et al.*, 1998; Bianchi *et al.*, 2000; Jennings & Blanchard, 2004). According to FAO (2012) as much as 87% of the global fish stocks are either overexploited or fully exploited. In European waters, recent estimates indicate that between 40 and 70% of fish stocks are currently at unsustainable levels, either overfished or at their lower biomass limits (Sumaila & Tai, 2020). The current size and capacity of the European Union (EU) fleet was estimated to be 2-3 times above the sustainable level in 2008 (European Commission, 2008). Several offshore fisheries capture species that are classified fully exploited (STECF, 2017).

Overfishing refers to both fishing down the marine food web (Pauly *et al.*, 1998, 2005), and depleting populations due to excessive fishing mortality (McCauley *et al.*, 2015; Baum & Fuller, 2016). Both effects threaten ocean health by causing changes in population size, age, size and spatial distribution, making populations more susceptible to environmental fluctuations (Pauly *et al.*, 1998, 2005; McCauley *et al.*, 2015). This is particularly relevant for highly impacted areas and vulnerable species (Issifu *et al.*, 2022). Overfishing the top predators may affect the trophic levels in the food chain, which can further lead to trophic cascades and ecosystem regime changes (Eriksson *et al.*, 2023). For example, after the collapse of Atlantic cod (*Gadus morhua*) stocks in Canada due to overfishing, Newfoundland

and other Canadian coastal areas changed to targeting shellfish, ie. shrimp, lobster, and crab which today dominate the fishing industry. This transition is known as fishing down the food web and is often the result of unsustainable fishing practices (Pauly *et al.*, 1998). A study by B. Worm and R. A. Myers (2003) showed that shrimp populations in the North Atlantic Ocean are inversely related to predator abundance, with increases in shrimp populations coinciding with declines in cod stocks.

Fishing methods such as bottom trawling, bycatch, and harmful subsidies are responsible for destructive fishing practices, leading to overfishing (Sumaila *et al.*, 2006, 2021; Agnew *et al.*, 2009; Moomaw & Blankenship, 2014). Bottom trawling, for example, damages both targeted and non-targeted species, and harms the seabed (Issifu *et al.*, 2022). Bycatch leads to discarded non-target species and is estimated at 27 million tons globally per year (Alverson *et al.*, 1994). Prawn trawling is particularly detrimental, resulting in more bycatch than prawns (Saila, 1983; Andrew & Pepperell, 1992), and responsible for a third of all fisheries discards (Alverson *et al.*, 1994). Bottom trawling reduces predator species abundance, leading to prey species productivity (Collie *et al.*, 2017), and indirectly benefits prey species due to size selectivity (Collie *et al.*, 2017). However, it also destroys habitats and affects species such as herring (*Clupea harengus*) and cod, which depend on bottom habitats at different stages of their life cycle (Kritzer *et al.*, 2016). The lack of suitable habitat affects the survival and reproduction (Tupper & Boutilier 1995).

1.3 Anthropogenic effects on deep-sea communities

Many species in deep-sea communities are very sensitive to changes or impacts (Bergstad *et al.* 2014). The most important characteristic they share is the low productivity rate. This is reflected in the life history strategies in many deep-water species that are characterized by long lifespans, relatively low fecundity, slow growth, and high age at first maturity. These strategies are considered adaptations to the generally low production rates in deep-water ecosystems (Merrett & Haedrich, 1997; Drazen & Haedrich, 2012). Therefore, major changes in communities can have a negative impact on these species (Bergstad *et al.* 2014). With their slow development and late maturation, there is little to no time to adapt to new conditions. A high fishing pressure on deep-water fish species may lead to overexploitation of populations

with low productivity when trawling in deep areas (Bergstad *et al.* 2014). This leads to high mortality in these species, leading to decline or in the worst case, extinctions (Large *et al.*, 2003; Gordon, 2005; Clark *et al.*, 2007).

1.4 Deep waters in Skagerrak

The Norwegian trench is a deep channel running along the Norwegian coast from the inner Skagerrak to the shelf edge bordering the Norwegian Sea (Skjæråsen & Bjergstad, 2000). One important characteristic of the Norwegian trench is the inflow of comparatively saline and warm Atlantic water from the Norwegian Sea along its western slopes (Otto et al., 1990). These strong bottom currents are up to 20 m-sq, which enter the Skagerrak (Rosenberg et al., 1996). These currents occur down to 500 meters, especially on the southern side of the trench (Rodhe, 1987; Rodhe 1996), and resuspend and distribute the suspended matter on the slopes (Skjæråsen & Bjergstad, 2000). The deepest parts of the Norwegian trench are in the central Skagerrak with a maximum depth of 710 meters (Longva & Thorsnes, 1997). At a depth of 200 meters, there is a faunal transition zone, where the fish community proper differs from that in surrounding areas (Daan et al., 1990; Bergstad, 1990). The change in species composition coincides with a transition from relatively coarse to fine sediments like sand and silt, which characterize the lower slope and bottom of the channel (van Weering et al., 1973; Longva & Thorsnes, 1997). Deep slope channels are hence often rather productive areas which can be utilized by animals from adjacent shallower areas, upper continental slope and upper mesopelagic of the open ocean (Bergstad, 1990).

The fish community in Skagerrak contains various pelagic, semi-pelagic and benthic fish species. This community has a complicated structure, where factors such as flow, depths and seasons are shaping the structure (Bergstad, 1990). There are indications of a certain downslope migration in winter of fish from shallower areas, which suggests that the relatively warm Atlantic water masses also offer satisfactory wintering conditions for some populations of shallow North Sea species. The Atlantic inflow largely determines which fish species will occur in the Norwegian trench (Bergstad, 1990). The area is deep enough for the immigration of species to adapt to the large means of traveling from the open sea into the shelf channel. This provides favorable conditions for fish species that colonize the area permanently or temporarily (Bergstad, 1990). Since Norwegian trench in Skagerrak has ranged maximum

depths from 150 to 700 meters, the community structure changes a lot from the shallower areas compared to deeper areas (Bergstad, 1990). In the shallower areas Norway pout (*Trisopterus esmarkii*), saithe (*Pollachius virens*) and haddock (*Melanogrammus aeglefinus*) dominate (Bergstad, 1990; Albert, 1994). In Skagerrak, blue whiting (*Micromesistius poutassou*) is more dominant compared to the west side of Norwegian Deep (Bergstad, 1990; 1991). Skagerrak is a nursery and feeding area for blue whiting, where most juveniles are found (Bergstad, 1991). In the deeper areas, the community is characterized by a lot of roundnose grenadier (*Coryphaenoides rupestris*) and greater argentine (*Argentina silus*) (Bergstad, 1990; 1991).

1.5 Aims and objectives

The aim of this study is to investigate temporal and spatial changes in the fish community in the deep-water areas of Skagerrak, and discuss the implications in relation to overfishing and climate change. To achieve this, the study intends to test the following hypotheses based on trends in biodiversity and CPUE of some species populations in different depth strata and over the years 2006-2022.

- The fish community in the deep-water areas of Skagerrak has undergone significant alterations in biodiversity over the past decades.
- CPUE of the dominant species in deep water communities has experienced significant changes over the past decades, which has affected biodiversity.
- If overfishing is the primary driving force for changes in the fish community (a topdown impact), one would expect an increase in some species lower down in the food chain.
- Alternatively, if climate change were the principal driving force, one would expect an increase in the abundance of warm-water species and a decrease in cold-water species, or their migration to greater depths.

The study will compare different depth strata to uncover potential trends in fish (teleost and elasmobranch) evenness and species richness. This comparison may highlight deviations that stand out against the general trends. Additionally, by examining trends in diversity and evenness, the study aims to identify which species are primarily responsible for driving or masking these trends, if such trends exist. Addressing these hypotheses will provide insights into whether anthropogenic activities, such as overfishing and changes in temperature, have affected the deep-water fish community in Skagerrak's marine ecosystems.

2. Methods

2.1 Norwegian shrimp survey

The data utilized in this study are obtained from the Norwegian Bottom Trawl Survey for Northern Shrimp (*Pandalus borealis*) in Skagerrak and the Norwegian Deep (ICES Divisions 3.a and 4.a East), which is an annual survey conducted by the Norwegian Institute of Marine Research (IMR). The survey assesses the distribution, biomass, abundance, recruitment, size distribution and demographic composition of the shrimp stock, the size of the populations of shrimp predators, as well as measuring hydrographic conditions in the survey area.

The survey has been running since 1984 and continues to this day. The main focus has been monitoring the stock status of northern shrimp for input to the stock assessment, to provide advice on fishing quotas. However, the whole catch is worked up, and weight, abundance and lengths are registered for all fish species.

The survey time series consists of four parts due to shifts in timing and gear: 1) October/November in 1984-2002, 2) October/November in 2003 (different gear), 3) May/June in 2004-2005, and 4) January/February from 2006 until today.

2.2 Survey area

The Norwegian Bottom Trawl Survey for Northern Shrimp covers the Norwegian trench from south of Bergen to the inner parts of the Skagerrak. In 2021 and 2022, the Oslo fjord was also covered. The survey encompasses depths ranging from 100 to 550 meters. The survey area is stratified by area and four depth zones (100-200 meters, 200-300 meters, 300-500 meter and >500 meters). There are currently no trawl stations in strata 1, 3 and 8 (*Figure 1*). In 2006, a fixed station network was created based on the stations that were trawled during the shrimp survey in 2000. During the years, several stations have been moved, deleted, or added due to rough bottom conditions, new power cables, requests from fishers or stations too close to each other. Presently, there are 111 fixed stations where the survey is conducted.



Figure 1: Map over fixed trawl stations by stratum. Stations marked with a gray dot have been excluded from the station list. The black dots are all the stations used today, while star dots present the stations in Oslo fjord, which are new stations added in recent years. Reference: Trude Hauge Thangstad, IMR.

2.3 Vessel and trawling

Between 2006 and 2016, the vessel Håkon Mosby was utilized. In 2017 it was replaced by Kristine Bonnevie. The standard towing time for trawling is typically 30 minutes at the bottom. At shallow stations in the Norwegian trench west of Lindesnes, the towing time was previously reduced to 15 minutes due to very large catches of fish. The standard towing speed is 3 knots. Kristine Bonnevie has a symmetry sensor showing the water speed into the trawl opening. In previous years, when the survey was carried out with Håkon Mosby, the trawl was trawled according to speed from GPS. If you trawl according to speed on the symmetry sensor (3 knots), the speed on the GPS will be higher than 3 knots when you are trawling with the current and lower when you are trawling against the current.

The door spread and trawl opening have varied somewhat throughout the time series. In 2013-2016 the average door spread was between 49 and 51 meters, while in 2017-2020 it was between 52 and 55 meters, which is above the accepted range (48-51 meters). Door spread and trawl height are related, and it appears that when an acceptable door spread has been achieved, the vertical trawl opening has been too high and vice versa. Furthermore, the use of new and heavier doors (Thyborøn) on Kristine Bonnevie compared to the Waco doors on Håkon Mosby have also affected speed, door spread and trawl opening.

2.4 Equipment

2.4.1 Bottom trawl

The Campelen 1800 trawl, with a mesh size of 20 mm in the channel and cod end, and a 10 mm mesh size in the inner net, has been utilized for the shrimp survey since 1984 (except in 2003) (*Figure 2*). A rockhopper bottom gear is used. To prevent mud hauls, extra floats are added between the gear and the fishing line ("Nordsjørigging"). This rigging received a new gear code in 2019 (3296). In previous years, gear code 3271 was used (Campelen trawl with standard rigging). Even though code 3271 was used in the data, it was still "Nordsjørigging" that was used. In 2008, strapping was introduced to achieve a more constant trawl geometry regardless of depth. The trawl doors are Thyborøn 125. The sweep length is 40 meters. Scanmar sensors are used to monitor trawl geometry.

The procedure for rigging and use of the Campelen 1800 trawl in this survey, is described in more detail in this report from IMR:

https://www.hi.no/om_havforskningsinstituttet/rederi/sms_systemet/nb-no/pub/docs/6004.pdf



Figure 2: The Campelen 1800 trawl used in collecting data. Photographer Heidi Gabrielsen, 2021.

2.4.2 Fish lab

All fish in the catch are sorted and identified to species (*Figure 3*). During sorting, all large fish and not so common fish species are sorted out. If the catch of some species is too large for everything to be sorted, the "mix" is weighed together (for example a total of 200 kg). Then we take out a fraction and find the weight of this subsample (for example 20 kg). A factor of 10 will give us the total weight of the species in the fraction. The fraction is sorted by species, for example Norway pout, blue whiting, and haddock. All the species in the fraction are weighed and multiplied by 10 to find the total weight in the trawl haul. If there are 5.3 kg of blue whiting in the fraction that was sorted, then there is $5.3 \times 10 = 53$ kg of blue whiting in the entire trawl catch.



Figure 3: In the fish lab, where measurements, counting and identification takes place. Picture right: photographer Heidi Gabrielsen, 2021.

The data are registered using a data registration system called Fish2Data (F2D). For all fish species, the total catch weight, as well as length measurements of up to 30 fish and sample weight (weight of all length measured specimens) are recorded. F2D estimates the abundance of fish per species in the catch by using the sample number and weight, and total weight. When measuring the length of fish, the Scantrol FishMeter100 electronic measuring board is used.

2.5 Dataset

In this study, only time series 4 (2006-2022) is used. Using data obtained from three different seasons may have affected the data regarding abundance, individual sizes and distribution of

species in the different depth strata. This is because the ecological dynamics within the study area (seasonal variation, reproductive cycles, environmental conditions, food availability and trophic interactions) differs in each season. Throughout the entire survey time period, species identification may have been done with varying precision and quality. The species identification in the latter part of the time series starting in 2006 is probably better than in the 1980s and 1990s, especially for the less common species. For example, the skates during the earlier periods were not identified to species but were registered as "skate". Only data from Skagerrak are used in this study. In January/February, weather conditions are often rough, which resulted in several trawl stations in some years not being taken due to poor trawling possibilities. Since Skagerrak is not as exposed to the weather compared to areas further west, problems with a lack of stations are avoided here. Furthermore, a fixed station network was established in 2006. This makes it easier to map and compare fish populations between years.

In this study, only the biodiversity and CPUE of demersal fish species was studied. The catches contain everything from crustaceans (Norway lobster (*Nephrops norvegicus*), shrimps, crabs), fish, jellyfish to squid. All registrations that were not fish were filtered out of the data set. Fish that have not been identified to species, but for instance to family, were also filtered out. The reasons for filtering these out are 1) few individuals placed in families, and 2) utilizing data identifying individuals at several taxonomic levels can lead to inaccurate estimates of biodiversity. Finally, pelagic fish which are caught in the trawl on its way up or down were also filtered out.

Instead of calculating the biodiversity at fixed stations or areas, depth intervals were used. Indices were created for 100-200 meters, 200-300 meters, 300-400 meters, 400-500 meters, and 500+ meters depth intervals. Reason for dividing the data in depth intervals is because of the differences in species distribution and community structure in the different depth strata. Both species richness and abundance differ by depth. Calculating the trends in biodiversity and population size then provides a more accurate estimate of what changes have occurred over the years.

2.6 Diversity indices and statistical data analysis

Most of the analyses were done using R (version 4.2.1). Annual survey files were extracted from the IMR database. After adding all the years (2006-2022) into one large data set and filtering the unnecessary species, a new data set was created.

With the new data set containing the selected data, indices were created to analyze changes in biodiversity in Skagerrak.

2.6.1 Shannon diversity index

The Shannon index, also known as the Shannon-Weaver diversity index or Shannon entropy, is a measure of biodiversity or the amount of uncertainty in a system. The Shannon index, denoted by H, is often used in ecology to measure the diversity of species in a particular community. It considers both the number of species present and the relative abundance of each species (Fath, 2019). The higher the value of H, the higher the diversity of species in a particular community. H is given by:

$$H - \sum_{i=1}^{S} (pi * \ln(pi))$$

where S is species richness, p_i is the relative abundance of each species in the system representing the proportion of individuals belonging to the species *i* in the total population, and ln is the natural logarithm.

An Equitability Index was also used, which is measuring the evenness of species in a community. The term "evenness" simply refers to how similar the abundances of different species are in the community (Fath, 2019). The value ranges from 0 to 1 where 1 indicates complete evenness. A value of EH = 0 indicates a community that only contains one species. The Equitability Index (*EH*) is given by:

$$EH = H/lnS$$

where *H* is the diversity index, and *S* is species richness (Fath, 2019).

2.6.2 Simpson diversity index

The Shannon index is the most used method for calculating diversity, together with the Simpson index (Fath, 2019). Both methods were used to calculate the diversity in this thesis, to compare the results from the two indices. The Simpson index D is a measure of probability and is given by:

$$D = 1 - \sum_{i=1}^{S} (pi^2)$$

where pi is the proportion of individuals belonging to species *i*. The value of the Simpson index ranges from 0 to 1, where 0 represents infinite diversity and 1 represents no diversity. The larger the value of *D*, the lower the diversity (Fath, 2019).

The difference between the two indices is that the Simpson index focuses heavily on the species that dominate the community the most, while the Shannon index takes more account of the rarer species as well (Fath, 2019). This is an important factor when the data that are used contain many rare species. With the Simpson index, the diversity is a measure of probability. The less diversity, the greater the probability that two randomly selected individuals will be of the same species (Fath, 2019). The Shannon index considers both species richness and evenness and is a measurement related to the concept of uncertainty. If a community has very low diversity, we can be more certain of the identity of an organism we choose by random (Fath, 2019). Both Shannon and Simpson (*Appendix C, figure 40*) indices were used to calculate the biodiversity in five different depth intervals.

To examine the influence of potential dominant species on the diversity index, the *H* value was recalculated adopting a leave-one-out approach. This involved removing one species at a time from the data and calculating new H values for each modified dataset. Species not mentioned in the CPUE data were also considered (*Appendix B*).

2.6.3 Heatmap

Heatmap is a useful tool for visualizing multivariate data and represents two-dimensional tables of numbers as shades of colors. The dense and intuitive display makes heatmaps wellsuited for presentation of high-throughput data. Heatmap relies fundamentally on color encoding and meaningful reordering of rows and columns. Heatmaps were made in R with the package pheatmap (Kolde, 2019). This technique is very useful for datasets with hundreds of rows and columns. Heatmaps were used to illustrate which species, as well as the abundance of these species, that were caught each year on the survey, as a tool to understand the annual trends in the diversity indices. Since each species has a different amount of catch of individuals, the total catch was normalized. A statistical normalization is a proportion without measurement units (dimensionless or scale invariant) that allows us to compare elements of different variables and different measurement units. In this case, there are a number of individuals all from 0 to sixty thousand. Without the normalization, most of the species would have disappeared in the figures, because some of the measurement values were higher than others. Formula used in R:

$$Normalized_X = (X - min(X)) / (max(X) - min(X))$$

where *X* is the total catch of a certain species, per year.

2.6.4 Catch per unit effort (CPUE)

Catch per unit effort (CPUE) indices were calculated to look at the temporal trends in catch rate in selected species from 2006 to 2022. By assuming that CPUE (catch rate) is proportional to fish abundance, trends in fish populations can be monitored by tracking changes in CPUE over time. Researchers can estimate trends in fish populations and identify periods of population growth or decline. Looking at trends in populations can further tell us something about community structure and help explain trends in biodiversity. CPUE is calculated by dividing the total catch of a fish species by the amount of fishing effort (the number of hours fished (distance) or the amount of fishing gear used). To calculate the CPUE, the abundance per species was divided by distance trawled, to get a standardized catch rate

per station (catch per nautical mile). An average catch rate was calculated for each depth stratum for each year.

2.6.5 Simple linear regression

When analyzing the index data and CPUE data, simple linear regression was used. Linear regression models describe the relationship between two variables by fitting a straight line to the observed data. Regression allows us to estimate how a dependent variable changes as the independent variable changes. The formula for a simple linear regression is $y=\beta_0 + \beta_1 X + \epsilon$. Y is the predicted value of the dependent variable (y) for any given value of the independent variable (x). β_0 is the intercept, which is the predicted value of y when x is 0. β_1 is the regression coefficient, which indicates how much we expect y to change as x increases. ϵ is the error term. Simple linear regression is a parametric test, meaning that it makes certain assumptions about the data. These assumptions are homogeneity of variance (homoscedasticity), independence of observations (no hidden relationships among observations) and normality (normal distribution) (Crawley, 2015).

2.6.6 Model testing

After analyzing the data, the models were tested with an emphasis on constancy of variance and normality of error. For testing these models, one can use four built-in model-checking plots. First plot test is residuals versus predicted values, which is used to check the assumption of linearity and homoscedasticity. If the model doesn't meet the linear model assumption, the residuals give either big positive value or big negative value. To assess the assumption of linearity we want to ensure that the residuals are not too far away from 0. The QQ-plot, which is the second figure, evaluates the normality based on the residuals, by comparing the residuals to "ideal" normal observations. The plots need to be along the 45degree line in the QQ-plot, to assume that normality holds in the data. The third plot is a scale-location plot (square rooted standardized residual vs. predicted value). This is useful for testing the assumption of homoscedasticity. Last one is residuals vs. leverage plots which are a type of diagnostic plot that allows us to identify influential observations in a regression model (Crawley, 2015).

2.6.7 Trawling and Temperature data

Trawling data from Norwegian commercial fishing were used to look at the amount of trawling in Skagerrak from 2011-2022. They were used to compare if the potential increases had any effect on the biodiversity or CPUE of species. These data are electronic logbooks that are filled out at sea, by all vessels with a length greater than or equal to 12 m. Information is filled in per trawl haulage.

Conductivity-Temperature-Depth (CTD) samples were taken at each station at the shrimp survey. IMR calculated the mean bottom temperature (\pm SD) per area in Skagerrak and the Norwegian Deep in 2006 to 2023. These data are used to look at the temperature changes over the years and compare it with the results. Both the trawling data and temperature data are found in Appendix E.

2.7 R-Script

In order to create several indices from a dataset, the dataset was divided into lists with the function list(). In addition, the function for-loop was also used when creating the lists. This is necessary with the intention of the data set being divided into years and depth, as well as containing lots of species and number of individuals' data. After the division of data, new columns were created where the calculation of number of species with the number of individuals for each species was made to find the H-value. The H value was calculated at each depth for each year, to see the change in the fish population. To visualize the H value and CPUE, the package ggplot was used. This package is used to create different figures that visualize the specific data from a dataset. With package girdExtra (Auguie, 2017), all the plot figures of each depth stratum were inserted into one figure. Pheatmap (Kolde, 2019) was used to create a heatmap, for visualization development in total catch per year. Ggplotify was used to convert pheatmap to ggplot2. Package vegan (Oksanen et al., 2022) were used to create the clusters in the heatmaps. This package provides tools for descriptive community ecology. With ggplotify (Yu, 2021), we are able to use 'cowplot' to align plots produced by pheatmap by converting them to 'ggplot' objects. After making most of the figures, some detailed work was done on each figure. The package plotrix (Lemon, 2006), provided with various labeling and color scaling functions, to make the figures more representative. For the coloring of most figures, the package viridis (Garnier et al., 2021) was also used.

3. Results

The dataset used in this study contained 66 demersal fish species. In total catch of all 66 species (*Appendix A, Table 12 and 13*), made between 2006 and 2022, it is Norway pout that dominates the most in numbers with 82% (*Figure 4*). Then there are long rough dab (*Hippoglossoides platessoides*), haddock, blue whiting and whiting (*Merlangius merlangus*) with a total of 13% of the abundance. The last 5% is distributed among the rest, including among other species saithe, roundnose grenadier, velvet belly (*Etmopterus spinax*) and witch (*Glyptocephalus cynoglossus*).



Figure 4: Species' proportion (%) of total catch in numbers during the time period from 2006 to 2022.

3.1 CPUE of dominating fish species

3.1.1 CPUE of Norway pout

Among all the species, Norway pout dominated the total catch in numbers. Figure 5 shows large fluctuations in Norway pout in depth stratum 100-200 meters. Few years (2010, 2013 and 2020) showed a high catch rate of Norway pout in this stratum. The three depth strata from 200 to 500 meters started with low catch rates in 2006-2008, and have had large

fluctuations after, throughout the years. The trend lines in depth strata 300-400 and 400-500 meters show a positive trend over the years. In depth stratum 500-600 meters, the catch rate was very low throughout this time series, with a negative trend. The analysis shows no significant trends in Norway pout in any of the depth strata (*Table 1*).



Figure 5: Trends in catch rate (specimens per trawled nm) of Norway pout in the five depth strata over the timeperiod 2006-2022. Note different values on the y-axes.

Estimate	Slope	P-value	Adjusted R-squared	Multiple R-squared
19886.91	-9.57	0.8	-0.0634	0.00305
-17373.27	9.14	0.8	-0.0621	0,803
-72670.2	36.7	0.4	-0.0217	0.0421
-116001.7	58.1	0.3	0.0223	0.0834
5598.78	-2.76	0.3	-4.77e05	0.0769
	Estimate 19886.91 -17373.27 -72670.2 -116001.7 5598.78	Estimate Slope 19886.91 -9.57 -17373.27 9.14 -72670.2 36.7 -116001.7 58.1 5598.78 -2.76	EstimateSlopeP-value19886.91-9.570.8-17373.279.140.8-72670.236.70.4-116001.758.10.35598.78-2.760.3	EstimateSlopeP-valueAdjusted R-squared19886.91-9.570.8-0.0634-17373.279.140.8-0.0621-72670.236.70.4-0.0217-116001.758.10.30.02235598.78-2.760.3-4.77e05

Table 1: Simple regression analysis of CPUE Norway Pout.

3.1.2 CPUE of blue whiting

Another species appearing to be dominant in abundance in some of the trawl catches was blue whiting. Not as dominant as the Norway pout, but it still stood out compared to many other species. In Figure 6, in depth stratum 100-200 meters, the catch rate was low in blue whiting during the years, resulting in minimal change over time. In the depth strata from 200 to 600 meters, there is more stability and low catch rate from 2006 to 2011/2012. After 2012, large fluctuations appear in the catch rate, resulting in significant positive trends in each of these depth strata. Analyzing this data, all depth strata except 100-200 meters shows a significant trend (*Table 2*).



Figure 6: Trends in catch rate (specimens per trawled nm) of blue whiting in the five depth strata over the timeperiod 2006-2022. Note different values on the y-axes.

Depth	Estimate	Slope	P-value	Adjusted R-squared	Multiple R- squared
100-200m	282.84	-0.14	0.15	-0.1452	0.2402
200-300m	-354.98	0.177	0.01	0.3047	0.3482
300-400m	-452.87	0.226	0.02	0.2696	0.3183
400-500m	-690.02	0.344	0.0001	0.5946	0.6199
500-600m	-445.63	0.223	0.01	0.3724	0.4207

Table 2: Simple regression analysis of CPUE blue whiting, after log transforming the residuals.

3.1.3 CPUE of dominating predatory species

Saithe showed a slight decrease in catch rate (CPUE) in all five depth stratums over the studied time period (*Figure 17, Appendix B*), but only the decrease in the deepest stratum (500-600 meters) was found to be significant (p = 0.03, adjusted R² = 0.429) (*Table 3*). The 200-300 meters depth stratum had more fluctuation in catch rate over the years compared with the other strata. In the deepest areas between 400-600 meters, the saithe catch rate was more stable, and the number of individuals caught at these depths are few. Saithe is found more in shallower areas (100-400 meters).

Whiting showed an annual fluctuating catch rate (CPUE) in the four shallowest depth strata over the studied time period (*Figure 19, Appendix B*). 100-200 meters had the strongest increase and was the only stratum to be found significant (p = 0.005, adjusted R² = 0.38) (*Table 3*). In the deepest areas between 400-600 meters, the catch rate in whiting was more stable, and the number of individuals caught at these depths are few. Whiting is found more in shallower areas (100-400 meters).

Roundnose grenadier showed a decreasing trend in depth strata 200-600 meters in the four deepest depth strata over the studied time period (*Figure 21, Appendix B*). Depth strata 300-400 (p = 0.0007, adjusted R² = 0.51), 400-500 (p = 0.004, adjusted R² = 0.51) and 500-600 (p = 0.02, adjusted R² = 0.29) meters presented significant negative trends (*Table 3*). In the shallowest areas between 100-300 meters, the catch rate in roundnose grenadier had few numbers of individuals caught. This species is found more in deeper areas (300-600 meters).

Haddock showed an annual fluctuating catch rate (CPUE) in all five depth stratums over the studied time period (*Figure 25, Appendix B*). Only a decrease trend in stratum 300-400 meters was found to be significant (p = 0.04, adjusted R² = 0.211) (*Table 3*). The largest fluctuation in catch rate over the years were in depth strata 100-400 meters. In the deepest areas between 400-600 meters, the catch rate in haddock was more stable, and the number of individuals caught at these depths were few. Haddock is found more in shallower areas (100-400 meters).

CPUE of these species and more, in all depth strata are found in Appendix B. Figure 7 presents all the significant trends in saithe, whiting, haddock, and roundnose grenadier. Table 3 presents all the analysis of the predator species with significant trends.



Figure 7: Predator species with significant trends in different depth strata from the period 2006-2022. Note different values on the y-axes.

Table 3: Simple regression analysis of significant trends in CPUE predatory species, after using 1	og
transformation or square root transformation in some of the residuals.	

Species	Depth	Estimate	Slope	P-value	Adjusted R-squared	Multiple R-squared
Whiting	100-200m	-7052.32	3.525	0.00485	0.3821	0.4208
Saithe	500-600m	861.249	-0.426	0.03	0.429	0.5
Haddock	300-400m	2191.24	-1.083	0.04196	0.211	0.2636
Roundnose Grenadier	300-400m	369.58	-0.182	0.0007	0.5142	0.5446
Roundnose Grenadier	400-500m	299.05	-0.147	0.004	0.3898	0.428
Roundnose Grenadier	500-600m	329.84	-0.1613	0.02	0.2935	0.3439

3.2 Diversity in the fish communities

3.2.1 Biodiversity of all demersal fish species in deep water areas.

To analyze changes in diversity of the fish community in deep-water species in Skagerrak, the Shannon diversity index (H) was used. Figures 8-11 present large annual fluctuations in H value in the four shallowest depth strata. 500-600 meters (*Figure 12*) has less fluctuations. In 100-200 meters (*Figure 8*) the diversity has no changing trend from 2006 to 2022. Depth strata 200-400 meters showed a similar pattern in H value each year. But 300-400 meters (*Figure 10*) present a larger decrease in diversity than 200-300 meters (*Figure 9*). 400-500 meters (*Figure 11*) has the largest decrease in diversity compared to the other depth strata. Even with large fluctuations, there is clearly a higher H value in the first years of this period compared to recent years. 500-600 meters (*Figure 12*) is the only depth stratum presenting an increasing trend in diversity. This increasing trend results mainly from the low H value in 2008, where the number of roundnose grenadiers caught was high by looking at the heatmap (*Figure 12*). Both depth strata 100-200 (*Figure 8*) and 500-600 meters (*Figure 12*) have kept the H value above 1, while the other depth strata have stayed below 1, giving a low diversity in these communities (*Figure 9-11*).

Each diversity index is accompanied by a heatmap. The heatmap provides an overview of species richness and abundance per species and year, which are two important factors used to calculate the Shannon index. Together they present both the trend that has occurred and some of the reasons for this occurring trend. The species richness was highest in 100-200 meters, with 59 species (*Figure 8*). 200-300 meters had 50 (*Figure 9*), while 300-400 meters had 43 species (*Figure 10*). 400-500 meters (*Figure 11*) and 500-600 meters (*Figure 10*) had respectively 40 and 28 species caught during these years. Species richness decreases with depth. All depth strata lower than 400 meters show very few changes in species richness over the years. The largest changes are found in abundance in these depth strata. In 500-600 meters, there are both increases in species richness and abundance.



Figure 8: Trend in diversity (H value) from 2006-2022 in depth stratum 100-200 meters. The values in the heatmap were normally distributed to give a scale from 0-1, to make it easier to compare the amount in different years.



Figure 9: Trend in diversity (H value) from 2006-2022 in depth stratum 200-300 meters. The values in the heatmap were normally distributed to give a scale from 0-1, to make it easier to compare the amount in different years.



Figure 10: Trend in diversity (H value) from 2006-2022 in depth stratum 300-400 meters. The values in the heatmap were normally distributed to give a scale from 0-1, to make it easier to compare the amount in different years.



Figure 11: Trend in diversity (H value) from 2006-2022 in depth stratum 400-500 meters. The values in the heatmap were normally distributed to give a scale from 0-1, to make it easier to compare the amount in different years.



Figure 12: Trend in diversity (H value) from 2006-2022 in depth stratum 500-600 meters. The values in the heatmap were normally distributed to give a scale from 0-1, to make it easier to compare the amount in different years.

400-500 meters was the only depth stratum with a significant negative trend in *H* value from 2006 to 2022 (p = 0.0186, adjusted R² = 0.272) (*Table 4*).

Table 4: Simple regression analysis of the trends in H-value in each depth strata.

Depth	Estimate	Slope	P-value	Adjusted R-squared	Multiple R-squared
100-200m	-58.9374	0.0299	0.9	0.045	0.113
200-300m	18.21668	-0.00866	0.7	-0.0572	0,009
300-400m	32.4030	-0.0158	0.5	-0.0375	0.0274
400-500m	91.6902	-0.0451	0.0186	0.272	0.317
500-600m	-58.9374	0.0299	0.22	0.045	0.113

3.2.2 Shannon Equitability index

Calculating the equitability or evenness of each depth strata, it presents a range from 0 to 1, where 1 indicates a perfect evenness in species abundance and 0 indicates complete dominance by one species. Figure 13 presents a low *EH* value in all depth strata. Most years stayed at a value <0.2.



Figure 13: Evenness (*EH*) of species abundance in each of the depth strata, which considers both species richness and the relative abundance of each species.

3.3. Species with the greatest impact on the diversity

3.3.1 Without roundnose grenadier

As written in the method, the leave-one out approach was used to look at the influence each of the dominant species has on the diversity index. Table 5 presents the differences in the H value in depth stratum 500-600 meters. When roundnose grenadier is removed from the equation, the H value in 2008 rises to a high value, indicating that the low value is attributable to the abundance of roundnose grenadier that year. When the roundnose grenadier is eliminated, the H values for the remaining years are slightly lower, as species richness is reduced by one species, which appears to matter at this depth when species richness is

normally low (*Figure 14*). Fluctuation in *H* values shows a non-significant trend over the time period.



Figure 14: Left graph: Diversity index without roundnose grenadier. Right graph: The original diversity index.

Table 5: Changes in the H value in the specific species that have removed their individual data from the index. These are compared to the H-value that contains all the species in the index, to see how much influence each of these dominant species has on the diversity index from 2006-2022, in depth stratum 500-600 meters. The species names colored yellow are those showing the greatest differences from the original H value (All Species).

500-600	All Species	Norway Pout	Blue Whiting	Saithe	Haddock	Whiting	Roundnose Grenadier	Velvet Belly	Long rough dab	Ratfish
2008	0,105	5 0,105	0,0867	0,105	0,105	0,105	1,561	0,0867	0,105	0,0724
2009	1,52	2 1,427	1,5199	1,52	1,444	1,289	1,884	1,3833	1,345	1,4836
2010	1,023	3 0,75	0,9531	0,987	1,009	1,023	1,64	0,855	0,946	0,8761
2011	. 1,384	1,379	1,3048	1,384	1,384	1,369	1,117	1,2846	1,328	1,2783
2012	1,105	5 1,054	0,9087	1,105	1,105	1,105	0,705	0,96	1,066	1,0319
2013	1,188	3 1	1,1279	1,171	1,188	1,188	0,824	1,0884	1,171	1,1445
2014	1,714	1,516	1,5169	1,642	1,714	1,714	1,939	1,593	1,655	1,6424
2015	1,821	l 1,785	1,663	1,795	1,821	1,821	1,672	1,6968	1,732	1,7391
2016	1,083	3 1,032	1,0162	1,083	1,083	1,083	0,996	0,9962	1,032	0,9962
2017	1,146	5 0,826	1,3651	1,127	1,146	1,146	0,907	1,0114	1,139	1,0732
2018	1,04	4 0,917	1,1178	1,02	1,04	1,04	0,645	0,8945	1,017	0,9914
2019	1,243	3 1,066	1,6382	1,241	1,243	1,243	0,966	1,1017	1,236	1,0938
2020	1,14	1 0,944	0,7703	1,14	1,14	1,14	0,874	1,0485	1,115	1,079
2021	. 1,481	1,287	1,4333	1,467	1,481	1,481	1,246	1,3043	1,425	1,402
2022	1,459) 1,372	1,2079	1,453	1,459	1,455	1,443	1,2555	1,379	1,3181

3.3.2 Without Norway pout

Figure 15 and Tables 6-9 shows what changes occurred in the diversity indices in the different depth strata from 2006 to 2022 when excluding Norway pout. Depth strata from 0-400 meters show several years with a H value around 2. Depth strata 100-200 meters have less fluctuations and more stable H value over time. The low H values in Norway pout (years 2009, 2010, 2013, 2020) are now gone, due to large abundance these years. 200-300 and 300-400 meters have much higher H values and less fluctuations. Norway pout affected the biodiversity in these depths to a lower extent, because this species dominates in numbers.
400-500 and 500-600 meters, the *H* values and the trend are unaffected by the removal of Norway pout. In 500-600 meters, the reason is lower amounts of Norway pout. While in 400-500 there is a lot of Norway pout, but the *H* values can be influenced by other species as well.

Table 6: Changes in the H value in the specific species that have removed their individual data from the index. These are compared to the H-value that contains all the species in the index, to see how much influence each of these dominant species has on the diversity trend from 2006-2022, in depth stratum 100-200 meters. The species names colored yellow are those showing the greatest differences from the original H value (All Species).

100-200	All Spieces	Norway Pout	Blue Whiting	Saithe	Haddock	Whiting	Roundnose Grenadier	Velvet Belly	Long rough dab	Ratfish
2006	5 1,552	1,91	1,552	1,492	1,33	1,433	1,552	1,287	1,332	1,53
200	7 1,912	1,79	1,912	1,878	1,765	1,786	1,909	1,742	1,891	1,898
2008	3 1,517	1,75	1,513	1,481	1,299	1,393	1,514	1,277	1,27	1,487
2009	9 0,724	1,74	0,724	0,699	0,499	0,627	0,724	0,484	0,59	0,704
2010	0,554	1,49	0,554	0,542	0,361	0,453	0,553	0,36	0,426	0,549
201	1 1,526	1,55	1,524	1,509	1,28	1,291	1,526	1,254	1,326	1,51
2012	2,029	1,98	2,009	1,991	1,946	1,889	2,029	1,89	1,91	1,998
2013	3 0,413	1,87	0,405	0,337	0,329	0,381	0,413	0,324	0,302	0,409
2014	4 1,78	1,67	1,777	1,681	1,651	1,648	1,78	1,596	1,859	1,736
201	5 1,602	1,54	1,602	1,577	1,468	1,454	1,602	1,424	1,496	1,579
2010	5 1,537	1,68	1,536	1,481	1,383	1,308	1,537	1,369	1,297	1,529
201	7 1,366	1,5	1,365	1,326	1,199	1,135	1,366	1,181	1,076	1,354
2018	3 1,632	1,55	1,632	1,604	1,509	1,417	1,632	1,479	1,438	1,582
2019	9 1,378	1,59	1,376	1,364	1,306	1,106	1,378	1,26	1,111	1,345
2020	0,584	1,81	0,584	0,582	0,425	0,46	0,584	0,407	0,484	0,563
2023	1 1,355	1,38	1,349	1,348	1,057	1,102	1,355	1,037	1,217	1,338
2022	2 1,636	1,55	1,636	1,613	1,43	1,454	1,636	1,388	1,419	1,627

Table 7: Changes in the H value in the specific species that have removed their individual data from the index. These are compared to the H-value that contains all the species in the index, to see how much influence each of these dominant species has on the diversity trend from 2006-2022, in depth stratum 200-300 meters. The species names colored yellow are those showing the greatest differences from the original H value (All Species).

200-300	All Species	Norway Pout	Blue Whiting	Saithe	Haddock	Whiting	Roundnose Grenadier	Velvet Belly	Long rough dab	Ratfish
2000	5 0,514	2,5	0,508	0,435	0,488	0,465	0,514	0,465	0,423	0,479
200	7 1,593	1,84	1,591	1,527	1,497	1,533	1,587	1,457	1,383	1,491
2008	в 0,689	2,09	0,688	0,655	0,583	0,634	0,683	0,564	0,508	0,627
2009	9 0,236	1,93	0,235	0,163	0,228	0,228	0,235	0,213	0,176	0,224
2010	0,223	1,69	0,222	0,198	0,206	0,21	0,223	0,199	0,122	0,212
201:	0,539	1,69	0,537	0,528	0,375	0,432	0,539	0,369	0,429	0,523
2012	2 1,353	1,71	1,334	1,328	1,119	1,296	1,353	1,096	1,079	1,315
2013	3 0,519	2,19	0,443	0,467	0,471	0,511	0,518	0,455	0,39	0,489
201	4 1,354	1,77	1,344	1,259	1,296	1,3	1,354	1,244	1,061	1,268
201	5 1,347	1,85	1,291	1,318	1,244	1,265	1,347	1,188	1,057	1,294
2010	5 1,482	2,23	1,399	1,375	1,442	1,409	1,47	1,379	1,256	1,405
201	7 0,857	2,32	0,777	0,804	0,829	0,77	0,857	0,762	0,692	0,786
201	в 0,609	2,14	0,608	0,545	0,589	0,523	0,609	0,536	0,471	0,538
2019	9 0,329	2,25	0,315	0,32	0,325	0,266	0,329	0,283	0,257	0,301
2020	0,364	2,23	0,361	0,358	0,328	0,312	0,364	0,28	0,287	0,315
2023	0,516	2,31	0,426	0,508	0,469	0,433	0,516	0,428	0,454	0,474
2022	0,753	2,12	0,739	0,742	0,696	0,663	0,752	0,603	0,572	0,688

Table 8: Changes in the H value in the specific species that have removed their individual data from the index. These are compared to the H-value that contains all the species in the index, to see how much influence each of these dominant species has on the diversity trend from 2006-2022, in depth stratum 300-400 meters. The species names colored yellow are those showing the greatest differences from the original H value (All Species).

300-400	All Species	Norway Pout	Blue Whiting	Saithe	Haddock	Whiting	Roundnose Grenadier	Velvet Belly	Long rough dab	Ratfish
2006	5 1,151	2,23	1,1284	1,1015	1,1419	1,146	0,9398	1,0059	1,0899	1,0899
2007	1,3412	2,37	1,3412	1,263	1,1967	1,275	1,2444	1,1242	1,1939	1,3036
2008	3 0,4795	2,22	0,4764	0,4394	0,3758	0,4691	0,4541	0,3645	0,4166	0,4583
2009	9 0,225	2,23	0,2212	0,1936	0,2218	0,2242	0,2092	0,177	0,1873	0,199
2010) 0,0958	2,44	0,0947	0,0872	0,0816	0,0951	0,0896	0,0652	0,0891	0,0857
2011	L 0,2778	2,42	0,2503	0,2716	0,2778	0,2757	0,2486	0,2593	0,2549	0,2407
2012	0,8715	2,06	0,6509	0,8585	0,7663	0,828	0,8599	0,7262	0,7805	0,8424
2013	3 0,6412	2,17	0,4772	0,5886	0,6099	0,6351	0,6272	0,5568	0,5783	0,6008
2014	1 0,3601	2,15	0,3574	0,312	0,3443	0,3358	0,3591	0,3066	0,2791	0,3551
2015	5 1,3693	1,55	1,0763	1,3409	1,3437	1,3451	1,3672	1,2418	1,2229	1,2968
2016	5 1,7369	1,64	1,5702	1,6981	1,7369	1,7253	1,7223	1,6634	1,5682	1,6742
2017	7 0,6796	2,1	0,5252	0,66	0,6736	0,6463	0,674	0,5709	0,5854	0,6296
2018	3 0,2817	2,18	0,2719	0,2469	0,274	0,2749	0,2796	0,2005	0,2553	0,2291
2019	9 0,1629	2,01	0,1181	0,1531	0,1628	0,1612	0,1612	0,1215	0,1516	0,1482
2020	0,3981	1,33	0,1966	0,3943	0,3964	0,3843	0,397	0,3454	0,381	0,3618
2021	0,7238	1,48	0,444	0,7212	0,7203	0,7102	0,7198	0,6316	0,7111	0,6651
2022	0,4363	2,07	0,3971	0,4287	0,435	0,4257	0,4206	0,2954	0,4147	0,3943

Table 9: Changes in the H value in the specific species that have removed their individual data from the index. These are compared to the H-value that contains all the species in the index, to see how much influence each of these dominant species has on the diversity trend from 2006-2022, in depth stratum 400-500 meters. The species names colored yellow are those showing the greatest differences from the original H value (All Species).

400-500	All Species	Norway Pout	Blue Whiting	Saithe	Haddock	Whiting	Roundnose Grenadier	Velvet Belly	Long rough dab	Ratfish
2006	1,609	1,959	1,586	1,549	1,609	1,593	1,439	1,388	1,576	1,541
2007	1,12	1,12	1,038	1,038	1,12	1,12	1,125	0,732	1,12	1,038
2008	1,642	1,846	1,6	1,529	1,63	1,633	1,432	1,451	1,623	1,521
2009	0,604	1,379	0,587	0,592	0,602	0,603	0,338	0,52	0,559	0,529
2010	0,809	1,83	0,787	0,78	0,805	0,801	0,676	0,575	0,773	0,708
2011	1,402	1,91	1,28	1,398	1,392	1,392	1,202	1,16	1,352	1,256
2012	0,985	0,567	1,072	0,973	0,985	0,976	0,945	0,871	0,957	0,92
2013	0,64	1,736	0,392	0,615	0,632	0,636	0,612	0,57	0,61	0,61
2014	0,331	2,266	0,287	0,295	0,325	0,329	0,31	0,265	0,285	0,302
2015	1,186	1,732	1,097	1,147	1,162	1,182	1,105	1,055	1,111	1,073
2016	1,263	1,073	1,737	1,263	1,254	1,258	1,173	1,193	1,175	1,241
2017	0,568	0,728	0,192	0,562	0,567	0,565	0,56	0,511	0,56	0,531
2018	1,111	1,623	0,836	1,089	1,111	1,111	0,956	0,932	1,073	0,993
2019	0,619	0,868	0,248	0,614	0,618	0,614	0,611	0,539	0,609	0,586
2020	0,516	1,733	0,356	0,509	0,516	0,516	0,478	0,419	0,504	0,437
2021	0,721	0,166	0,328	0,721	0,721	0,721	0,716	0,676	0,721	0,698
2022	0,519	0,689	0,161	0,516	0,519	0,51	0,488	0,477	0,518	0,503



Figure 15: Trends in biodiversity (H value) from 2006 to 2022 in the five depth strata when excluding Norway pout.

Analyzing the data, using simple linear regression, are showing a significant negative trend in the depth strata 100-200 (p = 0.03, adjusted R² = 0.219), 300-400 (p = 0.005, adjusted R² = 0.378) and 400-500 meters (p = 0.01, adjusted R² = 0.185), without Norway pout (*Table 10*).

Depth	Intercept	Slope	P-value	Adjusted R-squared	Multiple R-squared	
100-200m	36.6	-0.02	0.03	0.219	0.268	
200-300m	-33.2	0.02	0.2	0.0609	0.12	
300-400m	88.1	-0.04	0.005	0.378	0.416	
400-500m	117.01	0.01	0.05	0.185	0.236	
500-600m	-45.7	0.02	0.3	-0.0029	0.0687	

Table 10: Simple regression analysis of the trends in H value without Norway pout, in each depth strata.

3.3.3 Without blue whiting

Removing blue whiting from the index data, shows a difference in the *H* values only in depth stratum 400-500 meters. Looking at both figure 16 and table 9, the *H* values are quite similar in the first part of this period. While in more recent years, after 2013, the *H* values with and without blue whiting are starting to be more different. The slope in 400-500 meters presents a significant decreasing trend in diversity during this period (p = 0.008, adjusted R² = 0.338) (*Table 11*). *H* value showed a higher significance without blue whiting, than with, in depth stratum 400-500 meters. The other depth strata have more identical *H* values with and without blue whiting.



Figure 16: Trends in biodiversity from 2006 to 2022 in various depth strata. The diversity index estimates contain the H value without individual data from blue whiting.

Depth	Intercept	Slope	P-value	Adjusted R-squared	Multiple R- squared
100-200m	8.75	-0.003	0.9	-0.0651	0.00145
200-300m	-23.6	-0.01	0.6	-0.0498	0.0158
300-400m	51.6	-0.03	0.3	0.022	0.0831
400-500m	132.0	-0.07	0.008	0.338	0.379
500-600m	-58.9	0.03	0.2	0.0392	0.108

Table 11: Simple regression analysis of the trends in H value without blue whiting, in each depth strata.

The other species that also dominated the survey catch in numbers, such as haddock, whiting, saithe, rabbit fish (*Chimaera monstrosa*), velvet belly, and long rough dab, had little impact on *H* value when their individual data were removed from the index data.

4. Discussion

The investigation specifically targets benthic and semi-pelagic fish species captured during the shrimp survey in the Skagerrak region, strategically excluding pelagic fish and unidentified species. This leaves us with a total of 66 fish species for comprehensive analysis. The selection criteria focused on these species due to their prevalent and crucial roles in the benthic and semi-pelagic ecosystems. The annual catch rates of these species demonstrated substantial variations across the examined period, enabling us to easily discern dominant species. This study aimed thus to understand the fluctuations in their population trends and the potential influencing factors and could contribute significantly to the management and conservation strategies of these crucial marine ecosystems.

4.1 What changes have occurred in species dominating the systems?

Norway pout emerged as the dominant species (in numbers) in catch rate from 2006-2022, showing substantial fluctuations (Figure 4 and 5). Factors such as recruitment, growth, maturation, mortality, and fishing pressure, as well as predation by North Sea herring, significantly affect its spawning stock (Huse et al., 2008). Their spawning area is distributed west of Scotland and in the Irish Sea, with offspring transported towards Skagerrak with the currents (Albert, 1994), possibly causing observed stock fluctuations (Huse et al., 2008). Although Norway pout is found in all depth strata, a reduced catch rate at the depths of 500-600 meters suggests they usually inhabit shallower areas. Previous research in the Norwegian trench indicated that Norway pout stayed at a maximum depth of 200 meters (Albert, 1994). However, our data showed large amounts of Norway pout down to 400-500 meters. Figure 5 showed a catch rate of >3000 specimens per trawled nm in 2010 between 300-500 meters. Further, this study reveals an unusually low catch rate in the 100-200 meter depth stratum, contrasting with the species' tendency to migrate deeper as they age (Albert, 1994). Since Norway pout have their spawning period in January-April (Albert, 1994; Nash et al., 2012), and the survey occurs in January to early February, several individuals may have moved to deeper areas during this time of year, after development. Therefore, the catch rate of Norway pout can be greater in deeper depth strata than shallower in winter. However, the discovery of Norway pout at depths of 500-600 meters in this study challenges Albert's findings of a maximum depth of 200 meters, suggesting the need for further research to validate these observations.

Blue whiting, though not as dominant as Norway pout, featured predominantly in catch quantities (*Figure 4*). From 2006 to 2013, catch rates remained low across all depth strata, barring 400-600 meters, which experienced an increase in 2012 (*Figure 6*). After 2012 and 2013, there was a large fluctuation in catch rate. The reason for the sudden increases in recent 10 years are uncertain, but this species has a similar life cycle as Norway pout in their juvenile stage (Bergstad, 1991). Skagerrak is an area dominated by juvenile blue whiting, due to good nursery and feeding areas (Bergstad, 1991). It is found in shallower areas in the juvenile stage but moves to deeper areas after development (Bergstad, 1991). They also have a spawning area west of Scotland and in the Irish Sea, and eggs and larvae are transported to Skagerrak through ocean currents (Bailey, 1982; Bergstad, 1991). Therefore, the fluctuations occurring in recent years may be influenced by the number of surviving recruitments. ICES (2022b) confirm this with the measurements they've performed over the years on spawning biomass and recruitments in their report of blue whiting's stock measurements.

Norway pout and blue whiting are vital prey Skagerrak fish species, and pivotal in the food chain (Bergstad, 1991, Daan, 1989; Hislop *et al.*, 1997). Predators include larger fish like saithe, whiting, and haddock with catch rate fluctuating from 2006 to 2022 (*Figure 17, 19, and 25, Appendix B*). Saithe showed a decline across all depth strata (*Figure 22, Appendix B*), with a significant trend only at 500-600 meters. Conversely, whiting had a strong positive trend in 100-200 meters, and was the only depth stratum showing a significant trend. Haddock had a significant negative trend in 300-400 meters. Both saithe and whiting rely on Norway pout as a food source (Bergstad, 1991; Daan, 1989; Hislop *et al.*, 1997). Saithe has Norway pout as an important resource in winter (Bergstad, 1991). They both had similar catch rate patterns in shallower depths, but these trends were not observed in deeper strata. Bergstad's (1990) research noted high Norway pout abundance and saithe biomass in these communities during the 80s. However, 2006-2022 CPUE data indicated higher catch rates for haddock, whiting, and velvet belly over saithe in most depth strata (*Appendix B*), suggesting a substantial saithe population decline since 1980 (ICES, 2022a). Increased Norway pout

about saithe's distribution in the early 1980s, where most of the stock stayed in shallower areas in summer and autumn, compared to winter. As Norway pout may migrate to deeper areas after growth, the number of individuals that grow from the juvenile stage may have increased, which can increase the trend in Norway pout at deeper areas in winter. This could result in reduced predation pressure, leading to lower juvenile mortality in Skagerrak. Predation pressure during the larval stage may be the main factor influencing changes in Norway pout populations, but it can ease later in the stage, leading to long-term increases. Saithe also feeds on blue whiting, but not as extensively as on Norway pout (Bergstad, 1991). Some of the same reasons for population growth in recent years, may be due to the same reasons as Norway pout. While significant positive trends in blue whiting were observed in all depth strata, except 100-200 meters, there were no significant trends in Norway pout. Consequently, the correlation between trends among prey and predatory species remains uncertain.

4.2 How has diversity changed over time?

Biodiversity was analyzed using Shannon and Simpson diversity indices and heat maps demonstrating annual species richness and abundance per depth stratum (*Figure 40, Appendix C*). There is a clear decrease in the number of species with an increased depth. The abundance of several species at depth strata 100-500 meters seemed to increase in recent years. While the species richness seemed to have had few to no changes over the years, which were seen both in the dataset and heatmaps (*Figure 8-11*). The number of species caught annually has often stayed close to the average. This may indicate that the abundance has played a bigger role in the changes happening in biodiversity from 2006-2022 in these depth strata. Depth stratum 500-600 meters has the lowest species richness, but presents a strong increase in both species richness and in abundance in recent years (*Figure 12*). Data collected in this depth stratum is, however, poorer compared to the other strata. Trawling did not occur until 2008, and in the first years, there were fewer stations than today. Therefore, much of the data presented in this study, in depth stratum 500-600 meters, may not be as accurate compared to the other depth strata.

There were observed changes in biodiversity in some depth strata. Figure 8-12 presents greater changes in the diversity, the deeper the data is obtained. 100-200 meters present large variations in H value, but the figure showed no changes in diversity over time. Depth strata 200-300 and 300-400 meters present similar trends in H value during the years. Still, the figures presented a greater decrease in diversity at 300-400 meters compared to 200-300 meters. 400-500 meters was the depth stratum presenting the greatest decrease in diversity. Even with large fluctuations during the years, there was a clear decrease from 2006-2022. The deepest area, 500-600 meters, was the only stratum presenting a positive trend. Part of the reason was 2008, where the H value was close to zero. Over 1,800 individuals in total of roundnose grenadier were caught, which is the reason for the low H value this year. Of all the depth strata, 400-500 meters was the only depth stratum showing a significant negative trend over time in H value. The pronounced fluctuations across most depth strata potentially account for the lack of significant trends. Without clear trends, these changes in these strata cannot be confidently affirmed.

Norway pout had the highest catch rate (and total catch) and large fluctuations, which can be suspected to have had an influence in the diversity indices. After comparing the H values with and without some of the most dominant species, Norway pout showed that they had the largest impacts in most depth strata. The biggest changes occurred in depth strata 0-400 meters, where the large fluctuations of H value disappeared when Norway pout was removed (Figure 15). Figure 5, which presents the CPUE of Norway pout, showed large fluctuations in these depth strata. This confirms the reasons for the fluctuations in the diversity indices. The data analysis at the original index showed only a significant negative trend in depth stratum 400-500 meters (Table 4). The data analysis without Norway Pout showed however a significant negative trend in diversity at 100-200, 300-400 and 400-500 meters (Table 10). This suggests that the fluctuation in the number of Norway Pout has concealed the changes in H value in other depth strata than 400-500, the same that was speculated earlier. The least changes occurred in depth stratum 500-600 meters. Both table 5 and figure 15 present identical H values with and without Norway pout. The CPUE of Norway Pout in depth stratum 500-600 meter, showed a low catch rate (Figure 5), which indicates smaller quantities of Norway pout are found in such deep conditions. Even without changes in depth stratum 500-600 meters, there are still large changes in the H value without Norway Pout in other depth strata. The *H* value is much higher in the three shallowest depth strata without Norway

pout. While depth stratum 400-500 meters showed higher diversity in several years compared to the original index. This suggests that Norway pout dominates to a very large extent in most of the communities and contributes to a low biodiversity.

Another species that stood out was blue whiting. Looking at the tables 6-9 and figure 16, the H values are almost identical in the upper layers from <400 meters. In depth stratum 400-500 meters however, some differences between the H values were observed. The first period was almost identical to the original data, but in recent times there were observed more differences between the H values. There was a greater fluctuation, and some years showed higher and lower H-value without blue whiting. Looking at the CPUE of blue whiting in figure 6, there was a low catch rate of blue whiting until 2011. After 2011 there were more fluctuations and increases in catch rate. This proves, together with table 9 and figure 16, that blue whiting had no impact in the first period but had more impact in recent times. The analysis of the index without blue whiting resulted in significant negative trends in depth stratum 400-500 meters over time. The original index data also showed a significant negative trend, but the p-value was lower without blue whiting.

Depth stratum of 500-600 meters, no specific differences in the H-value occurred without Norway pout and blue whiting. However, roundnose grenadier showed large changes in Hvalue after removing the individual data. The biggest differences in H value were in 2008. After removing this species, the H value in 2008 got higher (*Figure 14*). When the roundnose grenadier was removed, the H values for the remaining years were slightly lower, as species richness was reduced by one species, which appears to matter at this depth when species richness is normally low. This depth stratum showed no significant trends. As mentioned earlier, the low number of stations in this depth stratum makes the result more uncertain compared to the other strata.

Norway pout dominates and influences most depth strata. The three shallowest depth strata from 100-400 meters had large fluctuations in H value during the entire period. Removing this species from the dataset, caused the fluctuations to disappear and gave a higher H value. With such a large catch rate and total catch of Norway pout compared to other species, contributed to low H values during this period. This proves how dominant Norway pout has been in 2006-2022, as the trends showed low diversity in most depth strata. By looking at the EH value in the Equitability index, the values showed low evenness, which indicates that some species in these communities have large dominance (Figure 13). In depth stratum 400-500 meters, Norway pout had a large impact, which gave a decline in diversity. But blue whiting also seemed to have an impact in diversity from 2011 and onwards in 400-500 meters. This suggests that these two species had a growth in population in this depth stratum from 2006 to 2022, which has affected the large decline in diversity. By looking at the CPUE figures in the depth stratum 400-500 meters in blue whiting and Norway pout, it presents a growth in catch rate during the entire period, even with large fluctuations. Although 400-500 meters in CPUE of Norway pout did not show a significant increase, we cannot ignore the fact that the population may have had a positive trend during the years. The heatmap (Figure 11) showed an increase in total catch of Norway pout the last couple of years in depth stratum 400-500 meters. Blue whiting had a significant increase in this depth stratum. Therefore, there is a probability that an increase in these populations had an impact in the decline in diversity. Looking at both species richness and abundance, the abundance has more influence on biodiversity than species richness. Abundance of Norway pout and blue whiting (400-500 meters) is what affects the biodiversity in most depth strata. Species richness was only affecting the deepest depth strata, when roundnose grenadier was removed.

The other species did not show any changes in H value, after removing them. That indicates none of these species influenced the changes in biodiversity that occurred in the depth strata.

4.3 What caused these changes in diversity and populations

Attributing the changes in the fish community to a specific cause is a challenging task, given the multitude of species present. However, it can be categorically stated that overfishing poses a significant problem in many parts of the world, including Skagerrak (Issifu et al., 2022). The observed changes in Skagerrak can be attributed to several decades of exploitation (Cardinale et al., 2012). Simultaneous changes in temperature due to global warming further compound the challenge of maintaining fish population sizes (Allison et al., 2009).

4.3.1 Is the alteration in fish communities brought on by overfishing?

High fishing intensity in the Skagerrak region has caused significant ecosystem alterations, leading to reduced diversity and over-dominance of certain species due to overfishing (Cardinale & Svedäng, 2004; Issifu et al., 2022)). CPUE and heatmaps show a marginal positive trend for Norway pout and a significant trend for blue whiting populations, with predatory species declining. Deep water species in Skagerrak have earlier been researched by dr. Odd Aksel Bergstad in various articles, with focus on their community structure, distribution, and trophic ecology between the 80s-90s. (Bergstad; 1990; Bergstad; 1991; Skjæraasen & Bergstad 2000; Bergstad et al., 2014). An article he wrote about the community structure, showed a lot of similarities then, with the community structure in this study (Bergstad, 1990). But still, there were some differences between how saithe was presented then to how total catch and CPUE of saithe is presented now. During that period, saithe was a dominant species in the higher upper slope. All depth strata have shown signs of decrease in CPUE, but not significantly (except 500-600 meters). The number of individuals were not any higher compared to other predator species in any of the depth strata. Therefore, a larger decline in saithe may have occurred from 1984 to 2022, as mentioned earlier, due to the influence of overfishing. Measurements in stock level of saithe from ICES (2022a) showed a large decrease in their population size from 1970 to present day. In their measurements from the early 80s when the time series (1984-2022) began, the population was much larger compared to now, which indicates that there has been a decline in saithe during the entire time series. This confirms that the population was larger in Bergstad's (1990) article than the study data. The total catch by weight was 62.783 tons in 2004 and 20.442 tons in 2021, which also indicates a decline in saithe population (ICES, 2022a). At the beginning of the 80s, there was a high fishing pressure until the mid-90s. Then, at the beginning of the 2000s, the fishing pressure was reduced, and has remained more stable until today in this population (ICES, 2022a).

ICES (2022d) presented stock measurements of Norway pout, showing changes in stock level from 1984. Their measurements showed a large fluctuation during the entire period. There was a growth in Norway pout' population between 2006 and 2022, which was also shown in CPUE and the heatmaps. Despite the non-significant trend in Norway pout's CPUE data, there are some certainties that population growth during these years may have taken place by comparing the data to ICES (2022d). These patterns can be compared to herring stock data from ICES (2022e), which shows that there may be a connection between herring and the increasing Norway pout recruitment rates at particular times. Herring has, in the last 15 years, been the weakest ever observed, which is due to reduced survival during the larval stage (Huse et al. 2008; Kvamme, 2022; ICES, 2022e). Spawning and rearing areas are sensitive to anthropogenic activities. Removal of gravel or other disturbances could negatively affect and reduce the extent of successful spawning (Kvamme, 2022) which may be some of the reasons for the potential increase in Norway pout in recent years.

The decline in saithe and other predatory species, coupled with a potential increase in prey species like blue whiting and Norway pout, indicates extensive overfishing of predators. ICES (2022a,c; 2023) reports confirm major declines in cod, haddock, and saithe from the 60s to 80s, primarily due to high fishing pressure, which was notably more intense than in the 2000s. Their measurements of fishing pressure from the 1970s to the 1990s reveals that it was significantly higher than in the 2000s. Additionally, several of these species endured a dramatic fall in population during this time. Therefore, the slight positive trends in Norway pout from 2006-2022 might not be due to lower predator pressure. Analyzing these species, no large declines occurred in 2006-2022, unlike the previous century. The primary driver influencing the fluctuations in Norway pout's population is most likely the number of survival recruits migrating from the spawning areas to Skagerrak. However, it is important to acknowledge that these predator species continue to prey upon the Norway pout. Nevertheless, the reason for these changes in the population is unlikely to originate solely from these predator species. But it should not be disregarded that the considerable abundance of Norway pout in deeper areas may have a positive impact with smaller populations in these predatory species.

Conversely, whiting has seen increased CPUE, potentially due to reduced resource competition with other predators

Overfishing, predominantly driven by advances in fishing technology, is the main culprit behind global declines in predator species (Issifu et al., 2022; Myers & Worm, 2003). The development of fishing equipment has made it much more efficient to fish larger quantities of fish and more selectively, which leads to a more rapid reduction in different populations, especially in predatory species (Jørgensen et al., 2009). Trawling, common in Skagerrak for catching northern shrimp, Norway lobster, and fish, results in substantial bycatch, impacting fish populations, biodiversity, and habitats (Cardinale & Svedäng, 2004; Collie et al., 2017). The table 24 in appendix E, presents the amount of trawling done in Skagerrak from 2011 to 2022 by Norwegian commercial fishing vessels. This table showed an increase in the number of times the trawl was released, over the years. Table 23 in Appendix E presents depth start and stop in each depth stratum from commercial fishing with trawl in Skagerrak. These data are showing a larger amount of trawling in deeper depth strata over the years. Whether this is the reason for the decline in biodiversity at 400-500 meters is uncertain. The duration of fishing at each station in this dataset can vary, with fishing lasting up to 11 hours. In this period, the trawl could have been in other depth strata without us knowing. Additionally, the size of the trawl used may differ across stations, seasons, and years. Irrespective of the depth strata that are predominantly trawled in Skagerrak, it is important to consider that some species are engaged in seasonal migrations throughout the water column (Bergstad, 1990). Therefore, some stocks may be equally impacted, regardless of whether they are located at deeper areas or shallower waters with high fishing intensity. Commercial fishing data indicates that trawling takes place in all seasons throughout the year. However, due to the lack of specific trawling data and the influence of biological and ecological factors within the communities, it is uncertain whether higher fishing intensity in certain depth strata is the primary cause for the significant trends observed in biodiversity (400-500 meter) or CPUE. This is something that can be further researched. Skagerrak has still quite intensive bottom trawling in all depth strata compared to other areas in the North Sea (Eigaard et al., 2017). Despite reduced trawling vessel numbers, increased vessel size and engine power have led to more efficient capture of larger quantities (ICES, 2017). ICES (2022f) report major restructuring in Danish and Norwegian fleets over the past 25 years, with decreasing vessel numbers but increased fleet efficiency due to twin trawls and larger trawl sizes. In Norway, the number of vessels has decreased from 423 in 1995 to 177 in 2021. While in Denmark, the number of vessels has decreased from 191 in 1987 to only eight in 2021. In Sweden, they had a decrease from more than 60 vessels in 1995–1997 to 30 in 2018–2021. Twin trawls were introduced in 2002, and within 2011–2021 more than half of the Norwegian trawlers were using this. The single trawl size or design has not gone through major changes, but during the last ten years, the landings of the twin trawlers have also increased from 7 to over 60% of the total Swedish Pandalus landings (ICES, 2022f).

With high fishing intensity and more efficient gear, has caused great destruction in the biodiversity in Skagerrak (Collie et al., 2017; Eigaard et al., 2017). With low biodiversity in all depth strata, may indicate that overfishing by trawls has affected many populations of different species in these communities. For example, in an article written by Pawlowski and Lorance (2009), shows that the roundnose grenadier have had a large decline from 1990 to 2008. The CPUE of the roundnose grenadier also presented a significant decrease in deeper depth strata (300-600 meters). The same trends are also shown in an article written by Bergstad et al. 2014, where overfishing affects the roundnose grenadier's recruitments, which results in low stocks. Since they have low productivity rates, they are even more vulnerable to overfishing than other species (Lorance et al., 2008). This species is supposed to be quite dominant in the deepest areas of the Skagerrak (Bergstad, 1990). This may therefore have an impact on low diversity in deeper areas. Less trawling was observed in the table 25, in depth strata 500-600 meters. Still, there are other countries, like Denmark and Sweden which also have high fishing intensity in these areas. At the same time, the population may also be affected by overexploitation in such deep areas, with higher trawling intensity in 300-500 meters. Other species such as rabbitfish (Chimaera monstrosa), lanternshark (Etmopterus spinax), blackmouth catshark (Galeus melastomus) and spurdog (Squalus acanthias), has earlier been exposed to overexploitation (Jac et al., 2021). Spurdog has a long history of exploitation in the North Sea and adjacent areas (Pawson et al., 2009), with peak landings in the 1950–1960s.

Due to prolonged high fishing intensity and unsustainable practices, the decline and generally low biodiversity from 2006-2022 can largely be attributed to long-term overexploitation and considerable bycatch. This may have reduced many populations in several decades, which has led to Norway pout becoming such a dominant species in the communities today. Looking back at the trends of Norway pout from 1984 (ICES, 2022d), the population did not show large increases to create these changes. But rather the reason for low diversity, especially at depths of 200-400 meters, could be a decline in several species' populations due to overexploitation. The heatmaps showed higher abundance in many species in recent times. But most of these species showed a low total catch in the dataset (*Table 13, Appendix A*) throughout the time series (2006-2022), which constitutes no impact on biodiversity. The observed patterns in the dataset from 2006 to 2022 are likely attributable to extensive

exploitation prior to the 2000s. Multiple indicators, including various stock measurements conducted by ICES, demonstrate declines occurring earlier. From the early 2000s to now, changes in deep-water fish populations have been relatively minor compared to trends observed in the late 20th century (ICES 2022 a,c,d,e; 2023). The CPUE has mostly shown either small decreases in some populations in different depth strata, or more stability with few to no changes. Most of the CPUE data did not show a significant trend in each of the depth strata. Notably, many stocks remain depleted due to historical exploitation, implying persistent high fishing intensity in the Skagerrak region, as demonstrated by the lack of recovery in several stocks over the past two decades. A trend indicative of expansion gradual expansion into deeper strata has been shown for bottom trawling globally (Morato et al. 2006). Whether this has been the case for Skagerrak and the Norwegian trench remains to be thoroughly researched.

Note that most stock measurement reports from ICES do not only contain measurements from Skagerrak, but also surrounding areas.

4.3.2 Is the apparent alteration in fish communities brought on by temperature changes?

At the beginning in 2006, Conductivity-Temperature-Depth (CTD) samples were taken at each station at the shrimp survey. The temperature measurements for the entire time series showed no changes during the years (*Figure 51 and 52, Appendix E*). The mean annual bottom temperature has remained around 7-8 degrees Celsius from 2006 to 2022 except in 2011, when the temperature dropped to around 5-6 degrees celsius. Changes in temperature in deeper areas do not occur at the same extent as in shallow areas along the coast (Albretsen *et al.,* 2023). Therefore, it seems unlikely that temperature is the cause of the changes that have occurred. Numerous studies have shown that many species and populations subjected to global warming have not shown the expected changes, or have even shown contradictory changes (Lenoir *et al.,* 2010; Fei *et al.,* 2017). A report written by IMR about risk of temperature changes, described some of the effects that can occur from changes in temperature in these communities (Sandø *et al.,* 2022). They assume that an increase in temperature will have a positive effect on hake (*Merluccius merluccius*). However, the CPUE

of hake from 2006 to 2022 (*Figure 33, Appendix B*) reveals a decrease in the catch rate across all depth strata. Given that none of the depth strata have shown a significant negative trend, it is inconclusive to claim a definitive decline. Hake, known for their generally deep distribution, are less susceptible to high summer temperatures as well as low winter temperatures, occurring in the surface layers (Sandø *et al.*, 2022). The species also has a large latitudinal range indicating its wide temperature tolerance (Dulvy *et al.*, 2008). Boarfish (*Capros aper*) and john dory (*Zeus faber*), two warm-water species, did not exhibit any changes in population. These are still uncommon species, and just a few of them were found in the entire dataset (*Table 13, Appendix A*). These trends are also observed in other similar species. But there are many indications that the effect of temperature is not the main reason for changes in deeper areas from 2006 to 2022. Research done by IMR (Albretsen *et al.*, 2023) suggests that the temperature has remained normal in the deep areas since 1991. At the same time, the inflows of Atlantic deep water have kept low and stayed in the same pattern as it was observed in 2006.

4.4 Other studies reporting on similar research

There are many studies that have researched the biodiversity in different communities over the years. Impact of fishing on size composition and diversity of demersal fish communities, is a study done by Bianchi et al (2000). They looked at possible changes in diversity in terms of species composition and dominance in different places. Overall, they found no evidence in any of the data sets that were analyzed, that fishing had changed community structure in the direction of lower diversity in the 90s. Their diversity index increased (e.g., eastern Scotian Shelf) following many years of high exploitation. The high diversities were related to a higher number of species identified, to increased evenness or both. In the eastern Scotian Shelf, there was an increase in the number of species identified. Whether that increase was caused by an influx of new species, increased abundance of formerly rare species, or by an improved survey protocol were to remain ascertained.

Bianchi et al (2000) compared their study with Rijnsdorp et al. (1996) and Greenstreet and Hall (1996). Rijnsdorp et al. (1996) compared trawl survey data collected in the southern North Sea in 1906 to 1909 and 1990 to 1995. They found lower species diversity and evenness in the latter period, and a shift in the size distributions of flatfish and roundfish

towards smaller fish. Changes in the survey gear between the periods hampered comparisons of overall abundance, but the data still suggested a large reduction. As for the studies done by Greenstreet and Hall (1996) and Greenstreet et al. (1999), they studied the fish community in the North-western North Sea from trawl survey data collected during 1925–1996. They found minor changes, but their analyses revealed a modest decrease in diversity over time, an increase in dominance, and a shift in size composition towards smaller fish. Jennings et al. (1999) used the same data set as Greenstreet and Hall (1996) and Greenstreet et al. (1999) to study whether the response of individual species was linked to their life histories, and observed a relative decrease in the abundance of the slower growing, late maturing species.

Some of the same trends are also seen in this study, with higher dominance of Norway pout and blue whiting in depth stratum 400-500 meters, which can be the cause of a negative trend in diversity. The high exploitations are probably the reasons for the changes between 2006-2022, like most of these studies. The changes in CPUE of roundnose grenadier during this period, can relate to Jennings et al. (1999) study. As Bianchi et.al 2000 mentions in the article, many of these examples are data collected throughout the 19th century. Huge parts of this data have an inconsistency in species identifications over time, which effectively reduces the possibility of detecting real changes that may have occurred. Proper taxonomic classification of non-commercial species has earlier not been a huge priority, even in scientific surveys. The lack of proper and readily available taxonomic literature has aggravated this problem, particularly in the highly diverse regions (Bianchi et al., 2000). The same can also be seen in the time series used in this study. Parts of the data obtained before 2006 have not been properly identified, leading to the difficulties in calculation of diversity from 1984 to 2022. In addition, the data collection was also obtained in different seasons during the time series, which means that the seasonal variation in the community would have affected the results.

5. Conclusion

Long-term biodiversity trend datasets are vital for researchers studying the impact of natural and anthropogenic influences on marine ecosystems. Unfortunately, these datasets are often unavailable, making it challenging to establish baseline diversity metrics, comprehend shifts in species composition, and understand ecological variability.

Our analysis utilizing the Shannon index revealed significant biodiversity fluctuations in the shallower depth strata, down to 400 meters, without a clear trend. Only depth stratum 400-500 meters showed a significant decrease in biodiversity over time (2006-2022). Depth strata down to 500 meters were more influenced with changes in abundance than species richness. In 500-600 meters, a weak, non-significant positive trend was noted. Both increased species richness and abundance were observed over the years in 500-600 meters. But this depth stratum doesn't contain a good collection of data compared to the other strata. The dominance of Norway pout in terms of population size has a profound impact on diversity indices. This species' considerable population fluctuations, primarily driven by recruitment levels from spawning areas, impact biodiversity within depths down to 500 meters. Although the trends in catch per unit effort (CPUE) for Norway pout did not indicate a significant change, it would be premature to dismiss the possibility of a stock increase. Consideration of the stock measurements provided by ICES, as well as the analysis of heatmaps within the 400-500 meter depth range, suggests that Norway pout may have played a role in shaping the biodiversity alongside blue whiting, contributing to the observed decrease in biodiversity in depth stratum 400-500 meters.

Note that the overall biodiversity across all depth strata (except 500-600 meters) remains remarkably low, primarily due to the dominance of Norway pout. However, predatory species such as saithe, haddock, and cod have not experienced that large significant changes between 2006 and 2022. Many of these species have either exhibited no significant change or displayed relative stability with a slightly decreasing trend. In contrast, several species in the dataset consistently yielded low catches compared to the dominant species. The Norway pout itself has not undergone substantial changes to account for its high level of dominance.

The depletion of the entire fish community, resulting from extensive fishing activities in the Skagerrak region throughout history, likely plays a significant role in the overall reduced biodiversity. The historical period of intense fishing, particularly from the 1970s to the 1990s, has likely resulted in persistently low populations that have struggled to recover due to ongoing high fishing intensity. This continued pressure in fish communities has prevented them from recovering, even in recent times. The Skagerrak region, characterized by high trawling intensity and substantial fishing pressure from Norway, Denmark, and Sweden, has maintained population suppression over the past two decades. Consequently, Norway pout's population has emerged as the dominant species in multiple communities without going through significant changes, as a consequence of these circumstances.

While selective fishing of predators and large bycatches of non-targeted species is a crucial factor contributing to this decline, the exacerbating effects of a warming climate cannot be ignored. Although rising water temperatures have not yet significantly impacted deep-water fish, several climate reports project future temperature increases that could affect these deeper water populations. The combined effects of increasing temperatures and overfishing will make it more challenging for fish populations to recuperate from losses. Without prompt interventions, multiple stocks may collapse, leading to the loss of essential resources in Skagerrak.

References

- Agnew, D. J., Pearce, J., Pramod, G., Peatman, T., Watson, R., Beddington, J. R., & Pitcher, T. J. (2009). Estimating the Worldwide Extent of Illegal Fishing. PLOS ONE, 4(2), e4570.<u>https://doi.org/10.1371/journal.pone.0004570</u>
- Albert, O. T. (1994). Biology and ecology of Norway pout (Trisopterus esmarki Nilsson, 1855) in the Norwegian Deep. ICES Journal of Marine Science, 51(1), 45–61. https://doi.org/10.1006/jmsc.1994.1005

Albretsen, J., Skogen, M. D., & Hjøllo, S. S. (2023, March 23). *The climate in the North Sea and Skagerrak*. Havforsknings Instituttet. Retrieved May 9, 2023, from <u>https://www.hi.no/hi/temasider/hav-og-kyst/klimaet-i-havet/klimastatus/nordsjoen-og-skagerrak</u>

- Allison, E. H., Perry, A. L., Badjeck, M. C., Adger, W. N., Brown, K., Conway, D., et al. (2009). Vulnerability of national economies to the impacts of climate change on fisheries. Fish Fish. 10, 173–196. doi: 10.1111/j.1467-2979.2008.00310.x
- Alverson, D.L., Freeber, M.H., Murawski, S.A. & Pope, J.G. (1994). A global assessment of fisheries bycatch and discards. FAO Fisheries Technical Paper 339: 233 pp.
- Andrew, N.L. & Pepperell, J.G. (1992). The by-catch of shrimp trawl fisheries. Oceanography and Marine Biology Annual Review 30: 527–565.
- Bailey, R..(1982). The population biology of Blue whiting. Advances in Marine Biology, 19, 257-355. <u>https://doi.org/10.1016/S0065-2881(08)60089-9</u>
- Barceló, C., Ciannelli, L., Olsen, E. M., Johannessen, T., & Knutsen, H. (2016). Eight decades of sampling reveal a contemporary novel fish assemblage in coastal nursery habitats. Global Change Biology, 22(3), 1155–1167. https://doi.org/10.1111/gcb.13047
- Bates, A.E., Pecl,G.T., Frusher,S., Hobday, A.J., Wernberg, T., Smale, D.A., Sunday, J.M., Hill, N.A., Dulvy, N. K., Colwell, R K., Holbrook, N.J., Fulton, E.A., Slawinski, D., Feng, M., Edgar, G.J., Radford, B.T., Thompson, P.A., & Watson, R.A.. (2014). Defining and observing stages of climate-mediated range shifts in marine systems. Global Environmental Change, Volume 26, May 2014, Pages 27-38. <u>https://doi.org/10.1016/j.gloenvcha.2014.03.009</u>
- Baum, J. K., & Fuller, S. D.. (2016). Canada's Marine Fisheries: Status, Recovery Potential and Pathways to Success. Toronto, ON: Ocean Canada.
- Baum, J. K., & Worm, B. (2009). Cascading top-down effects of changing oceanic predator abundances. Journal of Animal Ecology, 78(4), 699–714. <u>https://doi.org/10.1111/j.1365-2656.2009.01531.x</u>

- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. Ecology Letters, 15(4), 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x
- Bergstad, O. A.. (1990). Ecology of the fishes of the norwegian deep: distribution and species assemblages. Netherlands Journal of sea research 25 (1/2): 237-266. https://doi.org/10.1016/0077-7579(90)90025-C
- Bergstad, O. A..(1991). Distribution and trophic ecology of some gadoid fish of the Norwegian deep.1. Accounts of individual species. Sarsia 75:269-313. Bergen. INNS 0036-4827.
- Bergstad, O. A., Øverbø Hansen, H., & Jørgensen, T. 2014. Intermittent recruitment and exploitation pulse underlying temporal variability in a demersal deep-water fish population. ICES Journal of Marine Science, 71: 2088–2100._ https://doi.org/10.1093/icesjms/fst202
- Bianchi, G., Gislason, H., Graham, K., Hill, L., Jin, X., Koranteng, K., et al. (2000). Impact of fishing on size composition and diversity of demersal fish communities. ICES Journal of Marine Science, Volume 57, Issue 3, Pages 558–571,<u>https://doi.org/10.1006/jmsc.2000.0727</u>
- Blanchard J.L., Dulvy, N.K., Jennings. S., Ellis.J. R., Pinnegar. J. K., Tidd.A., & Kell.L. T.. (2005). Do climate and fishing influence size- based indicators of Celtic Sea fish community structure. Journal of Marine Science, Volume 62, Issue 3, 2005, Pages 405–411, <u>https://doi.org/10.1016/j.icesjms.2005.01.006</u>
- Campana, S. E., Stefánsdóttir, R. B., Jakobsdóttir, K., & Sólmundsson, J. (2020). Shifting fish distributions in warming sub-Arctic oceans. Scientific Reports, 10(1). https://doi.org/10.1038/s41598-020-73444-y
- Cardinale, M., & Svedäng, H. (2004). Modelling recruitment and abundance of Atlantic cod, *Gadus morhua*, in the eastern Skagerrak–Kattegat (North Sea): Evidence of severe depletion due to a prolonged period of high fishing pressure. *Science Direct*, 69(2). <u>https://doi.org/10.1016/j.fishres.2004.04.001</u>
- Cardinale, M., Svedäng, H., Bartolino, V., Maiorano, L., Casini, M., & Linderholm, H.. (2012). Spatial and temporal depletion of haddock and pollack during the last century in the Kattegat-Skagerrak. *Journal of Applied Ichthyology*, 28(2), 200–208. <u>https://doi.org/10.1111/j.1439-0426.2012.01937.x</u>
- Cartes, J., Fanelli, E., Lloris, D., & Matallanas, J. (2013). Effect of environmental variations on sharks and other top predators in the deep Mediterranean Sea over the last 60 years. Climate Research, 55(3), 239–251. <u>https://doi.org/10.3354/cr01137</u>
- Clark, M. R., Vinnichenko, V. I., Gordon, J. D. M., Beck-Bulat, G. Z., Kukharev, N. N., & Kakora, A. F. (2007). Large-scale distant-water trawl fisheries on seamounts. In Seamounts: Ecology, Fisheries, and Conservation, pp. 361–399.

- Collie, J., Hiddink, J. G., Van Kooten, T., Rijnsdorp, A. D., Kaiser, M. J., Jennings, S., & Hilborn, R.. (2017). Indirect effects of bottom fishing on the productivity of marine fish. Fish and Fisheries, 18(4), 619–637.<u>https://doi.org/10.1111/faf.12193</u>
- Crawley, M. J. (2015). *Statistics: An Introduction Using R* (2nd ed.). Wiley. ISBN:9781118941096
- Daan, N. (1989). Data base report of the stomach sampling project 1981 (ICES Cooperative Research Report No. 164; ICES Cooperative Research Report, p. 144). ICES.
- Daan, N., Bromley, P.J., Hislop, J.R.G., & Nielsen, N.A. (1990). Ecology of North Sea. Netherlands Journal of Sea Research. 26: 343-386. https://doi.org/10.1016/0077-7579(90)90096-Y
- Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C., & Mace, G.M. (2011) Beyond predictions: biodiversity conservation in a changing climate. Science, 332,53–58. DOI: 10.1126/science.1200303
- Doney, S. C., Ruckelshaus, M., Emmett Duffy, J., Barry, J. P., Chan, F., English, C. A., Galindo, H. M., Grebmeier, J. M., Hollowed, A. B., Knowlton, N., Polovina, J., Rabalais, N. N., Sydeman, W. J., & Talley, L. D.. (2012). Climate Change Impacts on Marine Ecosystems. Annual Review of Marine Science, 4(1), 11–37. <u>https://doi.org/10.1146/annurev-marine-041911-111611</u>
- Drazen, J. C., & Haedrich, R. L. (2012). A continuum of life histories in deep-sea demersal fishes. Deep Sea Research I, 61: 34–42. <u>https://doi.org/10.1016/j.dsr.2011.11.002</u>
- Duarte, C. M., Agusti, S., Barbier, E., Britten, G. L., Castilla, J. C., Gattuso, J.-P., Fulweiler, R. W., Hughes, T. P., Knowlton, N., Lovelock, C. E., Lotze, H. K., Predragovic, M., Poloczanska, E., Roberts, C., & Worm, B. (2020). Rebuilding marine life. *Nature*, 580(7801), 39–51. <u>https://doi.org/10.1038/s41586-020-2146-7</u>
- Dulvy, N. K., Rogers, S. I., Jennings, S., Stelzenmller, V., Dye, S. R., & Skjoldal, H. R.. (2008). Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. Journal of Applied Ecology, 45(4), 1029–1039. <u>https://doi.org/10.1111/j.1365-2664.2008.01488.x</u>
- Eigaard, O. R., Bastardie, F., Hintzen, N. T., Buhl-Mortensen, L., Buhl-Mortensen, P., Catarino, R., Dinesen, G. E., et al. (2016). The footprint of bottom trawling in European waters: distribution, intensity, and seabed integrity. – ICES Journal of Marine Science, 74: 847–865. <u>https://doi.org/10.1093/icesjms/fsw194</u>
- Eriksson, B.K., Bergström, U., Govers, L.L., & Eklöf, J.S. (2023). Trophic Cascades in Coastal Ecosystems. Reference Module in Earth Systems and Environmental Sciences. https://doi.org/10.1016/B978-0-323-90798-9.00006-8
- European Commission (2008). Reflections on Further Reform of the Common Fisheries Policy. Brussels: European Commission.

FAO (2012). The State of the World Fisheries and Aquaculture. Rome: FAO. Dulvy, N. K., Sadovy, Y., & Reynolds, J. D.. (2003). Extinction vulnerability in marine populations. Fish and Fisheries, 4(1), 25–64. <u>https://doi.org/10.1046/j.1467-2979.2003.00105.x</u>

Fath, B. D. (2019). *Encyclopedia of Ecology* (2nd ed., p. 337–346). Elsevier. https://books.google.no/books?hl=no&lr=&id=x1h7DwAAQBAJ&oi=fnd&pg=PP1&dq=Enc yclopedia+of+Ecology+Av+Brian+D.+Fath+2019&ots=cr12AQx3E9&sig=3hLwhZoUnvK4 JvRQtioaxdnuYm4&redir_esc=y#v=onepage&q=Encyclopedia%20of%20Ecology%20Av%2 0Brian%20D.%20Fath%202019&f=false

- Fei, S., Desprez, J.M., Potter, K.M., Jo, I., Knott, J.A., & Oswalt, C.M. (2017). Divergence of species responses to climate change. Science Advances: 3(8). DOI: 10.1126/sciadv.1603055
- Fisher, J. A. D., Frank, K. T., Petrie, B., Leggett, W. C., & Shackell, N. L. (2008). Temporal dynamics within a contemporary latitudinal diversity gradient. Ecology Letters, 11(9), 883–897. <u>https://doi.org/10.1111/j.1461-0248.2008.01216.x</u>
- Free, C. M., Thorson, J. T., Pinsky, M. L., Oken, K. L., Wiedenmann, J., & Jensen, O. P. (2019). Impacts of historical warming on marine fisheries production. Science 363, 979–983.<u>https://doi.org/10.1126/science.aau1758</u>
- Freitas, C., Olsen, E. M., Moland, E., Ciannelli, L., & Knutsen, H. (2015). Behavioral responses of Atlantic cod to sea temperature changes. *Ecology and Evolution*, 5(10), 2070–2083. <u>https://doi.org/10.1002/ece3.1496</u>
- Gattuso, J., Magnan, A. K., Bopp, L., Cheung, W. W. L., Duarte, C. M., Hinkel, J., et al. (2018). Ocean solutions to address climate change and its effects on marine ecosystems. Front. Mar. Sci. 5:337. <u>https://doi.org/10.3389/fmars.2018.00337</u>
- Greenstreet, S. P. R., & Hall, S. J. (1996). Fishing and the ground-fish assemblage structure in the North-western North Sea: an analysis of long-term and spatial trends. Journal of Animal Ecology, 65: 577–598. <u>https://doi.org/10.2307/5738</u>
- Greenstreet, S. P. R., Spence, F. E., & McMillan, J. A. (1999). Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. V. Changes in the structure of the North Sea groundfish species assemblage between 1925 and 1996. Fisheries Research, 40(2): 153–183. <u>https://doi.org/10.1016/S0165-7836(98)00210-0</u>
- Gonzalez, P.C., Larsen, K.M. H., Fratantoni, P., & Beszczynska, M.A. (2019). ICES Report on Ocean Climate 2018. ICES Cooperative Research Report, Vol. 349. <u>https://doi.org/10.17895/ices.pub.5461</u>
- Gordon, J. D. M. (2005). Environmental and biological aspects of deepwater demersal fishes. In Deep Sea 2003: Conference on the Governance and Management of Deep-Sea Fisheries, pp. 70–88. Ed. by R. Shotton. FAO Fisheries Proceedings, 3/1. FAO, Rome. 718 pp.

- Halpern, B. S., Frazier, M., Potapenko, J., Casey, K. S., Koenig, K., Longo, C., Lowndes, J. S., Rockwood, R. C., Selig, E. R., Selkoe, K. A., & Walbridge, S.. (2015). Spatial and temporal changes in cumulative human impacts on the world's ocean. Nature Communications, 6(1), 7615. <u>https://doi.org/10.1038/ncomms8615</u>
- Hislop, J., Bromley, P., Daan, N., Gislason, H., Heessen, H., Robb, A., Skagen, D., Sparholt, H., & Temming, A. (1997). Database report of the stomach sampling project, 1991 (ICES Cooperative Research Report No. 219; ICES Cooperative Research Report, p. 422). ICES.
- Hobday, A. J., & Pecl, G. T.. (2014). Identification of global marine hotspots: sentinels for change and vanguards for adaptation action. Reviews in Fish Biology and Fisheries, 24(2), 415–425. <u>https://doi.org/10.1007/s11160-013-9326-6</u>
- Huse, G., Salthaug, A., and Skogen, M. D. 2008. Indications of a negative impact of herring on recruitment of Norway pout. – ICES Journal of Marine Science, 65: 906–911. <u>https://doi.org/10.1093/icesjms/fsn074</u>
- ICES. (2016). Norway pout (Trisopterus esmarkii) in Subarea 4 and Division 3.a (North Sea, Skagerrak, and Kattegat) (Version 1). ICES Advice: Recurrent Advice. https://doi.org/10.17895/ices.pub.18667826.v1
- ICES. (2019). Norwegian Sea Ecoregion Ecosystem overview. In Report of the ICES Advisory Committee, 2019. ICES Advice 2019, Section 12.1, <u>https://doi.org/10.17895/ices.advice.5748</u>.
- ICES. (2020). Working group on elasmobranch fishes (WGEF). 789 pp. ICES Scientific Reports. 2:77. 789pp. Retrieved from <u>http://doi.org/10.17895/ices.pub.7470</u>
- ICES. (2022a). Saithe (*Pollachius virens*) in subareas 4 and 6, and in Division 3.a (North Sea, Rockall and West of Scotland, Skagerrak, and Kattegat). In Report of the ICES Advisory Committee, 2022. ICES Advice 2022, pok.27.3a46. <u>https://doi.org/10.17895/ices.advice.19453649</u>.
- ICES. (2022b). Blue whiting (*Micromesistius poutassou*) in subareas 1–9, 12, and 14 (Northeast Atlantic and adjacent waters). ICES Advice 2022 whb.27.1-91214 <u>https://doi.org/10.17895/ices.advice.21493974</u>
- ICES. (2022c). Cod (Gadus morhua) in Subarea 4, Division 7.d, and Subdivision 20 (North Sea, eastern English Channel, Skagerrak). ICES Advice 2022 cod.27.47d20 https://doi.org/10.17895/ices.advice.21406881
- ICES. (2022d). Norway pout (Trisopterus esmarkii) in Subarea 4 and Division 3.a (North Sea, Skagerrak, and Kattegat). ICES Advice 2022 nop.27.3a4 <u>https://doi.org/10.17895/ices.advice.19772446</u>

- ICES. (2022e). Herring (Clupea harengus) in subdivisions 20–24, spring spawners (Skagerrak, Kattegat, and western Baltic). ICES Advice 2022 her.27.20-24 <u>https://doi.org/10.17895/ices.advice.19447964</u>
- ICES. (2022f). Joint NAFO\ICES Pandalus Assessment Working Group (NIPAG). ICES Scientific Reports. 4:38. 25 pp. <u>http://doi.org/10.17895/ices.pub.19692181</u>
- ICES. (2023). Haddock (Melanogrammus aeglefinus) in Subarea 4, Division 6.a, and Subdivision 20 (North Sea, West of Scotland, Skagerrak). The ICES Advice 2023 had.27.46a20. https://doi.org/10.17895/ices.advice.22269400
- Isbell, F., Gonzalez, A., Loreau, M., Cowles, J., Díaz, S., Hector, A., Mace, G. M., Wardle, D. A., O'Connor, M. I., Duffy, J. E., Turnbull, L. A., Thompson, P. L., & Larigauderie, A.. (2017). Linking the influence and dependence of people on biodiversity across scales. Nature, 546(7656), 65–72. <u>https://doi.org/10.1038/nature22899</u>
- Issifu, I., Alava, J.J., Lam, V.W.Y., & Sumaila, U.R. (2022) Impact of Ocean Warming, Overfishing and Mercury on European Fisheries: A Risk Assessment and Policy Solution Framework. Front. Mar. Sci. 8:770805. doi: 10.3389/fmars.2021.770805
- Jac, R., Höffle, H., Albretsen, J., Jakobsdóttir, K., Staby, A., Søvik, G., & Junge, C. (2022). Of three sharks and one chimaera: varied habitat preferences across a latitudinal range revealed by coastal and offshore surveys. Journal of Fish Biology, 100(3), 660–674. <u>https://doi.org/10.1111/jfb.14979</u>
- Jennings, S., & Blanchard, J. L. (2004). Fish abundance with no fishing: predictions based on macroecological theory. J. Anim. Ecol. 73, 632–642. doi: 10.1111/j.1365-2656.2008.01466.x
- Jennings, S., Greenstreet, S. P. R., & Reynolds, J. D.. (1999). Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. Journal of Animal Ecology, 68(3), 617–627. https://doi.org/10.1046/j.1365-2656.1999.00312.x
- Jørgensen, C., Ernande, B., & Fiksen, Ø.. (2009). ORIGINAL ARTICLE: Size-selective fishing gear and life history evolution in the Northeast Arctic cod. *Evolutionary Applications*, 2(3), 356–370. <u>https://doi.org/10.1111/j.1752-4571.2009.00075.x</u>
- Kjesbu, O. S., Alix, M., Sandø, A. B., Strand, E., Wright, P. J., Johns, D. G., Thorsen, A., Marshall, C. T., Bakkeplass, K. G., Vikebø, F. B., Mari, Ottersen, G., Allan, B. J. M., Fossheim, M., Stiansen, J. E., Huse, G., & Sundby, S.. (2023). Latitudinally distinct stocks of Atlantic cod face fundamentally different biophysical challenges under on-going climate change. *Fish and Fisheries*, 24(2), 297–320. <u>https://doi.org/10.1111/faf.12728</u>
- Kritzer, J.P., DeLucia, M.B., Green, E. et al. (2016) The importance of benthic habitats for coastal fisheries. BioScience 66, 274–284. <u>https://doi.org/10.1093/biosci/biw014</u>

Kvamme, C. (2022, May 6). *Nordsjøsilda*. Miljostatus.Miljodirektoratet.no. Retrieved May 9, 2023, from https://miljostatus.miljodirektoratet.no/tema/hav-og-kyst/havindikatorer/nordsjoen-skagerrak/fiskebestander/nordsjosild/

- Large, P. A., Hammer, C., Bergstad, O. A., Gordon, J. D. M., & Lorance, P. 2003. Deep-water fisheries of the Northeast Atlantic: II. Assessment and management approaches. Journal of Northwest Atlantic Fishery Science, 31: 151–163.
- Lenoir, J., Gégout, J.-C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N. E., Dullinger, S., Pauli, H., Willner, W., & Svenning, J. C.. (2010). Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. Ecography. <u>https://doi.org/10.1111/j.1600-0587.2010.06279.x</u>
- Longva, O., & Thorsnes, T. (eds) (1997). Skagerrak in the past and at the present an integrated study of geology, chemistry, hydrography and microfossil ecology. Geological Survey of Norway, Special Publication, 8: 1–98.
- Lorance, P., Bergstad, O. A., Large, P. A., & Gordon, J. D. M. (2008). Grenadiers in the Northeast Atlantic - distribution, biology, fisheries and their impacts, and developments in stock assessment and management. American Fisheries Society Symposium, 63: 365 – 397.
- McCauley, D. J., Pinsky, M. L., Palumbi, S. R., Estes, J. A., Joyce, F. H., & Warner, R. R. (2015). Marine defaunation: animal loss in the global ocean. Science 347:1255641. doi: 10.1126/science.1255641
- Merrett, N. R., & Haedrich, R. L. 1997. Deep-Sea Demersal Fish and Fisheries. Chapman & Hall, London, UK. 282 pp.
- Moomaw, W., & Blankenship, S. (2014). Charting a New Course for the Ceans: A Report on the State of the World's Oceans, Global Fisheries and Fisheries Treaties, and Potential Strategies for Reversing the Decline in Ocean Health and Productivity. The Center for International Environment & Resource Policy, Number 011. Medford, MA: Center for International Environment and Resource Policy
- Morato, T., Watson, R., Pitcher, T. J., & Pauly, D. (2006). Fishing down the deep. Fish and Fisheries, 7(1), 24–34. <u>https://doi.org/10.1111/j.1467-2979.2006.00205.x</u>
- Mace, G. M., Barrett, M., Burgess, N. D., Cornell, S. E., Freeman, R., Grooten, M., & Purvis, A.. (2018). Aiming higher to bend the curve of biodiversity loss. *Nature Sustainability*, 1(9), 448–451. <u>https://doi.org/10.1038/s41893-018-0130-0</u>
- Möllmann, C., & Diekmann, R.. (2012). Marine Ecosystem Regime Shifts Induced by Climate and Overfishing. A Review for the Northern Hemisphere. Advances in Ecological Research, Volume 47, 2012, Pages 303-347. ScienceDirect, <u>https://doi.org/10.1016/B978-0-12-398315-2.00004-1</u>

- Murgier, J., Mclean, M., Maire, A., Mouillot, D., Loiseau, N., Munoz, F., Violle, C., & Auber, A.. (2021). Rebound in functional distinctiveness following warming and reduced fishing in the North Sea. Proceedings of the Royal Society B: Biological Sciences, 288(1942), 20201600. <u>https://doi.org/10.1098/rspb.2020.1600</u>
- Myers, R. A., & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature*, 423(6937), 280–283. <u>https://doi.org/10.1038/nature01610</u>
- Nash, R. D., Wright, P. J., Matejusova, I., Dimitrov, S. P., O'Sullivan, M., Augley, J., & Höffle, H. (2012). Spawning location of Norway pout (Trisopterus esmarkii Nilsson) in the North Sea. ICES Journal of Marine Science, 69(8), 1338–1346._ <u>https://doi.org/10.1093/icesjms/fss130</u>
- Otto, L., Zimmermann, J. T. F., Furnes, G. K., Mork, M., Sætre, R., & Becker, G. (1990). Review of the physical oceanography of the North Sea. Netherlands Journal of Sea Research, 26: 161–238. <u>https://doi.org/10.1016/0077-7579(90)90091-T</u>
- Parmesan, C., Burrows, M. T., Duarte, C. M., Poloczanska, E. S., Richardson, A. J., Schoeman, D. S., & Singer, M. C.. (2013). Beyond climate change attribution in conservation and ecological research. Ecology Letters, 16, 58–71. <u>https://doi.org/10.1111/ele.12098</u>
- Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. Nature, 421(6918), 37–42. <u>https://doi.org/10.1038/nature01286</u>
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., & Torres, F. (1998). Fishing down marine food webs. Science 279, 860–863. DOI: 10.1126/science.279.5352.860
- Pauly, D., Watson, R., & Alder, J. (2005). Global trends in world fisheries: impacts on marine ecosystems and food security. Philos. Trans. R. Soc. B Biol. Sci. 360, 5–12. doi:10.1098/rstb.2004.1574
- Pawson, M. G., Ellis, J. R., & Dobby, H. (2009). The evolution and man-gement of spiny dogfish (spurdog) fisheries in the Northeast Atlantic. In V. F. Gallucci, G. A. McFarlane, & G. C. Bargamann (Eds.), Biology and Management of Spiny Dogfish Sharks (pp. 373–390). Bethesda, MD: American Fisheries Society.
- Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander, K., Bruno, J. F., Buckley, L. B., Burrows, M. T., Duarte, C. M., Halpern, B. S., Holding, J., Kappel, C. V., O'Connor, M. I., Pandolfi, J. M., Parmesan, C., Schwing, F., Thompson, S. A., & Richardson, A. J.. (2013). Global imprint of climate change on marine life. Nature Climate Change, 3(10), 919–925.
 <u>https://doi.org/10.1038/nclimate1958</u>
- Rijnsdorp, A. D., van Leeuwen, P. I., Daan, N., & Heesen, H. J. L. (1996). Changes in abundance of demersal fish species in the North Sea between 1906–1909 and 1990–1995. ICES Journal of Marine Science, 53: 1054–1062. <u>https://doi.org/10.1006/jmsc.1996.0132</u>

- Rilov G, Mazaris AD, Stelzenmüller V, Helmuth B, Wahl M, et al. (2019) Global Ecol. Cons. 17: e00566
- Rohde, J. (1996). On the dynamics of the large-scale circulation of the Skagerrak. Journal of Sea Research, 35: 9–21. <u>https://doi.org/10.1016/S1385-1101(96)90731-5</u>
- Rodhe, J.. (1987). The large-scale circulation in the Skagerrak; interpretation of some observations. Tellus A, 39A(3), 245–253. https://doi.org/10.1111/j.1600-0870.1987.tb00305.x
- Rogers, L. A., Stige, L. C., Olsen, E. M., Knutsen, H., Chan, K.-S., & Stenseth, N. C.. (2011). Climate and population density drive changes in cod body size throughout a century on the Norwegian coast. *Proceedings of the National Academy of Sciences*, 108(5), 1961–1966. <u>https://doi.org/10.1073/pnas.1010314108</u>
- Rosenberg, R., Hellmann, B., & Lundberg, A. (1996). Benthic macrofaunal community structure in the Norwegian Trench, deep Skagerrak. Journal of Sea Research, 35: 181–188. <u>https://doi.org/10.1016/S1385-1101(96)90745-5</u>
- Rosenzweig, C., Karoly, D., Vicarelli, M., Neofotis, P., Wu, Q., Casassa, G., Menzel, A., Root, T.L., Estrella, N., Seguin, B., Tryjanowski, P., Liu, C., Rawlins, S., & Imeson, A.. (2008). Attributing physical and biological impacts to anthropogenic climate change. Nature 453, 353–357..<u>https://doi.org/10.1038/nature06937</u>
- Rubenstein, M. A., Weiskopf, S. R., Carter, S. L., Eaton, M. J., Johnson, C., Lynch, A. J., Miller, B. W., Morelli, T. L., Rodriguez, M. A., Terando, A., & Thompson, L. M.. (2020). Do empirical observations support commonly-held climate change range shift hypotheses? A systematic review protocol. Environmental Evidence, 9(1). <u>https://doi.org/10.1186/s13750-020-00194-9</u>
- Saila, S.A. (1983) Importance and assessment of discards in commercial fisheries. FAO Fisheries Circular 765: 62 pp.
- Sandø, A.B., Hjøllo, S.S., Hansen, C., Skogen, M.D., Hordoir, R., & Sundby, S. (2022). Risk analysis for the Norwegian sea areas on direct and indirect effects of climate change on marine ecosystems under various emission scenarios. Rapport from havforskningen ISSN:1893-4536
- Sguotti, C., Lynam, C. P., García-Carreras, B., Ellis, J. R., & Engelhard, G. H. (2016). Distribution of skates and sharks in the North Sea: 112 years of change. Global Change Biology, 22(8), 2729–2743. <u>https://doi.org/10.1111/gcb.13316</u>
- Skjæraasen, J. E., & Bergstad, O. A. (2000). Distribution and feeding ecology of Raja radiata in the northeastern North Sea and Skagerrak (Norwegian Deep). ICES Journal of Marine Science, 57: 1249–1260. <u>https://doi.org/10.1006/jmsc.2000.0811</u>
- STECF (2017). The 2017 Annual Economic Report on the EU Fishing Fleet (STECF-17-12). Luxembourg: Scientific, Technical and Economic Committee for Fisheries (STECF).

- Sumaila, U. R., Alder, J., & Keith, H. (2006). Global scope and economics of illegal fishing. Marine Policy 30, 696–703. <u>https://doi.org/10.1016/j.marpol.2005.11.001</u>
- Sumaila, U. R., Skerritt, D. J., Schuhbauer, A., Villasante, S., Cisneros-Montemayor, A. M., Sinan, H., et al. (2021). WTO must ban harmful fisheries subsidies. Science 374, 544–544. <u>https://doi.org/10.1126/science.abm1680</u>
- Sunday, J. M., Bates, A. E., & Dulvy, N. K. (2012). Thermal tolerance and the global redistribution of animals. Nature Climate Change, 2(9), 686–690. <u>https://doi.org/10.1038/nclimate1539</u>
- Tanaka, K. R., Van Houtan, K. S., Mailander, E., Dias, B. S., Galginaitis, C., O'Sullivan, J., Lowe, C. G., & Jorgensen, S. J.. (2021). North Pacific warming shifts the juvenile range of a marine apex predator. Scientific Reports, 11(1). <u>https://doi.org/10.1038/s41598-021-82424-9</u>
- Tupper, M., & Boutilier, R. G. (1995) Size and priority at settlement determine growth and competitive success of newly settled Atlantic cod. Marine Ecology Progress Series, Vol. 118, No. 1/3, pp. 295-300. <u>https://www.jstor.org/stable/24849786</u>
- van Hal R, Smits K, & Rijnsdorp AD. (2010) How climate warming impacts the distribution and abundance of two small flat-fish species in the North Sea. Journal of Sea Research 64,76–84. <u>https://doi.org/10.1016/j.seares.2009.10.008</u>
- van Weering, T. C. E., Berger, G. W., & Kalf, J. (1987). Recent sediment accumulation in the Skagerrak, Northeastern North Sea. Journal of Sea Research, 21: 177–189.
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E.. (2007). Let the concept of trait be functional!. Oikos, 116(5), 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x
- Webb, C. T., Hoeting, J. A., Ames, G. M., Pyne, M. I., & Leroy Poff, N.. (2010). A structured and dynamic framework to advance traits-based theory and prediction in ecology. Ecology Letters, 13(3), 267–283. <u>https://doi.org/10.1111/j.1461-0248.2010.01444.x</u>
- Worm, B., & Myers, R. A.. (2003). META-ANALYSIS OF COD–SHRIMP INTERACTIONS REVEALS TOP-DOWN CONTROL IN OCEANIC FOOD WEBS. Ecology, 84(1), 162–173. <u>https://doi.org/10.1890/0012-9658(2003)084[0162:maocsi]2.0.co;2</u>
- Zhou, S., Smith, A. D. M., Punt, A. E., Richardson, A. J., Gibbs, M., Fulton, E. A., Pascoe, S., Bulman, C., Bayliss, P., & Sainsbury, K.. (2010). Ecosystem-based fisheries management requires a change to the selective fishing philosophy. *Proceedings of the National Academy of Sciences*, 107(21), 9485–9489. <u>https://doi.org/10.1073/pnas.0912771107</u>

References for R-packages

- Auguie, B, (2017). _gridExtra: Miscellaneous Functions for "Grid" Graphics_. R package version 2.3, <https://CRAN.R-project.org/package=gridExtra>.
- Kolde. R, (2019). _pheatmap: Pretty Heatmaps_. R package version 1.0.12, <<u>https://CRAN.R-project.org/package=pheatmap</u>>.
- Lemon, J. (2006) Plotrix: a package in the red light district of R. R-News, 6(4): 8-12. Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J (2022). vegan: Community Ecology. Package_. R package version 2.6-4, <<u>https://CRAN.R-project.org/package=vegan</u>>.
- Simon Garnier, Noam Ross, Robert Rudis, Antônio P. Camargo, Marco Sciaini, and Cédric Scherer (2021). Rvision - Colorblind-Friendly Color Maps for R. R package version 0.6.2.
- Yu, G. (2021). _ggplotify: Convert Plot to 'grob' or 'ggplot' Object_. R package version 0.1.0, <<u>https://CRAN.R-project.org/package=ggplotify</u>>.

7. Appendices

Appendix A List of Species

Table 12: List of species used in the data set used in this study.

Norwegian species name	English species name	Latin species name
Blåkjeft	Blue-mouth redfish	Helicolenus dactylopterus
Blåsteinbit	Northern wolffish	Anarhichas denticulatus
Breiflabb	Anglerfish	Lophius piscatorius
Brosme	Tusk	Brosme brosme
Firetrådet tangbrosme	Fourbeard rockling	Enchelyopus cimbrius
Flekket fløyfisk	Spotted dragonet	Callionymus maculatus
Flekkskate	Spotted ray	Raja montagui
Gapeflyndre	Long rough dab	Hippoglossoides platessoides
Glassvar	Megrim	Lepidorhombus whiffiagonis
Gråskate	Spinytail skate	Bathyraja spinicauda
Gråsteinbit	Atlantic catfish	Anarhichas lupus
Hågjel	Blackmouthed dogfish	Galeus melastomus
Havålebrosme	Moray wolf eel	Lycenchelys muraena
Havmus	Rabbit fish	Chimarea monstrosa
Havsil	Raitt's sand eel	Ammodytes marinus
Hornkvabbe	Yarrell's blenny	Chirolophis ascanii
Hvitflekket glatthai	Starry smooth-hound	Mustelus asterias
Hvitskate	Sailray	Dipturus linteus
Hvitting	Whiting	Merlangius merlangus

Нуѕе	Haddock	Melanogrammus aeglefinus
Kloskate	Thorny skate	Amblyraja radiata
Knurr	Gurnard	Eutrigla gurnardus
Kolmule	Blue whiting	Micromesistius poutassou
Krokulke	Atlantic hookear sculpin	Artediellus atlanticus
Kveite	Atlantic halibut	Hippoglossus hippoglossus
Lange	Ling	Molva molva
Langhalet langebarn	Snakeblenny	Lumpenus lampretaeformis
Lomre	Lemon sole	Microstomus kitt
Lusuer	Norway redfish	Sebastes viviparus
Lyr	Pollack	Pollachius pollachius
Lysing	Hake	Merluccius merluccius
Mudderkutling	Norway goby	Pomatoschistus norvegicus
Mulle	Red mullet	Mullus surmuletus
Øyepål	Norway Pout	Trisopterus esmarkii
Panserulke	Hooknose	Agonus cataphractus
Pigghå	Spiny dogfish	Squalus acanthias
Piggskate	Thornback ray	Raja clavata
Piggvar	Turbot	Scophthalmus maximus
Rødknurr	Tub gurnard	Chelidonichthys lucerna
Rødspette	European plaice	Pleuronectes platessa
Rundskate	Round ray	Rajella fyllae
Sandflyndre	Dab	Limanda limanda
Sandskate	Sandy ray	Leucoraja circularis
Sei	Saithe	Pollachius virens

Skjellbrosme	Greater forkbeard	Phycis blennoides
Skolest	Roundnose grenadier	Coryphaenoides rupestris
Skrubbe	European flounder	Platichthys flesus
Slimål	Hagfish	Myxine glutinosa
Småsil	Lesser sand eel	Ammodytes tobianus
småvar	Norwegian topknot	Phrynorhombus norvegicus
Småflekket rødhai	Small-spotted catshark	Scyliorhinus canicula
Smørflyndre	Witch	Glyptocephalus cynoglossus
Sølvtorsk	Silvery pout	Gadiculus argenteus
Spisskate	Longnosed skate	Dipturus oxyrinchus
St.petersfisk	John Dory	Zeus faber
Svarthå	Velvet belly	Scomber scombrus
Sypike	Poor-cod	Trisopterus minutus
Sørlige Ålebrosme	Sars' wolf eel	Lycenchelys sarsii
Torsk	Cod	Gadus morhua
Tverrstripet Knurr	Red gurnard	Chelidonichthys cuculus
Tunge	Common sole	Solea solea
Vanlig Ålebrosme	Vahl's eelpout	Lycodes vahlii
Vanlig fløyfisk	Common dragonet	Callionymus lyra
Vanlig ringbuk	Common seasnail	Liparis liparis
Vanlig Uer	Golden redfish	Sebastes norvegicus
Villsvinfisk	Boarfish	Capros aper

Table 13: Total numbers by species caught in the survey in the time-period 2006-2022. The list shows allspecies in the data set of this thesis.

SPECIES	Total Catch	SPECIES	Total Catch
Blue-mouth redfish	315	Norway pout	1072522
Northern wolffish	11	hooknose	9
Anglerfish	184	Spiny dogfish	670
Tusk	28	Thornback ray	12
Fourbeard rockling	1884	Turbot	1
Spotted dragonet	32	Tub gurnard	1
Spotted ray	1	European plaice	1172
Long rough dab	58712	Round ray	50
Megrim	1	Dab	328
Spinytail skate	13	Sandy ray	1
Atlantic catfish	3	Saithe	6633
Blackmouthed dogfish	48	Greater forkbeard	76
Moray wolf eel	253	Roundnose grenadier	9468
Rabbit fish	9155	European flounder	4
Raitt's sand eel	8	Hagfish	2602
Yarrell's blenny	1	Small-spotted catshark	5
Starry smooth-hound	1	Lesser sand eel	10
Sailray	140	Norwegian topknot	7
Whiting	29425	Witch	7024
Haddock	34256	Silvery pout	1516
Thorny skate	959	Sars' wolf eel	109
Gurnard	557	Longnosed skate	10
Blue whiting	40419	John Dory	3
Atlantic hookear sculpin	1	Velvet belly	11949
Atlantic halibut	34	Poor-cod	1844
Ling	143	Cod	4132
Snakeblenny	20	Common sole	8
Lemon sole	236	Red gurnard	1
Norway redfish	401	Vahl's eelpout	2002
Pollack	75	Common dragonet	52
Hake	3647	Common seasnail	1
Norway goby	172	Golden redfish	8
Red mullet	85	Boarfish	1



Saithe

Figure 17: Catch rate of saithe with linear trend line, by depth stratum and year, in the period 2006-2022.

Depth	Estimate	Slope	P-value	Adjusted R-squared	Multiple R-squared
100-200m	778.9	-0.38	0.5	-0.04	0.02
200-300m	1252.3	-0.61	0.1	0.101	0.16
300-400m	604.3	-0.29	0.3	0.07	0.006
400-500m	307.3	-0.15	0.4	-0.03	0.05
500-600m	861.2	-0.42	0.03	0.43	0.5

 Table 14: Simple regression analysis of CPUE saithe.


Figure 18: 500-600 meters. Testing how good the simple regression model is with this type of data. Shapiro-Wilk normality test \rightarrow p-value = 0.6443, which indicates that it passed the normality test, with use of simple linear regression. 2010 and 2014 had a higher catch of Saithe compared to other years, with 6 and 7 individuals caught per station in this depth stratum. This may be the reason for the large value of points 1 and 3. But the Shapiro test still indicates that this model is normally distributed. By log and squat transform the residuals, didn't make the models any better. Log transformation only helped the Residuals VS Fitted figure, but Normal Q-Q test and Scale location got worse. There is very little assumption of homoscedasticity in this test model. Some of the reason for these results, can be the lack of data in this depth stratum. In residuals vs leverage, all points are within Cook's distance which indicates that there are not any influential points.

Whiting



Figure 19: Trend in catch rate of whiting, in different depth strata from the period 2006-2022.

Depth	Estimate	Slope P-value A F		Adjusted R-squared	Multiple R-squared		
100-200m	-7052.32	3.52	0.004	0.38	0.42		
200-300m	-1487.01	0.74	0.34	0.05	-0.004		
300-400m	-131.3	0.07	0.81	-0.06	0.004		
400-500m	-361.43	0.18	0.27	0.02	0.09		
500-600m	11910.2	-5.89	0.56	-0.21	0.39		

 Table 15: Simple regression analysis of CPUE whiting.



Figure 20: 100–200 meters. Testing how good the simple regression model is with this type of data.Shapiro-Wilk normality test \rightarrow p-value = 0.471, which indicates that it passed the normality test, with use of simple linear regression. The modeltest are normally distributed. After using log transformation and square root transformation, Scale-Location did get better, but the normal Q-Q figure didn't. But still Scale-Location shows some assumption of homoscedasticity. Residuals vs leverage indicates that there are not any influential points. All these tests together indicate that this model is good.

Roundnose Grenadier



Figure 21: Trend in catch rate of roundnose grenadier, in different depth strata from the period 2006-2022.

Estimate	Slope P-value		Adjusted R-squared	Multiple R-squared
357.5	-0.178	0.3	0.6356	0.8178
189.53	-0.093	0.2	0.1521	0.2936
369.58	-0.182	0.0007	0.5142	0.5446
299.05	-0.147	0.004	0.5142	0.428
329.84	-0.1613	0.02	0.2935	0.3439
	Estimate 357.5 189.53 369.58 299.05 329.84	Estimate Slope 357.5 -0.178 189.53 -0.093 369.58 -0.182 299.05 -0.147 329.84 -0.1613	EstimateSlopeP-value357.5-0.1780.3189.53-0.0930.2369.58-0.1820.0007299.05-0.1470.004329.84-0.16130.02	EstimateSlopeP-valueAdjusted R-squared357.5-0.1780.30.6356189.53-0.0930.20.1521369.58-0.1820.00070.5142299.05-0.1470.0040.5142329.84-0.16130.020.2935

Table 16: Simple regression analysis of CPUE roundnose grenadier.



Figure 22: 300-400 meters. Testing how good the simple regression model is with this type of data.Shapiro-Wilk normality test \rightarrow p-value = 0.7192, which indicates that it passed the normality test, with use of simple linear regression. By checking this model, use of square root transformation showed the most acceptable model. Points which are standing out in most of the plots are point 1 and 17. These points are outside the Cook distance and are also very high in the other tests. Reason for point 1, is because 2006 had a large catch of Roundnose Grenadier, compared to recent years. Same goes for points 17 to. It may give high value because the catch was higher in 2022 compared to 2014-2021. Still the model is showing assumptions of homoscedasticity and normal distribution.



Figure 23: 400–500 meters. Testing how good the simple regression model is with this type of data.Shapiro-Wilk normality test \rightarrow p-value = 0.8246, which indicates that it passed the normality test, with use of simple linear regression. After log transform the residuals, the model assumed normal distribution. Scale- Location shows assumption of homoscedasticity. Residuals vs leverage indicates that there are not any influential points. All these tests together indicate that this model is good.



Figure 24: 500-600 meters. Testing how good the simple regression model is with this type of data.Shapiro-Wilk normality test \rightarrow p-value = 0.1598, which indicates that it passed the normality test, with use of simple linear regression. After log transform the residuals, the model assumed normal distribution. Scale- Location shows assumption of homoscedasticity. Residuals vs leverage indicates that there are not any influential points. All these tests together indicate that this model is good. Residuals VS fitted shows a U-shaped pattern, which often concludes that a linear model is not appropriate and that a non-linear model might fit better. But the reason for these points to have a high value, may have to do with the amount of catches these years.

Haddock



Figure 25: Trend in catch rate of haddock, in different depth strata from the period 2006-2022.

Depth	Estimate	Slope P-value		Adjusted R-squared	Multiple R-squared
100-200m	1946.28	-0.9325	0.7	-0.05563	0.01035
200-300m	1951.4	-0.9589	0.5034	-0.03425	0.03039
300-400m	2191.24	-1.083	0.04196	0.211	0.2636
400-500m	907.53	-0.4488	0.3508	-0.003177	0.09714
500-600m	30700.18	-15.27	NA	NA	NA

Table 17: Simple regression analysis of CPUE haddock.



Figure 26: 300–400 meters. Testing how good the simple regression model is with this type of data.Shapiro-Wilk normality test \rightarrow p-value = 0.4864, which indicates that it passed the normality test, with use of simple linear regression. The model used to analyze CPUE of haddock shows that the type of model that has been used is not good enough to tell anything about the changes that have occurred at 300–400 meters. Although the Shapiro Wilk test resulted in normal distribution, the figures still show that there is no normal distribution or homoscedasticity. Which indicates that this model doesn't fit the data.

Velvet belly



Figure 27: Trend in catch rate of velvet belly, in different depth strata from the period 2006-2022. CPUE of Velvet belly showed increases in catch in 200-300, 300-400 and 500-600 meters depth stratums. While it decreases in 100-200 and 400-500 meters. Only 200-300 and 300-400 meters showed a significant positive trend.

Depth	Estimate	Slope	P-value Adjusted R-squared		Multiple R-squared	
100-200m	166.85	-0.081	0.31	-0.0039	0.066	
200-300m	-230.91	0.116	0.002	0.4355	0.4708	
300-400m	-326.38	0.16	0.006	0.3975	0.3573	
400-500m	91.70	-0.043	0.3988	-0.015	0.04787	
500-600m	-98.96	0.05	0.4959	-0.037	0.036	

Table 18: Simple regression analysis of CPUE velvet belly.



Figure 28: 200-300 meters. Testing how good the simple regression model is with this type of data.Shapiro-Wilk normality test \rightarrow p-value = 0.2369, which indicates that it passed the normality test, with use of simple linear regression. After using square root transformation in the residuals, the model assumed normal distribution. But point 1 and 10, are still showing high values, and this is because the amount of catch per stations were higher these years. Scale- Location shows assumption of homoscedasticity. Residuals vs leverage indicates that point 10 is an influential point. All these tests together indicate that this is an okay model but may be better fitted models to use. Residuals VS fitted shows a U-shaped pattern, which often concludes that a linear model is not appropriate and that a non-linear model might fit better. But the reason for these points to have a high value, may have to do with the amount of catches these years.



Figure 29: 300–400 meters. Testing how good the simple regression model is with this type of data. Shapiro-Wilk normality test \rightarrow p-value = 0.6776, which indicates that it passed the normality test, with use

of simple linear regression. After square root transformation of the residuals, the model assumes normal distribution. Scale- Location shows assumption of homoscedasticity. Residuals vs leverage indicates that there are not any influential points. All these tests together indicate that this model is good.



Long rough dab

Figure 30: Trend in catch rate of long rough dab, in different depth strata from the period 2006-2022. All depth stratums have shown more stability over the years, compared to the other species seen further up in Appendix B. The three shallowest depth strata have larger fluctuations, compared to strata in deeper areas. None of the depth strata showed significant changes.

Depth	Estimate	Slope	P-value	Adjusted R-squared	Multiple R-squared		
100-200m	-2279.7	1.173	0.6	-0.04618	0.01921		
200-300m	1319.78	-0.6267	0.8114	-0.06249	0.00391		
300-400m	671.6	-0.3253	0.7	-0.055	0.01		
400-500m	66.41	-0.029	0.9	-0.07	0.0006		
500-600m	2079.78	-1.02	0.16	0.086	0.1571		

Table 19: Simple regression analysis of CPUE long rough dab.

Rabbit fish



Figure 31: trend in catch rate of rabbit fish, in different depth strata from the period 2006-2022. 200-300 and 300-400 meters have shown an increase over the years. While the other depth stratums had more stability during the years. All depth strata have fluctuations. Only 300-400 meters showed a significant positive trend with p-value 0.016.

Depth	Estimate	Slope	P-value	Adjusted R-squared	Multiple R-squared
100-200m	12.49	-0.004	0.9	-0.065	0.0012
200-300m	-52.93	-0.02	0.46	-0.028	0.035
300-400m	-178.09	0.08	0.02	0.2534	0.3
400-500m	-5.37	0.004	0.94	-0.0663	0.0003
500-600m	37.08	-0.017	0.78	-0.07	0.0056

Table 20: Simple regression analysis of CPUE rabbit fish.



Figure 32: 300-400 meters. Testing how good the simple regression model is with this type of data. Shapiro-Wilk normality test \rightarrow p-value = 0.7367, which indicates that it passed the normality test, with use of simple linear regression. After square root transformation of the residuals, the model assumes normal distribution. Scale- Location does not show any assumption of homoscedasticity since it's not as horizontal as it should be. Residuals vs leverage indicates that there are not any influential points. But still, the model is okay.

Hake



Figure 33: trend in catch rate of hake, in different depth strata from the period 2006-2022. CPUE of hake showed decrease in all depth stratums, but none of them showed any significant changes. The three shallowest areas have large fluctuation the entire period from 2006 to 2022. While deeper areas (400-600 meters) also have some fluctuations, but not to the same extent as the other strata.

Depth	Estimate	Slope	Slope P-value		Multiple R-squared
100-200m	491.3469	-0.2418	0.1411	0.081	0.1386
200-300m	112.40	-0.053	0.686	-0.054	0.0112
300-400m	312.42	-0.1533	0.153	0.07332	0.1312
400-500m	534.31	-0.2639	0.1398	0.08207	0.1394
500-600m	219.34	-0.107	0.2646	0.03481	0.1226

 Table 21: Simple regression analysis of CPUE hake.

Blue Whiting



Figure 34: 200-300 meters. Testing how good the simple regression model is with this type of data. Shapiro-Wilk normality test \rightarrow p-value = 0.5533, which indicates that it passed the normality test, with use of simple linear regression. After log transformation of the residuals, the model assumes normal distribution. Scale- Location shows assumption of homoscedasticity. Residuals vs leverage indicates that there are not any influential points. All these tests together indicate that this model is good.



Figure 35: 300-400 meters. Testing how good the simple regression model is with this type of data. Shapiro-Wilk normality test \rightarrow p-value = 0.7897, which indicates that it passed the normality test, with use of simple linear regression. After log transformation of the residuals, the model assumes normal distribution. Scale- Location shows assumption of homoscedasticity. Residuals vs leverage indicates that there are not any influential points. All these tests together indicate that this model is good.



Figure 36: 400-500 meters. Testing how good the simple regression model is with this type of data.Shapiro-Wilk normality test \rightarrow p-value = 0.9041 , which indicates that it did not pass the normality test, with use of simple linear regression. After log transformation of the residuals, the model assumes normal distribution. Scale- Location shows assumption of homoscedasticity. Residuals vs leverage indicates that there are not any influential points. All these tests together indicate that this model is good.



Figure 37: 500-600 meters. Testing how good the simple regression model is with this type of data. Shapiro-Wilk normality test \rightarrow p-value = 0.06, which indicates that it passed the normality test, with use of simple linear regression. After log transformation of the residuals, the model assumes normal distribution, but still there is one point in Normal Q-Q which is more outside than the others. Scale- Location shows assumption of homoscedasticity. Residuals vs leverage indicates that there are not any influential points. Residuals VS fitted, are not showing good results. All these tests together indicate that this model is okay, but there may be better models fitting these data.



Analysis of Shannon index

Figure 38: Graph showing the predicted value of H-value at a depth of 400-500 meters



Figure 39: 400-500 meters. Testing how good the simple regression model is with this type of data. The model assumes normal distribution. Scale-Location shows assumption of homoscedasticity. Residuals vs leverage indicates that there are not any influential points. All these tests together indicate that this model is good. Shapiro-Wilk normality test residuals *p*-value = 0.3. For 400-500 meters, which indicates that this model is normally distributed.

Simpson Index



Figure 40: Trends in D-value, in different depth strata from the period 2006-2022. The Simpson index showed the same trends as the Shannon index but has more focus on the dominant species. None of the depth stratums showed significant changes over time, but the negative trend in the index i depth stratum 400-500 meters was almost significant (p = 0.052).

Depth	Estimate	Slope	P-value	Adjusted R-squared	Multiple R-squared		
100-200m	-3.891	-0.002	0.844	-0.06383	0.00266		
200-300m	10.02	-0.0048	0.6512	-0.051	0.01398		
300-400m	9.553	-0.004	0.673	-0.053	0.0122		
400-500m	33.91	-0.016	0.052	0.1759	0.2274		
500-600m	-34.28	0.017	0.094	0.139	0.2005		

 Table 22: Simple regression analysis of Simpson diversity index.
 D_value ~ year

Appendix D. Shannon Index Without Species

Without Norway Pout



Figure 41: Graph showing the predicted value of H-value at a depth of 100-200 meters



Figure 42: 100-200 meters. Testing how good the simple regression model is with this type of data. Shapiro-Wilk normality test W = 1, p-value = 0.6, which indicates that this model is normally distributed. The model assumes normal distribution. Scale- Location shows assumption of homoscedasticity. Residuals vs leverage indicates that there are not any influential points. All these tests together indicate that this model is good.



Figure 43: Graph showing the predicted value of H-value at a depth of 300-400 meters



Figure 44: 300-400 meters. Testing how good the simple regression model is with this type of data. Shapiro-Wilk normality test W = 0.9, p-value = 0.4, which indicates that this model is normally distributed. The model assumes normal distribution. Scale- Location shows assumption of homoscedasticity. Residuals vs leverage indicates that there are not any influential points. All these tests together indicate that this model is good.



Figure 45: Graph showing the predicted value of H-value at a depth of 400-500 meters



Figure 46: 400-500 meters. Testing how good the simple regression model is with this type of data. Shapiro-Wilk normality test W = 1, p-value = 0.9, which indicates that this model is normally distributed. The model assumes normal distribution. Scale- Location shows assumption of homoscedasticity. Residuals vs leverage indicates that there are not any influential points. All these tests together indicate that this model is good.

Without blue whiting



Figure 47: Graph showing the predicted value of H-value at a depth of 400-500 meters



Figure 48: 400-500 meters. Testing how good the simple regression model is with this type of data. Shapiro-Wilk normality test W = 0.9, p-value = 0.2 which indicates that this model is normally distributed. The model assumes normal distribution. Scale- Location shows assumption of homoscedasticity. Residuals vs leverage indicates that there are not any influential points. All these tests together indicate that this model is good.



EH-value Without Norway Pout

Figure 49: Illustrate the measurement of the evenness of species abundance in each of the depth strata, which considers both species richness and the relative abundance of each species. H-value without Norway pout.

EH-value Without Blue whiting



Figure 50: Illustrate the measurement of the evenness of species abundance in each of the depth strata, which considers both species richness and the relative abundance of each species. H-value without blue whiting.

Appendix E Fisheries and temperature data

Table 23:Commercial fishing data by depth stratum and year. The table contains the number of stop and start depths from each station during one year. Many stations contain several depth strata in one trawl. Example: A trawl has a starting depth of 247 meters, a stopping depth of 421m. Then a trawl was added in 200-300 meters, and one in 400-500 meters.

Depths	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022
0-200	807	733	804	768	743	1103	1145	792	1093	1239	1034	981
200-300	1619	1590	1567	1733	1354	1963	2263	2259	1540	2253	1818	1740
300-400	562	829	1133	900	802	961	903	920	568	620	573	561
400-500	111	202	435	429	349	376	306	252	150	88	135	155
500-600	5	8	8	16	15	13	20	21	2	9	11	7

Table 24: Total number of times the Norwegian trawls were used in Skagerrak between 2011 and 2022.

Year	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022
Count Trawling	2320	3102	3523	3375	2994	4106	4264	3932	3262	3957	3268	3396



Figure 51: Mean bottom temperature (± SD) per area from CTD from the shrimp survey in Skagerrak and the Norwegian Deep, 2006-2023. Reference: Guldborg Søvik, IMR.



Figure 52: Bottom temperature from CTD from the shrimp survey in Skagerrak and the Norwegian Deep, 2006-2023. Reference: Trude Hauge Thangstad, IMR.