

Environmental Drivers of Demersal Fish and Crustacean Community Structure in West Norwegian Fjords



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Abstract

Norwegian fjords, with their complex bathymetry and deep basins, are easily accessible study areas for deep sea communities. Impacts of climate change and increasing pressure from anthropogenic activities on fjord ecosystems, especially the aquaculture industry, reinforce the need to assess the state of the often poorly studied ecosystems. Less frequent basin water renewal linked to ocean warming can result in deoxygenation and hypoxic conditions, with unknown implications on the fjord communities. This study aimed to identify environmental drivers of benthopelagic and hyperbenthic community structures in West-Norwegian fjords, with a particular focus on fish and crustacean species composition, diversity and catch rates. Catch rates and distributions of *P. periphylla* were also investigated. The datasets consisted of 88 bottom trawl stations paired with CTDs, sampled from 2011 to 2022. The data was analyzed with generalized regression models, hierarchical clustering together with Indicator Species (IndVal) analysis to determine community clusters with associated key species, and NMDS ordination with fitted environmental variables over the clusters.

The results show that diversity (H) decreases with bottom depth and is highest for stations located in fjords with intermediately deep sills (150 to 250 m). Fish and crustacean catch rates decreased with distance to the coastline, whereas catch rates of *P. periphylla* were linked to lower temperatures. Catch rates of *P. periphylla* were also lower in basins with intermediately deep sills, where diversity was highest. Four community clusters were identified, in which bottom depth and geographic distributions had the strongest differentiation effects: 1) fjord stations at intermediate depths ($\bar{H} = 1.91$) linked to higher temperatures and salinity, 2) mostly coastal stations at shallower depths ($\bar{H} = 1.85$) linked to higher oxygenation, 3) deeper fjord stations ($\bar{H} = 1.26$) with inverse relationships to oxygen, and 4) both coastal and fjord stations with high prevalence of *P. periphylla* ($\bar{H} = 0.87$) linked to lower temperatures. Fjord communities were dominated by vulnerable key species with complex life history traits and lacked gadoid species in contrast to the coastal communities. These results illustrate how deep-sea fjord community composition, diversity and density responses are complex, with a multitude of interacting environmental variables shaping the observed communities. Long-term monitoring over a larger scale might be necessary to assess community responses to changing environments, which will be key for sustainable management of vulnerable fjord ecosystems. The present study provides a first thorough analysis of species communities in West-Norwegian fjords in relation to environment and, thus, an important baseline for future research.

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1 | Introduction

Norway has the world's second longest coastline, extending about 24 000 kilometers along the mainland and 103 000 kilometers if also accounting for islands. A major contributor to Norway's long coastline is the high prevalence of fjords, in which 1732 of them are named (Syvitski, Burrell and Skei, 1987). These fjords were carved by glaciers during the last ice age, and the fjord topography often consists of deep basins enclosed by sills (Syvitski, Burrell and Skei, 1987). The basins are typically much deeper than the adjacent coastal seas, and this makes fjords an easily accessible study area for unique, semi-enclosed deep-sea ecosystems (Storesund *et al.*, 2017; Meyer *et al.*, 2020). The deep sea generally refers to areas below 200 m depth and covers 95% of the ocean volume (Danovaro *et al.*, 2017). Despite being the world's largest biome, it is also the least studied due to the low accessibility (Ramirez-Llodra *et al.*, 2010; Danovaro *et al.*, 2017).

1.1 | Fjord Oceanography and Climate

Norwegian fjords have estuarine characteristics as the top layer is brackish from coastal freshwater runoffs. An estuarine circulation system transports some of the brackish water out of the fjord and into the northward flowing Norwegian Coastal Current (NCC) (Stigebrandt, 1981). Below the top brackish layer runs an intermediate layer with a compensation current, in which most of the water exchange between the fjords and the NCC takes place (Stigebrandt, 1981; Aksnes *et al.*, 2019). The well-oxygenated oceanic North Atlantic Water (NAW) runs below the NCC along the coast. Fjord basins often have different water mass properties than the intermediate layer as the water renewal frequency of the basins generally is lower (Aksnes *et al.*, 2019). For renewal to occur, the well-oxygenated NAW must be elevated above the sill depth and have a higher density than the basin water. Basin water renewal is thus dependent on the fjord topography and the density properties of the coastal water and the NAW. Multibasin fjords with multiple sills consequently have more barriers for water renewal in the innermost basins. Microbial oxygen consumption is the major driver of oxygen loss, and infrequent basin water renewal can consequently lead to hypoxic conditions over time (Aksnes *et al.*, 2019).

Species might however be well-adapted to fluctuating or permanently hypoxic environments (oxygen minimum zones, OMZs), as documented at the continental margins of the eastern Pacific, Indian and eastern Atlantic Oceans (Childress and Seibel, 1998; Helly and Levin, 2004). As an example, the bearded goby (*Sufflogobius bibarbatus*) in the Northern Benguela

upwelling system have been found to have behavioral and physiological adaptations to hypoxic environments, for instance by performing diel vertical migration to oxygenated waters during the night (Salvanes *et al.*, 2011; Salvanes and Gibbons, 2018). Otoliths from fish living in OMZ-regions have also been recorded to have patterns of micro-elements and isotopic composition suggesting previous exposure to severely hypoxic and low-pH environments (Cavole *et al.*, 2023). It is uncertain whether adaptations to naturally occurring hypoxia are present for deep-sea fish and crustacean species in Norwegian fjords. The HypOnFjordFish project aims to investigate evidence of hypoxia in deep-sea fish otoliths (Forskningsrådet, 2020). The Northern krill (*Meganyctiphanes norvegica*) was found to uphold diel vertical migration into hypoxic depths in a Swedish fjord despite having poor anaerobic metabolism capacity, causing accumulation of lactate (Spicer, Thomasson and Strömberg, 1999). Such accumulation of lactate could over time lead to a higher mortality rate of krill, which further may cause implications up the food web of the fjords. A masters' thesis in the HypOnFjordFish project found that populations of the mesopelagic shrimp species *Eusergestes arcticus* and *Pasiphaea* spp. have declined following a deoxygenation of a Norwegian fjord, Masfjord (Bukowski, 2022).

Climate change impacts fjord chemistry and hydrodynamics in many ways, including ocean acidification, increased coastal runoff, rising ocean temperatures, and changes in water mass stratification. Calcifying organisms are particularly sensitive to acidification, as it reduces their ability to form and uphold their exoskeleton (Guinotte and Fabry, 2008). Several deep-sea taxa can be affected by this acidification, such as cold water corals, crustaceans, benthic mollusks, and echinoderms (Guinotte and Fabry, 2008). Increased coastal run-offs with high organic content is expected to increase light attenuation of the water masses (Aksnes *et al.*, 2009). Such coastal water darkening does not only affect the primary production rates, but will also favor tactile species over visual species in terms of their feeding strategies (Eiane *et al.*, 1999; Aksnes *et al.*, 2009). This could potentially lead to mesopelagic regime shifts in fjords over time, and mass occurrences of the tactile scyphomedusa *Periphylla periphylla* in several Norwegian fjords are suggested to be due to the coastal water darkening (Sørnes *et al.*, 2007; Aksnes *et al.*, 2009). Increased freshwater run offs and rising ocean temperatures will also increase stratification, making fjord basin water renewals less frequent. A recent deoxygenation of one western Norwegian fjord, Masfjord, is suggested to be due to a 1 °C warming of NAW and thus less frequent basin water renewal (Aksnes *et al.*, 2019). High nutrient input from run-offs could lead to eutrophication and further deoxygenation, as

recorded in other estuaries, such as the Chesapeake Bay in USA, and coastal systems of the Baltic Sea (Malone and Newton, 2020). Anthropogenic nutrient input from sewage and agricultural fertilizers are of particular concern in densely populated coastal areas (Malone and Newton, 2020).

1.2 | Aquaculture Impact

Norwegian fjords have a socioeconomic value in terms of cultural history, tourism, industrial activities, fisheries, and most importantly the ascending aquaculture industry. Norway produces more than half of the farmed Atlantic salmon (*Salmo salar*) in the world, which is reflected in aquaculture sites scattered all along the Norwegian coast (Hersoug, 2021). Eutrophication from aquaculture nutrient inputs is considered to be of low risk in Norwegian fjords, but high input of particulate organic matter from fish feed and feces can accumulate in the bottom sediment if not sufficiently transported away with currents (Grefsrud *et al.*, 2022). Aquaculture sites in fjords therefore have higher risk of local environmental impact than coastal sites due to the lower water exchange. Increased particulate matter in the bottom sediments can lead to microbial deoxygenation and hypoxic conditions unfavorable for many species (Grefsrud *et al.*, 2022). Simulations of the dissolved oxygen development in Masfjord from 1975 to 2017, found that about 9% of the observed variation was due to oxygen consumption, which would also include consumption of organic matter from aquaculture sites. They concluded that the holding capacity for aquaculture is lower in poorly ventilated fjords (Aksnes *et al.*, 2019).

Environmental monitoring of Norwegian salmon farms shows that there is low impact from particulate organic matter on soft bottom areas, but for hard bottoms and mixed bottoms there is no standardized monitoring program in place yet (Grefsrud *et al.*, 2022). Because of this, there is limited knowledge on the environmental impacts of salmon farms on these locations (Grefsrud *et al.*, 2022). Fjord habitats can vary on small spatial scales, which should be accounted for in future management (Molina *et al.*, 2019). Especially filter- and suspension feeders are susceptible to the harms of suspended particulate matter, as their filters can clog if the particulate matter concentration exceeds their filtration capacity (Kutti, Krogness and Husa, 2016; Grefsrud *et al.*, 2022).

Modelling studies have shown that nitrogen and phosphorous substances can be traced up to 2 km from an aquaculture site with high fish biomass (Price *et al.*, 2015). The main form of

nitrogen waste from fish production is ammonia, and the main form of phosphorus is phosphate. Norwegian coastal waters are limited in nitrogen, especially during summer months (Grefsrud *et al.*, 2022). Ecosystems adapted to this low-nitrogen environment may therefore be negatively impacted by high nitrogen inputs from aquaculture. Regional impacts are mainly associated with increased microalgae production, as it supports zooplankton proliferation and thus increased biological sedimentation. This may in turn contribute to deoxygenation of the bottom sediment and water masses above, affecting the benthic communities (Grefsrud *et al.*, 2022). The study area in this thesis coincides with the Norwegian aquaculture Production areas 3 and 4 (Karmøy – Sotra - Stad), which have yearly discharges of respectively 1468 and 979 kg nitrogen per km², and 195 and 130 kg phosphorus per km² (Grefsrud *et al.*, 2022).

Chemical delousing of salmon might also impact the biological communities surrounding aquaculture sites. Dispersion and dilution of these substances depend on wind, ocean currents, depth and temperature at the locations (Grefsrud *et al.*, 2022). Modelling studies show that the chemicals hydrogen-peroxide, azamethiphos (organophosphate) and deltamethrin will be diluted to 1% at a radius of 1.9 km, with median dissolution time of 6.8 hours and possible impacted area of 0.9 km² (Saevik *et al.*, 2022). Pelagic crustaceans and larvae are most vulnerable to chemical delousing agents (Grefsrud *et al.*, 2022). The usage of chemical delousing in Norwegian salmon farms has however been reduced since 2014. Hydrogen-peroxide usage has been reduced from 33800 tons on average in 2014-2016, to 4060 tons in 2021. Azamethiphos usage was reduced from respectively 4630 and 3904 kg in 2014 and 2015 to 453 kg in 2021. Deltamethrin usage was reduced from 158 kg in 2014, to 5 kg in 2021 (Grefsrud *et al.*, 2022).

1.3 | Fjord Habitats and Communities

Norwegian coastal areas, located in the temperate and subpolar zones, have high primary production rates due to strong upwelling followed by stable stratification in the upper layers during spring and summer. Upwelling along the Norwegian coast is mainly driven by northerly winds, breaking the stratification of NAW and the Norwegian Coastal water (NCW) (Asplin, Salvanes and Kristoffersen, 1999). This increases the vertical mixing, fluxing nutrients from the deep sea to the euphotic zone. Research has shown that fjords such as Masfjord, are dependent on advection of zooplankton into the fjord for new production

(Aksnes *et al.*, 1989; Salvanes, Aksnes and Giske, 1992). Advection into the fjord occurs during southerly winds and downwelling, and frequent strong advection could increase the retention of planktonic organisms and thus increase the carrying capacity for planktivorous fish in the fjords (Asplin, Salvanes and Kristoffersen, 1999). The abundance and distribution of zooplankton are therefore important in bottom-up control in fjord communities, as they function as an interconnection between the primary producers and the higher trophic levels in the food web.

Fjords have an ecological importance for marine organisms by providing sheltered feeding areas and acting as nursery grounds, as well as having high carbon sequestration through sedimentation (Meyer *et al.*, 2020). Fjords can be considered as underwater valleys, with bedrock slope habitats on the sides and soft or mixed bottom habitats in the deep basins (Buhl-Mortensen *et al.*, 2020). A study done in the longest and deepest fjord in Norway, the Sognefjord, identified six different benthic biotopes along the slope gradient towards the soft deep bottom (Buhl-Mortensen *et al.*, 2020). The majority of the soft sediment in the basins are glaciomarine, but sedimentation is also increasing with both marine and terrestrial organic input. Soft bottom sediments range from sandy to muddy, and can contain different species compositions (Buhl-Mortensen *et al.*, 2020). Fjord habitats are thus diverse and heterogenous both within and between fjords, supporting a range of different communities.

Fjords with shallow sills have a higher degree of retention of organisms compared to fjords with deeper sills, as the sills act as topographic barriers to adjacent coastal areas (Buhl-Mortensen *et al.*, 2020). Multibasin fjords have multiple sills restricting water flow from the coast, creating a gradient of water exchange from the coast to the innermost basins. This isolation between the fjords and coastal areas can have implications on the connectivity between sub-populations of a species, as in the theory of island biogeography. For instance, the benthopelagic deep-sea species roundnose grenadier (*Coryphaenoides rupestris*) has sub-populations in different south-western Norwegian fjords with significant genetic heterogeneity (Delaval *et al.*, 2018; Sjøvik *et al.*, 2023). The mesopelagic species pearlside (*Maurolicus muelleri*) and glacier lanternfish (*Benthoosema glaciale*) have also been found to have some genetic differentiation between fjord sub-populations (Suneetha and Nævdal, 2001; Suneetha and Salvanes, 2001; Kristoffersen and Salvanes, 2009).

Deep-sea communities in general have high biodiversity and evenness, consisting of mainly macro- and meiofauna (Ramirez-Llodra *et al.*, 2010). A study in the Sognefjord found clear

gradients in species richness and composition of benthic communities related to distance into the fjord, depth, and landscape features, where the results showed a trend of decreasing number of taxa with depth and in fjord arms (Buhl-Mortensen *et al.*, 2020). Another study of the same fjord found that benthic species richness and diversity were stable in the fjord basin and decreased with proximity to the sill, decreasing water depth, and at the boundary between intermediate and basin water (Meyer *et al.*, 2020). The basin communities were homogeneous and characterized by sponges, echinoderms, and crustaceans, whereas the shallower regions were dominated by mobile invertebrate scavengers, as well as the fish species *Chimaera monstrosa*, *Coryphaenoides rupestris*, and *Sebastes viviparus*. Oxygen and salinity were identified as the most influential environmental variables on diversity (Meyer *et al.*, 2020).

Basin communities in multibasin fjords might also differentiate from each other. This was described in the three-basin sub-Arctic fjord Tysfjord, where the community differences were suggested to be caused by different environmental drivers (Molina *et al.*, 2019). The community in the innermost basin was for instance adapted to periodic hypoxic conditions with low food availability, whereas the deepest basin had community structure similar to that outside of the fjord (Molina *et al.*, 2019). Their main finding suggested that oxygen and organic matter content in the sediment were the main drivers of the benthic community structure. Oxygen has also been found to be the best explanatory variable for diversity and community composition for deep-sea fish in the Gulf of California, while temperature best explained variance in the fish density (Gallo *et al.*, 2020).

1.4 | Objectives and Hypotheses

Most studies present on Norwegian deep-sea fjord communities have focused on benthic epi- and infauna species composition, collected with video annotation (Buhl-Mortensen and Buhl-Mortensen, 2014; Buhl-Mortensen *et al.*, 2020; Meyer *et al.*, 2020) and grabs (Molina *et al.*, 2019). There is limited knowledge on hyperbenthic and benthopelagic community structures in the deep fjords, and how these are affected by environmental drivers. These communities are often dominated by fish and crustacean species with different ecological importance and niches. Scavengers are common in the deep sea and are important for breaking down organic matter and recycling nutrients. Common scavengers in Norwegian fjords include most deep-sea crustaceans (amphipods, decapod shrimps, squat lobsters (Galatheididae), Norway lobster

(*Nephrops norvegicus*)), as well as some fish species such as the Atlantic hagfish (*Myxine glutinosa*) (Sweetman *et al.*, 2014). Other species of the deep-sea fjord communities are predators, which are important for top-down control in the ecosystem. Common predators in the deep waters of the Norwegian fjords are rabbit fish (*Chimaera monstrosa*), roundnose grenadier (*Coryphaenoides rupestris*), blackmouth catshark (*Galeus melastomus*), velvet-belly lanternshark (*Etmopterus spinax*), spiny dogfish (*Squalus acanthias*), and different gadoid species such as the ling (*Molva molva*), blue ling (*Molva dypterygia*), tusk (*Brosme brosme*), saithe (*Pollachius virens*), pollack (*Pollachius pollachius*), and haddock (*Melanogrammus aeglefinus*). The gadoid species also include the Atlantic cod (*Gadus morhua*), an historically important species for the Norwegian fisheries that has been experiencing a stock decline (Lilly *et al.*, 2008).

Why is it important to study the hyperbenthic and benthopelagic communities? Norway has a long history of mineral mining, and is one of the few countries allowing disposal of mine tailings in the sea (Skei *et al.*, 2019). The western-Norwegian fjord Førdefjord has been subject for public debate, after the mining company Nordic Mining ASA has been granted permission to dispose of ~4 million tonnes of mine tailings annually for about 50 years (Skei *et al.*, 2019). The tailings will be transported to the fjord bottom in a tube, where most of it will settle at the seabed. However, one of the main concerns is the dispersion of smaller particles that can potentially affect the water column in a larger area. Another major concern is that toxic chemicals from the mineral extraction heavy metals can be dispersed together with the waste.

UN's Sustainable Development Goal 14 is about conserving and maintaining sustainable usage of marine resources, including protecting endangered species and vulnerable ecosystems. Deep-sea ecosystems are the least studied, and organisms from the deep often have life history traits that make them vulnerable to anthropogenic impacts. Coastal ecosystems are also generally less studied than offshore ecosystems, as science has been directed towards economically important offshore stocks. Understanding how these species, communities, and ecosystems work, will be crucial in future sustainable management.

The main objective of this study is to identify environmental drivers of deep-sea community structures in Western Norwegian fjords (59.5 to 62 ° N), with a particular focus on fish and crustacean catch rates, composition and diversity, as well as *P. periphylla* catch distribution. This is obtained using benthic trawl data. Both static and climate driven covariates are

explored as explanatory drivers. The climate driven variables include oxygen, salinity, and temperature. The static variables include bottom depth, sill depth (ranges from coastal stations with no sill (1), sills between 300-250 m depth (2), 250-150 m depth (3), 150-50 m depth (4) and the shallowest sills at less than 50 m depth (5)), distance to the shallowest sill, distance to the coastline, distance to closest aquaculture site, and aquaculture impact score (tonnes biomass capacity at aquaculture site over the squared distance to the site).

The main hypothesis is that different deep-sea fjord communities are shaped by different environmental variables, as found in previous studies (Buhl-Mortensen *et al.*, 2020; Meyer *et al.*, 2020). The main hypothesis is further categorized into three sub-hypotheses:

- a) Bottom depth and distance to the coastline are the main drivers for community structure differentiation.
- b) Diversity is positively affected by higher oxygen levels and temperature, and negatively affected by increasing bottom depth and aquaculture impact. Stations with deeper sills will have greater diversity than stations located within shallow sills, due to more frequent water exchange, more available habitats, and higher food availability from advection. Shallow sills will have higher retention of organisms, for instance *P. periphylla*.
- c) Environmental drivers behind catchweights (catches per minute fishing time, kg/min) of fish and crustaceans will differ from environmental drivers behind catchweights of the jellyfish *P. periphylla*:
 - a. Fish and crustacean catchweights are positively affected by higher levels of oxygen and temperature, and negatively affected by distance to the coastline.
 - b. *P. periphylla* catchweights are positively related to lower salinity, lower temperature, and shallower sills (higher retention).

2 | Material and Methods

2.1 | Overview Projects, Stations, and Gear

The data consist of 88 bottom trawl stations paired with CTD casts and were collected during 11 different surveys from 2011 to 2022 (Table 2.1, Appendix Table A.1). Fifty of these stations were visited in 2021 and 2022 during two CoastRisk project surveys, whereas the rest were visited during student surveys from 2011 to 2018 and one survey in 2022 of the HypOnFjordFish project (Table 2.1). Most of the surveys were conducted between September to February, except for three stations in May during the HypOnFjordFish survey (Table 2.1). A Campelen 1800 bottom trawl and a Sea-Bird 911plus CTD were used at 10 of the 11 surveys, with a total of 56 stations (Table 2.1). The remaining 32 stations were conducted with a Flekkerøy-trawl and an RBR Concerto CTD during the 2021 CoastRisk survey (Table 2.1). Information on the gear, equipment and methodology is detailed in sections 2.3-2.5.

Table 2.1: Overview of surveys (responsible institute, timing, number of stations and gear) along the West Norwegian Coast and in fjords from 2011 to 2022.

Institution / Project	Year	Month	Stations	Vessel	Trawl gear	CTD
IMR / Coastrisk	2021	Nov	32	M.S. Brattholm	Flekkerøy	RBR concerto
IMR / Coastrisk	2022	Feb	18	Kristine Bonnevie	Campelen 1800	Sea-Bird 911plus
UiB / Student survey	2011	Oct	6	H. Mosby	Campelen 1800	Sea-Bird 911plus
UiB / Student survey	2012	Oct	3	G.O. Sars	Campelen 1800	Sea-Bird 911plus
UiB / Student survey	2013	Nov	2	H. Mosby	Campelen 1800	Sea-Bird 911plus
UiB / Student survey	2014	Oct	2	G.O. Sars	Campelen 1800	Sea-Bird 911plus
UiB / Student survey	2015	Sep	5	H. Mosby	Campelen 1800	Sea-Bird 911plus
UiB / Student survey	2016	Sep	8	H. Mosby	Campelen 1800	Sea-Bird 911plus
UiB / Student survey	2017	Oct	3	G.O. Sars	Campelen 1800	Sea-Bird 911plus
UiB / Student survey	2018	Oct	3	G.O. Sars	Campelen 1800	Sea-Bird 911plus
UiB / HypOnFjordFish	2022	May	3	Kristine Bonnevie	Campelen 1800	Sea-Bird 911plus
Total			88			

2.2 | Study Area

All trawl stations were located at latitudes from 59.5 to 62° N, from Haugesund in the south to Stad in the north (Figure 2.1). There are both coastal stations and stations located inside fjords. Fjords visited include, from south to north: Bømlafjord, Etnefjord, Kvinnheradsfjord, Sørfjord, Radfjord, Hjeltefjord, Lurefjord, Masfjord, Gulafjord, Fjærlandsfjord, Sogndalsfjord, Lustrafjord, Åfjord, Vilnesfjord, Dalsfjord, Førdefjord, and the inlet of Nordfjord. These fjords differ in topographical characteristics, from shallow to deep sills and basins. The deepest trawl station was at 651 m in Lustrafjord, and the shallowest station was coastal at 112 m outside Stad (Appendix Table A.1). The sills range from approximately 30 m depth in the Lurefjord and Sogndalsfjord, to 200-300 m depth at the inlet of the Sognefjord, Førdefjord and Hjeltefjord (Appendix Table A.2). Some of the stations are located in basins restricted by multiple sills. In the Sogndalsfjord for example, there are two sills restricting water exchange with the coastal waters, the deep sill at the inlet of the Sognefjord and the shallow sill at the inlet of the Sogndalsfjord.

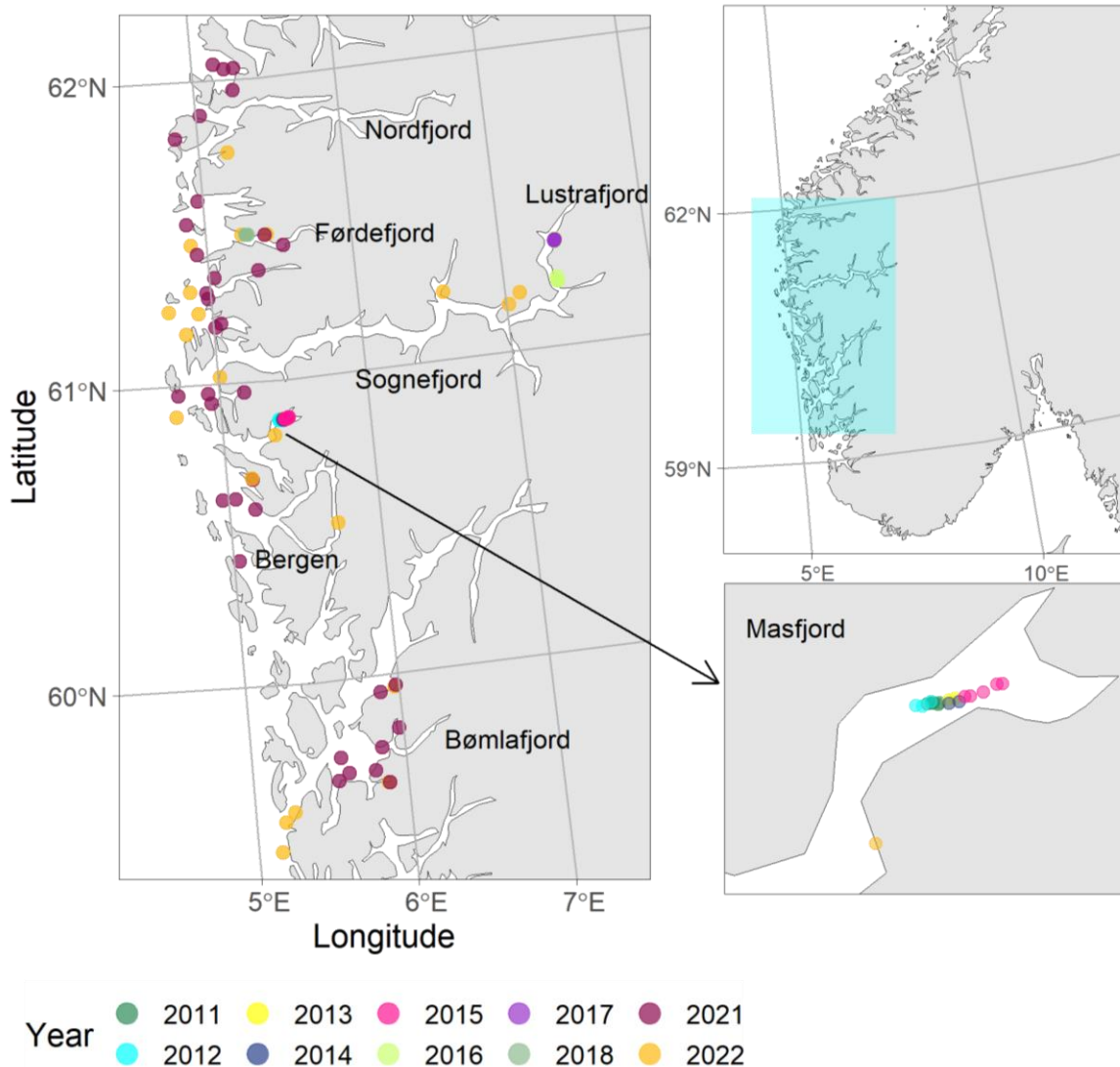


Figure 2.1: Map of 88 bottom trawl stations along the coast and in the adjacent fjords of West-Norway used in the analysis. There are 19 stations in Masfjord, of which 18 were visited from 2011 to 2015 (inner basin) and one was visited in 2022 (outer basin). Lustrafjord has 11 stations from 2016 and 2017. There are seven stations in Førdefjord, in which three are from 2018, two are from 2021 and two are from 2022. The rest of the stations are from 2021 and 2022, ranging from Bømlafjord to Stad.

2.3 | Sampling Gear

A Campelen 1800 trawl was used at 56 of the 88 stations (Table 2.1, Appendix Table A.1). This trawl has a cod-end of 22 mm mesh size; an inner net of 10 mm mesh size was used at the 2022 CoastRisk cruise. The targeted vertical trawl opening range is 4.0-4.6 m, and the

targeted door spread range is 47-53 m (Appendix Figure B.1). To ensure this setup at any trawling depth, the trawl wires were locked at 100-120 m ahead of the doors by a 10 m long strapping rope. Trawl opening and spread did however often occur outside these targeted ranges. For buoyancy, 104 8" floaters (259 kg uplift) were distributed evenly along the headrope besides the center (Appendix Figure B.1). The trawl was further rigged with "rockhoppergear". The trawl doors were of 125" Thyborøn type 7a and weighed 1810 kg each. Different Scanmar instruments were installed on the trawl. A depth sensor (model SS4) was mounted on the strapping rope to monitor the position of the trawl, where a steady distance of 35 m to the sea floor ensured that the trawl doors had constant contact with the floor. Door sensors (model SS4) gave information on the door spread and door angle. A trawl speed sensor was installed at the center of the headrope, and a trawl eye sonar was installed behind the trawl speed sensor.

The Campelen trawl was further rigged for different conditions and purposes at the different surveys. At the 18 trawl stations during the 2022 CoastRisk survey, it was rigged with "Nordsjø-rigging" with 32 extra 8" floats (80 kg uplift) between the bottom gear and ground rope to avoid mud hauls. The other surveys that used the Campelen trawl were rigged with "Tromsø-rigging", which included all the student surveys and the single HypOnFjordFish survey. This rigging also gave extra buoyancy to avoid mud hauls, with 63 8" floats extra on the gear (182 kg ± 6 kg uplift).

The 32 stations during the 2021 CoastRisk survey were trawled with the commercial Flekkerøy trawl (Appendix Table A.1). A 10 m long 16 mm mesh cod-end was sown onto the end of this trawl (Appendix Figure B.2). The trawl had a circumference of 2250 meshes, and 165 8" floats on the headrope. The groundgear had 8" Bobbin's chain (Appendix Figure B.2). No fish sorting device was installed on the trawl (permission granted by the Norwegian Directorate of Fisheries). The trawl doors were 115" Thyborøn and weighed 1200 kg each. A Simrad trawl door sensor was installed to measure trawl door spread, as well as a Simrad depth sensor to measure the depth. The trawl opening varied from 14 to 20 m, while door spread varied from 58 to 76 m. The trawling time varied from 10 to 15 minutes (Appendix Table A.1) at a speed of 1.3-1.8 knots, compared to a trawling time range from 2 to 41 minutes across all 88 stations (Appendix Table A.1).

2.4 | Processing of Catches

At the student surveys and the HypOnFjordFish survey, all catches were manually processed, calculated, and transferred to standardized Excel sheets. The sorting of the catches was done following the manual in Box 4.3 in Marine Ecological Field Methods (Salvanes *et al.*, 2018). Larger fish species and *Periphylla periphylla* were sorted out and weighed (kg total weight). The catches of smaller specimens were sorted together as mixed catch, which mostly included mesopelagic species such as *M. muelleri*, *B. glaciale*, krill (*Meganyctiphanes norvegica*) and shrimp species (*Pasiphaea* spp. and *Eusergestes arcticus*). The total weight of the mixed catch was registered, before taking a random subsample of approximately 1000 g from the mixed catch. The exact subsample weight was also registered. The different species in the subsample were then sorted and weighed to find the proportion of the species in the mixed catch (Formula 1).

$$(1) \text{ Proportion of species A} = \frac{\text{Weight of species A in the subsample}}{\text{Total weight of the subsample}}$$

The proportion of each species in the subsample was then used to find their total catch weight (Formula 2).

$$(2) \text{ Total catchweight of species A} = \text{Proportion of species A} * \text{Weight of the mixed catch}$$

The catches from the CoastRisk surveys were processed by a similar principle as on the student cruises, with sorting and weighing of the larger species and taking subsamples from the mixed catches. The species' catchweights were registered on tablet computers with the registration system Fish2Data (F2D) and Biotic Editor software to handle the calculations of species' total weights. The methodology is detailed in IMR's manual for sampling of fish, crustaceans and other invertebrates (Mjanger *et al.*, 2019). The digital registration systems are standard equipment on IMR survey ships, including on the 2022 CoastRisk survey with Kristine Bonnevie. As the 2021 survey was conducted with a commercial shrimp trawler (Table 2.1), a NUC server with F2D and a survey logger were installed below deck to create a local WLAN network for registration of catch and measurements. For position information, a GPS receiver from Globalsat was placed on the deck and connected to the server by a wire.

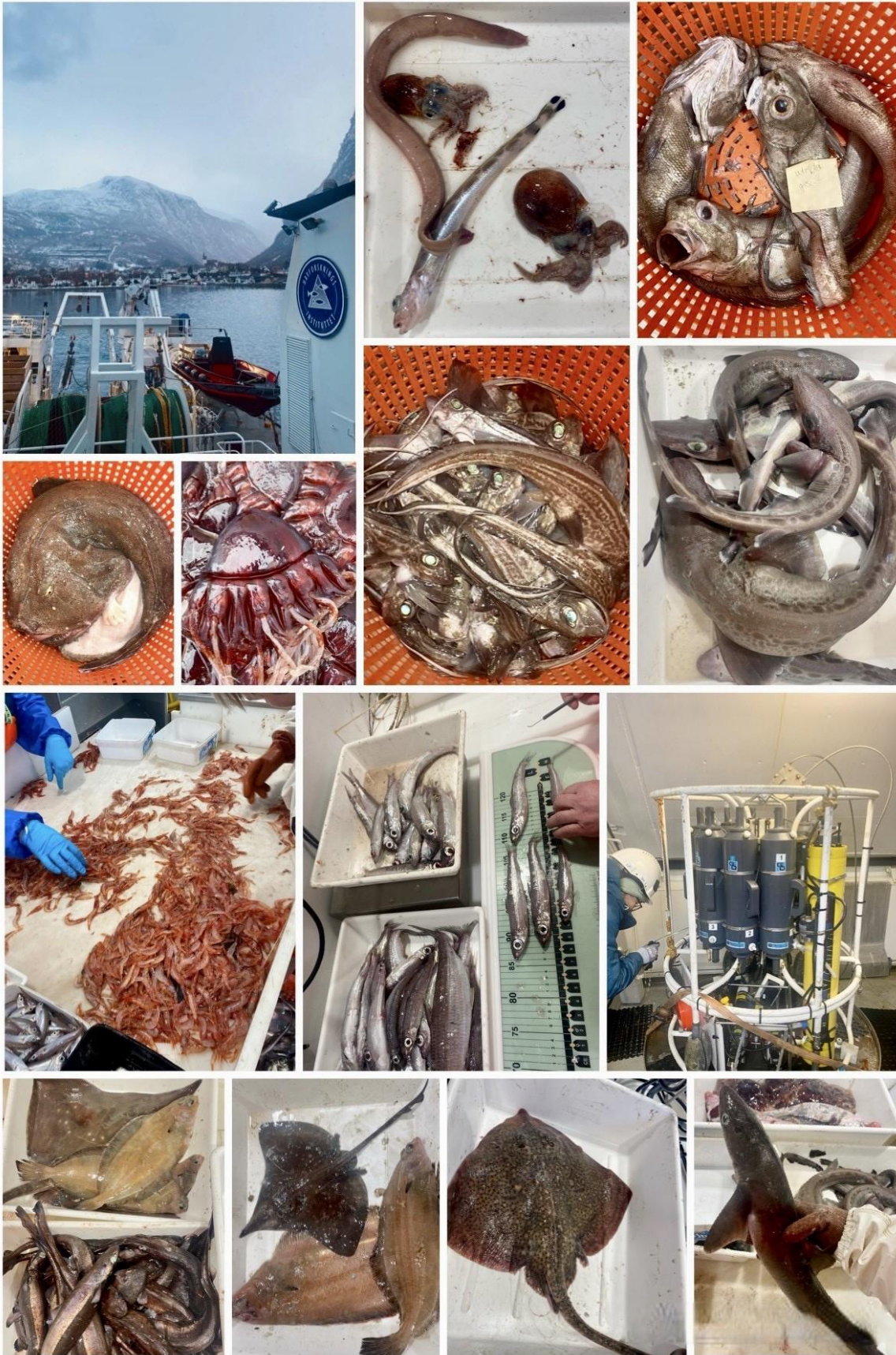


Figure 2.2: Collection of images from the 2022 CoastRisk research cruise. The cruise was conducted with the vessel Kristine Bonnevie (top left image, in Høyangsfjord). Photos: Sigrid Kjelstad

2.5 | Environmental Data Sampling

The environmental variables used in this study include: the hydrological variables oxygen, temperature, and salinity at bottom depth, as well as bottom depth, distance to the coastline, distance to the shallowest sill west (corresponding to the direction of the fjord opening) of the trawl station, distance to closest aquaculture site(s) and a calculated aquaculture impact score (Formula 3).

Oxygen, temperature, and salinity were measured with a CTD equipped with an oximeter and temperature gauge. A Sea-Bird 911plus CTD was utilized at 56 of the 88 stations (Table 2.1). The deployment speed of this CTD was about 0.5 m/s and it stopped approximately 10 m above the seabed, where the bottom hydrological data were measured. An RBR Concerto CTD was used at the remaining 32 stations. This CTD was attached to a winch at the back of the trawler, with a plumb at the end of the wire to ensure a vertical position in the water. Data registration (8 Hz) started as soon as the CTD hit the water due to a Marine wet switch setting. The CTD was held still for 60 seconds after hitting the water to acclimate to the water temperature. The RBR CTD was also stopped at approximately 10 m above seabed. After each CTD-haul, the data was loaded onto the PC onboard with Ruskin software.

Distance from each trawl station to the coastline, to the shallowest sill west of the trawl station, and to the closest aquaculture facility were measured manually using the Norwegian Fisheries Directorate ArcGIS map Yggdrasil (Norwegian Fisheries Directorate, 2023), as shown in Figure 2.2. Sill depths (Appendix Table A.2) were determined by looking at ENC (Electronic Navigational Charts) with depth grids. The sill depths were then used to create sill depth categories, ranging from coastal stations with no sill (1), sills between 300-250 m depth (2), 250-150 m depth (3), 150-50 m depth (4) to the shallowest sills at less than 50 m depth (5).

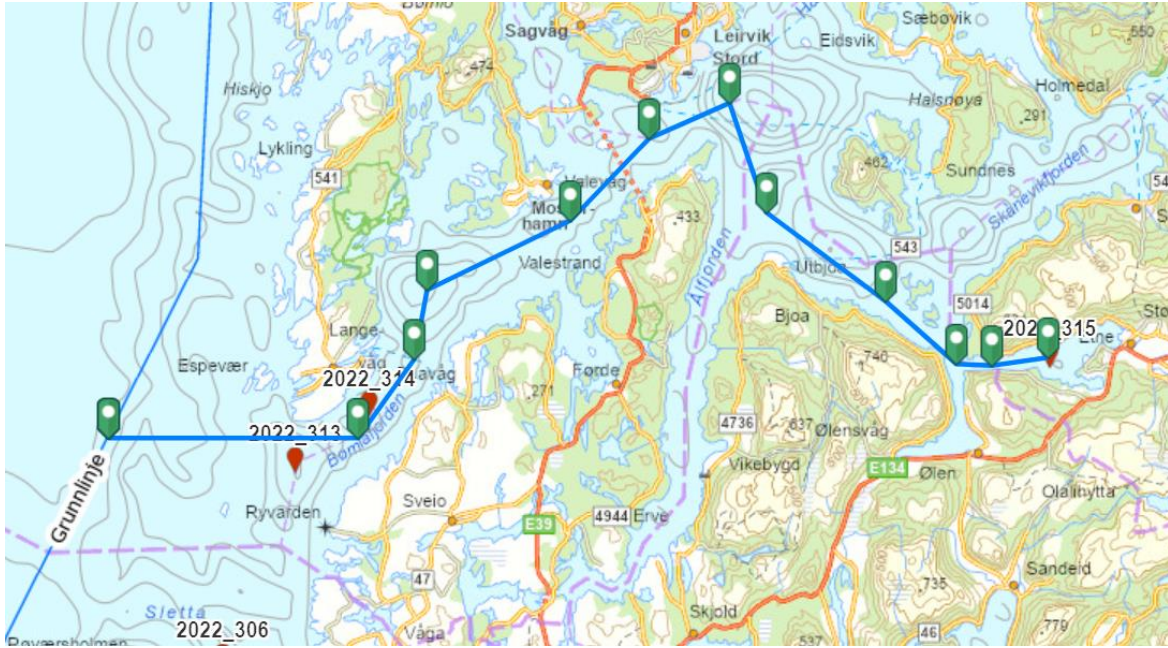


Figure 2.3: Example of distance measuring from the trawl stations to the coastline, defined here as the baseline (“grunnlinje”) (drawn by geodetic line segments between the outer points of the coast, including islands and islets not covered by waves at low tide). Distances from trawl stations to shallowest sill and aquaculture facilities were measured by the same method.

The aquaculture impact score for each trawl station was calculated by dividing the biomass capacity (tonnes) (retrieved from Norwegian Fisheries Directorate) at the closest aquaculture site by the squared distance to the site (km). The distance was squared to give larger weight (higher score) to the smaller distances, assuming that the aquaculture impact does not decrease linearly with distance but is greater at smaller distances. When there were several aquaculture sites in relatively close range to a station (5 km radius), the impact score was calculated by summing together the biomass over squared distance for each aquaculture site (Formula 3), where n is the number of aquaculture sites within a 5 km radius of the trawling stations.

$$(3) \text{ Impact score} = \sum_{i=1}^n \left(\frac{\text{Biomass capacity at aquaculture site A}}{(\text{Distance to aquaculture site A})^2} \right)_1 + \left(\frac{\text{Biomass capacity at aquaculture site B}}{(\text{Distance to aquaculture site B})^2} \right)_2 + \dots + \left(\frac{\text{Biomass capacity at aquaculture site C}}{(\text{Distance to aquaculture site C})^2} \right)_n$$

Example of the impact score calculation is shown below for station ID 7, which had one of the highest aquaculture impact scores of the 88 stations. The station, located by Sognesjøen in Gulen municipality, had three aquaculture sites within a 5 km radius: Hardbakkenset, Lyngholmen, and Mjånes (Figure 2.3).

Impact score (ID 7)

$$= \left(\frac{4500 \text{ tonnes}}{1.3^2 \text{ km}}\right)_{\text{Lyngholmen}} + \left(\frac{3120 \text{ tonnes}}{3.7^2 \text{ km}}\right)_{\text{Hardbakkeneset}} + \left(\frac{2340 \text{ tonnes}}{3.5^2 \text{ km}}\right)_{\text{Mjånes}} = 3081 \text{ tonnes/km}$$



Figure 2.4: Example of how some of the trawling stations are close to several aquaculture sites. Station ID 7, located by Sognesjøen in Gulen municipality, had three aquaculture sites within a 5 km radius: Hardbakkeneset (capacity of 3120 tonnes biomass), Lyngholmen (capacity of 4500 tonnes biomass) and Mjånes (capacity of 2340 tonnes biomass).

2.6 | Data Processing and Analysis

All data processing, visualizations and statistical analyses were performed in R version 4.1.3 (R Core Team, 2022). Figures with maps, species abundance and distributions were created using tidyverse and ggplot2 (Wickham *et al.*, 2019)

2.6.1 | Data Preparation and Visualization

All benthos except for crustaceans were removed from the catch data, leaving only fish, crustaceans, cephalopods, and jellyfish species. Several crustaceans, cephalopods and jellyfish were pooled into higher taxonomic groups due to inconsistent species characterization across the different survey cruises. Cephalopoda included unspecified *Cephalopoda spp.*, *Todaropsis eblana*, *Rossia macrosoma* and *Sepietta neglecta*. All jellyfish

species except *P. periphylla* were combined, which included *Cyanea capillata* and other unspecified jellies. The crustaceans were pooled into: Shrimp spp. (*Atlantopandalus propinquus*, *Dichelopandalus bonnieri*, *Pandalus borealis*, *Pontophilus* spp., *Crangon crangon*, and unspecified *Pandalina* spp.), Dendrobranchiata (*Pasiphaea* spp. and *Euergestes arcticus*), Galatheidae (*Munida* spp. and unspecified Galatheidae spp.), krill (*Meganyctiphanes norvegica* and unspecified euphausiids), isopods, as well as other unspecified crustaceans in its own group.

To account for the varying tow times between stations, the catch weights(kg) were standardized by trawling time to give catch per unit effort (CPUE, kg/min) (Formula 4). All species/taxonomic groups (*i*) were also transformed to their relative catchweight (proportion *p*) of the trawl catch (Formula 5).

$$(4) CPUE = \frac{\text{Trawl catch (kg)}}{\text{Fishing time (min)}}$$

$$(5) p = \frac{\text{Catchweight of species } i \text{ in trawl}}{\text{Total catchweight of trawl}}$$

The Shannon-Wiener diversity index (*H*) was calculated per trawl station, using the proportion of the entire community made up of species *i* (*p_i*) (Formula 6). This was done with the vegan package in R. The index provides an aggregate measure of the species diversity in the community, here assessed by trawl station. Values range from 0 to 5 (usually 1.5 to 3.5), where higher *H* indicates higher diversity in the community. If *H* = 0, the community only has one species (Ortiz-Burgos, 2016).

$$(6) H = - \sum_{i=1}^R p_i \cdot \log - (p_i)$$

The RBR Concerto CTD's oximeter measured oxygen in μmol/L, which later was converted to ml/L to match the other measurements. Oxygen's molar volume at standard pressure and temperature (0.022391 mL/mol) was used to calculate the volume of oxygen per liter sea water (Formula 7).

$$(7) \text{Oxygen (ml)} = (\text{Oxygen } (\mu\text{mol}) * 0.022391 \text{ ml}/\mu\text{mol})$$

The package sp (Bivand, Pebesma and Gomez-Rubio, 2013) was used to pair the closest CTD to each trawl station in the 2022 CoastRisk cruise and all student cruises. The pairings were then double checked manually to also match in time and depth. The longest distance between a CTD and the start position of a trawling station was 4.4 km in Masfjord in 2015 (ID 68), and the second longest was 3 km in Sogndalsfjord in 2022 (ID 9). Most trawl stations were

however within 1 km from the closest CTD. Due to the distance between the CTD- and trawling stations, some of the CTD bottom depths reached deeper than the trawling bottom depth. Where the difference exceeded 30 m, the environmental variable values were manually edited to match the bottom depth of the trawl station. This was done for ID 67 (60 m difference) and 68 (120 m difference) from Masfjord in 2015.

2.6.2 | Statistical Analyses

The environmental variables were tested for correlations prior to the statistical analyses by using a correlation matrix (Appendix C.1). This was generated by the function `ggpairs` from the package `GGally` (Schloerke *et al.*, 2022). Distance to shallowest sill was highly correlated with distance to the coastline (0.928) and was therefore removed from further analyses. Distance to closest aquaculture site was also highly correlated with distance to coastline (0.946), which was probably due to long distances from the trawling stations in Fjærlandsfjord, Sogndalsfjord and Lustrafjord to the closest aquaculture site by Høyanger further west in the Sognefjord. As the aquaculture impact score also includes distance in its equation, this variable was kept and distance to aquaculture dropped as a variable on its own. Temperature was correlated with bottom depth (-0.456) and distance to coastline (-0.488). Oxygen correlated with sill depth category (0.483), aquaculture impact score (0.315), bottom depth (-0.299), as well as distance to the coastline (-0.482). Both temperature and oxygen were however kept as variables, as previous studies have shown that they can potentially have a large influence on deep-sea community structures (Molina *et al.*, 2019; Gallo *et al.*, 2020; Meyer *et al.*, 2020).

Generalized linear models (GLMs) were used to explore relationships between the response variables diversity (H) and standardized catchweights (CPUE, catches in kg per minute fishing time), and the predictor environmental variables. The standardized catchweights were split into two models, a) summed fish and crustacean CPUE, and b) *P. periphylla* CPUE. This was done to explore differences in significant environmental variables between fish and crustaceans on one hand, and *P. periphylla* on the other hand. The GLMs were performed with the R stats package (R core team). The CPUE models were log-transformed with an added constant value of +1 (for observations with CPUE = 0), to make the response distributions more normal. In the *P. periphylla* data, there were a few stations with very high CPUE (highest 429 kg/min), whereas most stations had low or no catches of *P. periphylla* (30

stations had no catches). In addition to the environmental variables, trawl type was added as a categorical predictor variable with the Campelen 1800 as the reference category. For the sill depth categories, category 1 (coastal stations with no sill) was set as the reference category for the other sill categories. The models were checked with model-checking plots to ensure that assumptions were met (residuals vs fitted-, QQ-, scale-location-, residuals vs leverage-plots) (Appendix C).

Hierarchical clustering by Ward's method was performed on Bray-Curtis distance matrix to identify clusterings in the data. The data was transformed to relative abundance (Formula 5) and square-rooted prior to the analysis to make the response distributions more uniform. The package *factoextra* was used to determine the optimal number of clusters by the elbow method, and the package *dendextend* was used to visualize the cluster dendrogram. Key species in each cluster were determined by the Dufrene-Legendre Indicator Species Analysis (IndVal). This was done with the *labdsv* package (Roberts, 2023). Most abundant species/taxa in average per trawl were also presented for each cluster.

The same distance matrix was used in a non-metric multidimensional scaling (NMDS) plot with the package *vegan* (Oksanen *et al.*, 2022). Dimensions were set to $k=2$, giving stress of 0.2028. Several of the key species determined by the IndVal were plotted on the NMDS to validate their position relative to the clusters. Lastly, the environmental variables were fitted to the NMDS with *envfit*. This output was compared to a constrained RDA ordination to see if any variation was missing from other dimensions, as the NMDS only includes two dimensions.

3 | Results

3.1 | Catches and Trawls

3.1.1 | Catches - Distributions, Species and Diversity

The largest total catch was 429.9 kg/min in Lurefjord in 2021 (ID 32), and the smallest total catch was 0.098 kg/min in Lustrafjord in 2016 (ID 72). The median of the total catches was 4.2 kg/min, whereas the mean was 13.8 kg/min. There are clear differences between catches containing large abundances of *P. periphylla* compared to catches containing mainly fish and crustaceans (Figure 3.1). The fish and crustacean catches had a median of 3.0 kg/min and a mean of 4.8 kg/min. The largest catch of fish and crustaceans was 25.8 kg/min in Masfjord in 2014 (ID 66) (Figure 3.1A). The Periphylla catches had a median of 0.1 kg/min and a mean of 9.0 kg/min. The largest catch of Periphylla was, however, 428.6 kg/min in Lurefjord in 2021 (ID 32), followed by catches in Matersfjord and Skåneviksfjord (Figure 3.1B).

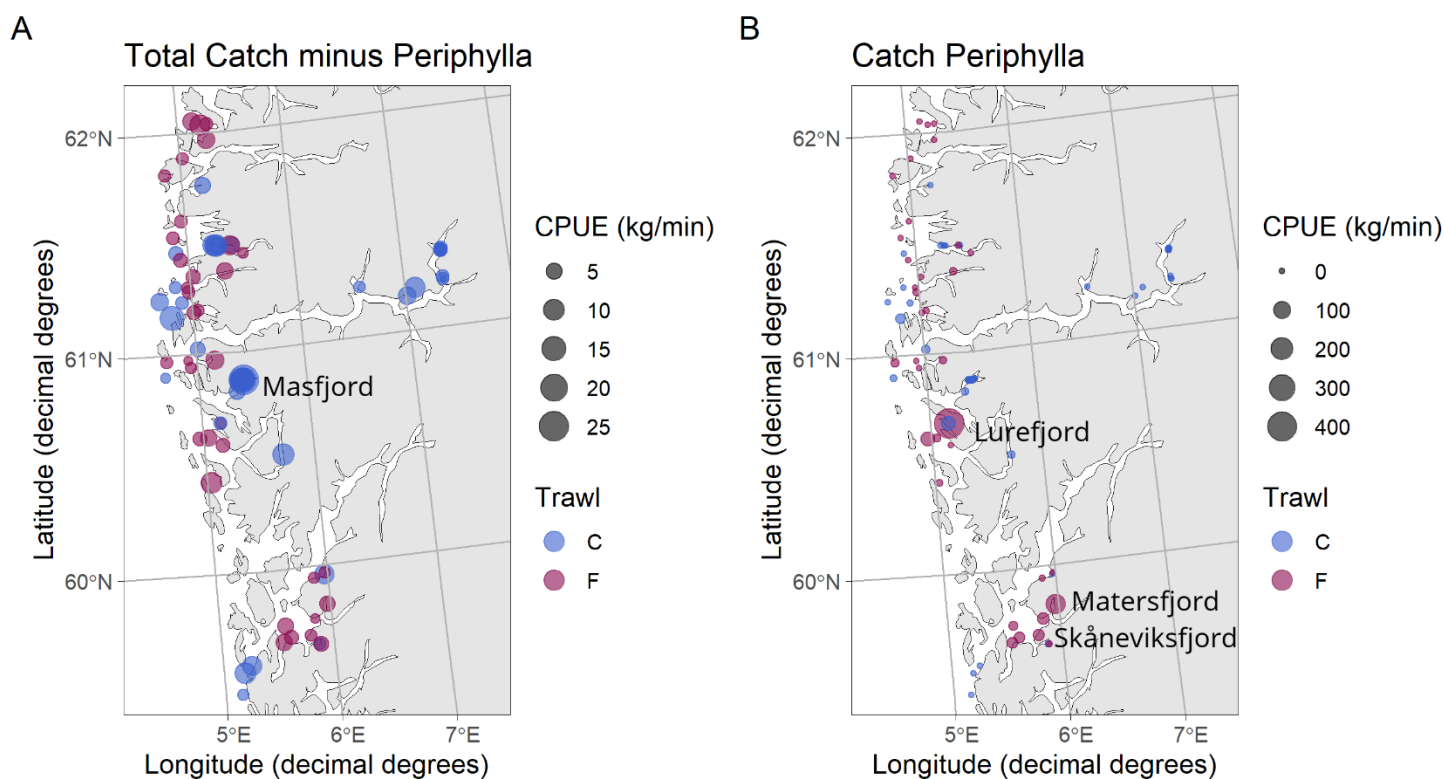


Figure 3.1: Trawl station catches in CPUE (catch per minute, kg/min) of total catch minus *P. periphylla* (A) and catch of *P. periphylla* only (B), where size of bubbles is proportional to catch weights. Trawl gear annotated as C (blue) refers to the Campelen 1800 trawl, whereas F (purple) refers to the Flekkerøy-trawl. Note different scales for CPUE in A and B. Fjord names are added to the largest CPUEs (Fish and crustaceans: Masfjord, *P. periphylla*: Lurefjord, Skåneviksfjord and Matersfjord).

A total of 67 species or taxonomic groups are present in the data, of which 53 are fish species. *P. periphylla* is the dominating species when measured in total CPUE across stations (65%) (Figure 3.2.A). But on average, each station CPUE consisted of 18% *P. periphylla*, closely followed by roundnose grenadier at 16 % (Figure 3.2.B). Other common species on average per CPUE are rabbit fish (11%), velvet-belly lanternshark (8 %), blackmouth catshark (5%), blue whiting (5 %), glacier lantern fish (4%), greater Argentine (4 %), and spiny dogfish (3%) (Figure 3.2.B). The remaining 58 species/taxa (other group (c)) each contributed less than 3% to the catches (Figure 3.2.B).

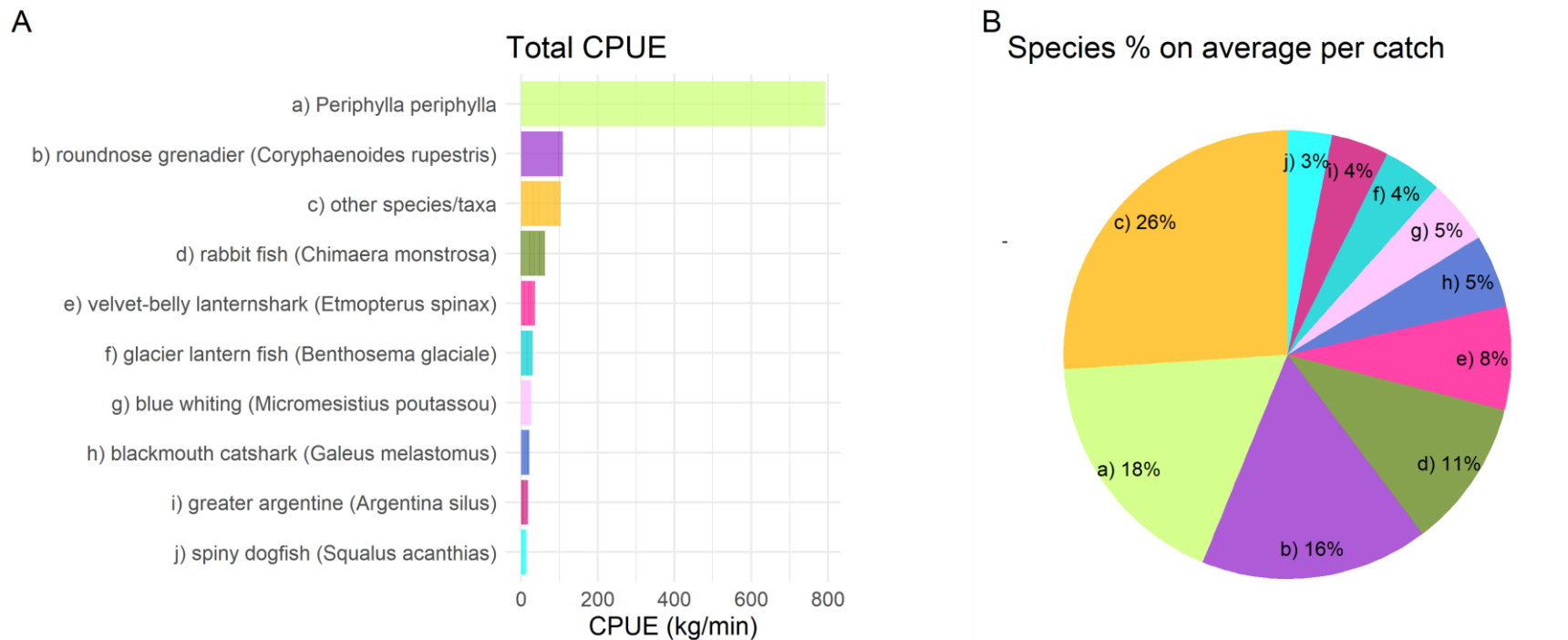


Figure 3.2: The 9 most common species in total catchweight (A) and their average share per trawl CPUE in % (B). The 'other' group includes the remaining species/taxa of the 88 trawl stations. Total catchweight is the total CPUE of each species summed across all stations, where CPUE refers to catch per minute (kg/min). Species average share in % was calculated by finding each species' relative proportion for each trawl station (Formula 5, sum each station = 1), then finding their average percentage across the 88 stations (for example for *P. periphylla* (sum relative proportion = 15.64) = $15.64 / 88 * 100\% = 18\%$).

The geographical distributions of the four most common fish species are shown in Figure 3.3. The largest catchweight of roundnose grenadier was in the Masfjord, with otherwise relatively lower occurrence in the study area (Figure 3.3A). Rabbit fish seems to be more evenly distributed between catches, with the largest catchweights in Fjærlandsfjord and outside Bømlafjord (Figure 3.3B). Velvet-belly lanternshark has an even distribution in the study area, with larger catchweights at Stad (62 ° N) than the other common species (Figure 3.3C). Blackmouth catshark has a notably similar distribution to rabbit fish, but here with the largest catchweight in Masfjord (Figure 3.3D).

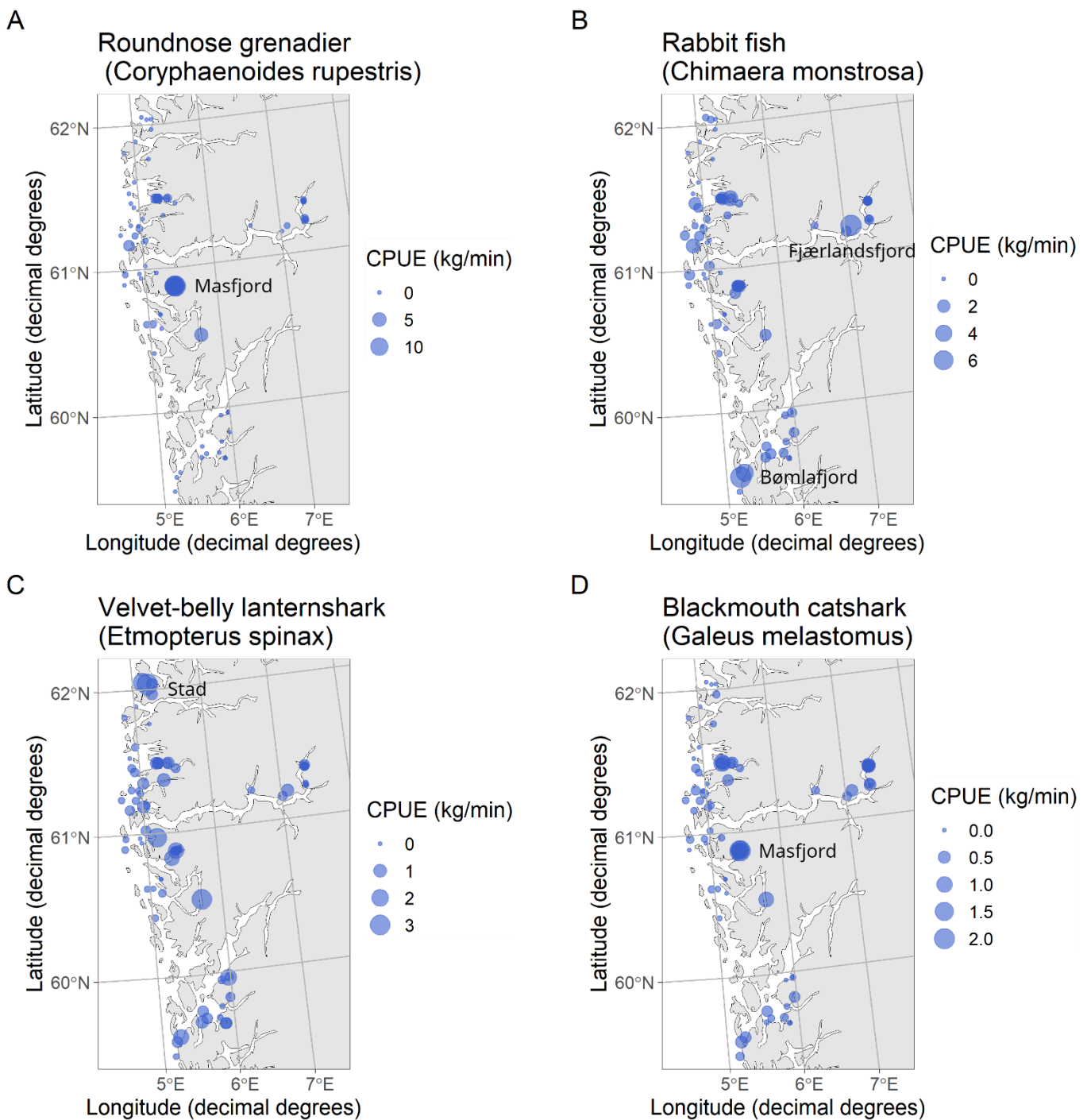


Figure 3.3: The geographical distribution of the four most common fish species; roundnose grenadier (A), rabbit fish (B), velvet-belly lanternshark (C), and blackmouth catshark (D). CPUE refers to catch per minute (kg/min).

The Shannon-Wiener diversity index (H) for each of the 88 trawl stations is illustrated on the map in Figure 3.4 (mean 1.54, median 1.65, max 2.42, min. 0.03) (Table 3.1). The stations with the highest and third-highest diversity score were in Førdefjord (Table 3.1). Out of the ten stations with the lowest diversity scores, four were in the Skåneviksfjord area, two in Lurefjord, two in Masfjord, and two were in the Mangersfjord area. Lurefjord had the lowest diversity index of these, with both stations among the four lowest index values.

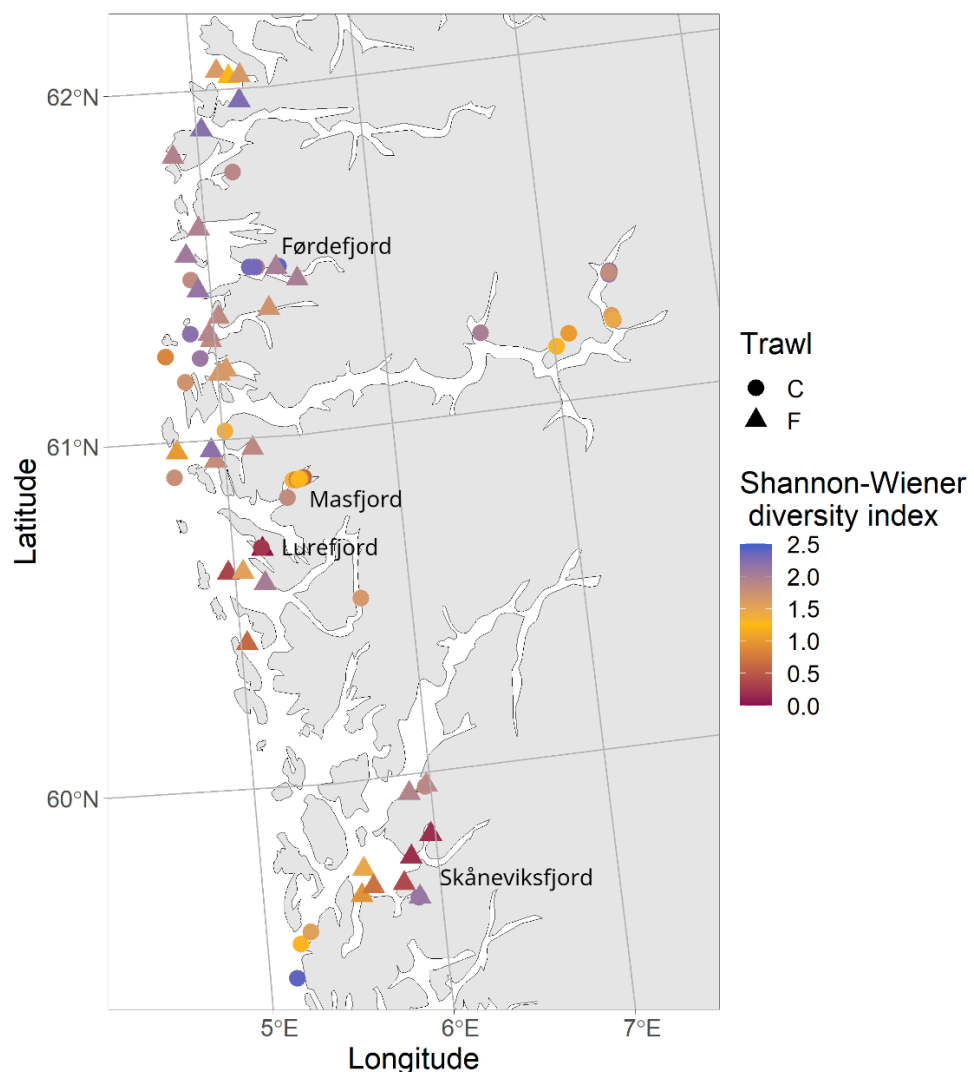


Figure 3.4: Shannon-Wiener diversity index (H) for the community data at trawling stations. Trawl gear annotated as C (round points) refers to the Campelen 1800 trawl, whereas F (triangle points) refers to the Flekkerøy-trawl. Fjord names are added by stations with high diversity (Førdefjord) and low diversity (Lurefjord, Skåneviksfjord, Masfjord).

Table 3.1: Top and bottom ten stations according to Shannon-Wiener diversity index.

Rank	Area	Shannon-Wiener diversity index	ID	Year	Trawl
1	Førdefjord, planned landfill area	2.42	12	2022	C
2	West of Haugesund	2.41	2	2022	C
3	Førdefjord	2.33	13	2022	C
4	Lustrafjord	2.32	85	2016	C
5	Nordpollen by Sildegapet, Stad	2.26	49	2021	F
6	Sogndalsfjord	2.24	79	2022	C
7	Lustrafjord	2.23	84	2016	C
8	Inlet Nordfjord	2.22	47	2021	F
9	Aldefjord	2.20	16	2022	C
10	West of Hisarøyna, Gulen	2.19	35	2018	C
...					
79	Masfjord	0.72	63	2013	C
80	Skåneviksfjord, Bjoafjord	0.69	23	2021	F
81	Hjeltefjord by Vindenes	0.61	28	2021	F
82	Masfjord	0.53	68	2015	C
83	Skåneviksfjord	0.37	20	2021	F
84	Mangerfjord	0.33	29	2021	F
85	Lurefjord	0.23	88	2022	C
86	Skåneviksfjord, Matersfjord	0.18	24	2021	F
87	Skåneviksfjord, Høylandssundet	0.17	25	2021	F
88	Lurefjord	0.03	32	2022	C

3.1.2 | Comparing Flekkerøy and Campelen 1800 Trawls

The Campelen and Flekkerøy trawls showed similar catch rates of fish and crustaceans (CPUE), and the Shannon-Wiener diversity index for the catches was also similar for the two trawl types (Figure 3.5). The Campelen 1800 trawl has a wider and higher range of catch rates than the Flekkerøy trawl, but the medians are relatively similar with respective values of 3.43 kg/min and 2.92 kg/min (Figure 3.6A). The Shannon-Wiener diversity distributions are also about the same for the two trawls' catches, with median values of 1.59 and 1.8 (Figure 3.6B). The means are very similar with values of 1.56 and 1.51. The lowest diversity catch was caught by the Flekkerøy, whereas the highest diversity catch was caught by the Campelen.

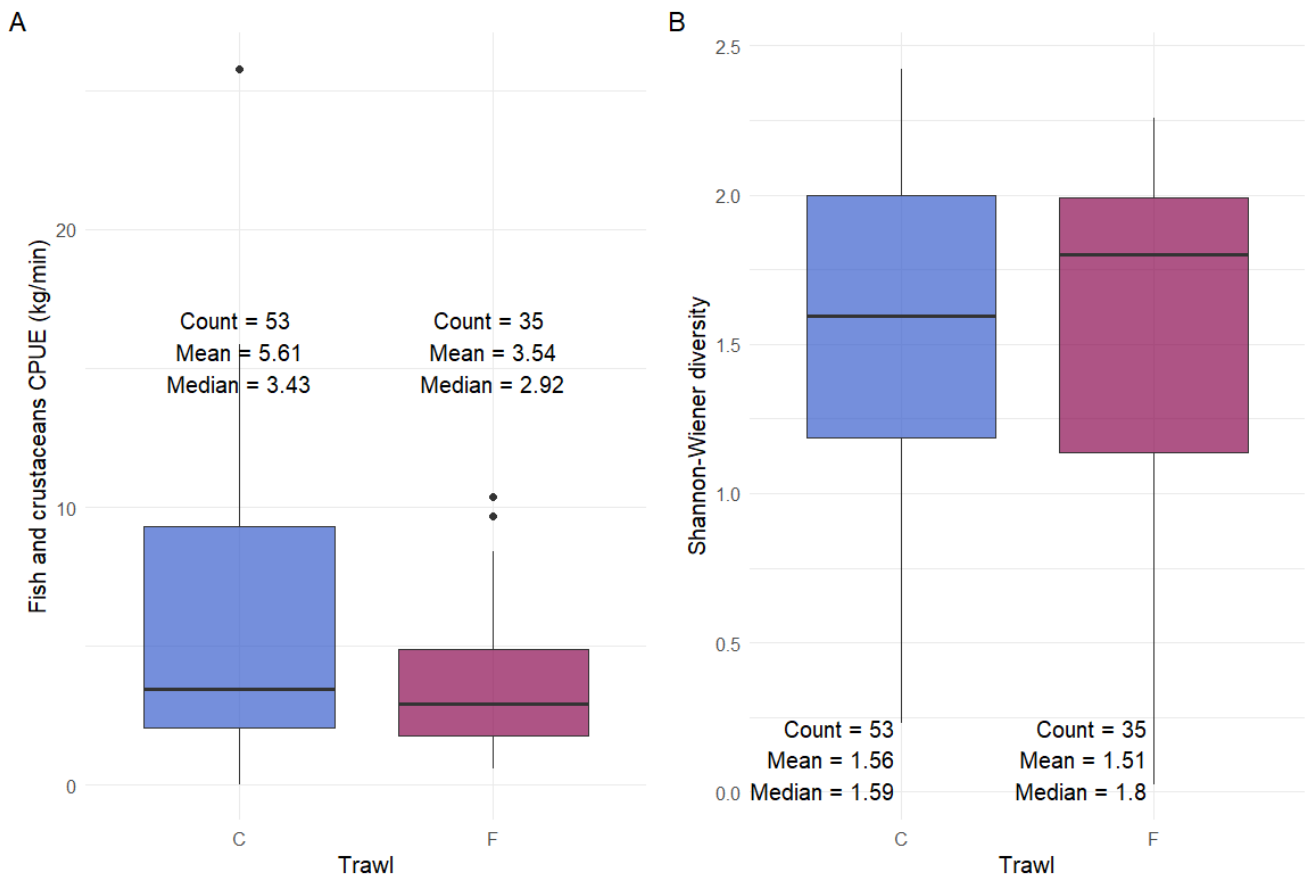


Figure 3.5: Comparisons of trawl CPUE (catch per minute, kg/min) of fish and crustaceans (A) and Shannon-Wiener diversity index (B). Trawl gear annotated as C refers to Campelen 1800 trawl, whereas F refers to Flekkerøy-trawl.

3.2 | Community Structure and Environmental Variables

3.2.1 | Environmental Variables – Relationships with Diversity and CPUEs

Bottom depth ($p < 0.001$) and sill category 3 ($p = 0.003$) are statistically significant environmental predictors for Shannon-Wiener diversity (H) (Figure 3.6). Diversity decreased with bottom depth, and stations located within 150 to 250 m deep sills (as the shallowest sill) had highest diversity (Figure 3.7). The Flekkerøy-trawl ($p = 0.06$) showed a tendency of lower diversity than the Campelen 1800 trawl. All other variables were found to be not relevant for the GLM explaining Shannon-Wiener diversity.

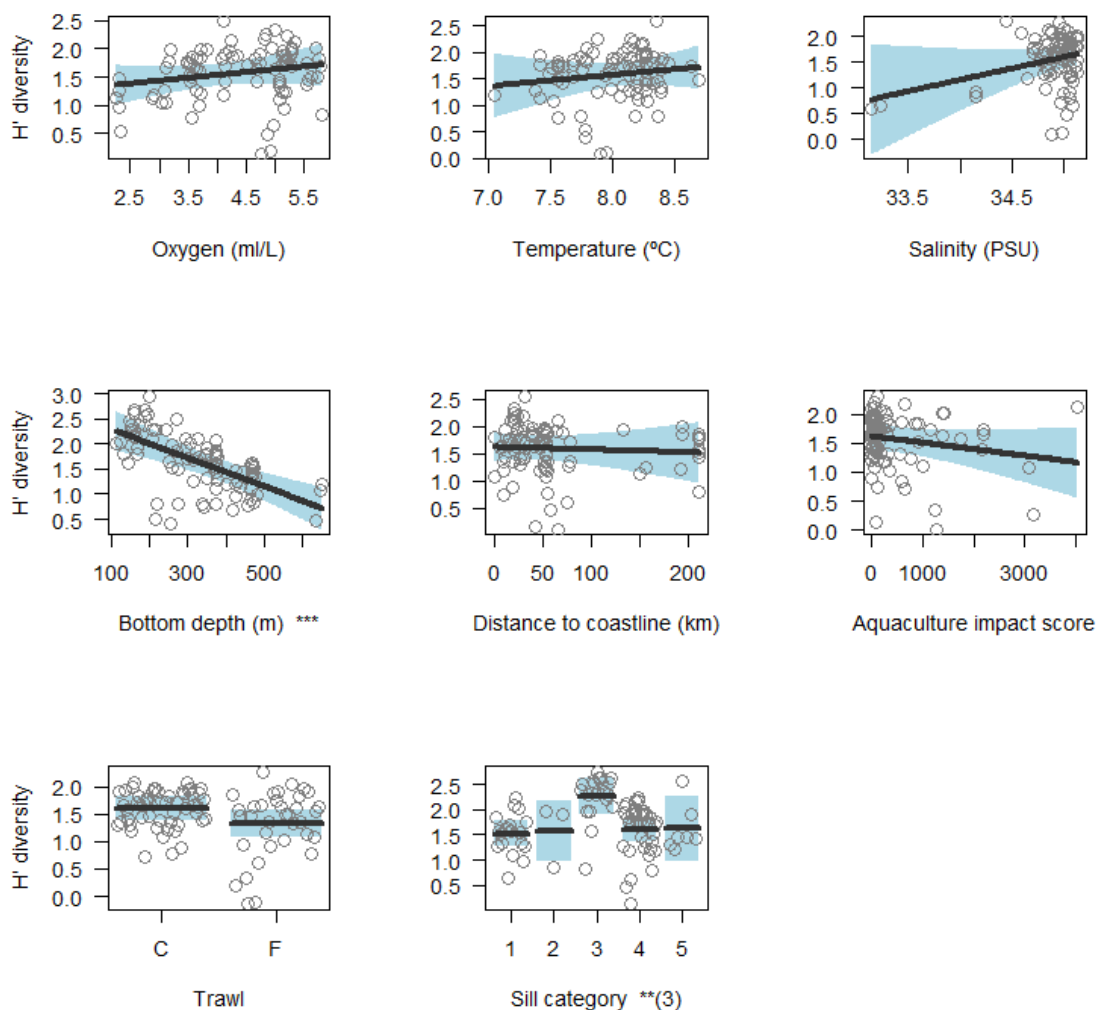


Figure 3.6: Relationships between Shannon-Wiener diversity index (H) and the environmental variables oxygen, temperature, salinity, bottom depth, distance to coastline, aquaculture impact score, trawl, and sill depth category. Trawl gear annotated as C refers to Campelen 1800 trawl, whereas F refers to Flekkerøy-trawl. Sill depth categories range from coastal stations with no sill (1), sills between 300-250 m depth (2), 250-150 m depth (3), 150-50 m depth (4) and the shallowest sills at less than 50 m depth (5). The 95 % confidence intervals are shaded in blue with the mean estimate as

black line. Significance codes for the p-values are given next to the variable label (0 '****' 0.001 '**' 0.01 '*' 0.05).

The only statistically significant predictor variable for fish and crustacean CPUE was distance to the coastline ($p = 0.002$), with lower CPUE at greater distances (Figure 3.7). Sill depth category 3 ($p = 0.07$) and the Flekkerøy-trawl ($p = 0.09$) showed a tendency toward higher and lower CPUE (Figure 3.7), respectively, but the effects were only marginally significant.

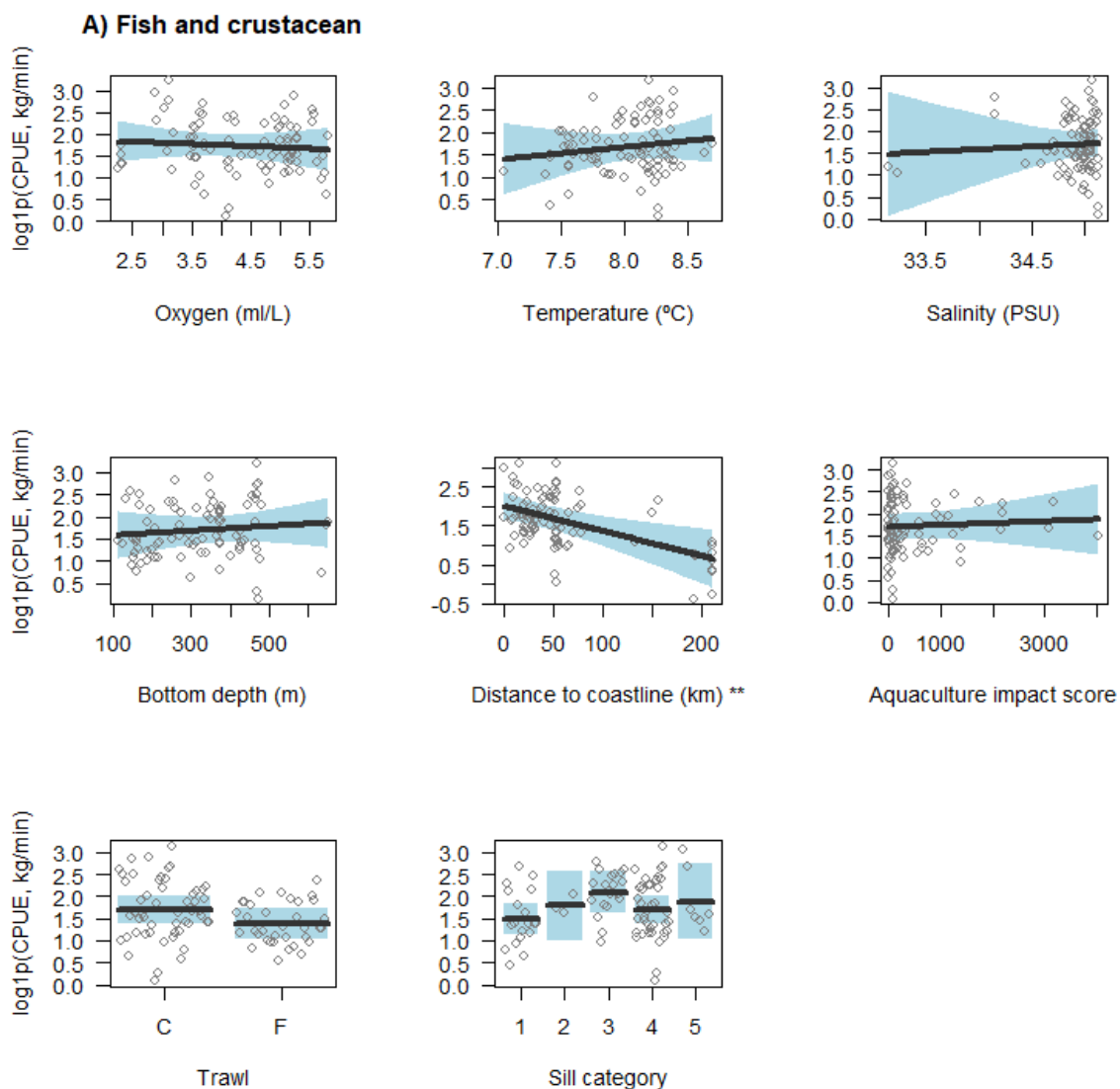


Figure 3.7: Relationships between log-transformed fish and crustacean CPUE (catches in kg per minute) and the environmental variables oxygen, temperature, salinity, bottom depth, distance to coastline, aquaculture impact score, trawl, and sill depth category. Trawl gear annotated as C refers to Campelen 1800 trawl, whereas F refers to Flekkerøy-trawl. Sill depth categories ranges from coastal stations with no sill (1), sills between 300-250 m depth (2), 250-150 m depth (3), 150-50 m depth (4) and the shallowest sills at less than 50 m depth (5). The 95 % confidence intervals are shaded in blue

with the mean estimate as black line. Significance codes for the p-values are given next to the variable label (0 ‘****’ 0.001 ‘***’ 0.01 ‘*’ 0.05), in this case only applicable for distance to the coastline.

For *P. periphylla* CPUE, temperature ($p < 0.001$), sill category 3 ($p = 0.03$) and trawl type ($p = 0.04$) were statistically significant variables (Figure 3.8). The CPUE decreased with increasing temperature. Stations with sill category 3 (150 to 250 m deep sills) had lower CPUE than the other sill categories, and stations that utilized the Flekkerøy-trawl had higher CPUE. Salinity ($p = 0.06$) and aquaculture impact score ($p = 0.09$) showed marginally significant trends, these were however mostly driven by a few observations at the low and high extremes of both variables, respectively.

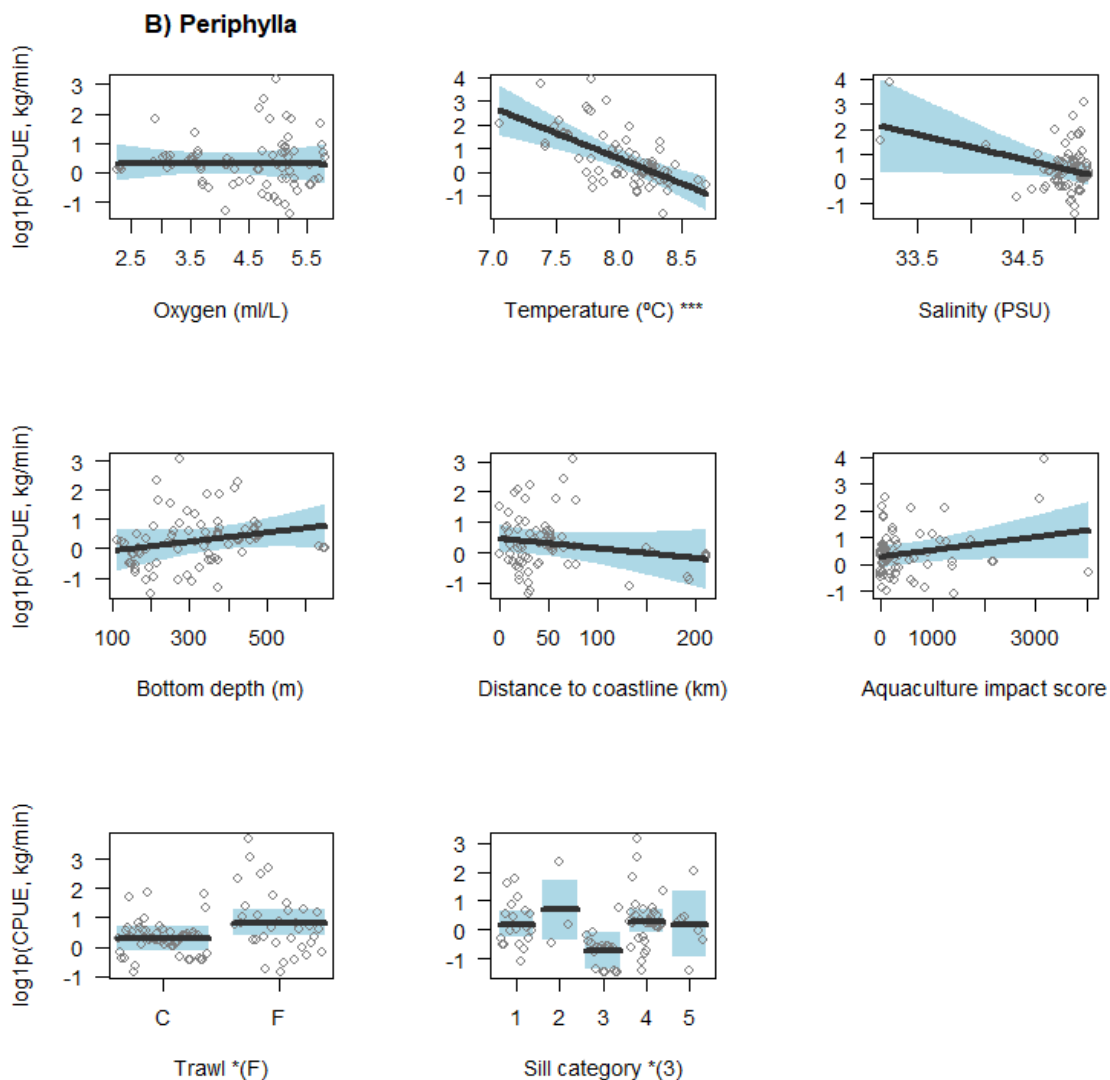


Figure 3.8: Relationships between log-transformed *P. periphylla* CPUE (catches in kg per minute) and the environmental variables oxygen, temperature, salinity, bottom depth, distance to coastline, aquaculture impact score, trawl, and sill depth category. Trawl gear annotated as C refers to Campelen

1800 trawl, whereas F refers to Flekkerøy-trawl. Sill depth categories ranges from coastal stations with no sill (1), sills between 300-250 m depth (2), 250-150 m depth (3), 150-50 m depth (4) and the shallowest sills at less than 50 m depth (5). The 95 % confidence intervals are shaded in blue with the mean estimate as black line. Significance codes for the p-values are given next to the variable label (0 '***' 0.001 '**' 0.01 '*' 0.05).

3.2.2 | Cluster and Multivariate Community Analysis

Hierarchical clustering by Ward's method identified four clusters in the data (Figure 3.8).

Cluster 1 stations (pink) are mainly in the Sognefjord and Førdefjord area (61 – 61.5 ° N), but there are also a few stations outside Bømlafjord as well as one inside Kvinnheradsfjord.

Cluster 2 stations (green) are mainly coastal stations all along the Study area and is the only cluster extending north of Førdefjord. Cluster 3 stations (yellow) are only located inside

Lustrafjord, Masfjord and Sørfjord. Cluster 4 stations

(blue) are in the Skåneviksfjord, Lurefjord and

Mangerfjord, as well as some coastal stations up to the inlet of Vilnesfjord.

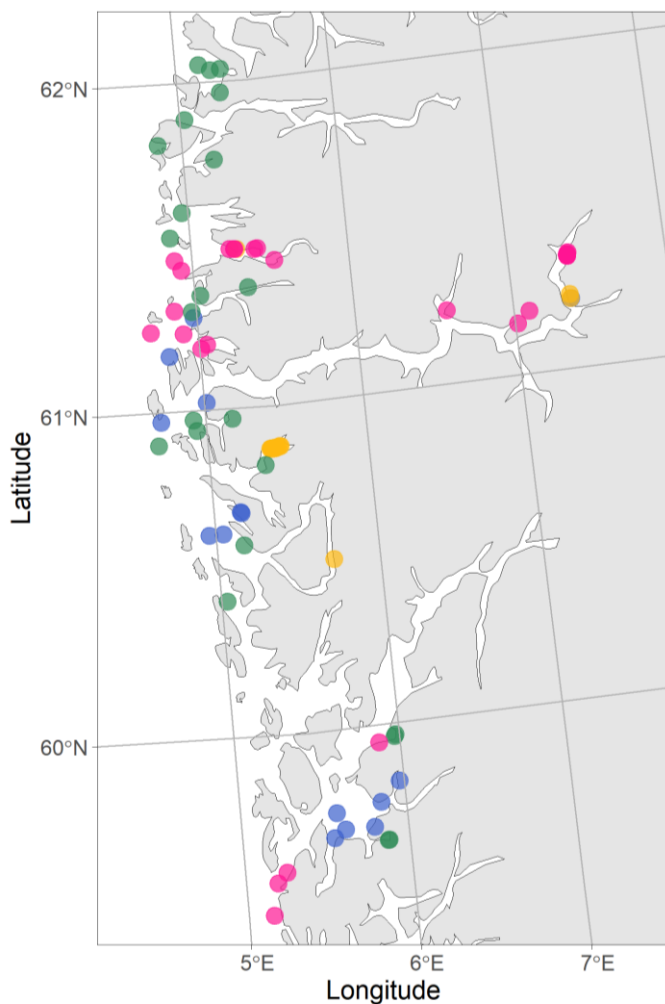
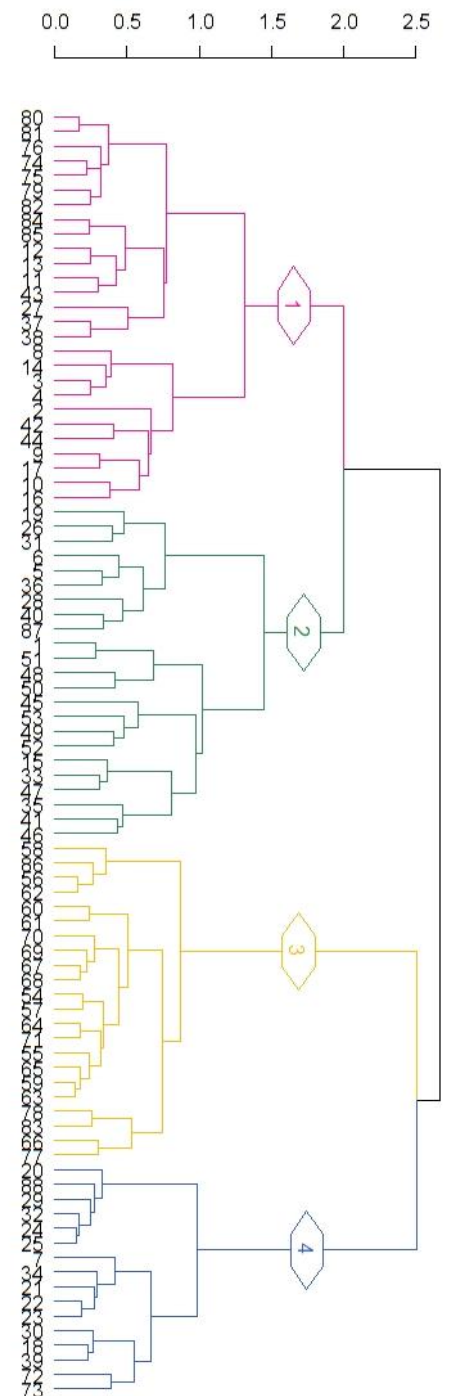


Figure 3.9.: Hierarchical clustering by Ward's method, containing cluster 1 (pink), cluster 2 (green), cluster 3 (yellow), and cluster 4 (blue) with station IDs and positions on map.



The diversity is decreasing from cluster 1 to cluster 4 (Table 3.2). The average CPUE is about the same for cluster 1 and 2 (~9 kg/min), followed by cluster 3 with a bit higher CPUE (14.3 kg/min). Cluster 4 has over 10 times larger CPUE than cluster 1 and 2 with 104 kg/min. Cluster 1 consists mostly of stations with intermediate depth in fjords (ranging 130 to 377 m, average 311 m). Cluster 2 mostly has coastal stations at shallower depth (ranging 113 to 298 m, average 189 m). Cluster 3 has the deepest stations in the fjords (ranging 340 to 651 m, average 462 m). Cluster 4 also consists of mainly deep-sea stations in the fjords, but with a bit lower average than cluster 3 (ranging 216 to 635 m, average 357 m). The most abundant species are rabbit fish (*Chimaera monstrosa*, 22%) in cluster 1, velvet-belly lanternshark (*Etmopterus spinax*, 13%) in cluster 2, roundnose grenadier (*Coryphaenoides rupestris*, 58%) in cluster 3, and *P. periphylla* (75%) in cluster 4. The IndVal analysis suggests that cluster 1 has six key species, cluster 2 has 11, cluster 3 has four and cluster 4 has only one key species. The species/taxa with the highest IndVal score for each cluster are shrimp spp. in cluster 1 (IndVal = 0.58, p = 0.027), Mueller’s pearlside in cluster 2 (IndVal = 0.63, p = 0.003), roundnose grenadier in cluster 3 (IndVal = 0.89, p = 0.001), and *P. periphylla* in cluster 4 (IndVal = 0.99, p = 0.001) (Table 3.2).

Table 3.2: Cluster characteristics with mean Shannon-Wiener diversity index (*H*), average CPUE (catch per minute, kg/min), depth range and average, most abundant species in average per trawl (%), and key species determined from indicator species analysis (IndVal).

	Cluster 1	Cluster 2	Cluster 3	Cluster 4
Average <i>H</i>	1.91	1.85	1.26	0.87
Average CPUE (kg/min)	9.1	8.9	14.3	104.0
Bottom depth (m)				
Range:	130-377	113-298	340-651	216-635
Average:	311	189	462	357

Most abundant species in average per trawl (%)	<p>1. <i>Chimaera monstrosa</i> (22%) 2. <i>Argentina silus</i> (11%) 3. <i>Etmopterus spinax</i> (10%) 4. <i>Galeus melastomus</i> (9%) 5. <i>Squalus acanthias</i> (9%)</p>			<p>1. <i>Etmopterus spinax</i> (13%) 2. <i>Pollachius virens</i> (12%) 3. <i>Benthosema glaciale</i> (9%) 4. <i>Pollachius pollachius</i> (7%) 5. <i>P. periphylla</i> (7%)</p>			<p>1. <i>Coryphaenoides rupestris</i> (58%) 2. <i>Chimaera monstrosa</i> (10%) 3. <i>Galeus melastomus</i> (8%) 4. <i>P. periphylla</i> (5%) 5. <i>Molva dypterygia</i> (4%)</p>			<p>1. <i>P. periphylla</i> (75%) 2. <i>Chimaera monstrosa</i> (5%) 3. <i>Micromesistius poutassou</i> (5%) 4. <i>Coryphaenoides rupestris</i> (3%) 5. <i>Benthosema glaciale</i> (3%)</p>		
IndVal	Species / taxa	Ind.v	p									
Shrimp spp.	0.58	0.027	<i>Mauroliticus Muelleri</i>	0.63	0.003	<i>Coryphaenoides rupestris</i>	0.89	0.001	<i>P. periphylla</i>	0.99	0.001	
<i>Argentina silus</i>	0.46	0.014	<i>Pollachius virens</i>	0.62	0.001	<i>Galeus melastomus</i>	0.54	0.001				
<i>Chimaeara monstrosa</i>	0.45	0.014	Krill	0.61	0.002	<i>Myxine glutinosa</i>	0.42	0.001				
<i>Squalus acanthias</i>	0.35	0.010	<i>Trisopterus esmarkii</i>	0.58	0.001	<i>Molva dypterygia</i>	0.38	0.002				
Jellyfish spp.	0.22	0.007	Pelagic shrimp spp.	0.46	0.008							
<i>Pomatoschistus norvegicus</i>	0.21	0.037	<i>Merluccius merluccius</i>	0.40	0.002							
			Galatheidae	0.40	0.044							
			<i>Pollachius pollachius</i>	0.35	0.001							
			Cephalopoda	0.34	0.002							
			<i>Argentina sphyraea</i>	0.25	0.011							
			<i>Cyclopterus lumpus</i>	0.22	0.010							

Cluster and selected species dissimilarities are presented on a non-metric multidimensional scaling plot (NMDS-plot) (Figure 3.9). The NMDS confirms the key species (IndVal) in cluster 3 (*C. rupestris*, *M. glutinosa*, *M. dypterygia* and *G. melastomus*) and 4 (*P. periphylla*). Some of the key species for cluster 1 are also located in close proximity to cluster 1 stations in the NMDS (Shrimp spp., *S. acanthias*, *C. monstrosa*). Not all key species for cluster 2 are shown on the NMDS plot, but there are clear closeness between some of the key species and cluster 2 (*P. virens*, Cephalopoda). Other species are located intermediate between stations from cluster 1, 2 and 4; pelagic shrimp (*Pasiphaea* and *Eusergestes* spp.), *B. glaciale*, *M. muelleri*, *A. silus*, Galatheidae and *M. poutassou*.

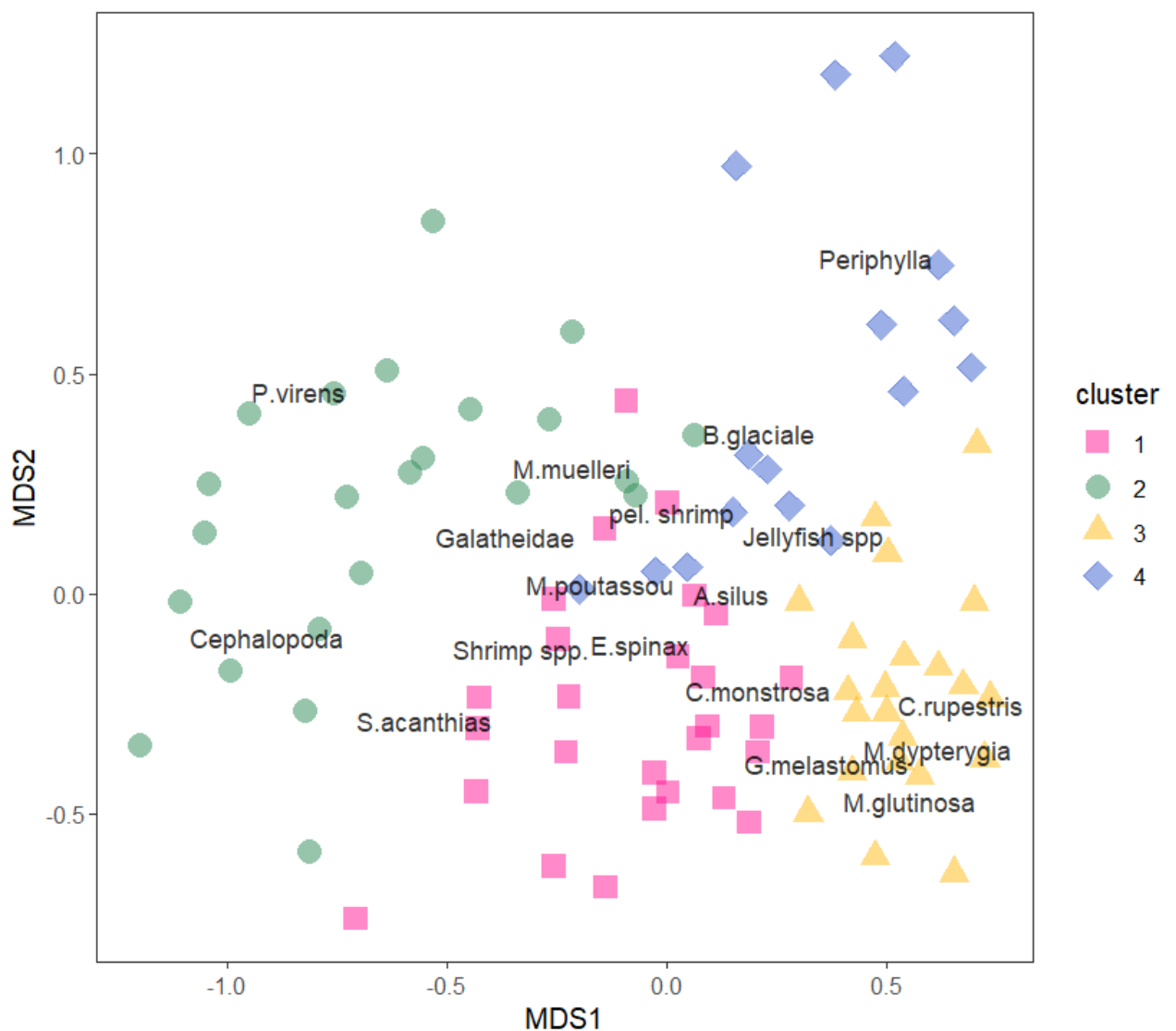


Figure 3.10: NMDS plot of stations colored by cluster, and selected species. 2D stress = 0.2028.

Bottom depth ($p = 0.001$), salinity ($p = 0.001$), and temperature ($p = 0.001$) had highest significance when fitting the predictor variables to the NMDS ordination, followed by oxygen ($p = 0.004$) and distance to the coastline ($p = 0.013$). Aquaculture impact score had no significance ($p = 0.798$). When plotting the environmental fits, bottom depth and oxygen display an inverse relationship. Bottom depth has the longest vector with deeper stations related to cluster 3, and shallower stations related to cluster 2 (Figure 3.11). Higher temperatures are related to cluster 1 and 2, and lower temperatures to cluster 3 and 4. Cluster 1 correlates with higher salinity values (Figure 3.11). Well-oxygenated stations are mostly located in cluster 2, with lower oxygen levels stations from cluster 3 (Figure 3.11). Distance to the coastline is longest for cluster 1 and 3 (Figure 3.11).

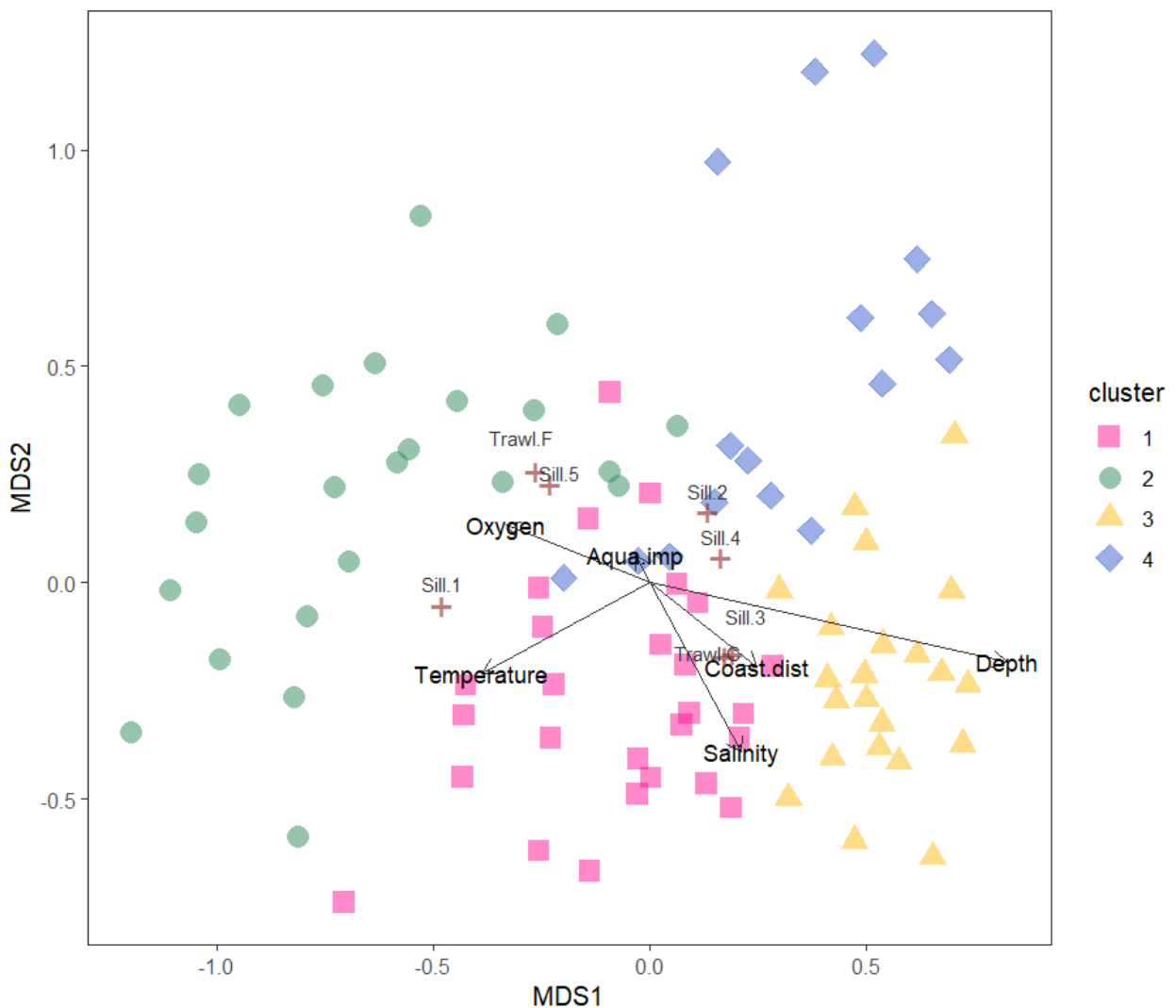


Figure 3.11: NMDS plot of stations colored and shaped by cluster, with fitted environmental variables as vectors, and trawl type and sill categories as factors (brown crosses). Trawl F refers to Flekkerøy-trawl, and Trawl C refers to Campelen 1800 trawl (overlap with distance to coastline in the plot). 2D stress = 0.2028.

4 | Discussion

This study aimed to identify environmental drivers of deep-sea community structures in Western Norwegian fjords, with a particular focus on fish and crustacean species composition, catch rates (CPUE) and diversity, as well as *P. periphylla* distribution and catch rate. The results show that diversity (H) is decreasing with bottom depth and is highest for stations located in fjords with intermediately deep sills (150 to 250 m). Environmental variables explaining fish and crustacean CPUEs differ from those explaining *P. periphylla* CPUEs: fish and crustacean CPUEs depend on distance to coastline, where CPUE decreased with distance, while CPUEs of *P. periphylla* were linked to temperature, with higher CPUEs at lower temperatures. *P. periphylla* CPUEs were also significantly lower for stations located inside intermediately deep sills (150 to 250 m). Four community clusters were identified amongst the 88 bottom trawl stations, and these differed in average diversity and key species. The identified clusters consisted of 1) fjord stations at intermediate depths, 2) mostly coastal stations at shallower depths, 3) deeper fjord stations, and 4) both coastal and fjord stations with high prevalence of *P. periphylla*.

4.1 | Catches, Diversity and Environmental Variables

From the 88 bottom trawl stations, 67 different species or taxonomic groups were identified, of which 53 were fish species. The catch rates (CPUE) of fish and crustaceans were evenly distributed in the study area. *P. periphylla* however, had a few very large CPUEs in Lurefjord, Skåneviksfjord and Matersfjord. Due to these large catches, *P. periphylla* were clearly the dominating species in total CPUE across all stations (65%). *P. periphylla* were also dominating in average CPUE per trawl (18%). Following *P. periphylla*, the four most common species in average CPUE per trawl were the roundnose grenadier (16%) and three chondrichthyans, the rabbit fish (11%), velvet-belly lanternshark (8%), and blackmouth catshark (5%).

Significant environmental variables were different for fish and crustacean CPUEs compared to *P. periphylla* CPUE. The only statistically significant variable for fish and crustacean CPUE was distance to the coastline, where CPUE decreased with distance. The stations located in the inner fjord arms of Sognefjord (Fjærlandsfjord, Sogndalsfjord and Lustrafjord) had the longest distances and lowest CPUEs. These fjord systems are restricted by multiple sills in direction to the coastline, which may reduce the level of advection of zooplankton

needed for new production in these ecosystems. Note that oxygen did not affect CPUEs, implying that the fjord arms have been well-ventilated during the time of sampling. For *P. periphylla*, CPUE decreased with increasing temperature. *P. periphylla* CPUEs were also significantly lower for stations located in basins constricted by 150 to 250 m deep sills (sill category 3). This may be caused by higher advection rates out of the fjord in the intermediate layer of fjords with deep sills, giving lower retention of *P. periphylla* in the fjord basins. However, the fjord stations restricted by the shallowest sills (<50 m) did not show significantly higher CPUEs of *P. periphylla*. There were indications that aquaculture impact score might be relevant for *P. periphylla* CPUE, but the effect was only marginally significant. Oxygen was also non-significant in the same model, which indicates that there was no significant deoxygenation caused by nutrient input from aquaculture sites.

Diversity (H) was significantly decreasing with bottom depth and highest for stations located inside 150 to 250 m deep sills (category 3). Coastal stations and the stations within the shallowest sills (<50 m) showed about the same diversity. Fjords with intermediately deep sills may act as a good middle ground with good ventilation from the NAC, good advection of organisms including zooplankton for new production, but with some retention needed for species settlement, and spawning- and nursery- grounds. Oxygen had no effect on diversity, but no true hypoxic values (0-2 ml/L) were measured (lowest was 2.25 ml/L). The regression model does however show a weak positive correlation between diversity and oxygen level. The station with the highest Shannon-Wiener diversity was located in Førdefjord, and was located inside the area designated for mine tailings of 5 million tonnes yearly (Skei *et al.*, 2019). The station with the third highest diversity score was also in Førdefjord. The stations with the lowest diversity, in Lurefjord and Skåneviksfjord, also had the highest prevalences of *P. periphylla* (Fig 3.4; Fig 3.1).

Fjords communities in fjords with 150-250 m deep sills had significantly higher diversity, and the CPUEs of *P. periphylla* were significantly lower within the same sill depths. Fjord communities with high abundances of *P. periphylla* show clear tendencies towards lower diversity, and these results suggest that sill depths might be a driver behind this trend. The sill depth category effect could also be correlated with other unobserved processes that can cause variation in diversity of these fjords. Coastal water darkening driven by increased coastal run-offs with lower salinity and dissolved oxygen, may favor tactile species such as *P. periphylla* (Aksnes *et al.*, 2009). This can cause mesopelagic regime shifts where other species are suppressed (Aksnes *et al.*, 2009). Fjords with shallow sills are more likely to have lower

salinity due to poor ventilation from the more saline NAC, whereas fjords with deep sills will have better ventilation and higher salinity levels. Salinity was, however, not significant for either diversity or *P. periphylla* CPUE in this study, which might suggest that ventilation from the NAC is not the only main driver of diversity or *P. periphylla* abundance. One other possible explanation to the sill depth significance might be that *P. periphylla* have low retention in fjords with sills between 150-250 m and is transported out of the fjord with the compensation current. The results underline that explaining diversity and species distribution can be complex, as often a multitude of interacting environmental variables shape the observed species communities.

The environmental variables oxygen, temperature and salinity provide a snapshot of the environmental conditions at the time of the surveys, but species communities will likely be shaped by environmental conditions over a longer period of time. The species responses to these variables might also be non-linear with threshold values for their tolerances, and the observed environmental ranges in this study might be too narrow to witness these tipping-points, leaving out possible significant effects on community composition. As mentioned, no true hypoxic values were measured in this study. The results from IMR's CoastRisk cruise with extensive hydrological sampling in February 2022 showed no hypoxic conditions in the West-Norwegian fjords, which indicates that there might have been basin water renewals in many of these fjords sometime during spring or summer 2021 (Søvik *et al.*, 2023). Most of the stations in this study (60%) were sampled after this renewal event, in November 2021, February 2022, and May 2022. The observed community densities and diversities, however, have been likely shaped by environmental conditions prior to the suggested renewal event, including the mass occurrences of *P. periphylla*.

4.2 | Benthopelagic and Demersal Fjord Communities

Four community clusters were identified from the catch data, which were further investigated with IndVal analysis to determine key species, and NMDS ordination with plotted species and environmental variables. The cluster distributions indicate that there is some community structure differentiation between coastal and fjord stations, and between shallower and deeper fjord stations. In addition to this, stations with high abundances of *P. periphylla* make up a community cluster of their own. The shallower fjord communities had the highest average diversity, followed by coastal communities, deeper fjord communities and lastly the *P.*

periphylla dominated communities. The shallower fjord communities also had higher similarity with the coastal communities than the deeper fjord communities. Oxygen and depth were inversely related in the NMDS plot, where oxygen was most related to the coastal stations and depth most related to the deeper fjord stations. The deeper fjord stations were in the inner parts of multibasin fjords, which may also explain the inverse relationship to oxygen. A study in Sognefjord found evidence of lower diversity with bottom depth and inward the fjord (Buhl-Mortensen *et al.*, 2020), which coincides with these findings on the deeper fjord communities. The following paragraphs describe each community cluster in order, with key species descriptions from the book “Marine fish and invertebrates of Northern Europe” (Moen and Svensen, 2004).

The highest diversity (cluster 1, $\bar{H} = 1.91$) was mainly linked to shallower fjord stations (130 to 377 m) and included six key species or taxa, where shrimp species was most important. Shrimps can be considered as keystone species for deep-sea communities, as they are scavengers recycling nutrients and constitute important prey for other predators. The second key species, the greater Argentine (*Argentina silus*), is a deep-sea species common below 300 m depth that can live to 40 years of age. The third key species, the rabbit fish (*Chimaera monstrosa*), is a common soft-bottom chondrichthyan, living between 50 to 1000 m depth. They have internal fertilization and are also common on shrimp beds. Spiny dogfish (*Squalus acanthias*) was also a key species, a shark that can live to 25 years, have late maturation, and give birth to living fry. The last key species, the Norway goby (*Pomatoschistus norvegicus*) can be found on soft bottom between 30 and 300 m depth. Many of these fish species are long-lived with complex reproduction strategies, which can make them vulnerable to anthropogenic impacts. Amongst the environmental variables included in this study, higher temperature and salinity were mostly related to this cluster. Changes towards lower basin temperatures and salinity could therefore negatively impact the community structure of this cluster.

Coastal stations (113 to 298 m) were associated with the second highest diversity (cluster 2, $\bar{H} = 1.85$). Most of the 11 key species in this cluster were mesopelagic species and active predators. The main species was mueller’s pearlside (*Maurolicus muelleri*), a common mesopelagic fish in coastal areas and Norwegian fjords. This species is of great ecological importance, as an interconnection between the primary producers in the euphotic zone, and fish predators in the deep-sea. Other mesopelagic key species in this cluster were krill and pelagic shrimp (*Eusergestes arctius* and *Pasiphaea* spp.), also of importance as

interconnections in the food web. Other invertebrate key species were squat lobsters (Galatheididae) and cephalopods. There were four gadoid predators in this cluster: saithe (*Pollachius virens*), pollock (*Pollachius pollachius*), the European hake (*Merluccius merluccius*), and Norway pout (*Trisopterus esmarkii*). The last two key fish species were lesser silver smelt (*Argentina sphyraea*), a mostly pelagic fish that occurs shallower than its relative greater Argentine (in cluster 1), and lump sucker (*Cyclopterus lumpus*), which can be found swimming in the water masses during winter. All of these species are mostly related to coastal communities with links to higher oxygen levels, shallower depth, and shorter distances to the coastline compared to fjord communities. Lower oxygen levels could influence this community negatively, but that is rather unlikely as most of the stations were coastal.

The two clusters with lowest diversity were linked to deep fjord stations (340 to 651 m and 216 to 635 m, respectively), one consisting of deep-sea fish species such as roundnose grenadier (*Coryphaenoides rupestris*) and elasmobranchs (cluster 3), and the other dominated by *P. periphylla* (cluster 4). The species in cluster 3 ($\bar{H} = 1.26$) have in common that they are long lived (e.g. roundnose grenadier up to 60-70 years) with more complex reproduction strategies (e.g. internal fertilization of elasmobranchs) and can be found in very deep areas (e.g. Atlantic hagfish (*Myxine glutinosa*) is a soft-bottom scavenger that can live down to 1300 m). Among the elasmobranchs, blackmouth catshark (*Galeus melastomus*) was particularly common, and the cluster also included the blue ling (*Molva dypterygia*), an endangered gadoid species that is most common between 350 to 500 m depth and can live for at least 30 years. This cluster was mostly related to lower oxygen levels and deeper basins located further from the coast, which may also be restricted by multiple sills. This may indicate that these communities are better adapted to lower oxygen levels. All of the stations from this cluster were located in Masfjord, Sørfjord or Lustrafjord. Cluster 4 with lowest diversity ($\bar{H} = 0.87$), on the other hand, was mostly related to lower temperatures, which also was a significant predictor for *P. periphylla* CPUE.

Fjord communities, both the shallower and the deeper communities, have key species that are long-lived and have complex reproduction systems. These are often vulnerable to anthropogenic impacts due to their life history traits. Climate change impacts are also higher in these communities due to less frequent fjord basin water renewals. However, the communities found in the deeper basins may have a good tolerance to lower oxygen levels. Gadoid species are more commonly found in coastal communities that also are dominated by

mesopelagic species, rather than in fjord communities. Cluster 1 with the highest diversity was linked to higher temperatures, whereas cluster 4 with the lowest diversity and *P. periphylla* domination was linked to lower temperatures. This may indicate that temperature drives differences between fjord stations containing high or low abundances of *P. periphylla*.

A fish species record list from 1956-1963 in Hardangerfjord indicates that there might have been a decline in total number of fish species in West-Norwegian fjords to present day (Tambs-Lyche, 1987). A total of 126 fish species were registered with the use of different fishing equipment, sampled throughout the seasons. In comparison, the bottom trawl data in this study consisted of 53 fish species across all 88 trawl stations. Registered deep-water fish fauna from the 1950 and 1960s consisted of species also common today (for instance *Chimaera monstrosa*, *Etmopterus spinax*, *Galeus melastomas*), but in addition included several other species that in this study were found in low numbers or not at all, such as Atlantic cod (*Gadus morhua*) and other gadoid species. Stations trawled in the same area in 2021 and 2022 have communities linked to cluster 1 (3 stations), cluster 2 (4 stations) and cluster 4 (6 stations) – in which the latter had high abundances of *P. periphylla* (catch average of 75%). These results suggest that a mesopelagic regime shift might have happened in this area, in favor of the tactile species *P. periphylla*.

4.3 | Limitations

The study is limited by the data available and the lack of a time series that is consistent in space. Datasets prior to 2021 are mainly limited to Masfjord and Lustrafjord, whereas the surveys in 2021 and 2022 covered a much larger area but consist of only two years. It is therefore not possible to infer on changes in fish communities over time, or how environmental variation over time (e.g., years with lower oxygen due to a lack of water exchange in some fjords) might have affected the results. Further inconsistencies may be introduced by the use of different trawls that have great difference in trawl openings, especially the vertical trawl opening. The Campelen 1800 has a vertical trawl opening between 4.0 to 4.6 m, whereas the Flekkerøy-trawl has a vertical trawl opening between 14 and 20 m. This means that the Flekkerøy potentially and likely catch species higher in the water column than the Campelen 1800. However, they showed similar catch characteristics in terms of diversity and fish and crustacean CPUEs. Trawl type only became significant for *P. periphylla* CPUE, where the Flekkerøy had higher CPUEs. This can also be caused by

locations visited during the surveys rather than the catchability of *P. periphylla*, or a combination of these two.

Limitations on where bottom trawling was possible might also have impacted the species' catch distributions. In addition to omitting by default areas that were not accessible to bottom trawling (such as rocky or uneven sea floor), difficult weather conditions, power cables, aquaculture sites or fishing gear like lobster traps, prevented trawling at many of the planned trawling sites during the 2021 and 2022 CoastRisk surveys. Most of the selected trawling sites were placed on old commercial shrimp fields, but trawling was possible on only 51% of these and only 38.5% contained the targeted Northern shrimp (*Pandalus borealis*) in the catches (Søvik *et al.*, 2023). This was especially an issue south of Bergen where a very active *Nephrops* fishery occupies large areas with their traps. Due to these restrictions, survey coverage was patchy and not fully randomized. Thus, important shrimp grounds with associated communities may not have been included in the data for this study. In fjords, aquaculture sites often occupy areas that have higher water exchange. They may have moorings that can extend several hundred meters from the fish cages, making it impossible to trawl within these areas. That also leaves out possibly important trawling sites for benthopelagic and demersal fjord communities with a higher water exchange, as well as communities more directly affected by aquaculture impact.

Deep sea communities might be structured by other factors not accounted for in this study. Even though there were no hypoxic conditions measured at bottom trawl stations, former hypoxic conditions may have impacted the community structures as they were during the time of trawling. Historical environmental conditions and records of hypoxia in the fjords were not included as an impact factor in this study. The effect of fishing on the communities was not included either but might have been an important variable for the deep sea community structure over longer periods of time. For instance, bottom trawling in the fjords might have contributed to benthic habitat degradation and unsustainable fishing of non-target species (Clark *et al.*, 2016). The capacity of deep-sea ecosystems to recover is generally low, as many deep-sea species are long-lived, grow slow and have late maturation (Clark *et al.*, 2016).

Seasonality and species' phenology will also affect the fjord ecosystems, including benthopelagic and demersal species compositions and densities. Access to feed will vary with season and primary production, functioning as bottom-up control for fjord ecosystems. The

spring bloom generally starts in February to March in West-Norwegian fjords, and zooplankton densities will follow the phytoplankton bloom and provide energy and nutrients for mesopelagic fish species. Many fish species have annual spawning and feeding migration patterns affecting their spatiotemporal distributions. Spawning time and duration vary between species, but most species in Norwegian coastal areas and fjords spawn during spring. Gadoid species such as saithe and cod are highly migratory species that spawn during early spring (Jørgensen *et al.*, 2008; Homrum *et al.*, 2013). The CoastRisk survey also found spawning blue ling in Førdefjord in February 2022 (Søvik *et al.*, 2023). Other migratory benthopelagic species have also been found to spawn in Norwegian fjords: one tag-and-release study found spawning female lumpfish (*Cyclopterus lumpus*) in July in Øksfjord (Northern Norway) who all left the fjord within one week of spawning (Mitamura *et al.*, 2012). Another tag-and-release study found a few spawning Atlantic halibut (*Hippoglossus hippoglossus*) in Sognefjord in March (Seitz *et al.*, 2014). The intra-year resolution of the dataset is strongly limited, as most stations in this study are from late fall or the winter season, except from three stations that are from May 2022. The different sampling months might have affected the results of this study. However, 52 of 88 stations are sampled in November and February and might have been comparable in terms of season.

Sill depth category was assigned as discrete categorical variable to each station to also include coastal stations with no sill, but community responses are likely gradual to sill depths. There also seems to be large variation in some of the diversity and CPUE responses to the sill depth categories, which suggest that some of the variation is linked to other processes than sill depth. Further, the coverage of different sill depths was not balanced, as only three stations were assigned to sill category 2 (250-300 m deep sills, with the inlet of Hjeltefjord as the shallowest sill (Appendix Table A.2)). This is a very small sample size for the sill category, which likely reduces the statistical power of the regression analyses.

The aquaculture impact score used in this study is not present in other existing literature. The score for each trawl station was found by dividing the biomass capacity at the closest aquaculture site by the squared distance to this site. Where there were several sites within a 5 km radius of the trawl station, the impact scores of all sites were summed. The distance was squared to give larger weight (higher score) to smaller distances but might have been overestimated at the smallest distances. The biomass capacity is the maximum allowance in tonnes for the aquaculture site and may not have been equal to the actual biomass at the site during the survey periods. Moreover, the sites may also have been empty in between

production periods (one production cycle normally lasts 14 – 22 months, followed by a few months fallow). Deep-sea fish and crustacean communities will however likely be more reflected by impacts over longer periods of time, rather than the shorter windows of the production cycle. More importantly, the impact score does not consider the solubility of the waste, ocean currents, or topography around the study sites. These factors are considered important for estimating and quantifying environmental impact from aquaculture sites (Grefsrud *et al.*, 2022). Future research on interactions between aquaculture and species communities should attempt to include more direct measurements of aquaculture effluents to assess potential impacts on surrounding ecosystems.

4.4 | Future Aspects

Two out of the three highest diversity scores in this study were from Førdefjord, and all seven stations from there belonged to cluster 1 with the highest average diversity and species vulnerable to anthropogenic impact. During the 2022 CoastRisk survey, several ecologically important species were found in Førdefjord. This included the endangered shark spiny dogfish (*Squalus acanthias*), the critically endangered endemic bamboo coral (*Isidella lofotensis*), and the critically endangered blue ling (*Molva dypterygia*) (Søvik *et al.*, 2023). Out of the four specimens of blue ling found in Førdefjord, one was non-mature, two were maturing, and one was spawning. This indicates that Førdefjord may have spawning and nursery grounds for blue ling, which has not been scientifically documented before along the Norwegian coast (Søvik *et al.*, 2023). High diversity fjord communities here might also be linked to cold water coral reefs. In addition, the roundnose grenadier in Førdefjord likely has its own genetic subpopulation that differs from Trondheimsleia, Skagerrak and Korsfjorden (Søvik *et al.*, 2023). This coincides with other studies that also have found genetic subpopulations of roundnose grenadier in Norwegian fjords (Delaval *et al.*, 2018). These results indicate that there are ecologically valuable and vulnerable communities in Førdefjord, which should be further investigated considering the planned disposal of 140 million m³ mine tailings in the fjord (Skei *et al.*, 2019) that may impact them negatively. Northern shrimp and common demersal predators, notably Atlantic cod, were either absent or only found in very low densities on former shrimp fishing grounds within fjords, raising questions about the status of the coastal shrimp stock in this region and changes that may have occurred. The lack of monitoring time series from western Norway prevents a

comparison of the findings from this study with past densities of shrimp and gadoids. However, landings data indicates that former abundances on surveyed shrimp grounds were sufficient to sustain commercial fishing activities during the second half of the last century (Melaa *et al.*, 2022). The findings here may therefore indicate the disappearance of previously relevant fisheries resources as result of environmental change and lack of regulation, underlining the need for a more consistent monitoring and management of coastal resources.

UN's sustainable development goal 14 emphasizes the importance of conserving marine ecosystems and sustainable development of marine resource utilization, especially in relation to climate change impacts. A modelling study showed trends towards more infrequent fjord basin water renewal for Norwegian fjords, when comparing the time period 1990-2020 to 1960-1990 (Johnsen *et al.*, 2021). This may have had great implications on fjord communities, where deoxygenation is of special concern. The results in this study might indicate that shallower fjord communities might be more susceptible to hypoxic conditions than deeper fjord communities. Communities in deep multibasin fjords might also have higher tolerance and adaptations to lower oxygen levels. Masfjord has been experiencing dissolved oxygen decline over a decade due to reduced basin water renewal (Aksnes *et al.*, 2019), and a recent circulation modelling study found that adding a continuous freshwater injection to the deep sea might mitigate the deoxygenation (Aksnes, Darelius and Berntsen, 2023). Masfjord is the only fjord with longer time series from this area, including hypoxia effects on mesopelagic communities. Regular monitoring on fjord basin water renewal and community responses should be implemented on a larger scale to comply with the goals of sustainable management of these ecosystems prone to deoxygenation.

5 | Conclusion

This study aimed to investigate how environmental variables shape deep-sea communities in West-Norwegian fjords, with a particular focus on fish and crustacean diversity and catches as well as *P. periphylla* distribution. Novel information on the benthopelagic community structures has been introduced in this analysis, as it has been a rather unexplored area of the fjord ecosystems. The results confirm the hypothesis on decreasing diversity (H) with bottom depth. As also hypothesized, CPUEs (catch per minute) of fish and crustaceans were linked to different environmental variables than CPUE of *P. periphylla*. Fish and crustacean CPUEs were found to decrease with distance to the coastline, this trend was however mainly driven by a few observations. There were large catches of *P. periphylla* in Lurefjord, Skåneviksfjord and Matersfjord, and *P. periphylla* CPUE was coinciding with lower temperatures. Sill depths were also significant for diversity and *P. periphylla* distributions, where diversity was highest in basins with 150-250 m deep sills and *P. periphylla* CPUEs were lowest for the same sill depths. This confirms the hypothesis on the significance of sill depth on community compositions.

Four community clusters were identified amongst the 88 bottom trawl stations. Bottom depth and geographic distribution had the strongest differentiation effects between these, which coincides with the hypothesis on their effect on community structure. The cluster with the highest diversity contained shallow fjord communities and was mostly related to higher temperatures and salinity. Coastal communities had the second highest diversity with oxygen as most explanatory variable. The deeper fjord communities had the second lowest diversity and was mostly related to bottom depth with inverse relationship to oxygen. The last cluster was dominated by *P. periphylla* and therefore the least diverse, mainly driven by lower temperatures. This, together with the fact that the cluster with the highest diversity was linked to higher temperatures, indicate that temperature might be an underlying driver behind high or low diversity communities.

In contradiction to some of the hypotheses, neither oxygen, salinity nor aquaculture impact were significant predictors for diversity or CPUEs. However, no stations had true hypoxic conditions and the range of observed salinity was limited. Community compositions and densities likely reflect environmental conditions over longer timeframes than snapshots in time, which might have affected the results of this study. Observed variations might also have been caused by other variables not included in this study.

The results in this study illustrate that deep-sea fjord community composition, diversity and density responses are complex, with a multitude of interacting environmental variables shaping the observed communities. There might be evidence of a decline in total number of fish species in West-Norwegian fjords compared to Hardangerfjord in the 1950-1960's, with a shift towards high abundances of *P. periphylla* in certain areas. Modelling studies show that there has been a trend towards more infrequent basin water renewals for the same time period, with possible deoxygenation effects. This amplifies the significance of long-term monitoring on a larger scale, to assess vulnerable deep-sea community responses to changing environments.

6 | References

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7 | Appendices

Appendix A - Catch and Environmental Data

Table A.1: Bottom trawl stations along the West Norwegian coast and fjords sampled from 2011 to 2022, including month, fjord, trawl gear, latitude and longitude for the start-position, bottom depth, fishing time, total catch per trawl in CPUE (kg/min), and number of species. Trawl gear annotated C refers to a Campelen 1800 bottom trawl, whereas F refers to a commercial Flekkerøy-trawl.

ID	Year	Month	Fjord/Coastal	Trawl gear	Lat.	Lon.	Bottom depth (m)	Fishing time (min)	Total catch (kg/min)	Number of species
1	2022	2	Kvinnheradsfjord	C	59.9665	5.9702	167	13	8.526	22
2	2022	2	Coastal	C	59.4598	5.1503	147	15	1.301	20
3	2022	2	Coastal	C	59.5563	5.1890	350	15	10.652	24
4	2022	2	Coastal	C	59.5872	5.2498	358	15	8.531	21
5	2022	2	Etnefjord	C	59.6557	5.8693	188	11	1.889	20
6	2022	2	Coastal	C	60.9087	4.6953	298	8	1.675	17
7	2022	2	Coastal	C	61.0290	5.0137	252	11	8.942	23
8	2022	2	Sogndalsfjord	C	61.2038	7.0962	260	16	9.669	20
9	2022	2	Sogndalsfjord	C	61.1702	7.0145	130	5	6.206	18
10	2022	2	Fjærlandsfjord	C	61.2352	6.5777	296	8	1.770	20
11	2022	2	Åfjord	C	61.2423	4.9052	325	15	2.572	18
12	2022	2	Førdefjord	C	61.4840	5.4203	330	18	5.359	22
13	2022	2	Førdefjord	C	61.4897	5.2452	377	15	9.913	24
14	2022	2	Coastal	C	61.4677	4.8887	271	15	3.432	21
15	2022	2	Nordgulen	C	61.7650	5.1987	124	12	5.047	18
16	2022	2	Coastal	C	61.3138	4.8603	209	15	2.011	24
17	2022	2	Coastal	C	61.2534	4.7010	342	15	6.763	19
18	2022	2	Coastal	C	61.1769	4.8062	346	3	26.709	14
19	2021	11	Etnefjord	F	59.6565	5.8758	188	15	4.095	15
20	2021	11	Bømlafjord	F	59.6995	5.7963	221	15	23.041	9
21	2021	11	Bømlafjord	F	59.7513	5.5767	352	16	12.147	16
22	2021	11	Bømlafjord	F	59.6768	5.5530	447	16	22.196	15
23	2021	11	Bømlafjord	F	59.6993	5.6217	375	15	20.036	13

24	2021	11	Matersfjord	F	59.8305	5.9715	275	15	137.465	10
25	2021	11	Skånevikfjord	F	59.7727	5.8498	216	16	25.738	9
26	2021	11	Kvinnheradsfjord	F	59.9712	5.9773	162	10	1.466	12
27	2021	11	Kvinnheradsfjord	F	59.9528	5.8740	214	10	1.662	14
28	2021	11	Hjeltefjord	F	60.4215	5.0357	256	11	11.372	15
29	2021	11	Hjeltefjord	F	60.6252	4.9607	418	10	53.129	13
30	2021	11	Hjeltefjord	F	60.6248	5.0462	352	8	9.443	13
31	2021	11	Radfjord	F	60.5870	5.1692	200	10	3.136	16
32	2021	11	Lurefjord	F	60.6848	5.1713	425	7	429.941	7
33	2021	11	Coastal	F	60.9462	4.9402	155	8	1.372	15
34	2021	11	Coastal	F	60.9792	4.7212	313	10	6.960	11
35	2021	11	Coastal	F	60.9778	4.9222	159	10	0.588	15
36	2021	11	Gulafjord	F	60.9733	5.1662	244	10	9.099	15
37	2021	11	Åfjord	F	61.1940	5.0098	375	10	3.343	16
38	2021	11	Åfjord	F	61.2040	5.0507	305	10	2.296	13
39	2021	11	Vilnesfjord	F	61.2902	4.9773	277	10	4.315	19
40	2021	11	Dalsfjord	F	61.3685	5.3392	259	11	7.863	17
41	2021	11	Vilnesfjord	F	61.3083	4.9693	154	10	1.624	19
42	2021	11	Coastal	F	61.4367	4.9268	273	10	2.918	16
43	2021	11	Førdefjord	F	61.4828	5.4043	316	10	8.713	22
44	2021	11	Førdefjord	F	61.4433	5.5222	174	10	1.191	16
45	2021	11	Coastal	F	61.5373	4.8722	158	10	2.196	17
46	2021	11	Coastal	F	61.8220	4.8447	166	10	2.066	19
47	2021	11	Nordfjord	F	61.8933	5.0310	187	10	1.866	19
48	2021	11	Coastal	F	62.0578	5.1522	168	10	6.365	19
49	2021	11	Coastal	F	61.9682	5.2762	196	10	6.549	16
50	2021	11	Coastal	F	62.0383	5.2242	146	10	9.678	15
51	2021	11	Coastal	F	62.0400	5.2908	113	10	2.435	19
52	2021	11	Coastal	F	61.6117	4.9625	153	10	2.223	13
53	2021	11	Vilnesfjord	F	61.3552	5.0330	206	10	3.533	17
54	2011	10	Masfjord	C	60.8727	5.3986	468	19	2.661	15
55	2011	10	Masfjord	C	60.8719	5.4019	467	16	3.338	14
56	2011	10	Masfjord	C	60.8725	5.4027	475	22	0.310	10
57	2011	10	Masfjord	C	60.8727	5.3972	467	16	5.979	13

58	2011	10	Masfjord	C	60.8727	5.3977	468	9	0.692	8
59	2011	10	Masfjord	C	60.8726	5.3935	464	14	10.861	9
60	2012	10	Masfjord	C	60.8718	5.3902	468	3	13.027	14
61	2012	10	Masfjord	C	60.8732	5.3968	482	2	9.407	13
62	2012	10	Masfjord	C	60.8723	5.3853	478	7	2.553	10
63	2013	11	Masfjord	C	60.8731	5.4099	457	16	11.352	12
64	2013	11	Masfjord	C	60.8736	5.4146	468	8	14.893	10
65	2014	10	Masfjord	C	60.8720	5.4100	472	7	15.970	15
66	2014	10	Masfjord	C	60.8723	5.4173	469	5	26.338	17
67	2015	9	Masfjord	C	60.8772	5.4466	400	29	2.523	10
68	2015	9	Masfjord	C	60.8773	5.4506	340	20	2.701	9
69	2015	9	Masfjord	C	60.8739	5.4220	430	17	3.814	9
70	2015	9	Masfjord	C	60.8749	5.4360	425	29	5.029	14
71	2015	9	Masfjord	C	60.8740	5.4264	425	22	3.109	9
72	2016	9	Lustrafjord	C	61.2257	7.3679	635	30	0.099	10
73	2016	9	Lustrafjord	C	61.3603	7.3782	373	28	0.106	10
74	2016	9	Lustrafjord	C	61.3559	7.3768	374	40	1.069	16
75	2016	9	Lustrafjord	C	61.3562	7.3772	373	26	2.147	20
76	2016	9	Lustrafjord	C	61.3589	7.3773	374	28	1.056	17
77	2016	9	Lustrafjord	C	61.2389	7.3615	651	41	2.257	9
78	2016	9	Lustrafjord	C	61.2267	7.3644	646	31	2.064	8
79	2016	9	Lustrafjord	C	61.3663	7.3823	372	20	2.853	22
80	2017	10	Lustrafjord	C	61.3595	7.3760	373	15	2.199	17
81	2017	10	Lustrafjord	C	61.3583	7.3750	373	15	3.007	19
82	2017	10	Lustrafjord	C	61.3620	7.3785	373	15	1.515	16
83	2018	10	Førdefjord	C	61.4877	5.2884	366	15	5.953	19
84	2018	10	Førdefjord	C	61.4880	5.2733	373	16	11.885	18
85	2018	10	Førdefjord	C	61.4881	5.2754	372	15	9.292	21
86	2022	5	Sørfjord	C	60.5190	5.7130	377	11	12.670	13
87	2022	5	Masfjord	C	60.8240	5.3460	294	2	7.075	14
88	2022	5	Lurefjord	C	60.6881	5.1654	438	6	51.415	11

Table A.2: Environmental variables and characteristics sampled for each trawl station. It includes the hydrological variables oxygen, temperature, and salinity at bottom depths, as well as the distance to the coastline (defined by geodetic line segments between the outer points of the coast, including islands and islets not covered by waves at low tide), distance to the shallowest sill west of the station, the shallowest sill depth, sill location, the sill depth category retrieved from sill depth (ranges from coastal stations with no sill (1), sills between 300-250 m depth, 250-150 m depth (3), 150-50 m depth (4) and the shallowest sills at less than 50 m depth (5)), distance to closest aquaculture site, and a calculated aquaculture impact score. The NAs in sill depth and distance are coastal trawl stations not restricted by any sills.

ID	Oxygen (ml/L)	Temp. (°C)	Salinity (PSU)	Bottom depth (m)	Distance coast (km)	Distance sill (km)	Sill depth (m)	Sill location	Sill cat.	Distance aqua.site (km)	Aquaculture impact score
1	5.56	8.13	34.87	167	76.6	10.8	120	Kvinnheradsfjord, Snilstveitøy	4	7	47.8
2	5.70	8.00	34.84	147	10.8	0	0	coastal	1	4	289.2
3	5.57	7.99	34.91	350	10	0	0	coastal	1	4.8	169.3
4	5.56	7.98	34.91	358	13.7	0	0	coastal	1	4.3	274.0
5	3.16	8.24	34.85	188	64.5	4.3	60	Etnefjord, Etnesundet	4	12	32.5
6	5.77	8.14	34.99	298	6.8	0	0	coastal	1	9.5	34.6
7	5.72	8.34	34.97	252	27	0	0	coastal	1	1.3	3081.6
8	2.88	8.40	34.16	260	156.5	7.7	30	Sogndalsfjord, Nornes-Fimreite	5	60	0.9
9	3.03	8.40	34.15	130	150	1.3	30	Sogndalsfjord, Nornes-Fimreite	5	55	1.0
10	4.94	7.74	34.97	296	132.3	98.3	200	Sognesjøen, Losna	3	38	2.2
11	5.34	7.84	34.98	325	20.1	3.6	130	Inlet Åfjord	4	4.3	253.1
12	5.12	7.98	35.01	330	47.2	14.6	210	Inlet Førdefjord, Skjeljevikneset	3	2.4	270.8
13	5.14	8.00	35.01	377	38	5	210	Inlet Førdefjord, Skjeljevikneset	3	2.55	1138.4
14	5.21	8.15	34.88	271	18.4	0	0	coastal	1	9.7	33.2
15	3.08	8.29	34.83	124	32	2.6	50	Nordgulen, Hesvikneset	5	7.8	89.7
16	5.75	8.46	34.95	209	20	0	0	coastal	1	5	93.6

17	5.80	8.37	34.97	342	9.9	0	0	coastal	1	3.8	108.0
18	5.23	7.76	35.05	346	16	0	0	coastal	1	9.6	42.3
19	3.20	8.23	34.88	188	64.9	4.6	60	Etnefjord, Etnesundet	4	12	32.5
20	4.85	7.78	35.03	221	57.6	24.2	150	Bømlafjord, Bømlafjordtunnelen	4	2.4	1231.5
21	5.17	7.51	35.06	352	41.2	8.5	150	Bømlafjord, Bømlafjordtunnelen	4	3.7	350.7
22	5.17	7.48	35.06	447	49.4	14.8	150	Bømlafjord, Bømlafjordtunnelen	4	1.8	1754.4
23	5.13	7.52	35.06	375	47.5	15.3	150	Bømlafjord, Bømlafjordtunnelen	4	2.4	1005.3
24	4.98	7.79	35.08	275	74.5	43	150	Bømlafjord, Bømlafjordtunnelen	4	0.7	3183.7
25	4.75	7.90	34.98	216	66.4	35.3	150	Bømlafjord, Bømlafjordtunnelen	4	7	63.7
26	4.52	8.14	34.84	162	77.4	11	120	Kvinnheradsfjord, Snilstveitøy	4	7	47.8
27	4.35	8.04	34.95	214	70.9	4.7	120	Kvinnheradsfjord, Snilstveitøy	4	13	23.0
28	4.91	7.96	34.88	256	42.2	24.3	200	Hjeltefjord, Alvøya- Skjelanger	3	2	1279.2
29	5.14	7.75	35.06	418	18.3	9.9	300	Inlet Hjeltefjord	2	2.5	579.2
30	5.29	7.78	35.04	352	23.1	10.4	300	Inlet Hjeltefjord	2	2.3	898.3
31	4.10	8.35	34.44	200	31.9	5.4	50	Radfjord	5	1.1	4036.3
32	4.67	7.38	33.23	425	30.8	11.2	30	Inlet Lurefjorden	5	18	11.2
33	4.69	8.39	34.77	155	22.4	0	0	coastal	1	5.2	115.4
34	5.19	8.07	35.07	313	10.3	0	0	coastal	1	2.6	230.8
35	4.80	8.25	34.88	159	20.8	0	0	coastal	1	2.5	1372.8
36	4.21	8.09	34.82	244	34	10.3	70	Gulafjord, Kjeøyna	4	3.4	269.9
37	5.20	7.79	35.00	375	29.3	11.1	130	Åfjord, Tollesundet	4	1.6	1406.3
38	5.13	7.80	34.99	305	29.7	12.4	130	Åfjord	4	2.2	838.2
39	5.08	7.88	35.04	277	26	3	180	Vilnesfjord, Lammetun-Rauøy	3	2	758.3

40	4.73	8.09	34.99	259	48.3	1.8	100	Dalsfjord, Eikeneset	4	3.2	152.3
41	5.14	8.40	34.81	154	26.7	1.3	130	Vilnesfjord, Kalvskjenneset	4	1.2	1381.8
42	4.99	7.88	34.96	273	21.1	0	0	coastal	1	5.8	92.7
43	4.99	7.94	35.06	316	46.3	13.6	210	Inlet Førdefjord, Skjeljevikenet	3	1.3	923.1
44	4.28	8.34	34.75	174	54.9	4.5	50	Førdefjord, Ålasundterskel	5	10	15.6
45	3.83	8.13	34.72	158	17.2	0	0	coastal	1	5	156.0
46	5.28	8.64	34.92	166	8.2	0	0	coastal	1	5	31.2
47	4.83	8.15	34.60	187	20.2	9.5	150	Inlet Nordfjord	4	3.4	638.6
48	5.08	8.37	34.85	168	10.8	0	0	coastal	1	5.5	77.4
49	4.25	8.17	34.86	196	23.5	3	90	Nordpollen	4	6.4	57.1
50	5.09	8.28	34.82	146	0	0	0	coastal	1	2.6	346.2
51	5.07	8.71	34.64	113	18.5	0	0	coastal	1	3.8	324.1
52	4.65	8.41	34.70	153	23	0	0	coastal	1	5.8	92.7
53	4.73	8.15	34.71	206	30.6	2.4	100	Vilnesfjord, Granesundet	4	2	585.0
54	4.14	8.27	35.13	468	52.3	15.3	70	Inlet Masfjord	4	3.7	65.1
55	4.14	8.27	35.13	467	52.5	15.5	70	Inlet Masfjord	4	3.5	77.4
56	4.08	8.27	35.13	475	52.5	15.5	70	Inlet Masfjord	4	3.5	77.4
57	4.14	8.27	35.13	467	52.2	15.2	70	Inlet Masfjord	4	3.8	62.2
58	4.14	8.27	35.13	468	52.2	15.2	70	Inlet Masfjord	4	3.8	62.2
59	4.12	8.27	35.13	464	52	15	70	Inlet Masfjord	4	4	57.9
60	3.63	8.27	35.12	468	51.8	14.8	70	Inlet Masfjord	4	4.2	55.3
61	3.63	8.27	35.12	482	52.2	15.2	70	Inlet Masfjord	4	3.8	62.2
62	3.63	8.27	35.12	478	51.5	14.5	70	Inlet Masfjord	4	4.4	53.0
63	3.68	8.21	35.08	457	53	16	70	Inlet Masfjord	4	4.2	50.2
64	3.68	8.21	35.08	468	53.2	16.2	70	Inlet Masfjord	4	3.1	86.8
65	3.11	8.20	35.08	472	53	16	70	Inlet Masfjord	4	3	92.6
66	3.11	8.20	35.08	469	53.3	16.3	70	Inlet Masfjord	4	3.3	76.6
67	2.26	8.19	35.06	400	55	18	70	Inlet Masfjord	4	1.2	541.7
68	2.33	8.18	35.06	340	55.1	18.1	70	Inlet Masfjord	4	1.1	644.6
69	2.31	8.20	35.06	430	53.5	16.5	70	Inlet Masfjord	4	2.5	128.8

70	2.31	8.20	35.06	425	54.3	17.3	70	Inlet Masfjord	4	1.8	240.7
71	2.31	8.20	35.06	425	52.8	15.8	70	Inlet Masfjord	4	2.3	151.4
72	3.73	7.41	35.04	635	192.2	158.2	200	Sognesjøen, Losna	3	93	0.4
73	3.56	7.56	35.00	373	210.4	176.4	200	Sognesjøen, Losna	3	110	0.3
74	3.48	7.56	35.00	374	209.9	175.9	200	Sognesjøen, Losna	3	110	0.3
75	3.48	7.56	35.00	373	209.9	175.9	200	Sognesjøen, Losna	3	110	0.3
76	3.56	7.56	35.00	374	210.2	176.2	200	Sognesjøen, Losna	3	110	0.3
77	3.73	7.41	35.04	651	193.7	159.7	200	Sognesjøen, Losna	3	93	0.4
78	3.73	7.41	35.04	646	192.4	158.4	200	Sognesjøen, Losna	3	93	0.4
79	3.56	7.56	35.00	372	211	177	200	Sognesjøen, Losna	3	110	0.3
80	3.52	7.60	34.99	373	210.3	176.3	200	Sognesjøen, Losna	3	110	0.3
81	3.52	7.60	34.99	373	210.2	176.2	200	Sognesjøen, Losna	3	110	0.3
82	3.52	7.60	34.99	373	210.6	176.6	200	Sognesjøen, Losna	3	110	0.3
83	5.29	7.68	35.06	366	40.2	7.4	210	Inlet Førdefjord, Skjeljevikneset	3	1.3	2147.5
84	5.29	7.68	35.06	373	39.5	6.6	210	Inlet Førdefjord, Skjeljevikneset	3	1.3	2177.2
85	5.29	7.68	35.06	372	39.6	6.7	210	Inlet Førdefjord, Skjeljevikneset	3	1.3	2177.2
86	2.90	8.09	34.80	377	77.5	13	170	Sørfjord shallowest sill	3	8	36.6
87	3.59	8.33	34.92	294	0	8,1	70	Inlet Masfjord	4	4	220.0
88	5.62	7.04	33.15	438	30.3	11	30	Inlet Lurefjord	5	18	1.1

Appendix B - Trawl Gear

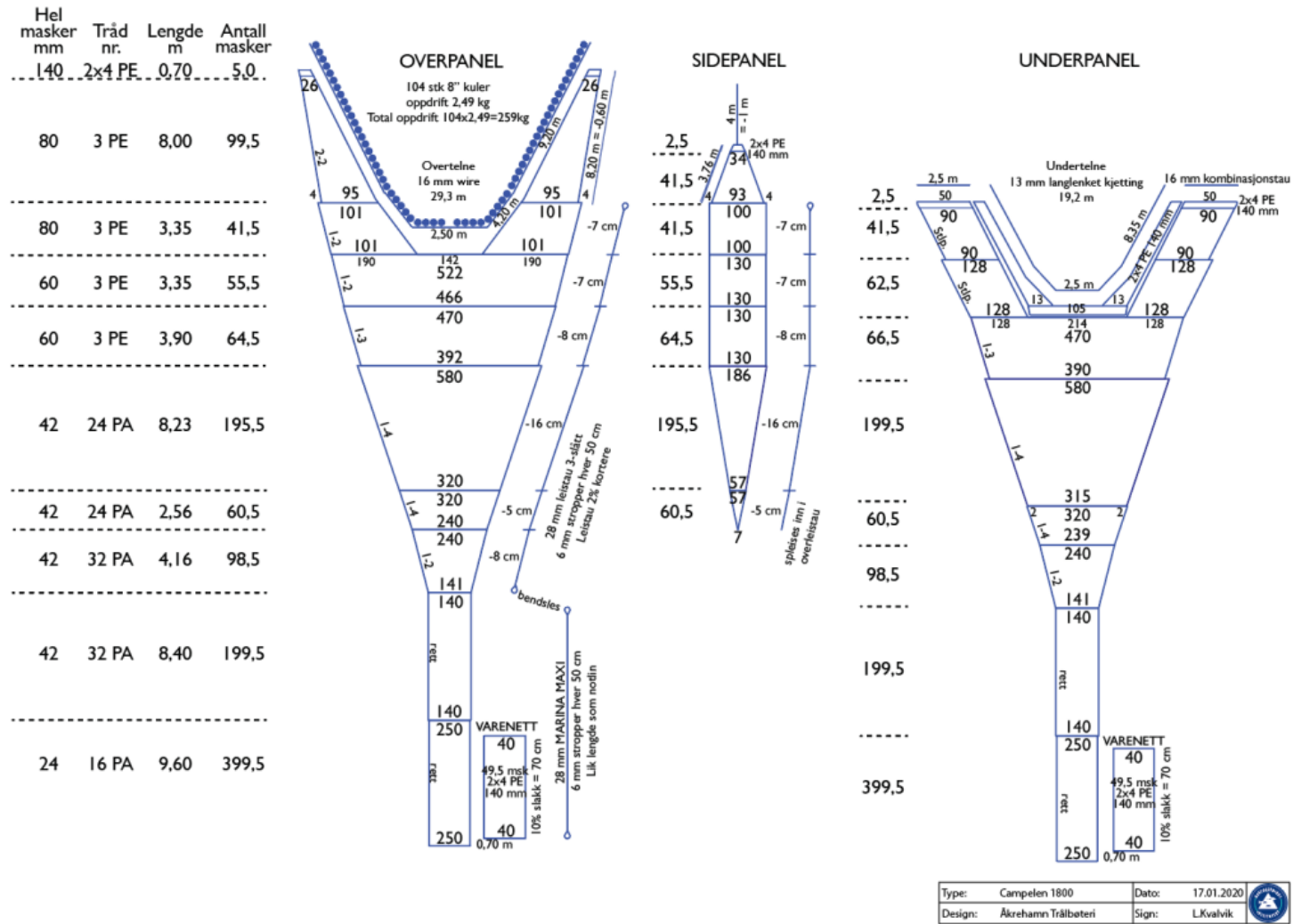


Figure B.1: Campelen 1800 trawl.

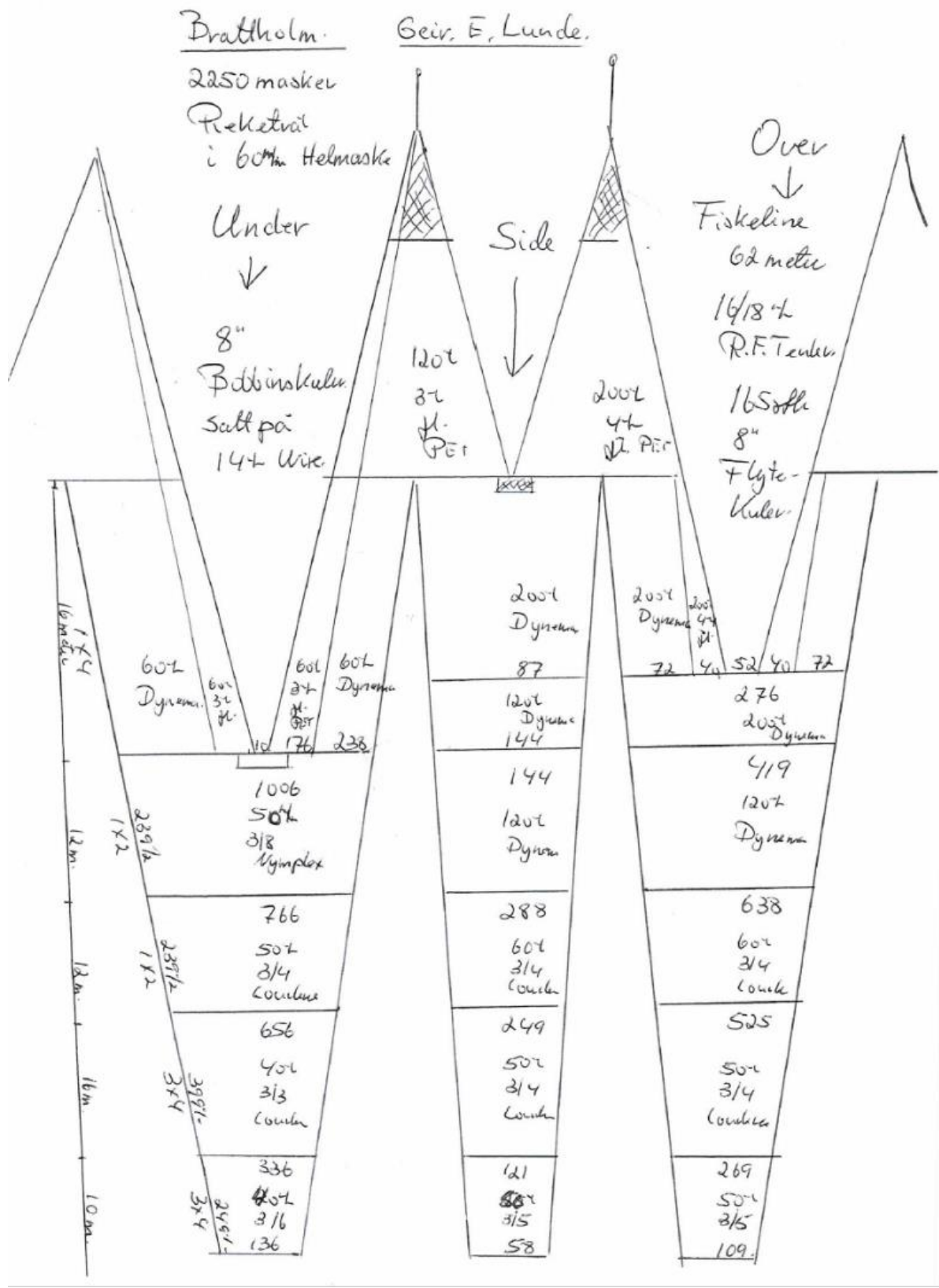


Figure B.2: Flekkerøy-trawl

Appendix C – Correlation Matrix and Model Diagnostic Plots

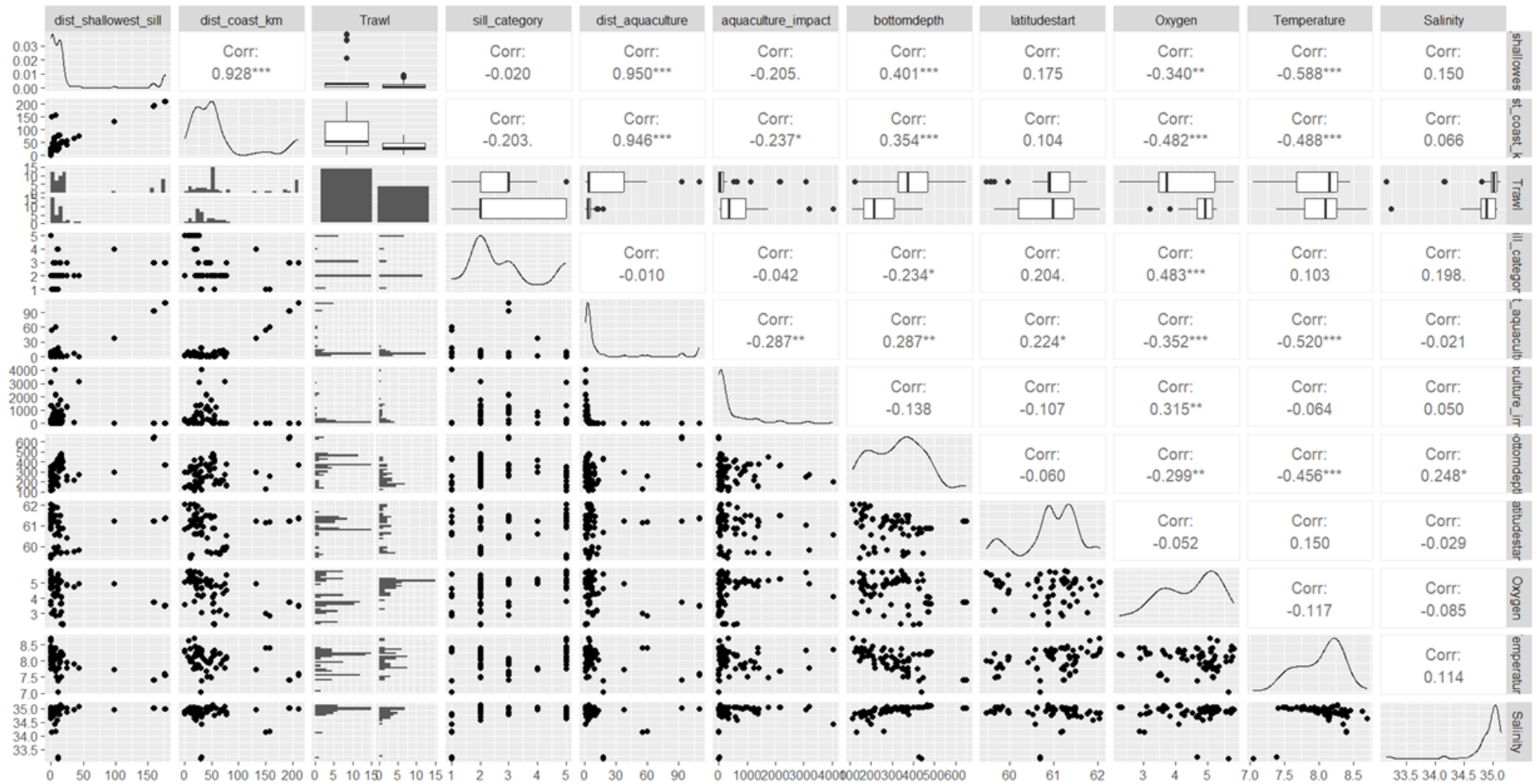


Figure C.1: Correlation matrix of the environmental variables with correlation coefficients and significance level (0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05). The correlation coefficients show strength (max of 1) and direction (positive or negative correlation) between the variables. The variables plotted against themselves can visualize possible outlier values for the variable.

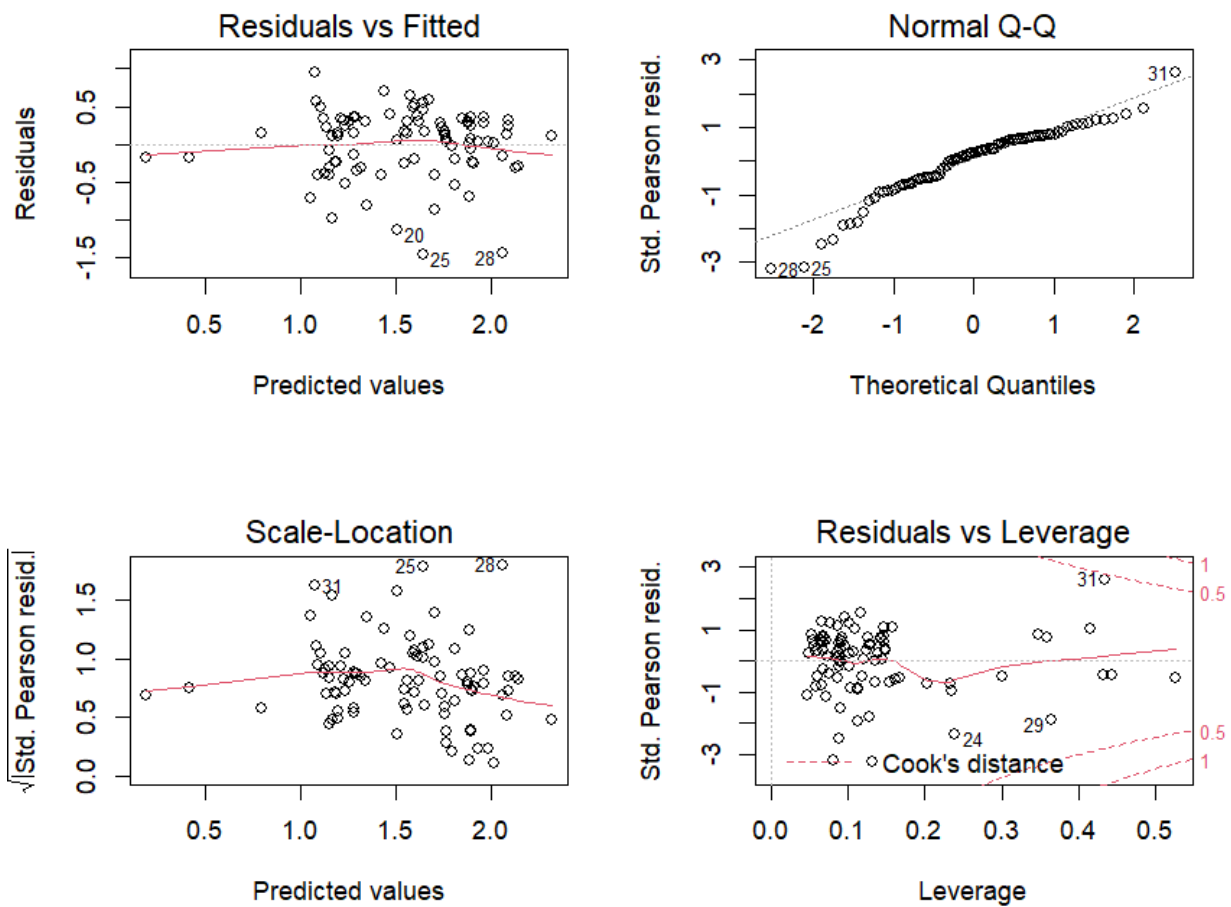


Figure C.2: Model diagnostic plot for the GLM with Shannon-Wiener diversity as response. Residuals vs fitted check for linearity of the residuals and should follow the line at $x=0$. This output shows that the assumption of linearity between the response variable and the predictor variables are met. Normal QQ check for normal distribution of the residuals and should follow a straight diagonal line. This output shows that there are some residuals outside normality. Scale-location check for homoscedasticity (equal variance) of the residuals and should follow a straight line. This output suggest that most residuals are spread equally along the predictors' ranges. Residuals vs leverage check if there are any influential cases that determine the regression line, where values in the upper or lower right corner outside the dashed lines are likely influential cases. This output suggests that there might be an influential case (31) on the regression.

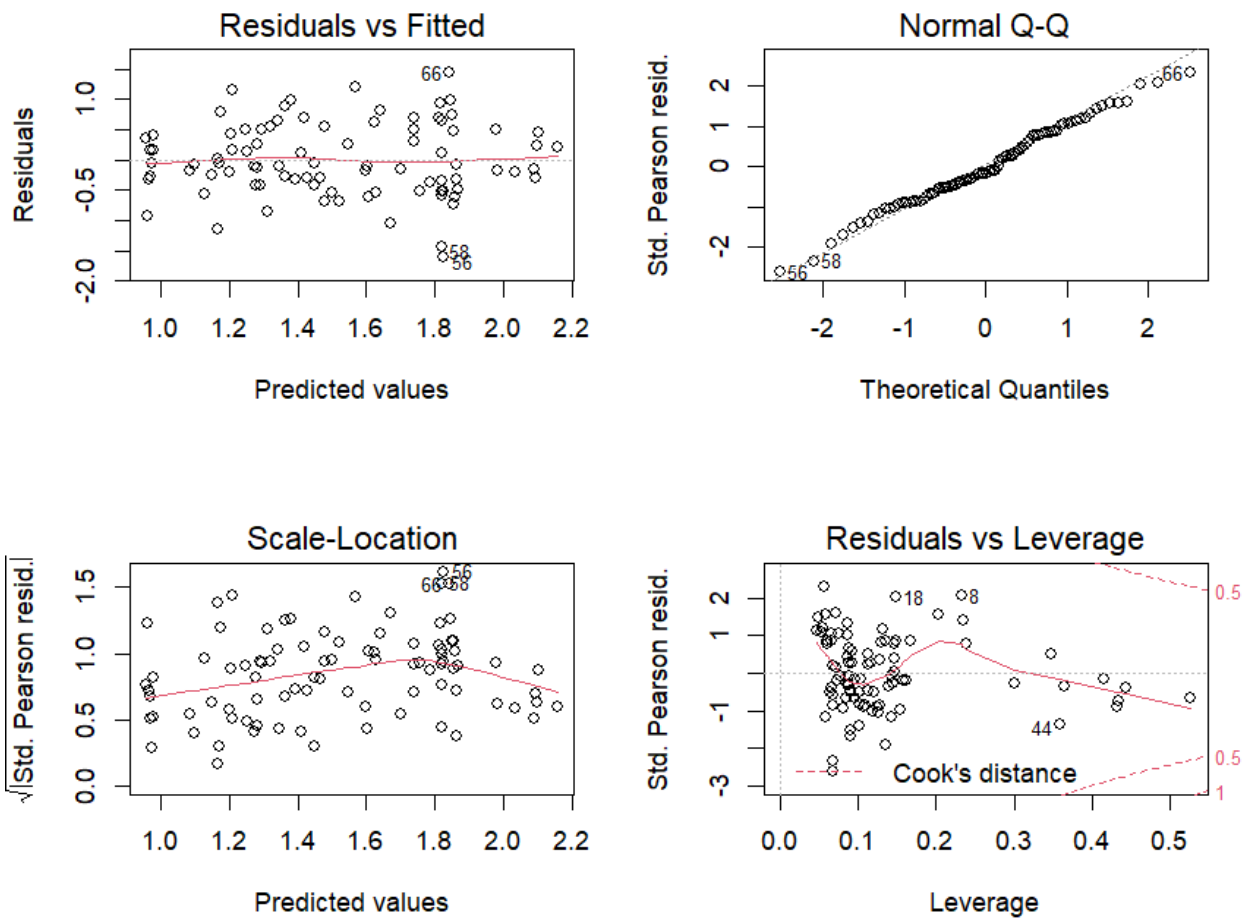


Figure C.3: Model diagnostic plot for the GLM with fish and crustacean CPUE as response. Residuals vs fitted check for linearity of the residuals and should follow the line at $x=0$. This output shows that the assumption of linearity between the response variable and the predictor variables are met. Normal QQ check for normal distribution of the residuals and should follow a straight diagonal line. This output shows that the normality is high. Scale-location check for homoscedasticity (equal variance) of the residuals and should follow a straight line. This output suggest that most residuals are spread equally along the predictors' ranges. Residuals vs leverage check if there are any influential cases that determine the regression line, where values in the upper or lower right corner outside the dashed lines are likely influential cases. This output suggests that there are no especially influential cases.

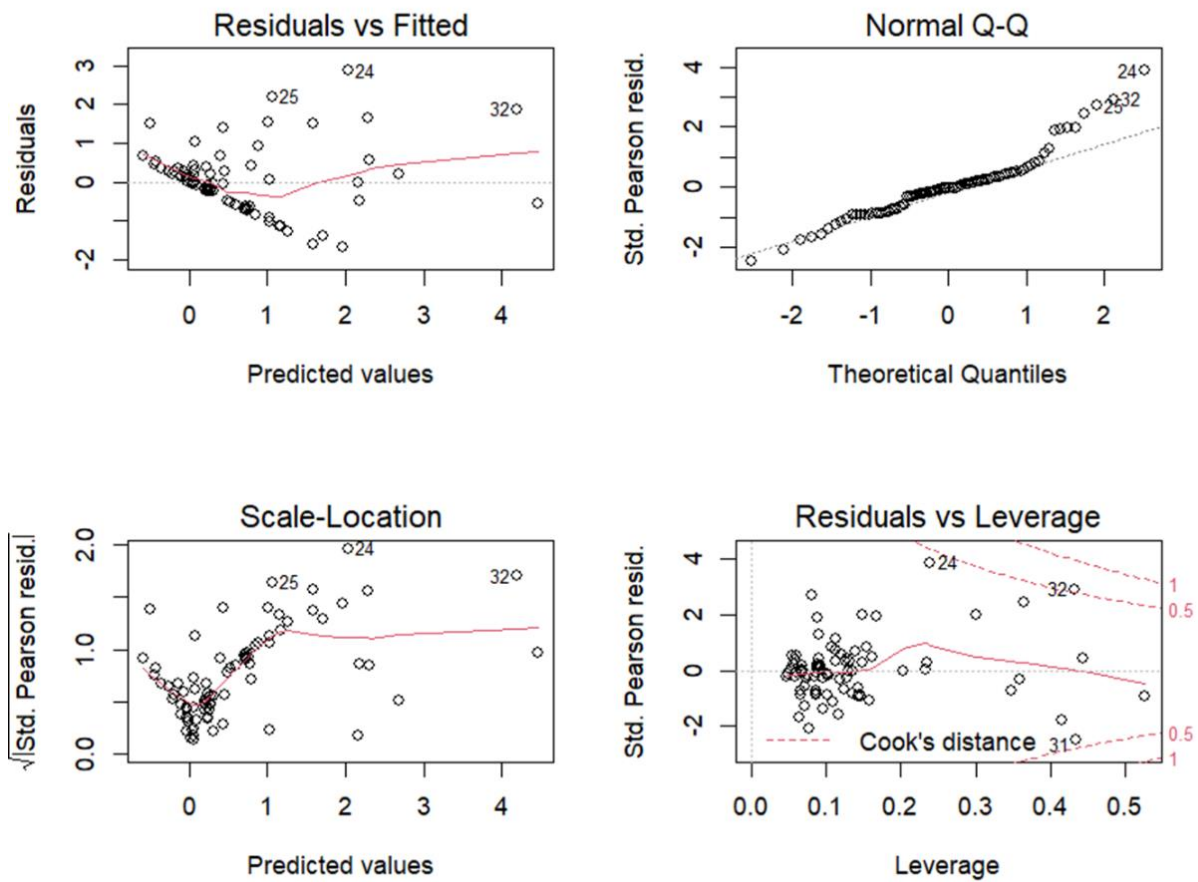


Figure C.4: Model diagnostic plot for the GLM with *P. periphylla* CPUE as response. Residuals vs fitted check for linearity of the residuals and should follow the line at $x=0$. This output shows that there might be some non-linearity not being detected by the model. Normal QQ check for normal distribution of the residuals and should follow a straight diagonal line. This output shows that there are some residuals outside normality. Scale-location check for homoscedasticity (equal variance) of the residuals and should follow a straight line. This output show that some residuals are not spread out equally along the predictors' ranges. Residuals vs leverage check if there are any influential cases that determine the regression line, where values in the upper or lower right corner outside the dashed lines are likely influential cases. This output suggests that there might be three influential cases (32, 31 and 24) on the regression.

