Norwegian College of Fishery Science
Faculty of Biosciences, Fisheries and Economics

Fish communities in shallow coastal waters

- a study of effects of season and bottom substrate

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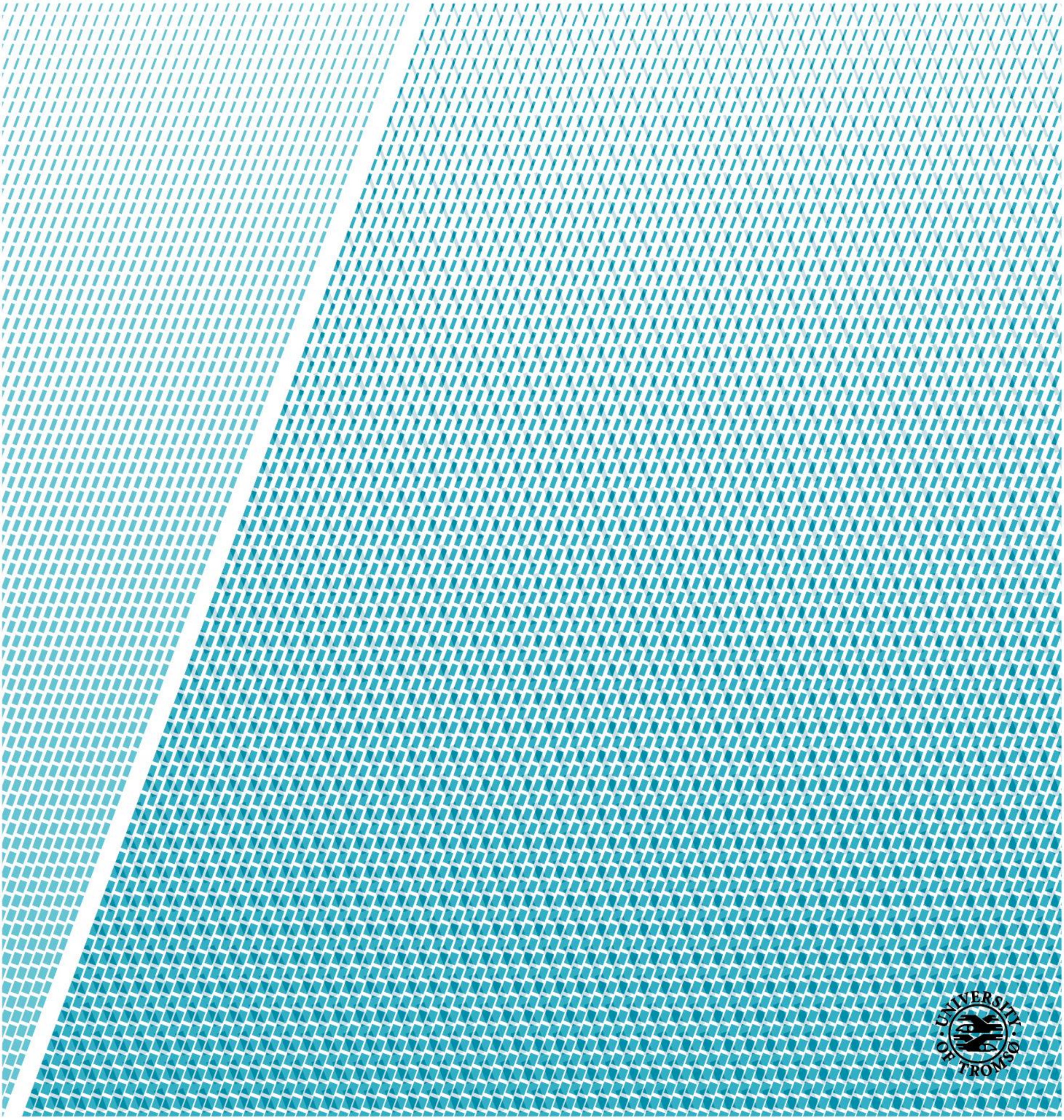

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"So long, and thanks for all the fish" -Douglas Adams

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Abstract

In this thesis, fish communities in the shallow waters of outer Malangen fjord, Troms county were studied to identify seasonal effect on fish assemblages and bottom substrate associations for the most abundant species of fish. Trammel nets, gill nets and underwater video were applied as sampling tools. Throughout four consecutive fieldtrips, a total of 17 species of fish were caught at depths between 9 – 20 m at four locations. A total of four species from Pleuronectidae and six from the Gadidae family were caught. Cod (*Gadus morhua* L.) was the most numerous species followed by plaice (*Pleuronectes platessa* L.), lemon sole (*Microstomus kitt* Walbaum, 1792) and halibut (*Hippoglossus hippoglossus* L.). Cod dominated the catches in all months except March, in which plaice and other flatfishes were most dominant. On a community scale, species richness was highest in October and lowest in March. Furthermore, the species richness and diversity were higher at locations with greater bottom substrate evenness. On a single species scale, lemon sole and saithe (*Pollachius virens* L.) had shorter length distributions in March compared to the other months. Von Bertalanffy's growth function were calculated for cod, plaice and lemon sole. The growth coefficient K of cod was higher than adjacent fjords populations and the L_∞ was considered low. The K value for place were comparably higher than North Sea populations and the mortality rate were also considerably lower than North Sea populations. Smaller individuals of common dab (*Limanda limanda* L.) and plaice were present at one location, where larger specimens were absent. Plaice and common dab showed positive associations with sand and pebble coverage, while lemon sole was more associated with maerl beds, cobble and low algae coverage. Only immature halibut were observed, and the three locations where halibut were present are suggested to be nursery grounds for this species. Cod showed a positive association with large macroalgae coverage and were less numerous at the location with the highest proportion of sand and pebble coverage. The edible crab (*Cancer pagurus* L.) had a clear seasonal pattern, but no clear spatial pattern. The present study highlights the importance of including shallow water studies for both coastal and fisheries management.

Key words: Shallow water habitats, habitat evenness, trammel net, seasonal catch variation, scale of diversity, fish population dynamics, management

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1 Introduction

1.1 Background

The Norwegian fjords and coastal areas have a varied topography, with both hard and soft bottom substrates (Bekkby et al., 2004; Buhl-Mortensen et al., 2012). Shallow coastal waters (< 50 m) are important areas for a variety of species such as such as the Norwegian Costal cod (*Gadus morhua* L.), saithe (*Pollachius virens* L.), Atlantic halibut (*Hippoglossus hippoglossus* L.) and other flatfishes, wolffish (*Anarhichas lupus* L.) and crabs as well as top predators such as coastal seals, harbor porpoise (*Phocoena phocoena* L.) and sea birds (Mann, 2000; Sundby et al., 2013; Havforskningsinstituttet et al., 2016). The knowledge of population and community dynamics for species in these areas are important for comprehensive coastal resource management. It is however inefficient to survey shallow waters with conventional bottom trawls due to bathymetric and biogenic structure complexity. As a result, habitats with depths shallower than 50 m are not covered by the annual autumn coastal surveys of the Institute of Marine Research (IMR) in Norway.

Fish assemblages are affected by many biogenic factors, such as macroalgae coverage, predation and competition (Fraser et al., 1996; Fahrig, 2003; Gratwicke and Speight, 2005; Pennock et al., 2018). Macroalgae habitats can for example function as a shelter for juvenile fish species (Demartini and Roberts, 1990; Michaelsen, 2012), thereby influencing the predator-prey dynamics (Sivertsen, 2006). Furthermore, species-specific habitat preference is also related to physical factors such as bathymetry, currents, wave exposure, temperature, salinity, light, turbidity and bottom substrate (Claireaux and Dutil, 1992; Ruppert et al., 2009; Buhl-Mortensen et al., 2012). It is more likely that several rather than a single factor determine how a species uses a habitat (Gili and Petraitis, 2009), and it would be overly comprehensive to investigate all factors in the present study. Physical factors such as temperature, light and turbidity change seasonally, while bottom substrate is a result of biogenic factors as well as physical factors, especially current and exposure levels (Sivertsen, 1997; Buhl-Mortensen et al., 2012; Rinde et al., 2014). For these reasons, seasonal- and bottom substrate effects were considered suitable variables for the present study.

Kelp forests are important ecosystems in the sublittoral coastal zone, e.g. high primary production, nutrient filtering, shelter, food for adjacent ecosystems or other ecosystem services (Mann, 2000; Persson et al., 2012; Filbee-Dexter and Wernberg, 2018). In the 1970s and 80s, kelp beds from mid Norway (63°30’N) to (70°N) and into Russian waters were grazed down predominantly by the green sea urchin (*Strongylocentrotus droebachiensis* O.F. Müller, 1776) (Sivertsen and Bjørge, 1980; Norderhaug and Christie, 2009). Different species of fish and crab use habitats differently, therefore a change or limitation to habitats can have cascading effects on their successive recruitment (Fraser et al., 1996; Persson et al., 2012). Steneck et al. (2013) describe kelp forests and barren grounds as stable ecological states, as sea urchin predator abundances are high in kelp forest and low in barren grounds. However, since the 1990s the southern and northern parts of the barren grounds have seen regrowth, namely near Vega (65.5°N, 12.5°E) and Kirkenes (70°N, 25°E) (Norderhaug and Christie, 2009). The southern recovery area has now moved as far north as the southern part of Troms county (Christie et al., 2019). Different causes have been hypothesized, e.g. temperature or top-down predation on sea urchins (Sivertsen, 2006; Fagerli et al., 2013; Christie et al., 2019).

The present study will focus on benthic and benthopelagic fish and crab species in the sublittoral zone at different habitats in the outer part of Malangen fjord (69°N, 18°E, from this point referred to as Malangen) in Troms, Norway. The adjacent deeper waters have been studied by the University of Tromsø (UiT) through various course field trips, but the shallow waters are largely understudied. The outer part of Malangen is an area with high natural kelp production. In this area UiT participated in a research project called “KELPEX Kelp export: fuel for adjacent communities in changing arctic ecosystems”. Most of the kelp production is not grazed on directly but transformed to detritus which is available for other organisms such as microorganisms and higher animals (Filbee-Dexter et al., 2018), making kelp forests important habitats for adjacent ecosystems (Mann, 2000).

Many studies have investigated the substrata association of cod (Fraser et al., 1996; Meager and Utne-Palm, 2008; Michaelsen, 2012; Persson et al., 2012) and flatfishes in the North Sea (Jennings et al., 1993; Gibson and Robb, 2000; Bergmann et al., 2006). Studies regarding fish community structure in shallow waters and the role of habitat in northern Norway are somehow lacking. Such studies are abundant in temperate marine habitats (Gratwicke and Speight, 2005; Mesa et al., 2006), and most of these studies conclude that species richness, diversity and densities are positively related with substratum complexity (Macpherson, 1995; Gratwicke and Speight, 2005). This was also shown to be true for benthic communities at deeper water (40 to 2200 m) in northern Norway (Buhl-Mortensen et al., 2012). One of the aims of the present research is to study whether bottom substrate complexity has the same effect for shallow water fish communities in the Malangen study area. Knowledge regarding species interactions with different habitats are vital for the understanding of natural population dynamics and marine resource- and coastal management. Furthermore, it can give an indicator of how the fish assemblages react to human externalities.

Juvenile fish generally display a more specific substrate type preference than adults (Hancock, 1975). If this is the case for the observed species, we expect that larger adult fish will be more dispersed than juvenile specimen. Lefcheck et al. (2019) reviewed articles on nursery habitats and found that three-dimentional "structured" habitats such as mangroves or submerged aquatic vegetation provided the greatest nursery benefits habitats compared with unstuctured habitats. Fraser et al. (1996) found that substrate use for age 0+ and 1+ Atlantic cod was affected by the presence of predators (age 3+ cod), either hiding in cobble substrata or refuging in sand and gravel substrate to avoid predators. It is therefore expected that juvenile cod are less abundant in areas where large adult cod are abundant. In general, it is expected that some species have different substrata preferences, e.g. plaice use sand and gravel to bury themselves in the substrate (Bergmann et al., 2006), while different benthopelagic species use kelp forests as refugee and nursing ground habitat (Mann, 2000; Steneck et al., 2003; Michaelsen, 2012).

Additional factors that are expected to affect the catch rates are time of year, e.g. seasons and population dynamics. The most important commercial fish stocks like coastal cod, saithe, plaice and halibut spawn during winter and early spring (Haug and Tjemsland, 1986; Jakobsen, 1987; Heino et al., 2012). It is therefore expected that larger mature fishes recruit to the spawning stock and leave these shallow waters during winter-early spring. Consequently, the numerical density of these large fishes should be highest in shallow waters during summer and autumn. Other population parameters such as growth and mortality also influence the biomass at different locations and thus will be included in the study.

Some previous studies have used trammel nets to survey shallow waters, and Salvanes (1991) studied the fish composition of Masfjorden (60°50'N, 5°20'E), western Norway, providing a good methodological description for research fishing with trammel nets. Their findings showed that cod had a higher abundance in winter and autumn than in summer and spring. The gadids were the most abundant family of fishes in Masfjorden, and in this family pollack (*Pollachius pollachius* L.*)*, saithe, poor-cod (*Trisopterus minutus* L.) and cod were the most numerous. Masfjorden is however a rather steep-sided fjord that opens to another fjord, in contrast to Malangen which has larger areas of shallow water and is largely influenced by coastal waters (Sælen, 1950). Similar studies with samplings throughout the year are not known from the two northernmost counties of Norway (Troms and Finnmark). A research project called KILO aimed to identify shallow water resources and associate bottom substrates with coastal species (Sundby et al., 2013). Their trammel net samplings were however only done in November 2011, and some of their data will be compared with findings from the present study.

Other research methodologies used were video surveys and analysis of the relation between bottom substrate and demersal species that have previously been done by Michaelsen (2012) and Wiesener (2015). These studies focused mostly on underwater video as a method to identify bottom substrate, and habitat associations of video-recorded juvenile cod and different flatfish, whereas the present study uses the same method to identify bottom substrate and algae coverage in order to compare it with trammel net catches.

1.2 Objectives, hypotheses and approach

The main objective of this study was to characterize the fish assemblages of outer Malangen by identifying the dominant fish species and their population dynamics, and how they vary in time and space. Furthermore, the study aims to identify habitat associations for the most abundant species. The following research questions were considered relevant for this study:

- Are catches equal at all locations and seasons?
- What are the bottom substrates at the different study locations, and are there any species associations with certain substrate types?
- Are the growth and mortality rates of the most abundant species comparable to other areas, such as fjords and the North Sea?

From the research questions above, the following null hypotheses are set to be tested:

- H01: There are no seasonal effects on trammel net catch composition and single species variables
- H02: There are no spatial effects on trammel net catch composition and single species variables
- H03: There are no effects caused by bottom substrates on trammel net catch composition and single species variables
- H04: Growth patterns and mortality are equal to other areas

Seasonal patterns are expected to be identified by comparing the different surveys, as four locations will be sampled four times throughout the year. Spatial patterns will be investigated by studying the different catch compositions at the different locations. The catch composition includes species composition, frequency and biomass. These variables will be used to identify community parameters such as species richness, diversity and evenness. Seasonal and spatial effects will also be tested for these indices, as they are important for a holistic ecosystem approach. Single species variables, such as length, age, growth and mortality rate will also be measured and calculated by applying von Bertalanffy's growth function and Chapman-Robson mortality for species with sufficient catch data. These variables are important factors that influence the population dynamics as well as standing biomass in the specific habitats. By quantifying bottom substrate coverage and habitat heterogeneity, or evenness, it should be possible to identify specific species-habitat interactions (Boström et al., 2011). The substrate evenness represents the complexity of the habitat. The study area is dominated by relatively warm coastal water compared to adjacent fjords. Therefore, we expect a higher K value compared with specimen inhabiting adjacent inner fjord habitats, and a lower K and higher L_∞ when comparing our findings with specimen from further south, e.g. the North Sea. These growth parameters, including mortality, will be discussed and compared, but it will not be tested if they differ from other areas. Thus, the H04 hypothesis must be interpreted as a research question instead of a strictly statistical hypothesis.

2 Method

2.1 Study area

Malangen is a 60 kilometers long subarctic fjord in Troms county, Norway, that stretches from Hekkingen lighthouse in the west to Nordfjordbotn in the east (Figure 1) (Sælen, 1950). The fjord has a deep sill/threshold at ca. 200 m depth and is relatively close to the adjoining continental shelf, feeding the fjord with a high influx of Atlantic Water and Coastal Water (Mankettikkara and Eilertsen, 2013). The Coastal Water is the more prominent in the intermediate and surface waters of the fjord (Hald et al., 2011). The fjord has an outer and an inner basin with depths of ca. 450 and 250 m respectively, and both basins are largely influenced by denser Atlantic Water (Sælen, 1950). Sea surface temperatures (SST) and temperatures at deeper waters (>100 m depth) vary with season. In general, temperatures are warmer at 100 m depth compared with SST during winter and spring while the SST is warmer during summer and autumn (Mankettikkara and Eilertsen, 2013). Average temperature at 10-20 m depths in outer Malangen vary from 4.5 C° in March to 10.8 C° in August, 9.8 C° in October and 9.0 C° in November (Mankettikkara, unpublished data).

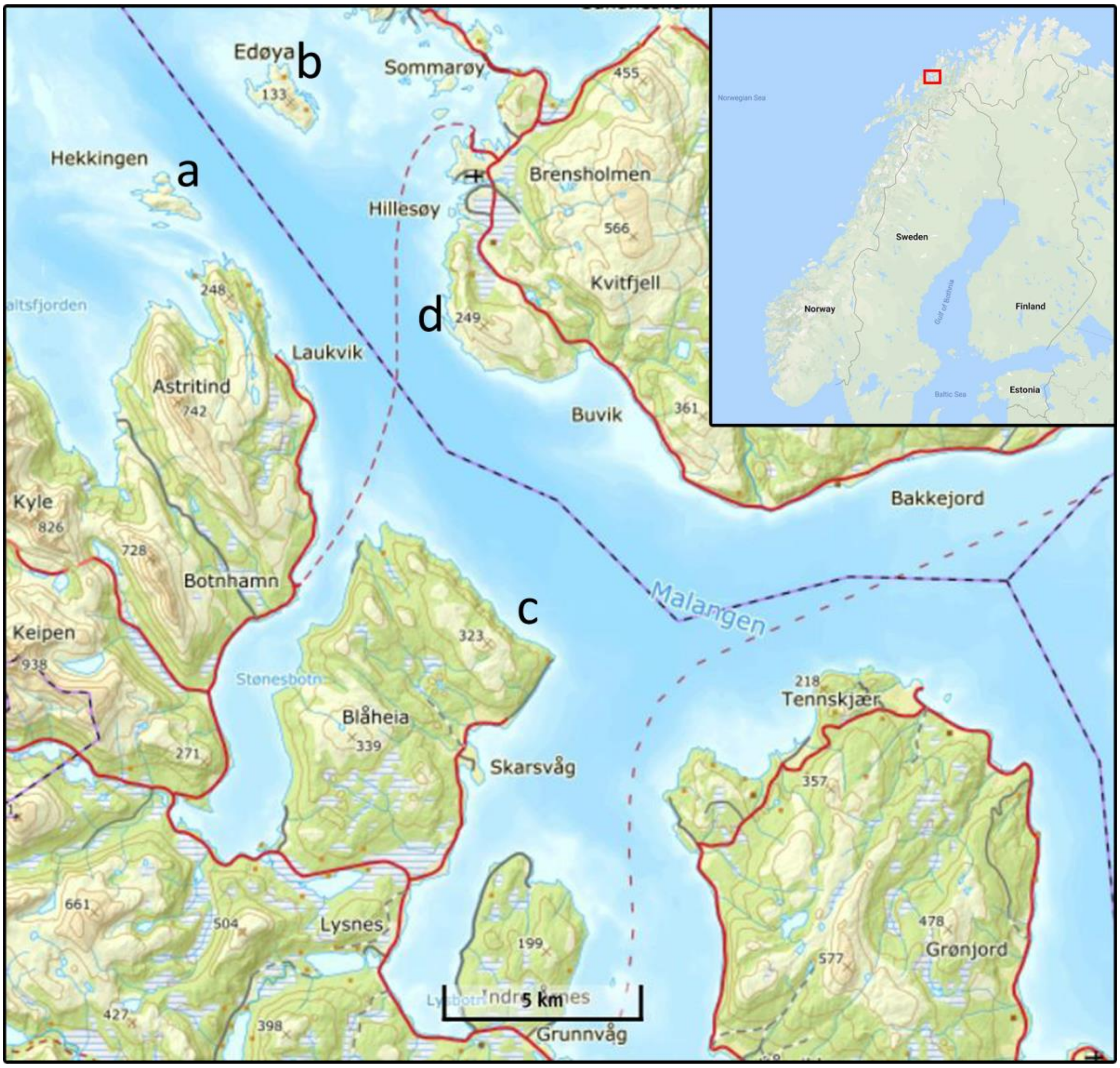

Figure 1: Positioning of Malangen (N 69°33, E 17°58) and sample locations. (a) Hekkingen, (b) Edøya, (c) Skårlia and (d) Molvika. Landmasses southwest of Malangen belong to the Senja island. (Kartverket, 2019)

Fieldtrips took place in shallow waters adjacent to the outer basin. These shallow waters are largely influenced by Coastal Water (Hald et al., 2011), making it an appropriate area for this study. Two of the locations were in the outer exposed areas of Malangen; Hekkingen and Edøya, another two further into the fjord; Molvika and Skårlia (Figure 1). Hekkingen and Edøya are both islands where the sample locations were placed on the east-northeast side of the islands. Hekkingen is the most exposed location due to its limited protection from winds and swells. There is a shallow area with kelp beds Northwest of Hekkingen that is exposed to the continental shelf and Norwegian Sea. The location at Edøya is surrounded by a shallow area with the deepest area being ca. 70 m deep. The other two stations have gradual slopes leading down to the outer basin, where the basin faces Molvika to the east and Skårlia to the southwest (Figure 1). Location names in figures are abbreviated as the first three English letters of the name, e.g. Skårlia (Ska).

2.2 Sampling

Data for this study were gathered by fishing with trammel nets and gill nets as well as underwater video recording at all four locations in Malangen (Appendix table 1, Figure 3). Four consecutive surveys were performed in November 2016 (Winter), March 2017 (Spring), August 2017 (Summer) and October 2017 (Autumn). Each fieldtrip lasted from Monday to Friday with departure and return from Tromsø Harbour. Fieldwork done in November, March and October was conducted with the research vessel (R/V) Johan Ruud (30.5 m long) and a smaller fiberglass dinghy (4.3 m long) with a 30 HP outboard engine, which was used to deploy and haul the trammel nets. In August, R/V Hyas (12.24 m long) was used and the trammel nets were directly deployed and hauled from the vessel. The nets were deployed at the same locations every time using a handheld Garmin Global Positioning System (GPS). Two net-sets were used at each location, roughly 200 meters apart and the nets fished between 14-24 hours at depths between 9-20 m (Appendix table 1). This depth range is ideal for net-fishing and as light declines with depth, so does the possibility of surveying the bottom with a video recorder. The most exposed location (Hekkingen) could not be sampled in March 2017 due to rough weather conditions. The locations needed to have a homogenous depth range over ca. 400 m distance to allow fishing with two net-sets placed ca. 200 m apart. The bottom substrate at the different locations was expected to vary due to levels of exposure.

Each of the trammel nets were 20 m long, 2 m deep with two slack outside panels (235 mm mesh bar length) and an inner net with 53 mm mesh bar length. A line with a weight and surface marker buoy were tied to the end of the chain, and a weight was attached to the bottom of each end of the net-sets (Figure 2). Trammel nets are robust nets, and were used for this reason, as some rough handling was expected in the winter months.

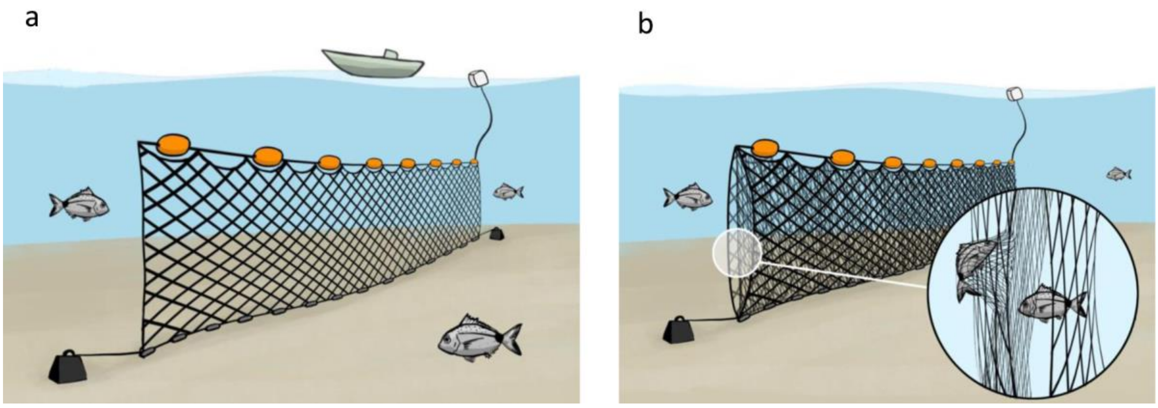

Figure 2: An illustration of the trammel nets used for this study. (a) A gill net, buoyed at the top and weighted below, with two larger weights on both sides of the net keeping it anchored, one float above the water surface for monitoring its location. (b) A trammel net made up of three panels, where two outer panels are of larger mesh sized nets and the inner panel is of smaller mesh size. Fish entangle when swimming through the net as illustrated (pocketing). Illustration obtained from Frid and Belmaker (2019).

In addition to wedging, gilling and entangling (i.e., held by teeth, spines or other protrusions), trammel nets also catch fish and invertebrates by a process called pocketing, where the fish is caught in the inner smaller mesh wall which then gets pushed through one of the larger mesh outer walls (Erzini et al., 2006). Trammel nets are therefore generally considered to be less size selective than gill nets, with size distributions frequently skewed to the right. If a significant proportion of large individuals is pocketed, the selectivity curve may not even decline or reach zero, which suggest very few individuals escape the catch process (Salvanes, 1991; Erzini et al., 2006). Erzini et al. (2006) found that trammel nets have a multi-species nature, meaning that they catch substantially more species than gill nets and long lines.

As the size distributions are often right-skewed for the trammel nets and since relatively large meshed trammel net were used (Erzini et al., 2006), an additional small meshed gillnet (26 mm bar length) was attached to each net-set for the August 2017 fieldwork to sample smaller fish. The gillnets were only used in August as the weather was expected to be better in this month and thereby not destroying the fragile nets.

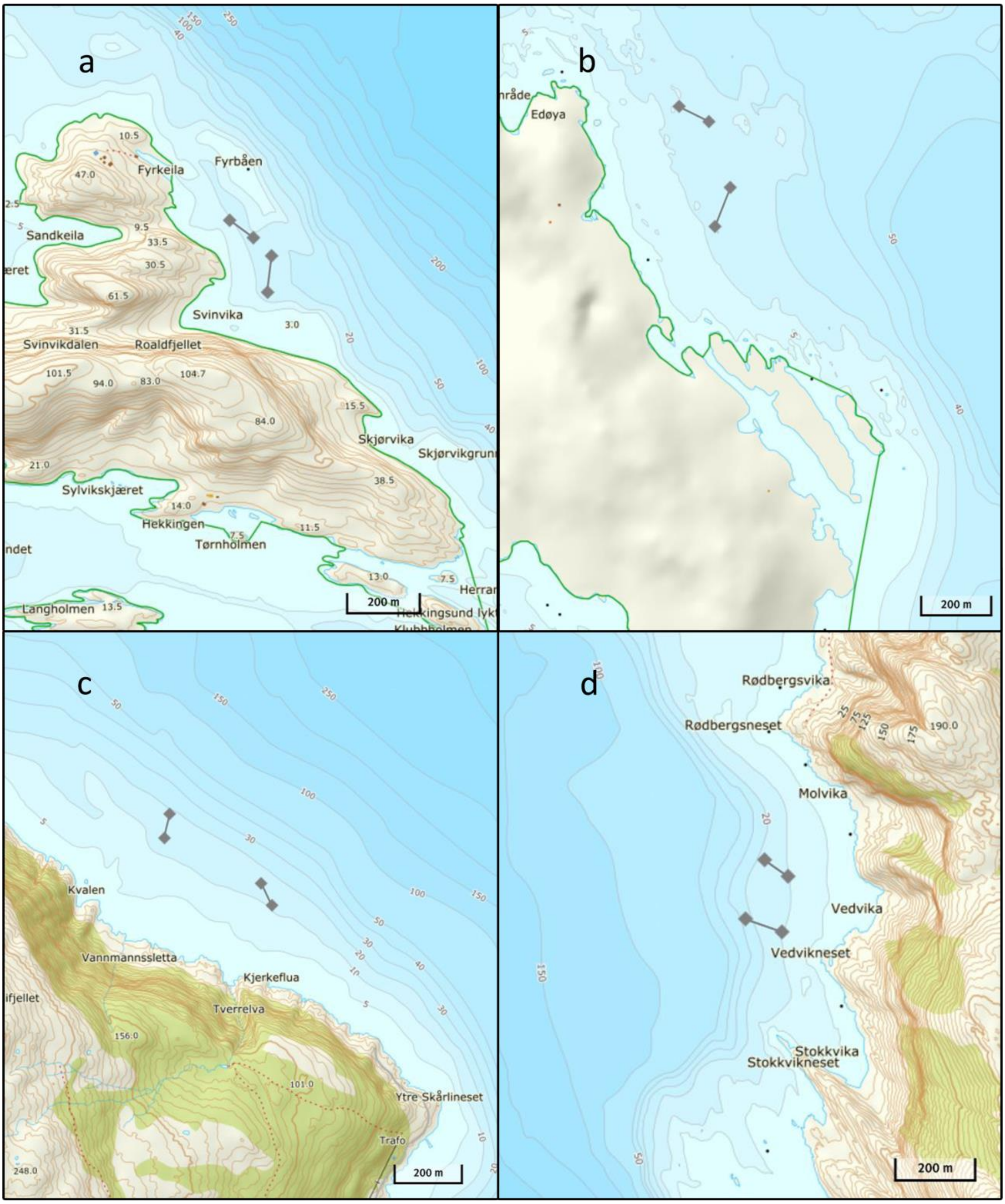

Figure 3: Location of trammel nets. Hekkingen (a), Edøya (b), Skårlia (c) and Molvika (d). Squares show endpoints of each net-set (Kartverket, 2019). Trammel nets are generally set between the 10 m and 20 m contour lines.

The catches were sorted on the deck of the main vessel at all surveys. The crew at R/V Johan Ruud welded a square frame in which the net was strung up. All catches could then easily be collected and placed in individual bins for each net-set. The fishes, crabs and other invertebrates were counted, individually length measured, weighted and otoliths were taken from the cod, halibut, lemon sole and plaice for later examination. Gonads of fish were identified, and sex was recorded. A maturity scale (1-4) was recorded according to the level of gonad development (Mjanger et al., 2011). Maturity scale 1 describe an immature specimen with small gonads without visible egg or milt. Scale 2 represent a mature individual with larger, but not “runny” gonads. A fish with maturity scale 3 will spray milt or eggs when the abdomen is pressed and are therefore considered to be spawning. Fish with maturity scale 4 have large gonads but no eggs or milt and were considered post spawning. Fish specimen total length was measured downwards to the nearest centimetre; e.g. a specimen of 6.7 cm would be recorded as 6 cm. The field laboratory at R/V Johan Ruud was equipped with a balance weight with a measuring accuracy of 2 gram, while one with 10 gram measuring accuracy was used on deck at R/V Hyas.

2.3 Age determination

Otolith reading was used to determine the age of the selected species. Otoliths were extracted with tweezers by making a cross section between the snout and neck of the fish. Otoliths from cod were stored in paper envelopes, while flatfishes’ otoliths were individually stored in glass veils with a 60 % ethanol solution. Otoliths were analyzed at a laboratory at the University of Tromsø. Different age estimation methods are described by various studies, and also differ between species. There are many pitfalls when determining age by otolith readings, such as false rings which are thought to be a consequence of post larval metamorphosis (Smith, 2014). Another common source of error is shadow rings or “checks” which are false rings between annuls (C.A.R.E, 2006). Measures were taken to combat these errors, which are detailed in the last paragraph of this section.

Fishes at high latitude (45-70°N) often start to form opaque zones in spring (April-May) and translucent winter zones in October-November. Generally, the period of fast growth starts later and lasts longer compared with fishes in more temperate waters (Høie et al., 2009). Annulus were interpreted as one opaque and one translucent zone. Cod and lemon sole were expected to be born in April, plaice in March and halibut in February.

In the present study, flatfish otoliths were not cut or broken, but rather glazed with glycol before reading growth zones under reflective light with a dark background. Otoliths from cod were broken transversely and placed in clay, leaving the cut end visible from above. Growth zones could then be studied and counted in a Motic SMZ-171 stereoscope at 16x magnification with a light source from the side.

Fish caught in October and November had a thin translucent zone at the edge, indicating that the translucent zone start to form in late autumn / early winter. Cod otoliths that were sampled in August had a prominent opaque zone in the outer part, indicating ca. 5 months of fast growth. A fish with 7 opaque zones caught in August was therefore identified as 6+ years old specimen (depending on the species). An experienced supervisor was present when reading otoliths, as to compare the results. Reading reliability was noted as one of three categories, (1) reliable, (2) uncertain and (3) low reliability. All cod otoliths with reliability (3) were double checked by an experienced supervisor. Cod otoliths were also read two times to double check for technical errors. When a different age of fish was read, a discussion took place to agree on the final noted age.

2.4 Video survey

The video survey was conducted with R/V Hyas at each of the locations in August. The filming rig was an aluminum construction with stabilization fins (Figure 4). The rig had a depth and temperature gauge, two parallel lasers used for estimating the distance to the bottom and an underwater camera. The video was paired with a sound recorder and written recording of coordinates and depth measures, and therefore could reasonably assure that the fishing net grounds were covered. As the depth gauge was faulty, we used the echo sounder on the vessel to record the depth manually. Transects were filmed back and forth roughly along the depth contours where the trammel nets stood. The rig was towed using a reinforced wire as well as a cable which also provided the live feed video. The wire had a coiling spool on deck. An aluminum triangle construction was attached at the front of the deck to easily lower and pull the camera rig. One person was controlling the depth (1-2 m above the bottom) of the rig by lowering and pulling the wire while another person read out the coordinates and depth, using a hand-held GPS and the boat echo-sounder. A third person wrote down coordinates and depth. The vessels’ skipper was driving the boat. Towing speed varied around 0.8 m sec^{-1}.

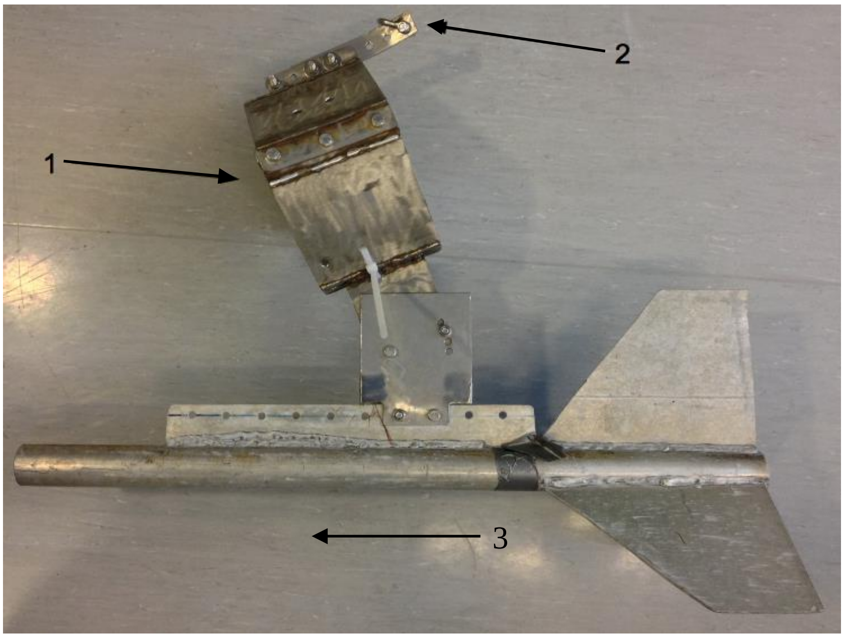

Figure 4: Towed video rig used to record video of bottom habitats in the subtidal zone; (1) camera and lasers pointing forwards, (2) cable attachment, (3) towing direction.

The videos were saved on an external hard drive and reviewed using VLC software and a 24-inch monitor at UiT. In total 24 minutes and 4 seconds were filmed at Edøya, 17 minutes and 2 seconds at Hekkingen, 22 minutes and 9 seconds at Molvika and 28 minutes and 17 seconds at Skårlia. Bottom substrate variables were divided into seven categories; sand/pebble, cobble, bedrock, low algae, high algae, shell fragments and other. These categories are relatively general as muddy bottom substrate were included in sand/pebble. Coralline algae and maerl were included in cobble coverage. Bedrock was defined as hard bottom with little-to-no algae cover. Algae cover was differentiated roughly into either low algae (< 30 cm height) or high algae (> 30 cm height) coverage. In general, high algae cover was present in areas with kelp such as *Laminaria hyperborea* and *Saccharina latissima*, while low algae cover consisted mostly of Dulse (*Palmaria palmata*) and *Desmarestia aculeata* as well as other unidentified clusters of turf algae. “Other” mostly represented sea cucumbers (*Holothuroidea*), sea anemones (*Actiniaria*) and sponges (*Porifera*). These simplifications were done to limit the variation of bottom substrates and the number of variables for a statistical analysis. When reviewing the footage from the built-in underwater camera, ten second intervals were analysed, and visually assessed proportions of various bottom substrate and abundance of sea urchins were recorded onto an Excel spreadsheet. The abundance of sea urchins, mainly *Strongylocentrotus droebachiensis* (Müller, 1776), was divided into categories of “none”, “some” and “many”. The percentage of each category of bottom substrate was noted for a ten second interval (8 meters filming), summing up to 100 percent for each ten second interval. A sum of 145 individual ten second clips were recorded at Edøya, 99 for Hekkingen, 133 for Molvika and 156 for Skårlia. These were then averaged for each location in order to calculate the average percentage of each category at the location. The proportional coverage data were arcsine-square root transformed prior to the canonical correspondence analysis to meet assumptions of normality (Zar, 1998).

2.5 Data analysis

Due to lack of sampling at Hekkingen in March 2017, the March data were excluded when testing spatial patterns for cod and saithe, and the Hekkingen data were excluded when analyzing spatial patterns for flatfishes. Hekkingen was excluded from seasonal pattern analysis. These measures were done so that all groups were equally represented in the statistical analysis. The eight species in focus were cod, common dab, halibut, lemon sole, saithe, plaice, thorny skate (*Amblyraja radiata*, Donovan) and the edible crab (*Cancer pagurus*, L.). Not all species were included in length and age determinations, due to lack of data in some cases. Figures include all catch data unless otherwise indicated in figure text.

Mann-Whitney U test and Kruskal-Wallis H test

A non-parametric Mann-Whitney U-test (MW) was used to test if age or length distribution of two groups differed from equality. Kruskal-Wallis H-test (KW) is another non-parametric test that was employed when more than two sample distributions were tested. In these tests, before the test-statistics are calculated, the actual measurements are converted to ranks (Zar, 1998).

Chi-Square test

When analyzing contingency table data, chi-square statistics was used to test whether frequencies of fish were equal for different seasons or locations (Zar, 1998). A criterion to the Chi-Square test is that the value of the expected cells should be 5 or above for at least 80 % of the cells, and no cells should be below 3. The test assumes a random sample from the population.

Box-plot

Box plots were used for displaying distributions of age and length for different species. The median is showed and the lower and upper quartile which each include 25% of the individuals. The fences, or “whiskers”, define the total data and asterisk and circles indicate outliers. Asterisks are outliers within 3x the height of the box whereas circles indicate values further away from the median.

Von Bertalanffy growth function

The von Bertalanffy growth function was estimated, which describes the growth of fishes. The parameters for this function were calculated with SYSTAT (2017) and the function was expressed as:

$$L_t = L_\infty(1 - e^{-K(t-t_{0)}})$$

L_t (cm) is the length at age (year) and L_∞ (cm) is the theoretical maximum length. K (year^{-1}) is the growth coefficient which describes how fast the length reaches its L_∞. t_0 (year) is the theoretical age of a fish when the length is equal to zero. Sex was not differentiated when creating length at age figures for halibut as studies show similar growth rates up to sexual maturity (Karlson et al., 2013).

Chapman-Robson mortality-rate analysis

The Chapman-Robson mortality was estimated (Chapman and Robson, 1960) by using the free statistical software R verson 3.5.3 (http://www.r-project.org) and applying the FSA package (Fisheries Stock Assessment methods). The function is expressed as:

$$Z = \log_e\left(\frac{1 + \bar{a} - 1/n}{\bar{a}}\right)$$

where Z is the total annual mortality rate, *n* the sample size and $\bar{a}$ is the average age of the individuals above recruitment age.

Spearman rank correlation coefficient (r_s)

The Spearman rank coefficient was used to identify associations between bottom substrates and the community indices or abundance of different fish species. The coefficient is a non-parametric correlation analysis that identify the correlations between variables (Zar, 1998). The coefficient ranges from -1 to +1.

Canonical correspondence analysis

Canonical correspondence analysis (CCA) is a multivariate parametric technique that highlight relationships between biological assemblages of species and the physical environment (Braak and Verdonschot, 1995). By quantifying ecological data such as bottom substrate, we can visualize the different associations of taxa and bottom substrate categories in an ordination diagram. The benefit of this method over other linear multivariate methods relating two set of variables, is that it can deal with the unimodal functions of habitat variables (Braak and Verdonschot, 1995). CCA attempts to define the primary independent dimension which relate one set of variables to another set of variables (Carpenter et al., 1981). CCA is also a good method when analyzing seasonal variation in communities and how much of that variation that could be explained by relevant environmental variation (Braak and Verdonschot, 1995). Eigenvalues represent the niche separation. A permutation test with 999 permutations was used to test the axes significance. Spearman rank correlation was used to study the association or correlation between bottom substrate category coverage and individual species occurrence.

Sample location and month were individually grouped in columns, and values for each net-set (row) were given for the different environmental values as well as catch numbers for various species (columns) (Appendix table 3). Five environmental variables – sand/pebble, cobble, low algae, high algae and urchin cover were used and eight species – cod, halibut, plaice, lemon sole, saithe, edible crab, common dab and thorny skate were used for the CCA.

Community indices

The fish assemblages were characterized by calculating species richness (S), Shannon-Wiener diversity index (H'), and evenness (J) as well as species catch proportions by number, frequency and biomass. A Spearman rank correlation coefficient was used to test if species composition parameters S, H' and J had any correlation with bottom substrate evenness (Jsub) and individual % coverage for each substrate.

Average S, H' and J for each net-set were calculated for each location and month. The Shannon-Wiener diversity index (H') formula is:

$$Shannon\ Wiener\ Index\ (H') = -\sum_{i=1}^{S} p_i \ln\ p_i$$

Where p_i is the proportion of individuals of species *i* found divided by the total number of species at the location or season, ln is the natural log, Σ is the sum for all species calculation and S is the total number of species. It is important to note that the H' is defined as the diversity for the catch population. It is not a sample of something greater, rather a representation of the diversity at the location or season where the trammel nets were used. Higher H' value indicates a higher diversity.

The evenness (J) is described as the "*the ratio of the observed diversity to the maximum possible in a collection having the same number of species*" (Pielou, 1966). The evenness (J) is then calculated as $J = H' / H'_{max}$ where $H'_{\max}$ is the natural logarithm of species richness (S).

The use of Shannon-Wiener diversity has received some criticism in regard to having a biased evenness (Strong, 2016), so other diversity indices were considered. Simpsons-D index were tested, but the indices displayed similar patterns (Appendix 1). The main difference is that Simpsons-D do not give a high value to rare species observations. This could perhaps be of value for this study, but in order to keep the results in line with similar literature, the Shannon-Wiener diversity index was used.

In addition, community similarity was calculated between two locations by using Sorenson's similarity index (Sorenson, 1948):

$$Sorenson's\ Coefficient\ (CC) = \frac{2C}{S1 + S2}$$

Where C is the number of species two locations have in common and S1 and S2 are the total number of species at location 1 and 2. The coefficient will be a value between 0 and 1, where complete similarity is found at 1.

Preliminary results and figures were handled by using Microsoft Excel (2016). SYSTAT (2017) 13 Version 13.2.01 was used when applying non-parametric tests (KW and MW) to test if a variable was equal in different groups. PAST V3 was used for the multivariate analysis applying CCA (Hammer et al., 2001). PAST V3 was also used for the following permutation tests and the spearman rank correlation coefficient. For all tests, a P-value < 0.05 was considered significant.

3 Results

A total of 337 organisms from 17 species of fish including the edible crab were caught and analyzed. Thirteen species from five families of Teleostei were recorded with four species from Pleuronectidae and six from the Gadidae family. Cod was the most numerous species followed by plaice, lemon sole and halibut (Table 1).

Table 1: Total trammel net fish and edible crab catch numbers (No.) and average weight and length + 1 standard deviation (SD). For edible crab the measuring were not consistent for each fieldtrip, hence length and weight are not included (*).

Family and species	English name	No.	Av. weight (kg) ± SD	Av. Length (cm) ± SD
Pleuronectidae				
Hippoglossus hippoglossus	Atlantic Halibut	27	1.22 ± 1.3	47.0 ± 11.8
Limanda limanda	Common dab	16	0.32 ± 0.2	30.3 ± 5.5
Microstomus kitt	Lemon Sole	34	0.43 ± 0.2	32.8 ± 4.7
Pleuronectes platessa	Plaice	55	0.88 ± 0.5	41.0 ± 7.8
Gadidae				
Gadus morhua	Cod	98	1.59 ± 1.1	53.2 ± 11.4
Melanogrammus aeglefinus	Haddock	3	0.57 ± 0.2	38.0 ± 2.9
Pollachius pollachius	Pollack	1	0.11	23.0
Pollachius virens	Saithe	21	0.51 ± 0.5	35.2 ± 10.5
Merlangius merlangus	Whiting	2		33.0 ± 1.0
Micromesistius poutassou	Blue whiting	1	0.11	25.0
Anarhichadidae				
Anarhichas lupus	Atlantic wolffish	7	3.54 ± 1.7	70.3 ± 10.2
Cyclopteridae				
Cyclopterus lumpus	Lumpsucker	13	1.72 ± 1.4	33.3 ± 8.9
Lophiidae				
Lophius piscatorius	Monkfish	1	7.00	77.0
Chimaeridae				
Chimaera monstrosa	Rabbitfish	1	2.09	64.0
Rajidae				
Amblyraja radiata	Thorny skate	16	0.93 ± 0.3	46.6 ± 9.4
Mynxinidae				
Myxine glutinosa	Hagfish	2	0.01 ± 0.0	
Cancridae				
Cancer pagurus	Edible crab	39	*	*

3.1 Seasonal patterns in catch composition

Community structure

Species richness (S) and diversity (H’) displayed highest scores in October and lowest in March (Figure 5), but only S had a significant variation between months (KW, H = 9.1, df = 3, P = 0.028). Species evenness (J) showed no clear seasonal patterns and remained high for all months.

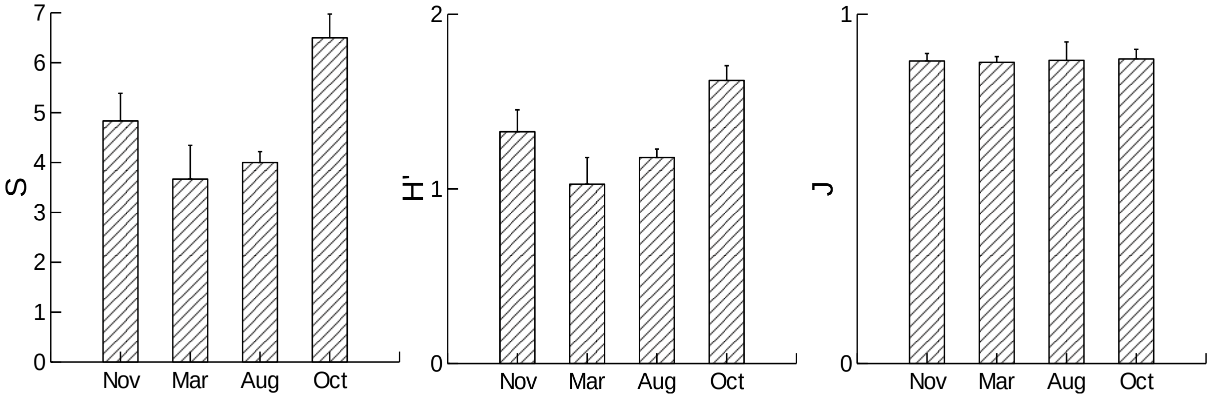

Figure 5: Mean (± SE) species richness (S), diversity (H') and evenness (J) for the net-sets at the different months excluding samples from Hekkingen. S proved significantly different from equal between months.

The species composition of the eight most numerous species showed a clear difference between months (χ^2 = 110.7, df = 21, P < 0.001). For all species at all locations and seasons see Appendix 3. Cod had the highest proportion of catch numbers for all months except March. Plaice was the most dominant species in March, followed by lemon sole and common dab. Both plaice and lemon sole displayed a decline in proportion throughout the seasonal calendar. Edible crab, halibut and skate showed higher proportion in October and November compared to March and August (Figure 6).

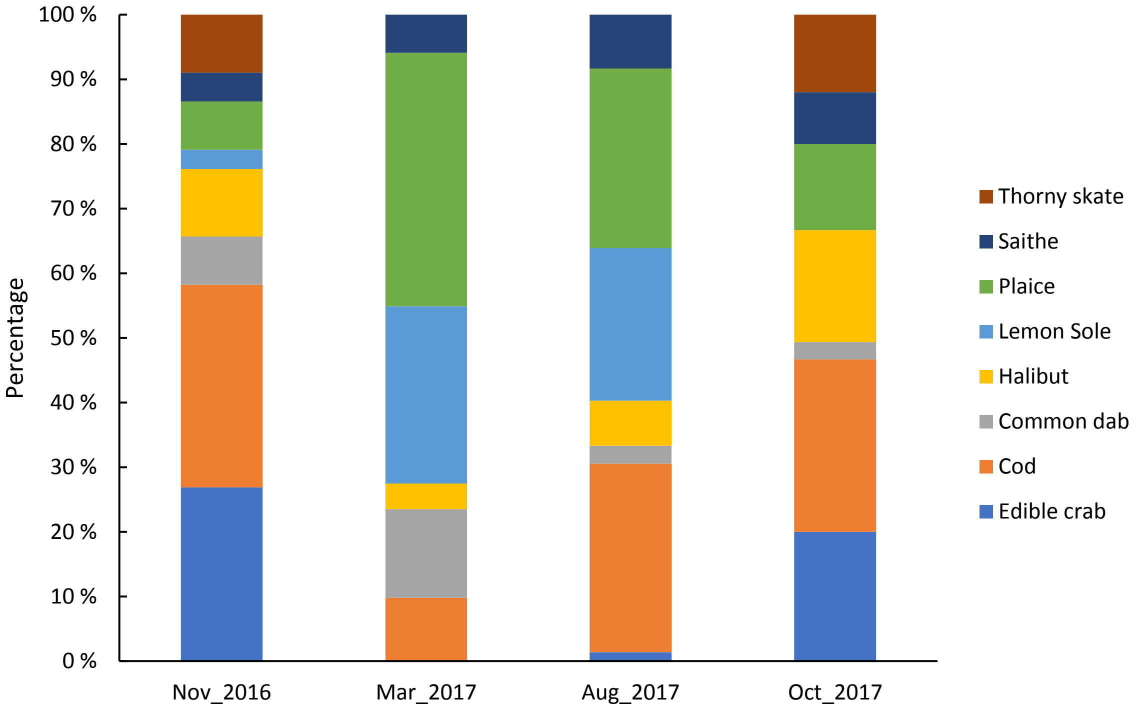

Figure 6: Species composition (% of catch numbers) by seasons, all catch data included. Percentages were calculated with the eight species summing up to 100 %.

Frequency

Edible crab, halibut and thorny skate showed higher frequency in November and October than in March and August (Figure 7). Common dab and plaice were the only species that had higher occurrence in March, while lemon sole was abundant in March, but more numerous in August. Cod showed lowest frequency in March with 5 individuals observed and 20 in October followed by 21 in both August and November (Figure 7). All species but saithe and common dab, which did not meet the assumptions of a Chi-Square test, had statistically different catch numbers between the seasons ($P < 0.05$).

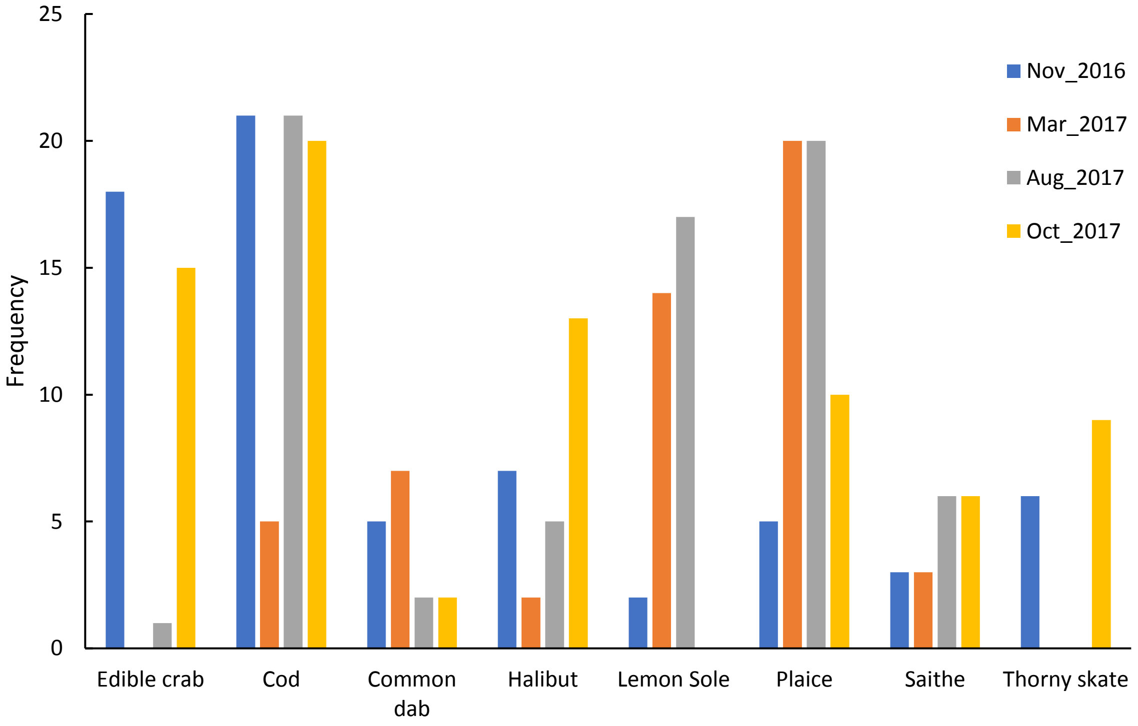

Figure 7: Total catch numbers of different commercial species at different seasons. Note that samples from Hekkingen are excluded. Areas with no bars indicate no catches. All except common dab and saithe were statistically different from equal between months.

Biomass

The total highest biomass was caught in October (125.1 kg) followed by August (97.7 kg), November (83.6 kg) and March being the lowest with 48.3 kg (Figure 8). The biomass in March was naturally lower due to no sampling at Hekkingen. All samples from Hekkingen were therefore excluded from the statistical test when testing for seasonal variation. By doing this, the rank remained the same, but the differences were less apparent with 80 kg caught in October, 78.8 kg in August, 59.3 kg in November and 48.3 kg in March. The net-set catch biomass could not be rejected to be equal between the months (KW, $H = 3.0$, $df = 3$, $P =$

0.40). The seasonal and spatial patterns of biomass were relatively similar to the patterns of catch numbers (Figure 9), however, the biomass observed at Hekkingen was comparably higher than the catch numbers (insinuation larger specimen). The seasonal variation in biomass was relatively equal at Edøya, while Skårlia peaked in August and Molvika had highest catch biomass in October (Figure 8).

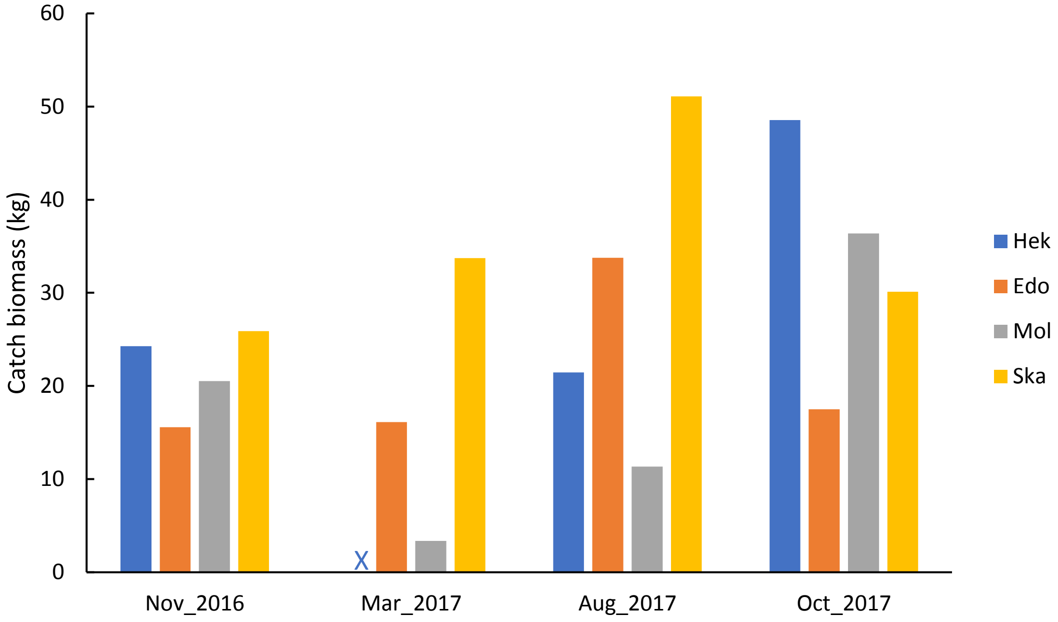

Figure 8: Total biomass of fish including edible crab at all locations at different seasons. X indicate no sampling at Hekkingen in March.

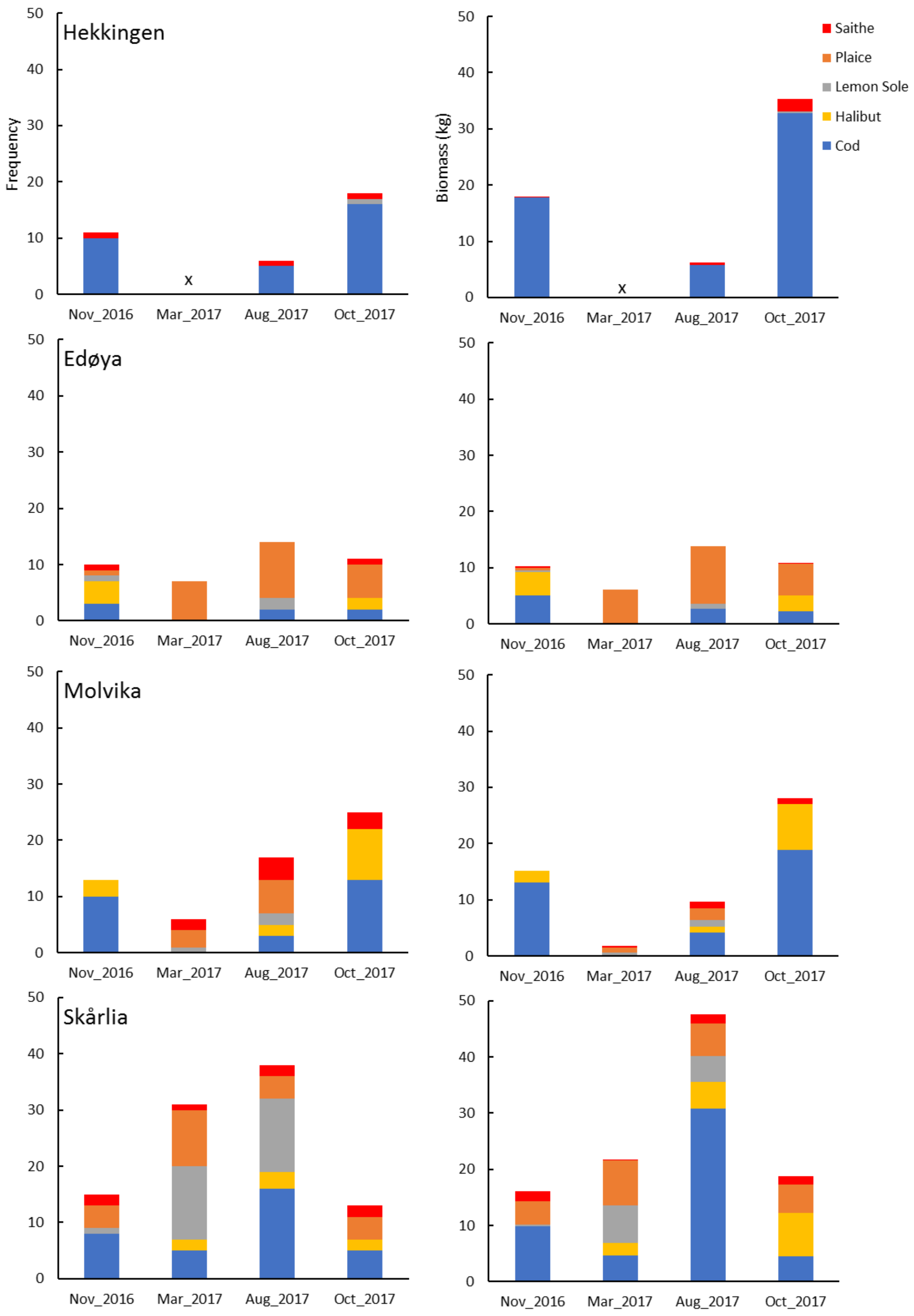

Figure 9: Numbers (left column) and biomasses (right column) for saithe, plaice, lemon sole, cod and halibut at different locations and seasons. Note that Hekkingen was not fished in March 2017 (x).

3.2 Seasonal patterns in length and age distributions

Length

Length frequency distributions were tested for equality between months for six species, and two species showed significant different distributions, namely lemon sole and saithe. Lemon soles were significantly longer in March, with a median of 36 cm, than in August (30 cm) and November (24 cm) (Table 2, Figure 10). There were however only 2 individuals in November, so an additional Mann-Whitney U test was done which also concluded that the length of lemon soles in March (n = 14) were longer than in August (n = 16) (MW, U = 39, P = 0.002). Saithe lengths were significantly longer in November (median = 42 cm) compared to the other months and saithe in March had the lowest median length of 25 cm (Table 2, Figure 10). It could not be rejected that the length distributions for cod, common dab, halibut and plaice in the different seasons was equal (Table 2). The cod caught in March had a median of 47 cm which was slightly shorter than the other three months, but the low sample size in March (5 individuals) contributed to a high and non-significant P value in the KW test.

Table 2: Kruskal-Wallis H-test result for test of length distribution at different seasons. P-values in bold are statistically significant. Total catch numbers (No.), test statistics (H) and degrees of freedom (Df).

Species	No.	H	Df	P-value
Cod	67	1.729	3	0.61
Common dab	16	4.346	3	0.20
Halibut	27	0.105	3	0.99
Lemon sole	33	13.62	2	**0.001**
Plaice	55	3.24	3	0.34
Saithe	18	7.87	3	**0.047**

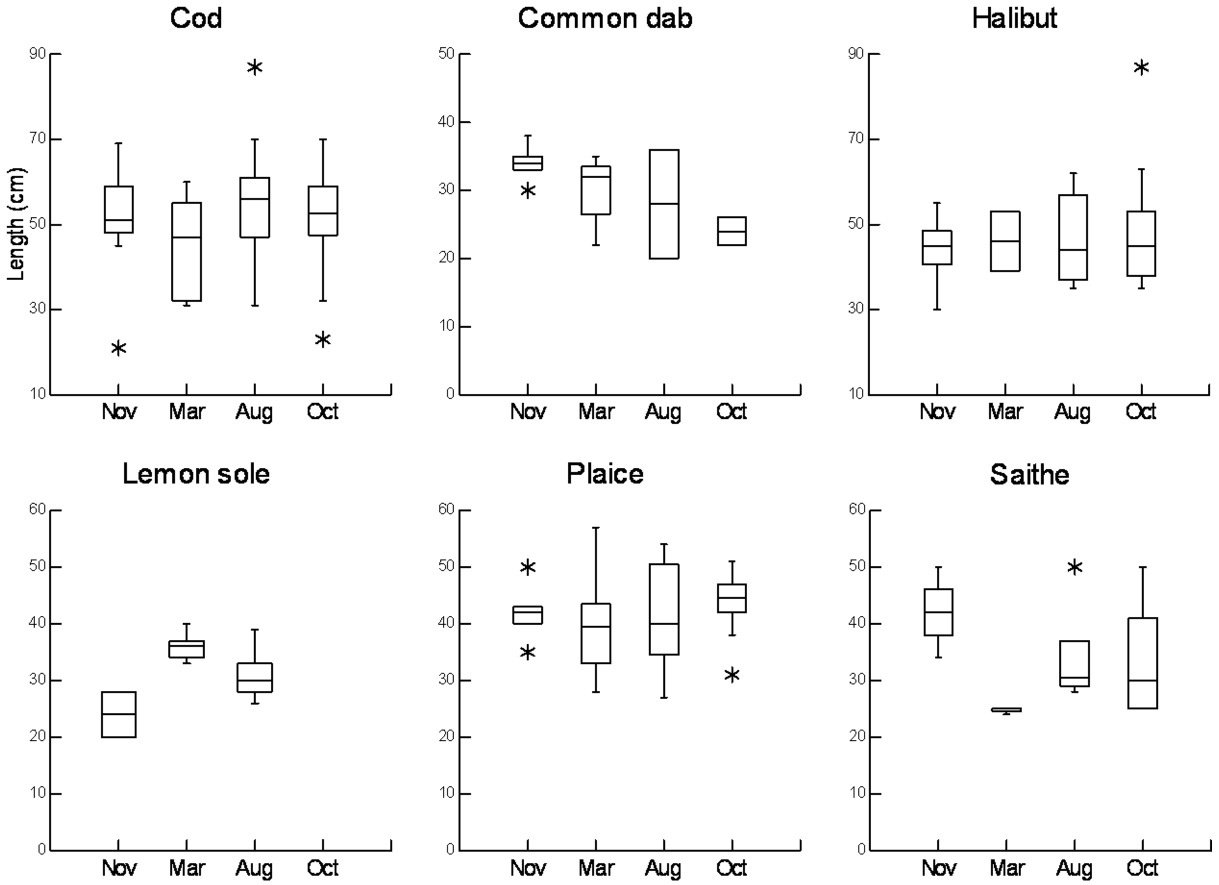

Figure 10: Box plot showing median (line), upper and lower quartile as well as maximum and minimum length for cod, common dab, halibut, lemon sole, plaice and saithe at different months. Note that samples from Hekkingen are excluded and that y-axis values differ between plots. Lemon sole and saithe statistically different from equal between the months. Stars indicate outliers.

Age distribution and length at age

Age distributions were not significant different from equality for most species at different months, but in line with the length distributions, equality was rejected for lemon sole (Table 3). The lemon soles observed in March were older than the lemon soles observed in August. Cod, lemon sole and plaice displayed asymptotic growth which declined as the fishes grew older whereas halibut seemed to have a linear growth (Figure 12). Lemon sole otoliths were only available from March and August, and they were significantly older in March (n = 14) with a median age of 7 years compared to 5 years in August (n = 9) (Table 3, Figure 11, Figure 12). Plaice showed a generally lower age distribution in November compared to the other months. However, there were only 3 fish caught in November and therefore it could not be rejected that the age distributions among the four months were equal (Table 3, Figure 11). Spawning individuals of lemon sole and plaice were observed in March.

Table 3: Kruskal-Wallis H-test results (H) and Mann-Whitney U-test results (U) with P-values for test of equality of age distributions between season for cod, halibut, lemon sole and plaice. P-values in bold indicate a significant result. Total number of individuals displayed as (No.), degrees of freedom as (Df).

Species	No.	U	H	Df	P-value
Cod	65	-	1.904	3	0.59
Halibut	27	-	1.45	3	0.69
Lemon sole	23	20	-	1	**0.005**
Plaice	51	-	1.93	3	0.59

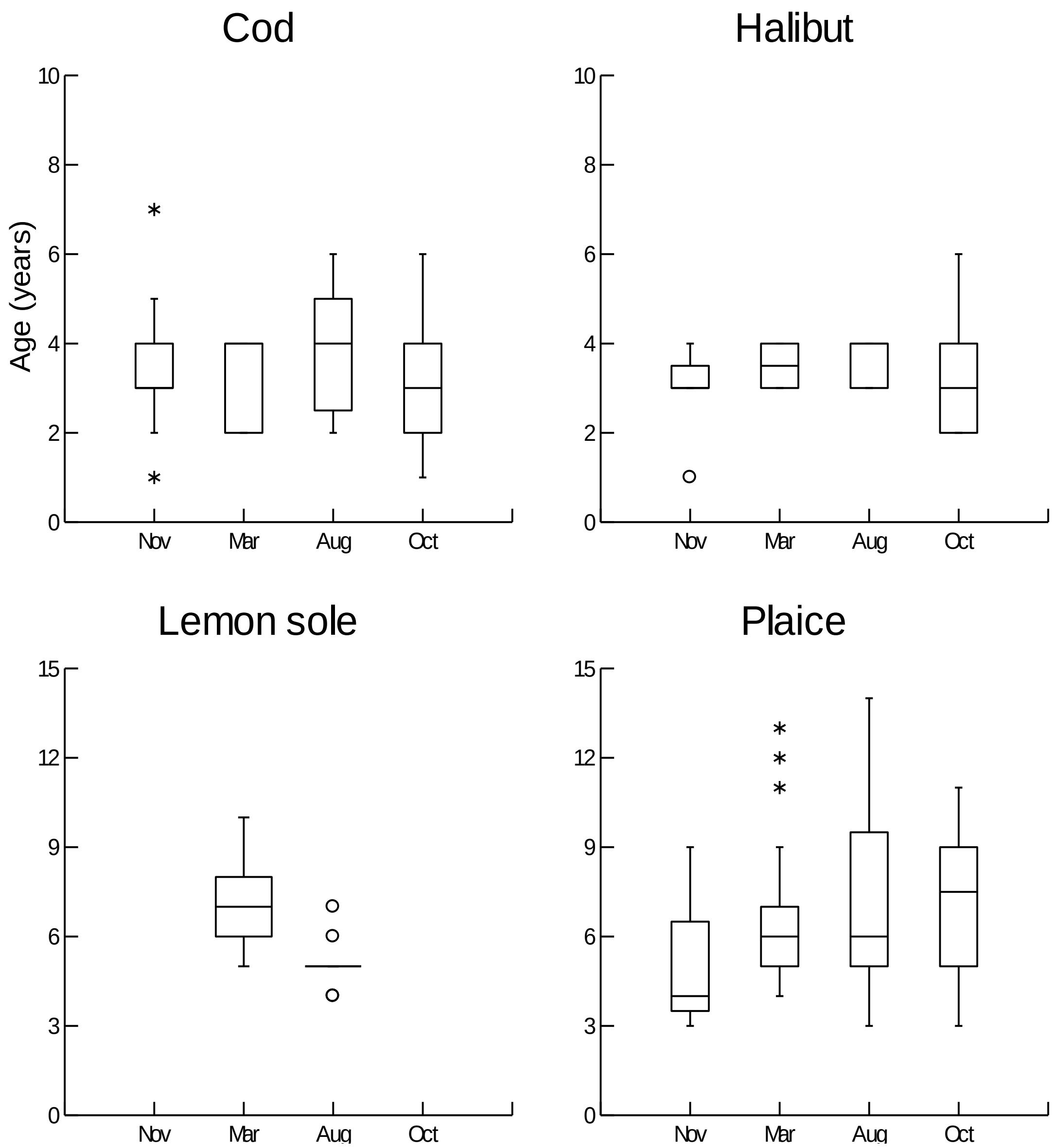

Figure 11: Box plot showing median (line), boarders for upper and lower quartile as well as maximum and minimum age for cod, halibut, lemon sole and plaice. Hekkingen data were excluded. Lemon sole statistically higher age distribution in March compared with August. Note different values for Y-axis between plots. Stars indicate outliers.

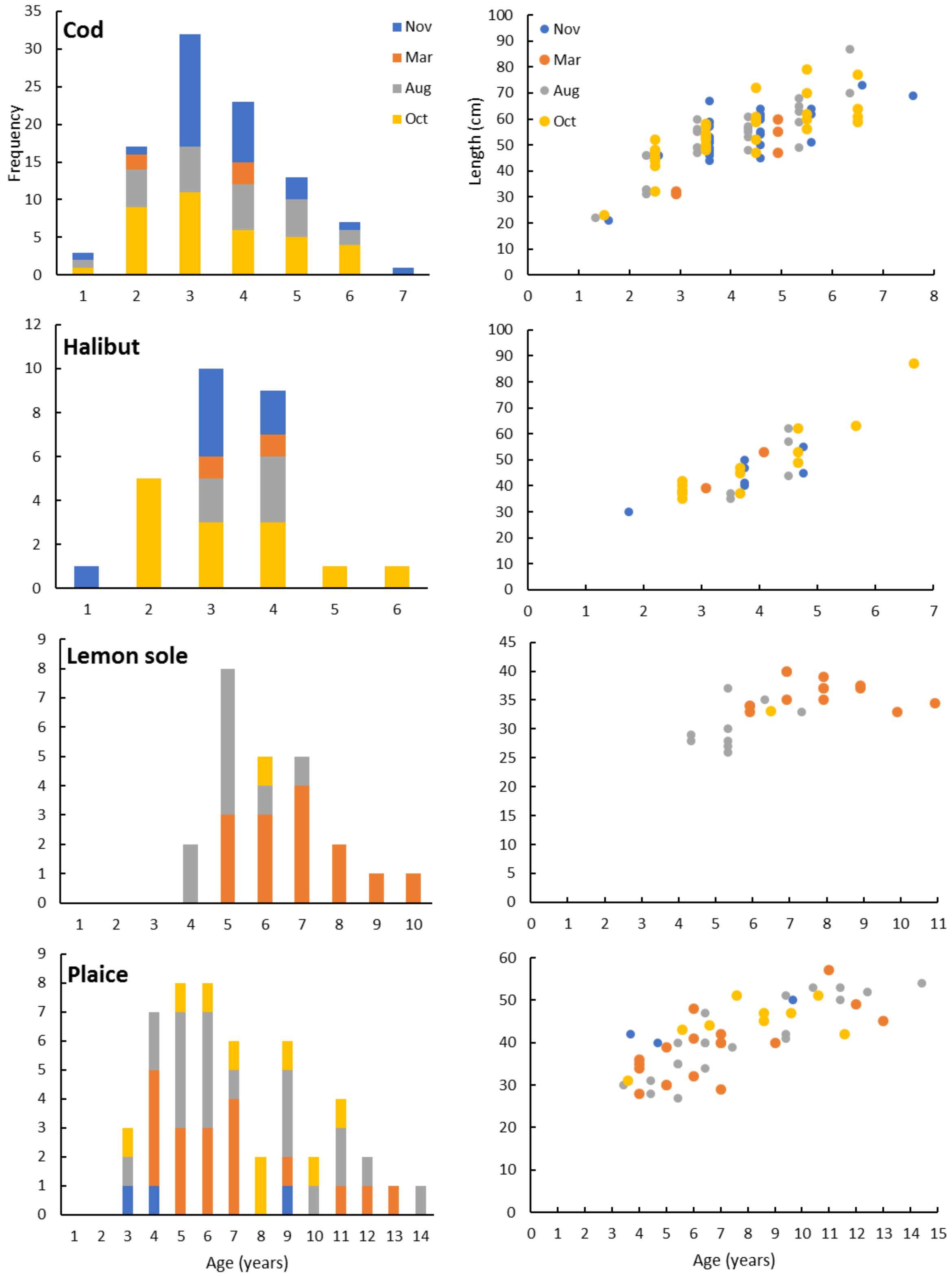

Figure 12: Age frequency distribution (Left panels) and length at age (right panels) for cod, halibut, lemon sole and plaice. Note that length at age is adjusted age according to expected spawning time. Cod and lemon sole born in April, plaice in March and halibut in February. Note different axis values. All trammel net data included.

3.3 Spatial patterns in catch composition

Species composition

Species richness (S) and diversity (H’) were highest at Skårlia and lowest at Hekkingen (Figure 13). The spatial effect on S and H’ was significant as indicated by Kruskal-Wallis tests (KW = 8.02, df = 3, P= 0.046 and KW = 10.1, df = 3, P = 0.018 respectively). There was no clear pattern for evenness (J) in relation to spatial effect.

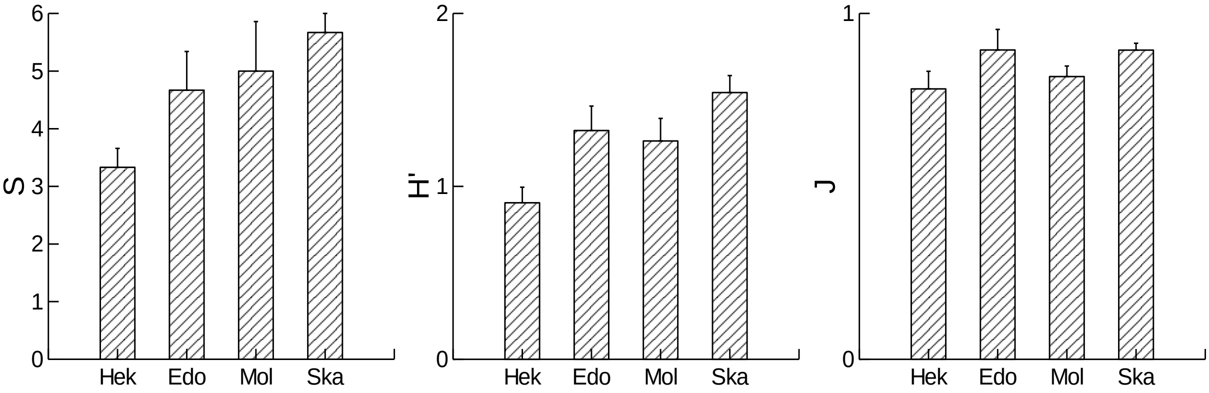

Figure 13: Mean (± SE) species richness (S), Shannon Wiener diversity (H'), evenness (J) for the net-sets at all four locations, excluding samples from March. Both S and H’ statistically different from equal between the locations.

The catch proportion of number of species at the different locations was not equal ($\chi^2 = 99.4$, df = 21, P < 0.001). Of the eight most numerous species, cod was the most dominant at all locations except Edøya, where plaice dominated the catches. The proportion of cod was highest at Hekkingen with the catches consisting of 75 % cod (Figure 14). Edøya, Molvika and Skårlia showed a somewhat similar species composition, but plaice showed a higher dominance at Edøya whereas cod were the more dominant species at Molvika and Skårlia (Figure 14). Edøya were generally dominated by flatfish, whereas both Molvika and Skårlia had a large proportion of cod.

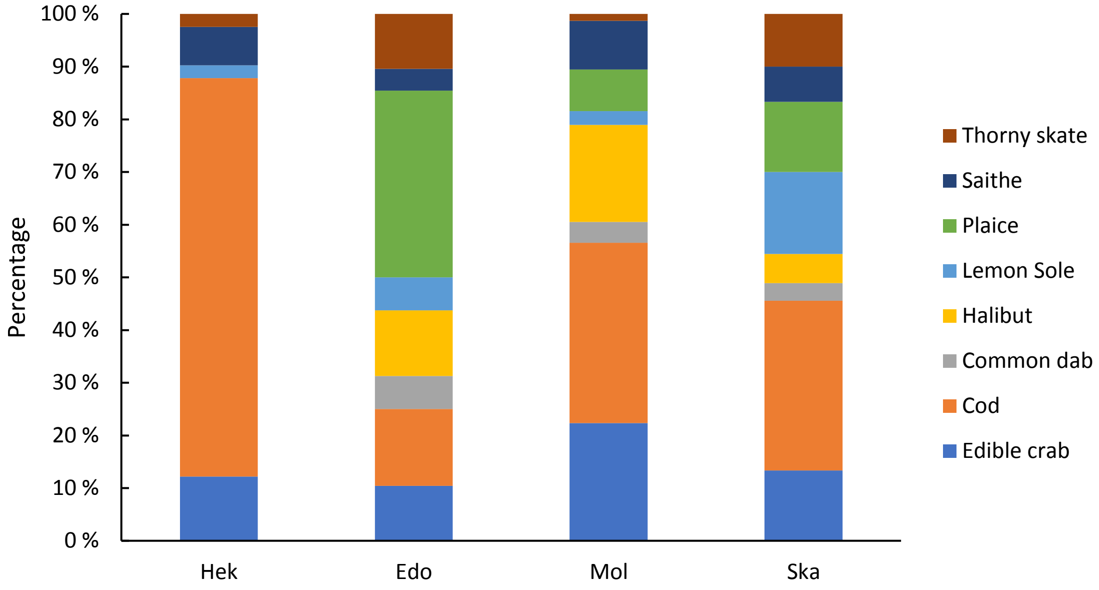

Figure 14: Species composition (% of catch numbers) by location for trammel net catches, excluding March data. Percentage calculated with the eight species being 100 %.

According to Sorenson's coefficient (CC), Edøya, Molvika and Skårlia had a high degree of pairwise overlap (CC > 0.8), whereas Hekkingen was more unique with lower pairwise overlap, all fish species accounted for (Table 4).

Table 4: Sorenson's coefficient (CC) for the four different locations. C represent species in common, S 1 and 2 represent species richness at each location.

Loc 1	Loc 2	C	S 1	S 2	CC
Ska	Edo	9	11	10	0.86
Ska	Hek	7	11	10	0.67
Ska	Mol	10	11	12	0.87
Edo	Mol	9	10	12	0.82
Edo	Hek	6	10	10	0.60
Hek	Mol	6	10	12	0.54

Total species frequency and biomass

Skårlia stood out as the locations where most species had relatively high catch numbers (Figure 15). Common dab, saithe and thorny skate did not meet the assumptions of expected values for Chi-square tests, while the rest of the species all had significantly different catch numbers at the different locations (Chi-square tests, $P < 0.05$). The highest frequency of lemon soles was observed at Skårlia, with a few observations at all other locations. Flatfishes were close to absent at Hekkingen, except for one lemon sole caught in October. Common dab and plaice were the species with the highest frequencies at Edøya. Cod catches were not equal at the different locations ($\chi^2 = 15.69$, df = 3, P = 0.001). Cod showed highest catch numbers at Hekkingen, but the clearest difference was the low frequency observed at Edøya (Figure 15).

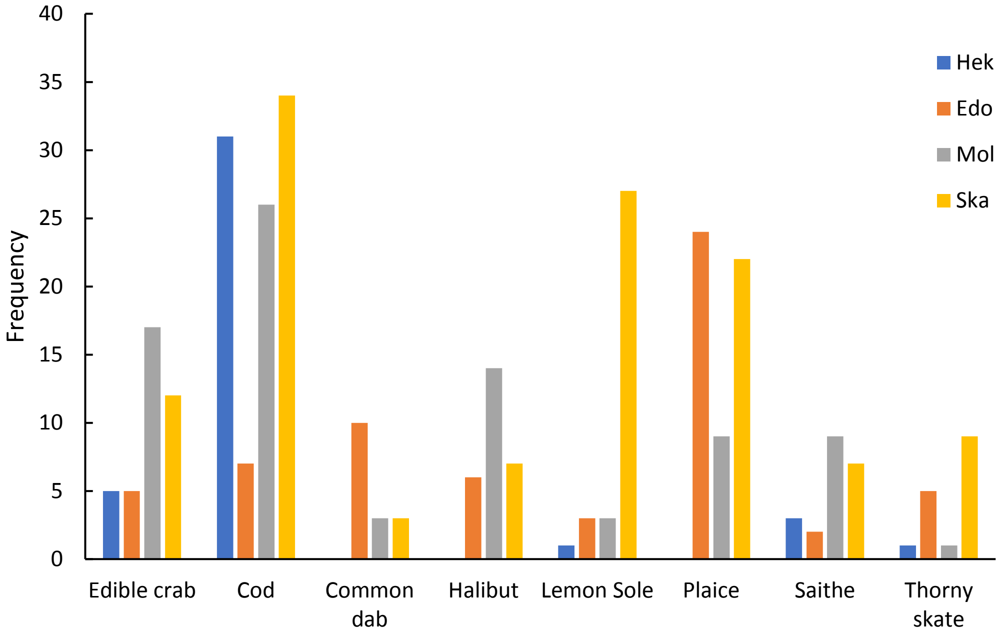

Figure 15: Total number of fishes at different locations, all data included. No bars indicate no catch.

When excluding samples from March, the total number of biomass was highest at Skårlia with 106 kg, followed by Hekkingen (88.5 kg), Molvika (65.5 kg) and Edøya (44.7 kg). It could not however, be rejected that the mean net-set biomass at each location was equal (KW, H = 6.738, df = 3, P = 0.08) (Figure 9).

3.4 Spatial patterns in length and age distributions

Length

The three flatfish halibut, plaice and common dab all showed a trend where shorter individuals were observed at Molvika compared with the other locations (Figure 16). The length distributions at the four locations were however only significantly different for plaice and common dab (Table 5). It could not be rejected that the length distributions for cod, halibut, lemon sole and saithe were equal for the different locations. The smallest common dab median length was found at Molvika (22 cm) followed by Edøya (32.5 cm) then Skårlia (35 cm) (Figure 16). The median length of plaice was 30 cm at Molvika (n = 9) which was shorter than Edøya (n = 22) and Skårlia (n = 23) (Figure 16).

Table 5: Kruskal-Wallis H-test results for equality in length distributions at different locations. P-values in bold indicate a significant result.

Species	No.	H	Df	P
Cod	93	1.523	3	0.6
Common dab	16	6.043	2	**0.049**
Halibut	27	4.371	2	0.11
Lemon sole	33	1.218	2	0.5
Plaice	54	19.15	2	**<0.001**
Saithe	18	5.471	3	0.14

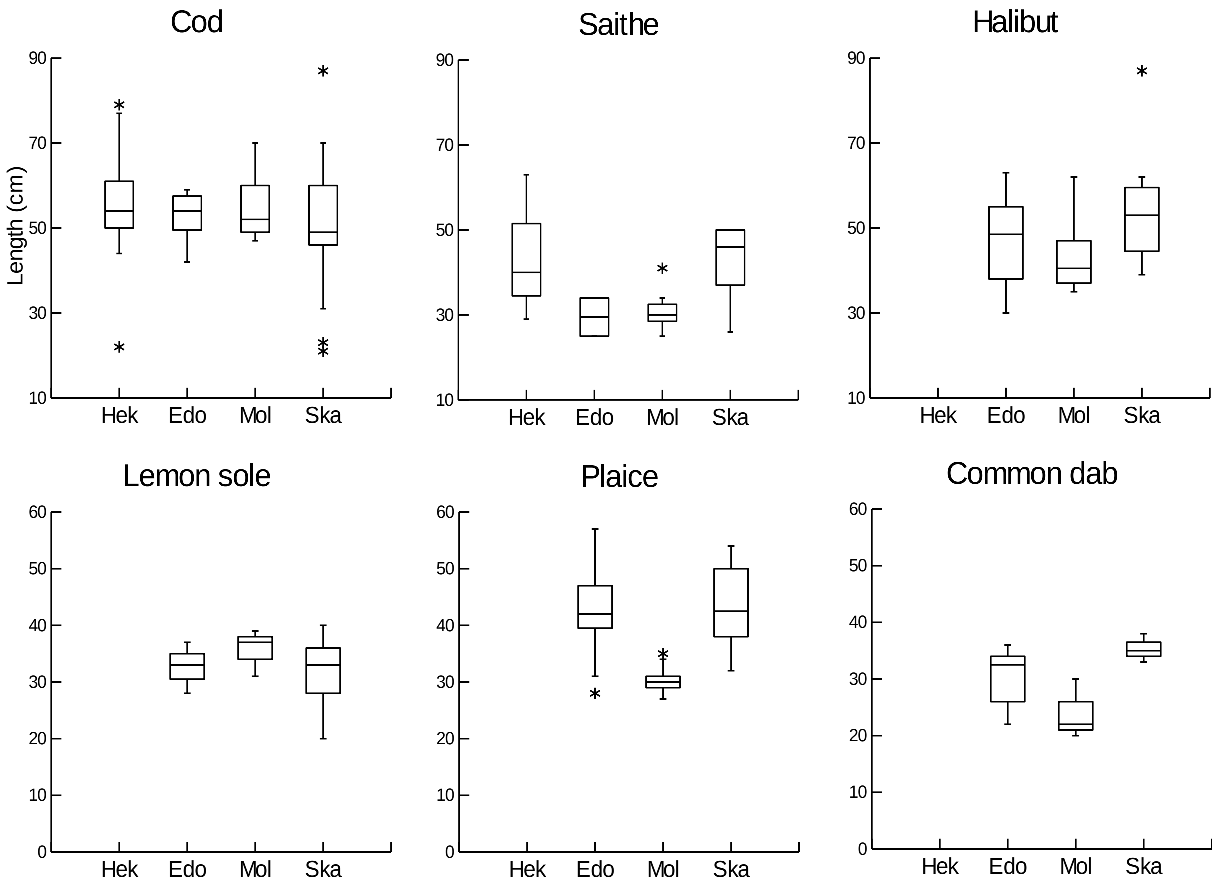

Figure 16: Box plot showing median (line), border for upper and lower quartile as well as maximum and minimum length for Cod, saithe, halibut, lemon sole, plaice and common dab. Stars indicating outliers. Note different Y-axis values. March data were excluded for cod and saithe and Hekkingen data were excluded for the flatfishes.

Age distribution and length at age

Only plaice showed a difference in age distribution between the locations. Plaice caught at Molvika were significantly younger (median 5 year) than plaice caught at Edøya and Skårlia (median 7 years) (Table 6, Figure 17). Both Edøya and Skårlia showed a large age-range of plaice (3-11 and 3-14 years respectively), whereas only younger individuals were observed at

Molvika (3-6 years) (Figure 17). It could not be rejected that the age distributions of cod, halibut and lemon sole were equal at the different locations (Table 6).

The oldest plaice males observed were 9 years while the oldest female was 14 years. Age distribution for plaice males were younger than females with a median age of 6 year and 7 years for females (MW, U=279, P = 0.047). The age distributions for the other species did not differ between sexes.

Table 6: Kruskal-Wallis H-test results for equality in age distributions at different locations. P-values in bold indicate a significant result.

Species	No.	H	Df	P
Cod	90	3.757	3	0.29
Halibut	27	4.388	2	0.11
Lemon sole	23	1.414	2	0.49
Plaice	50	6.417	2	**0.04**

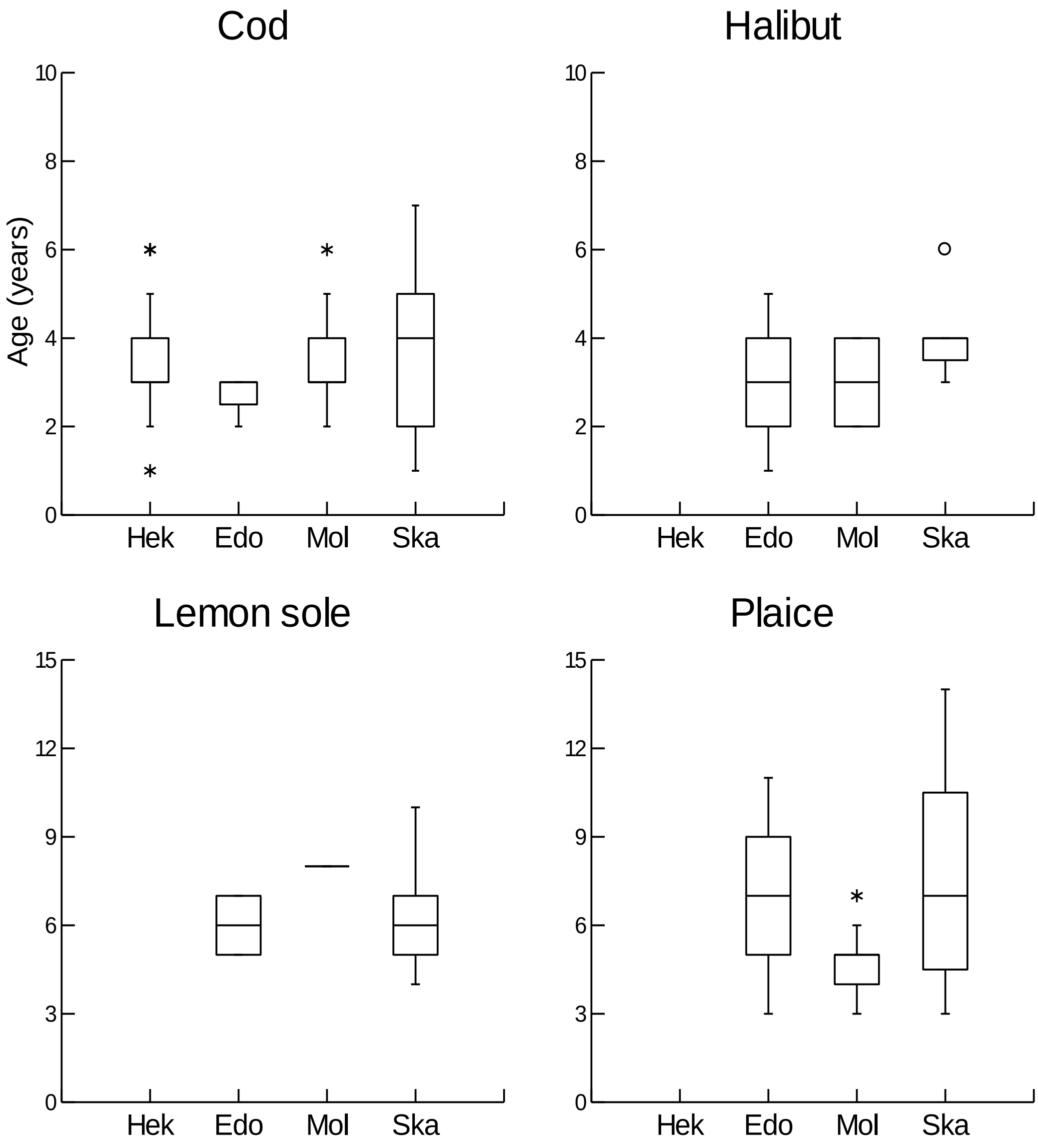

Figure 17: Box plot displaying median (line), border for upper and lower quartile age as well as maximum and minimum age for cod, halibut, lemon sole and plaice at different locations. Note that y-axis values differ.

Cod, lemon sole and plaice all had a general decline in catch rates from recruitment age (Figure 18), these catch rates were used to estimate annual mortality rates (Z) in the following chapter.

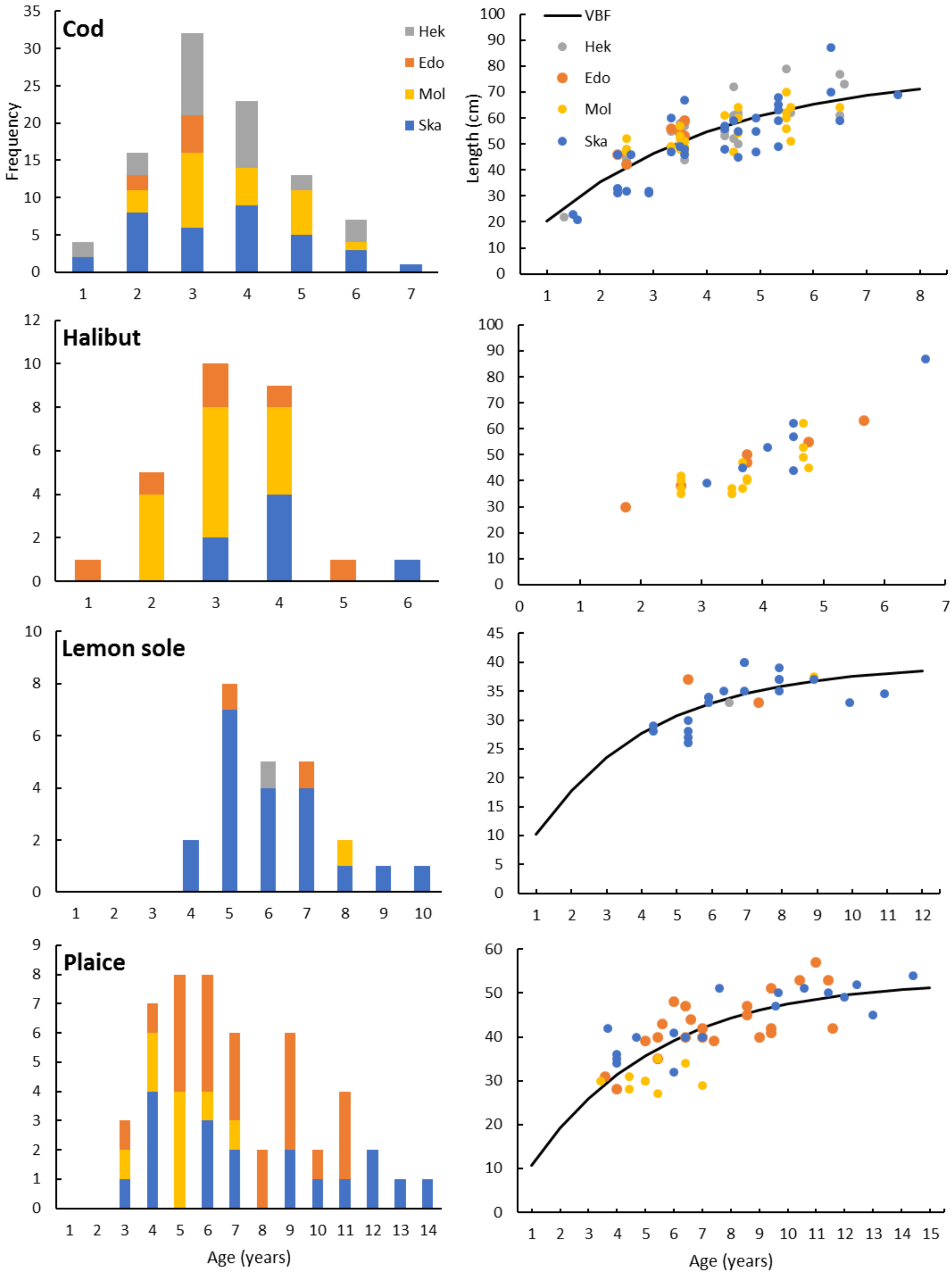

Figure 18: Age distribution (left column) and length at age (right column) for cod, plaice, halibut and lemon sole at different locations. Von Bertalanffy's growth function showed in black line. Cod and lemon sole born in April, plaice in March and halibut in February. Note that axis values differ. All trammel net data were included.

3.5 Growth and mortality rate

Von Bertalanffy parameters (L_∞ and K) and total mortality rate (Z) were estimated for plaice, cod and lemon sole (Table 7), sex was differentiated for plaice and cod, but lemon sole lacked sufficient data. Cod had the highest total mortality rate (0.69 $year^{-1}$) while plaice mortality was estimated to be 0.31 with a 95% confidence interval from 0.22 to 0.41 $year^{-1}$ (Table 7). Von Bertalanffy growth curves are displayed in (Figure 18). Cod and lemon sole had the same K coefficient, but lemon sole had a higher 95% CI. Female specimen had higher L_∞ and lower K for both plaice and cod.

Table 7: Von Bertalanffy's growth function parameters L_∞ and K, and total mortality (Z) estimates for Plaice, Cod and Lemon sole. 95 % Upper and lower 95% confidence interval (CI) showed in brackets. Text in bold are results for pooled sex.

SPECIES	SEX	L_∞ (95% CI)	K (95% CI)	Z (95% CI)
PLAICE	Pooled	**53.1 (47.77-58.42)**	**0.224 (0.168-0.280)**	**0.31 (0.22-0.41)**
	Female	53.2 (47.27-59-22)	0.240 (0.160-0.320)	
	Male	42.8 (37.03-48.59)	0.404 (0.184-0.624)	
COD	Pooled	**78.1 (68.77-87.39)**	**0.301 (0.229-0.373)**	**0.69 (0.50-0.89)**
	Female	83.9 (61.5-106.2)	0.260 (0.128-0.391)	
	Male	71.2 (61.35-81.08)	0.363 (0.253-0.473)	
LEMON SOLE	Pooled	**39.5 (34.39-44.63)**	**0.301 (0.177-0.425)**	**0.52 (0.38-0.65)**

3.6 Habitat and substrate coverage

Coverage of various substrate categories showed large variability between locations (Figure 19). Hekkingen had the highest coverage of high algae (93 %). Molvika and Edøya had similar coverage distributions where sand and pebble dominated the bottom substrates, however there were more low algae and shell fragments coverage and less cobble and bedrock at Molvika. Skårlia had high coverage of cobble and low algae as well as some patches with sand (Figure 19). Skårlia was the location with highest degree of substrate evenness, whereas Hekkingen was largely homogenously covered with high algae (Table 8).

Table 8: Habitat evenness (Jsub) at the four locations.

	Hekkingen	Edøya	Molvika	Skårlia
Jsub	0.199	0.647	0.670	0.790

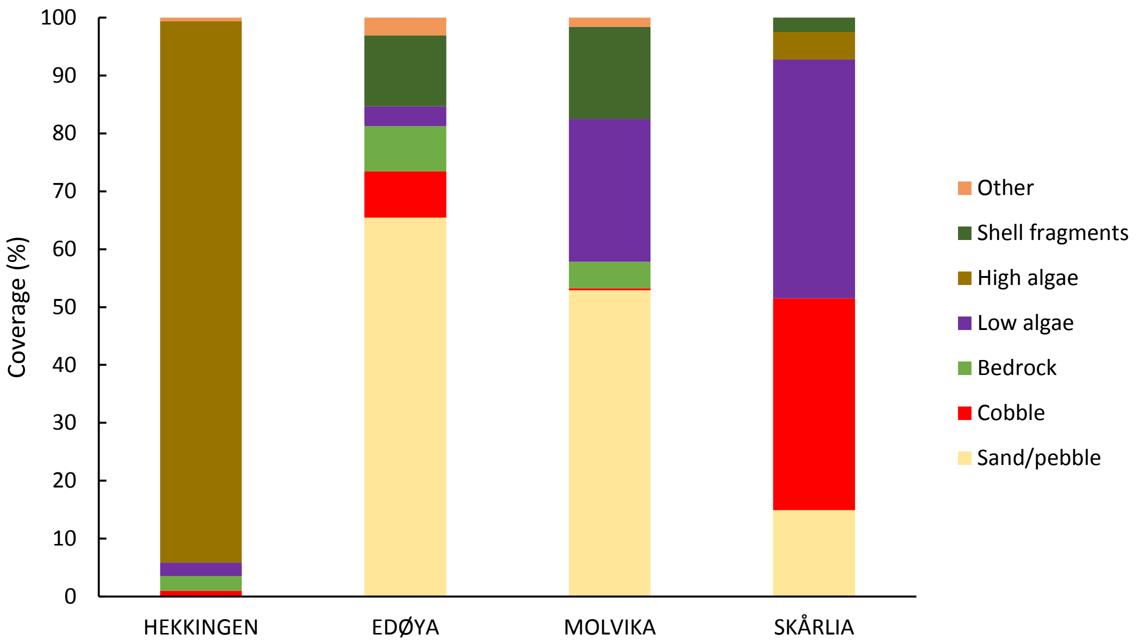

Figure 19: Coverage of various bottom substrate categories observed with video survey at different locations in August 2017.

3.7 Substrate associations

A Spearman rank correlation test was used to identify community parameters relationships with bottom substrate evenness. Both mean species richness (S) and diversity (H') were positively correlated with substrate evenness (Jsub) ($R_S = 0.5$, $P = 0.004$ and $R_S = 0.52$, $P = 0.003$) respectively). Halibut and lemon sole were both significantly positively correlated with substrate evenness (Jsub), ($r_S = 0.4$, $P = 0.03$) for halibut and lemon sole ($r_S = 0.37$, $P = 0.04$) whereas for plaice ($r_S = 0.34$) and saithe ($r_S = 0.33$), the test results were close to significant ($P = 0.067$ and $P = 0.073$, respectively).

The following canonical correspondence analysis (CCA) aimed to display habitat associations of the species in focus. The species-environment ordination diagram (Figure 20) display the CCA results from eight species and five environmental variables. Sand/pebble, cobble, low algae, high algae and urchin cover were used as environmental variables as they were the most prominent variables at all locations. The CCA explained 40 % of species variance at all four locations and seasons, and the first three axes accounted for close to 100 % of this variation. According to a permutation test with 999 permutations, the three first canonical axes were all significant ($P < 0.05$). Axis 1 explained 59.5% of the variance while axis 2 explained 26.3% with eigenvalues of 0.238 and 0.105 respectively. Axis 3 had an eigenvalue of 0.057 and explained 14.3% of the species-environmental variance (Table 9).

Table 9: Eigenvalues percentage of variation explained by each axis for the ordination plot in Figure 20, and Permutation test results (P-value).

Axis	Eigenvalue	%	P-value
1	0.238	59.5	0.006
2	0.105	26.25	0.012
3	0.057	14.25	0.004

The first synthetic gradient (axis 1) clearly separated locations with sand / pebble (negative) and high algae (positive) coverage (Table 10, Figure 20A), which is seen by net-set catch compositions at Edøya (negatively) and Hekkingen (positively) with the first axis. Hekkingen was largely unique with no overlap with the other locations. Molvika and Skårlia had some degree of overlap for the first axis (Figure 20A).

Axis 2 is mostly positively explained by cobble coverage (0.4) and to a lesser degree by low and high algae coverage (0.17). This habitat is mostly found at Skårlia which had the highest proportional coverage of both cobble and low algae. The second axis was weakly negatively related with urchin cover and sand/pebble (-0.21 and -0.32 respectively) (Table 10), which is found mostly at Edøya and Molvika.

Looking at the third axis a separation was prominent where Molvika in average was positively related with the axis, which was explained by low algae (0.53), and Hekkingen and Edøya negatively related with the axis which was explained by urchin and high algae coverage (Table 10, Figure 20B).

Table 10: Regression for environmental variables on the first three axes (AX1-AX3). L. and H. algae abbreviations for low and high algae and Ur.cover is urchin coverage.

	Sand/pebble	Cobble	L. algae	H. algae	Ur.cover
AX1	-0.61	-0.25	-0.04	0.61	-0.52
AX2	-0.32	0.41	0.17	0.17	-0.21
AX3	0.21	0.10	0.53	-0.38	-0.28

The results from the CCA highlighted many species-environmental relationships. Five of the eight most abundant species had significant correlation with one or more bottom substrates (Table 11). The first axis of the ordination plot seems to separate the flatfish (benthic species) from the more benthopelagic species (cod and saithe). The second axis shows some distinction between species related with sand / pebble to species that are more related with cobble, low and high algae coverage. The third axis separates halibut, lemon sole, saithe and edible crab which are positively related to the axis with common dab, cod, plaice and skate which are negatively related to the axis (Figure 20B). For axis scores for all species see Appendix table 2.

Cod seemed to be associated with habitats with high algae coverage rather than sand / pebble, as seen by axis 1 of the ordination plot (Figure 20A). This was supported by the Spearman rank correlation which showed that cod abundance was significantly ($P < 0.05$) positively correlated with high algae ($R_s = 0.53$) and negatively related with sand / pebble ($R_s = -0.58$) as well as urchin coverage ($R_s = -0.54$).

Halibut had the clearest association found for low algae coverage as demonstrated by a negative relationship to the third axis. Halibut abundance was significantly correlated with low algae coverage ($R_s = 0.4$) (Table 11).

We can suggest that plaice had a strong positive relation with sand / pebble and urchin coverage as demonstrated by its negative association with the first axis. The third axis also highlight a possible relation between plaice and cobble coverage (Figure 20B). The spearman rank test supports these findings to some degree, as plaice was significantly positively related with both sand / pebble and cobble ($P < 0.05$), but there was no correlation between plaice and urchin coverage (Table 11).

Lemon sole catches were associated with the second and third axis (Figure 20 A&B). At the second axis, lemon sole observations seem to be positively related with cobble, whereas the third axis suggests a strong positive association with low algae coverage. These findings are further supported by significant positive correlations ($R_s = 0.37$) with both substrate categories (Table 11).

Common dab was the species with the highest negative regression at the first axis, suggesting the species has a strong association with sand / pebble and urchin coverage. The Spearman rank correlations confirmed a significant positive correlation for sand / pebble as well as a significant negative relation towards high algae coverage (Table 11).

Table 11: Spearman rank correlations for species catches and substrate coverage categories, with net-set catches as observation units. Values in bold indicate significant correlations. P-values in brackets.

Species	Sand/pebble		Cobble		Low algae		High algae		Urchin cover	
Cod	**-0.58**	**(0.001)**	0.08		0.09		**0.53**	**(0.003)**	**-0.54**	**(0.002)**
Halibut	0.20		0.00		**0.40**	**(0.029)**	-0.29		-0.01	
Plaice	**0.36**	**(0.049)**	**0.50**	**(0.004)**	0.34	(0.067)	-0.24		0.07	
Lemon sole	-0.05		**0.37**	**(0.041)**	**0.37**	**(0.042)**	0.07		-0.27	
Saithe	-0.22		0.05		0.33	(0.073)	0.12		-0.34	(0.065)
Edible crab	-0.06		-0.12		0.17		-0.04		-0.11	
Common dab	**0.50**	**(0.005)**	-0.01		-0.04		**-0.44**	**(0.014)**	**0.44**	**(0.016)**
Thorny skate	0.06		0.29		0.14		0.01		-0.06	

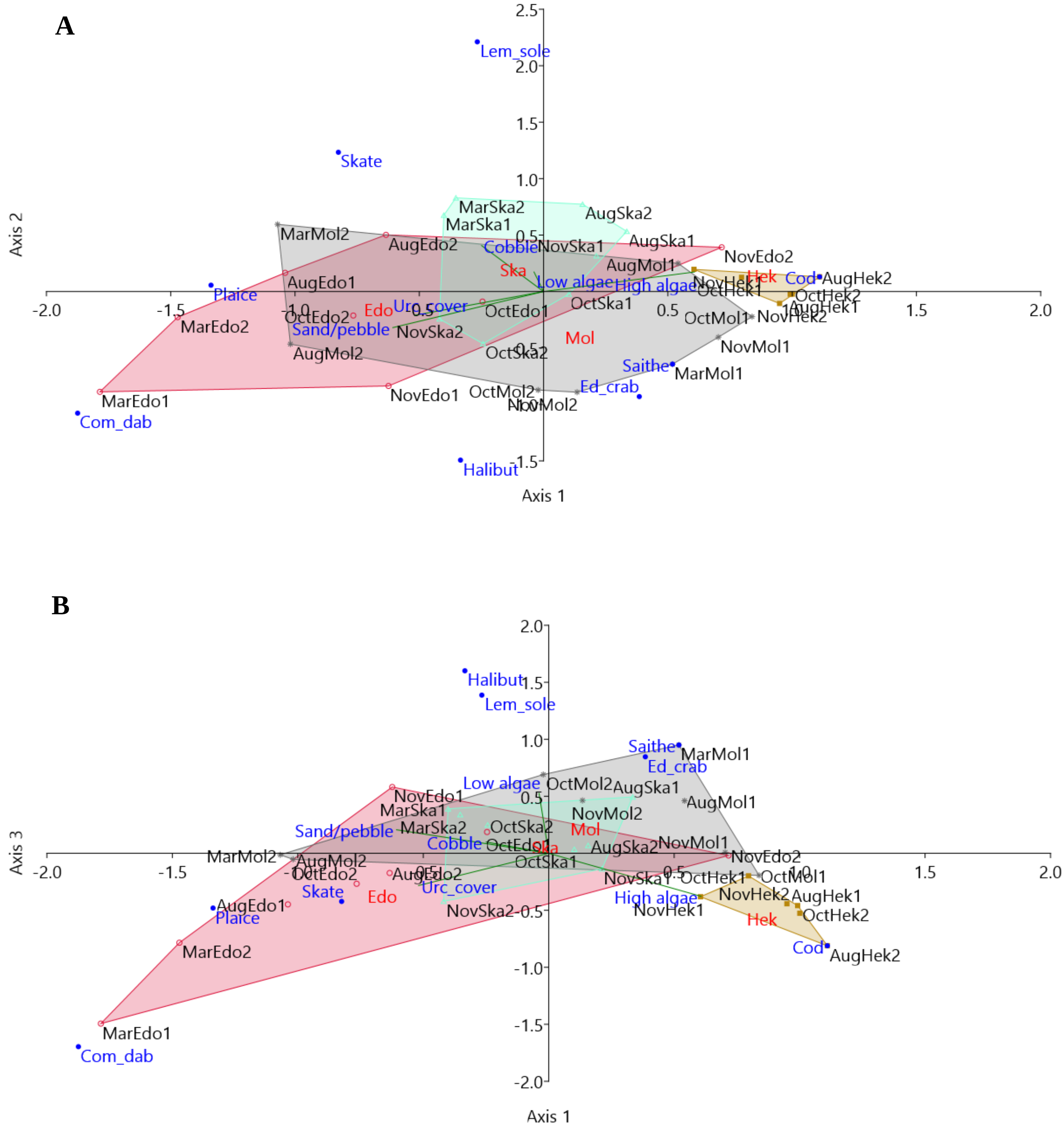

*Figure 20: Ordination diagram of Axis 1 and 2 (**A**) and Axis 1 and 3 (**B**) from the canonical correspondence analysis (CCA). Species points represent the centroid (weighted average) of the site points in which it occurs, and vectors represent the regression relationships of environmental variables with the canonical axes. The species points indicate the relative locations of the two-dimensional niches of the species in the ordination diagram (Braak and Verdonschot, 1995). The sites are abbreviated with first three letters of month then location. Hekkingen is represented by six points as there were no sampling in March. The abbreviated name of each location represents the centroid of the site, which is a weighted average. Edøya in red polygon, Molvika in grey, Skårlia in turquoise and Hekkingen in brown.*

An additional CCA was preformed to further highlight possible seasonal patterns (Figure 21). For this CCA the four months were used as binary environmental variables, as well as sand / pebble, cobble, low- and high algae coverage. Lumpsucker (*Cyclopterus lumpus* L.) and wolffish were included in order to have sufficient species for the increase in environmental variables. Axis 1 and 2 had eigenvalues of 0.398 and 0.209 respectively, and the first axis stood for 49% of the explained variance while the second axis explained 25.5%. Both the axes were significant (Permutation test, $P < 0.005$) (Table 12). The first axis identified a clear similarity between October / November as well as a separation between these two months (positive) and March (negative). August had a positive relation to the second axis whereas the other months were slightly negatively related with this axis. The third axis was not proven significant ($P > 0.05$). All flatfishes except halibut were negatively related with the first axis. This association was explained by the environmental variables March, August, sand/pebble and cobble. The second axis separated lemon sole, wolfish, cod and saithe (positive) with common dab, thorny skate, halibut, edible crab, plaice and lumpsucker (negative). Interestingly, the ordination diagram separates lemon sole as the only flatfish species positively associated with the second axis. Most of the explanation derive from positive relation with March on the first axis and from August on the second axis, whereas plaice and common dab seems to be more associated with sand/pebble (and March), than August.

Table 12: Eigenvalues, percentage explained and p-value for the first two axes of CCA in Figure 21.

Axis	Eigenvalue	%	P-value
1	0.398	48.96	0.001
2	0.209	25.57	0.004

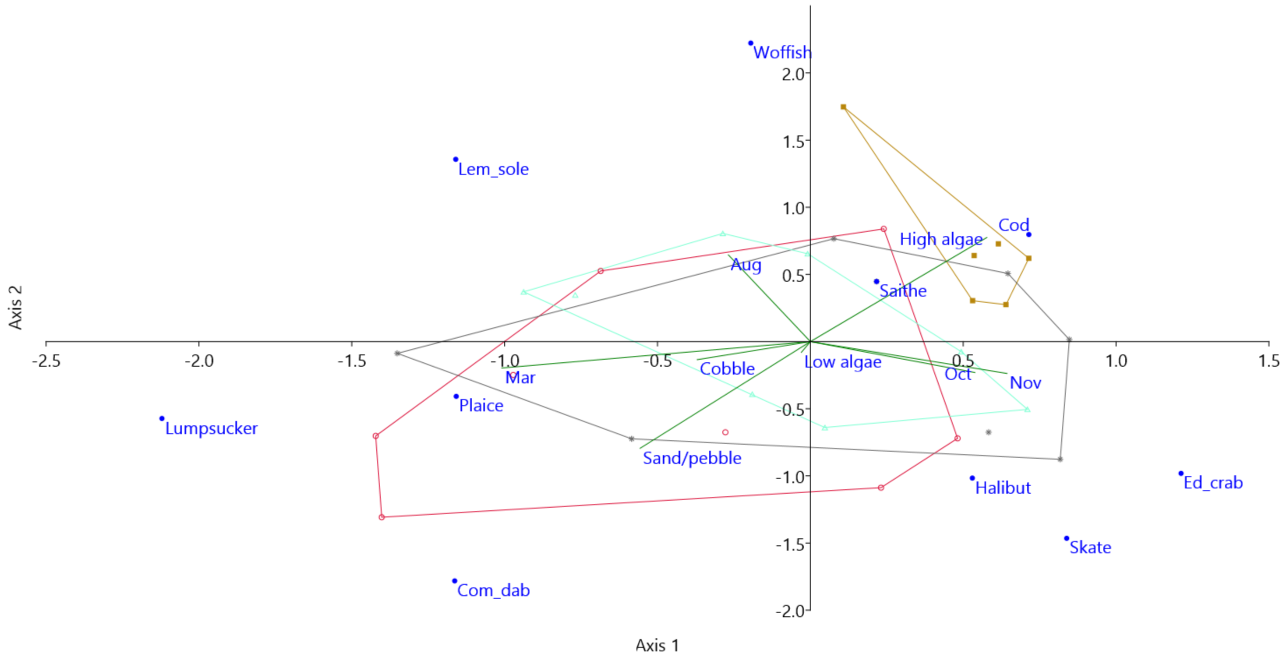

Figure 21: Ordination plot from canonical correspondence analysis (CCA) displaying seasonal patterns in catches. Vectors for environmental variables (green lines) are amplified by x1.5. Brown polygon represent Hekkingen, red is Edøya, turquois is Skårlia and grey is Molvika.

4 Discussion

4.1 Study design

The main goal of this study was to investigate whether fish communities were affected by seasonal and spatial variation on a community and species scale, and thereby to identify possible species habitat associations for the most abundant species in the coastal area. The present study offers an overview of the fish communities at four locations in the outer part of Malangen. The four locations portrayed different bottom substrate coverage and evenness, ranging from Hekkingen being largely homogenously covered with high algae to Skårlia which had a relatively heterogenous habitat covered with low algae, cobble and sand / pebble. The results from the trammel- and gillnets both support and negate the original hypotheses and expectations of seasonal and spatial effect, e.g. it was assumed that larger fish would leave the shallow waters in spring, leading to lower catch frequencies in March – which were the case for cod, halibut and saithe, but not so much for plaice and lemon sole. Interspecies patterns will therefore be discussed separately from the community compositions.

Biological trends and effects rely upon statistical analyses for support. The eight species in focus consisted of 305 individuals, where 32% were cod. When sample size is a limiting factor, the chances of conducting a type II error increase, e.g. failing to reject a null hypothesis that is false (Zar, 1998). Statistical test results for species with lower catch numbers should therefore be interpreted with care. Furthermore, species richness could be biased as we were dealing with a low number of species, where the flatfishes add up to a high percentage. Flatfishes were nearly absent at Hekkingen and most of the flatfish showed associations with sand/pebble, cobble or low algae coverage which were all substratum types that had low coverage proportion at Hekkingen. Catch data were pooled for all months to each location, vice versa, which could possibly lead to loss of biological or natural patterns (Bergmann et al., 2006). Community parameters such as species richness, diversity and evenness are based upon mean net-set catch data, to lessen the effect of single individual observations. These parameters assist in describing the fish community structure, which again was regarded as mirroring the population at the given location (Pielou, 1966). The total biodiversity is however expected to be higher as there is some bias towards catch selectivity, regardless, the focus of this study was fish species caught in the trammel nets. Another issue with the statistical power could occur when testing correlations between habitat evenness and other parameters, as the habitat evenness only had one unit per location. It can also be problematic to relate bottom substrate to certain species *in situ,* as a high density of one species at a location is not necessarily exclusively related to the bottom substrate. As previously described, fish aggregations could be due to other factors, e.g. competition or predator - prey interactions (Fraser et al., 1996; Bergmann et al., 2006). This will be addressed in depth later in the discussion.

4.2 Catch composition

Seasonal patterns

All the species with adequate data from the trammel net catches showed unequal numerical frequency at different seasons, thereby rejecting the null hypothesis of seasonal effect. More importantly and on a finer scale, the relative proportion of the various species highlighted different use of shallow waters by different species throughout the seasons. Spring and summer were largely dominated by flatfishes, whereas cod, edible crab and thorny skate were the most prominent species during autumn and winter months. Cod showed high catch numbers for all months except March and saithe had highest occurrence during summer and autumn. These findings are in line with observations from Masfjorden (Salvanes and Nordeide, 1993), suggesting that coastal cod and saithe have similar seasonal distribution patterns as fjord populations. Edible crab catch rate in numbers were lower for the present study than found by the KILO project for their trammel net catches at the western part of Senja in November 2011 (Sundby et al., 2013). Edible crab was more abundant in November than in August which was the case for both the KILO project and the present study.

The largest variation between the months were found in terms of species richness and composition, whereas the diversity and evenness were found to be statistically equal. It was observed that fewer species inhabited the shallow waters during spring and summer and the peak were found in autumn. There could be many reasons for this variation, but two fluctuating factors will be discussed, namely temperature and prey abundance.

The surface water in outer Malangen is warmer than at 50 m depths from around mid-April to the end of September (Mankettikkara and Eilertsen, 2013). It is possible that fishes migrate to deeper waters in winter and spring as the temperature is higher at depths. Both temperature and fish catch biomass seemed to have a negative trend from summer and autumn to spring (Figure 22), suggesting that temperature could be an important factor for seasonal variation. Trammel nets are passive fishing gear, and according to the Q10 temperature coefficient, biological reaction rates generally decrease with lower temperatures (Hegarty, 1973). The Q10 coefficient is a measurement rate of biological reactions to a 10 C° change in temperature. The efficiency of the gear would therefore decrease with temperature if fish movement and hence catch-rates in trammel nets are proportional to $exp^{(c*T)}$ where c corresponds to the value of Q10. With a temperature increase from 4.2 C° in March, to 10.8 C in August, the calculated increase in biological rate was expected to be 1.83 with a Q10 of 2.5 (Clarke, 2017). The total biomass of mobile fish increased by a ratio of 1.64 from March to August, being reasonably close to the calculated rate. In addition to this factor, spawning migrations out of the shallow water during spring and winter could also help to explain the biomass variation. This could be the case for saithe, which generally spawn in offshore waters in winter (Salvanes and Nordeide, 1993) or cod which spawn in deeper water in spring between March and April (Fevolden et al., 2015). The bathymetric distribution of the edible crab follows the temperature gradient. Most edible crabs were observed in October and November. In mid-Norway the crab is mainly distributed at depths of 40-50 meter from October and November (Woll et al., 2006).

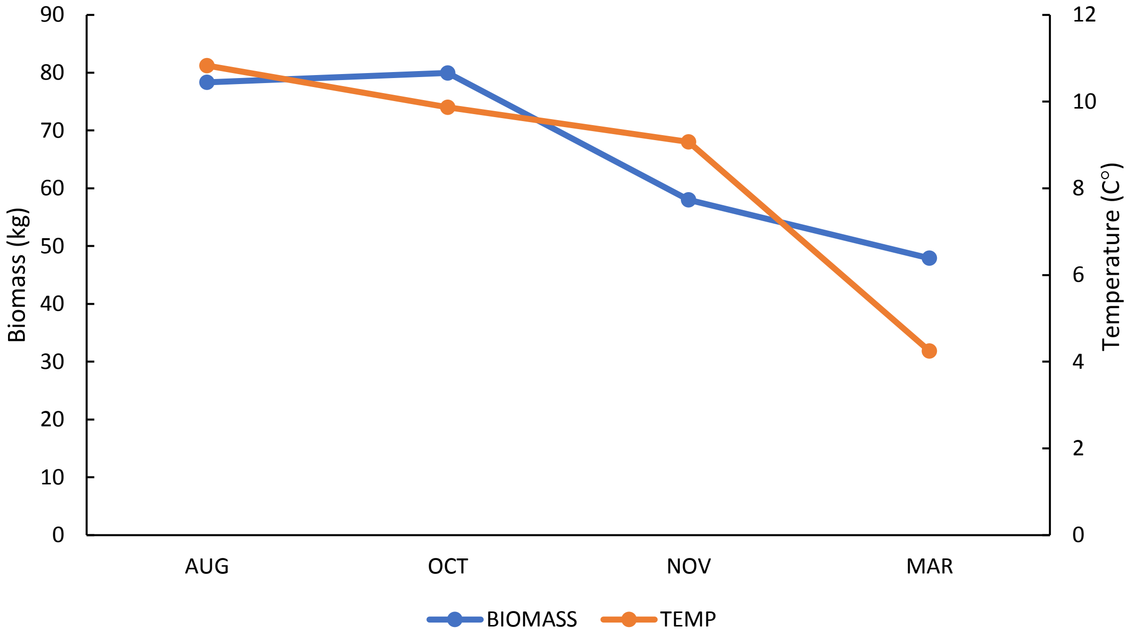

Figure 22: Total catch biomass and temperature data at the different months. Note that samples from Hekkingen are excluded and all fish species are included. Temperature data obtained from Mankettikkara, unpublished data.

The high species richness and biomass in October could also be explained by a period of high zooplankton biomass. This abundance of prey could increase the number of predators seeking to forage in shallow waters, either directly such as whiting (*Merlangius merlangus* Garsault, 1764), blue whiting (*Micromesistius poutassou* A. Risso, 1827) and saithe who all have *Calanus* spp. as an important prey (Nedreaas, 1987), or indirectly by predators of these three species. Surveys from Balsfjorden (69°N; 19°E) showed that copepod biomass generally reaches its maximum in late summer (August – October), and then decrease towards the winter (Tande, 1991). However, most of the *Calanus* spp. migrate to deeper water in the end of summer. The fish diversity (H') could not be rejected to be equal for the different months, it is however important to note that the total biodiversity of ecosystems north of 60°N is largely affected by season as these systems have high primary production in spring when daylight returns from the dark winter months (Sundby et al., 2013). It could therefore be hypothesized that the fish diversity in these areas are less affected by seasonal variation, and more by substrate coverage and biological interactions.

Spatial patterns

It was expected that species richness would increase with increased bottom complexity, e.g. habitats with mixed bottom substrates or a high degree of evenness. Results from the present study found that mean species richness and diversity increased with increasing substrate habitat evenness. The statistical power of these correlations is limited as each location had only one value of habitat evenness. However, the results of the present study are in line with literature regarding habitat complexity, which suggest that species richness and diversity are positively correlated with habitat complexity (Gratwicke and Speight, 2005; Buhl-Mortensen et al., 2012; Huang et al., 2019). The correlations are further supported by the significant differences (KW-test) of both S and H' between the four different locations. Regardless of statistical power, the results highlight the effect of bottom substrate type on fish community structure in shallow waters. It also indicates that bottom substrate evenness is important for species richness and diversity.

4.3 Growth and mortality

The observed cod age distribution had the highest frequency at three years. As age distributions for trammel net catches are skewed to the right we can assume that the total mortality (Z) estimate is relatively representative for the actual population in the area. The observed Z for cod in the present study (0.69 year^{-1}) was nearly identical to that found for cod by Larsen and Pedersen (2002) when sampling cod in the inner part of Malangen (Table 13). Comparing the von Bertalanffy coefficient K for cod observed in outer Malangen (0.30 year^{-1}) with cod found further south in Masfjorden (0.21 year^{-1}) (Table 13) (Heino et al., 2012) we confirm our expectations that outer coastal cod reach their maximum length faster than fjord resident cod, which could be due to prey availability and timing of sexual maturation (Morgan et al., 2010). Beverton (1992) found the L_∞ to be higher for populations further north. The L_∞ was 78 cm for the present study, whereas Rindorf et al. (2008) describes the cod populations in the North Sea found by various studies to be over 110 cm, contradicting the expectations of a higher L_∞. Length at age for the cod found in the present study was generally higher than found by Berg and Pedersen (2001) who sampled two adjacent fjords, namely Ullsfjorden and Sørfjorden (Figure 23). Length at age was found to be higher for coastal cod caught offshore than cod caught inshore (Berg and Albert, 2003), supporting the present findings. The high length at age also corresponds with the high K for cod of the present study. The faster growth could be explained by higher temperature in outer Malangen as optimal temperature for large cod growth was 9-12°C (Pedersen and Jobling, 1989), which are temperatures in line with outer Malangen in summer and autumn.

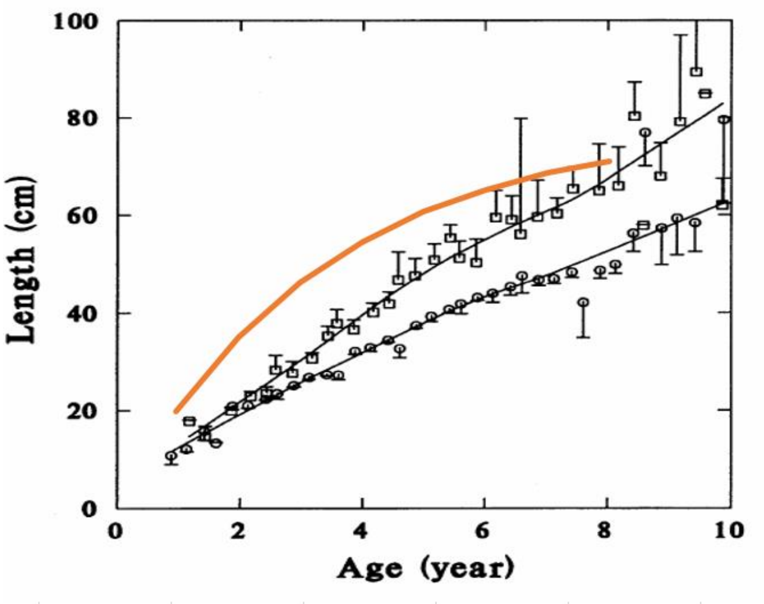

Figure 23: Length-at-age curves of cod caught in Sørfjord (black circles) and Ullsfjord (black squares) from 1989 to 1994 (Berg and Pedersen, 2001) and VBF for cod caught in the present study (orange line).

For plaice in outer Malangen, the L_∞ was 53 cm and the growth coefficient K was 0.22 year^{-1}. Plaice with similar L_∞ found in the North Sea had a lower K value of 0.11 year^{-1} (Table 13) (Jennings et al., 1998; Cardinale et al., 2010), thereby contradicting our expectations of a low K in my study area. The relatively high K value could suggest that the present study area is an optimal habitat for growth and survival of plaice, which is further supported by the low total mortality observed in the present study (0.31 year $^{-1}$) compared to total mortality rates found for North Sea plaice from 1990-2007 (0.6-0.8 year $^{-1}$) (Cardinale et al., 2010). For North Sea plaice, there was a decrease in L_∞ and an increase in K, in both males and females during the last century, especially from the 1980s to the 2000s (van Walraven et al., 2010). The L_∞ for female and male found at the present study were close to identical with plaice caught in the North Sea during the 1980s. Plaice in the North Sea was found to have had a fishery induced decline in L_∞ and an increase in K (van Walraven et al., 2010), which the northern population in the present study probably has avoided. The age distribution and large age range found in the present study suggest that plaice can grow to its maximum age and size in Malangen and that the population is characterized by long lived individuals compared with North Sea populations.

Table 13: Von Bertalanffy parameters L∞ (cm), Growth coefficient (K) and total annual mortality (Z) for present study and other areas.

Species	Area & Period	L∞ (cm)	K ($year^{-1}$)	Z ($year^{-1}$)	Reference
Cod	Malangen, this study	78	0.30	0.69	
	Inner Malangen 1988			0.7	(Larsen and Pedersen, 2002)
	Sørfjord 1990-1996			0.47	(Pedersen and Pope, 2003)
	Masfjorden 1986-1988	101	0.13	1.02	(Salvanes and Ulltang, 1992)
	Masfjorden 1985-1993	80	0.21	1.0	(Heino et al., 2012)
Plaice	Malangen, this study	53	0.22	0.31	
	Kattegat-Skagerrak 1990-2007	54.9	0.11	0.6-0.8	(Cardinale et al., 2010)
	North Sea 1975-1994	54.4	0.11		(Jennings et al., 1998)
Lemon sole	Malangen, this study	40	0.30	0.52	
	Karmøy 1992-1995	36	0.254		(Albert et al., 1998)
	North Sea	40	0.315		(Jennings et al., 1998)

Interestingly, lemon sole had higher total mortality than plaice. Part of this mortality could perhaps be explained by migration out of the study area, which could suggest that lemon sole undertake spawning migrations to a higher degree than plaice. Spawning individuals for both lemon sole and plaice were however observed in March, suggesting that both species spawn in outer Malangen. These shallow waters are therefore not only important for growth and survival as mentioned earlier, but also reproduction and hence the recruitment of these two species. Lemon sole age distribution was lower in August than in March which could indicate that the species have seasonal age dependent migrations, whether this is bathymetric or vertical is however unknown. The L∞ and K for lemon sole observed in the present study were slightly higher than observations by Albert et al. (1998) in southern Norway (Karmøy) (Table 13). It is worth noting that the 95% CI for K varied from 0.177-0.425, which could be due to the lack of age readings from younger specimen.

Only large mature adult lemon sole and plaice were caught (≥4 and ≥3 years respectively), suggesting that both species have a bathymetric or spatial distribution shift to shallow grounds when reaching maturity. Plaice settle in shallow water >1 m depth before moving deeper as they grow (Gibson et al., 2002). The ontogenetic distributional shift is a common phenomenon for flatfishes (Able et al., 2005), and Jennings et al. (1993) suggest that young lemon soles inhabit rocky areas between 50-100 m deep, which could explain the lack of juvenile and young specimen in the present study. These findings are also in line with observations from the Norwegian Coastal Surveys, which found juvenile lemon soles in deeper offshore areas. They also found that lemon sole length distribution was shorter at increased depth (Albert et al., 1998).

All the observed halibuts were immature and the majority was ≤ 4 years. These findings are in line with Godø and Haug (1988) who indicated that juveniles stayed in coastal nursery areas until the age of 4-6. This would in turn identify the present study area as an important nursery ground for halibut. The reason for its importance is that we could hypothesize that young halibut could have similar low mortality rate as plaice, due to relatively similar size. The length at age for the observed halibuts were similar to those of Karlson et al. (2013) from the coast of Norway north of 62°N. Adult halibut in coastal waters in norther Norway generally display a spawning migration to deeper waters during late winter (January-April) (Bygdnes, 2015), while younger individuals can stay shallow all year, which is supported by the present study. As mentioned, the Institute of Marine Research of Norway uses data from the yearly coastal survey when monitoring the development of younger individuals (Havforskningsinstituttet et al., 2016). The present findings could be used to argue that more shallow water surveys should be included, as these areas are identified as nursery grounds.

4.4 Species-environment relationships

Substratum type is an important environmental variable for habitat use for most species, especially flatfishes (Bergmann et al., 2006). The spatial patterns and canonical correspondence analysis (CCA) for the trammel net catch compositions displayed different bottom substrate associations for many of the species in focus. As mentioned, these substratum types might however not always be the direct causal factor for the observed distribution patterns as there could be several factors explaining fish aggregations. However, substratum type may influence fish habitat use both directly as refugee or resting areas, e.g. flatfish burying themselves in sand, or indirectly, as certain bottom substrates might have a higher prey abundance than others (Able et al., 2005). If predator and prey interactions play an important role for the species found in the present study, we can hypothesize that substrates with a high abundance of prey would be preferable for the given species.

Hekkingen stood out as a unique location which could be described as a kelp forest / bed. The cod catches had the clearest positive association with this bottom substrate displayed by the

CCA, this could be caused by the lack of other species at the location. Regardless, the total catch biomass was higher at Hekkingen than at Molvika and Edøya. Many studies highlight the importance of these kelp habitats as areas for nursery grounds, primary production, ecosystem services and biological diversity (Mann, 2000; Steneck et al., 2003; Norderhaug and Christie, 2009). Kelp forests are therefore important ecosystems, even though fish species richness or diversity were significantly negatively correlated with high algae coverage. However, Lefcheck et al. (2019) reviewed articles regarding nursery areas and found that kelp habitats had a negative effect on densities of juveniles when comparing the habitat with unstructured bottom substrates such as sand or mud. The review consisted of few articles regarding kelps, however it highlights the need of comparative studies when defining habitat associations. Lefcheck et al. (2019) also highlight the assumption of a nursery ground descried by Beck et al. (2011) – that the habitat cannot be considered a nursery ground if the fish inhabit the habitat throughout its' lifespan. According to this assumption and present findings, the kelp habitats cannot be considered a nursery ground for cod.

The edible crab was not found to be more abundant at Hekkingen. If this is the case, the theory that crabs such as *Cancer borealis* (Stimson, 1859) keep sea urchin from grazing kelps (Steneck et al., 2013), does not necessary apply for the edible crab. However, Christie et al. (2019) identified cobblestone habitats as good refugee habitats for settling sea urchins, and that the smaller sea urchins struggle to settle in kelps due to predation. It is therefore more likely that the low frequency of edible crab at Hekkingen was caused by the position of the nets being above the kelp. Regardless, the effect of predation on sea urchins as a limiting factor in kelp forests is not agreed upon by all. Sivertsen (2006) calculated the total predation, predominantly by edible crab and common eiders (*Somateria mollissima* L.) and could not find predation to have a significant effect on sea urchins. Without going too much into detail, it should be stressed that studies regarding predation should include stomach analysis and grounded theories such as Ivlev's electivity index, as the proportion of a specific prey in an environment is related to the observed proportion of the prey in the stomach of the predator (Ivlev, 1961).

Edøya was the only location with a relative low cod abundance. As indicated by the CCA this seemed to be due to a negative association with sand / pebble for cod. The KILO project could not identify bottom substrate preferences for cod older than one year (Sundby et al., 2013), which makes this observation somewhat novel. On the contrary to cod, most of the flatfishes were positively associated with sand / pebble. Habitats such as Edøya would therefore be a natural area for fishermen to target plaice. However, if commercial fisheries on plaice increase in northern Norway, it is likely that it would have a negative impact on the successive recruitment of halibut in the form of bycatch.

Molvika offered some unique habitat patterns that was not explained by the multivariate studies, but rather by individual species parameters. Cod length distributions were not different between the locations, there were however less older cod at Molvika in August, which is when a high frequency of age 1+ individuals were observed (Appendix 2). This could suggest that predator avoidance is more important than foraging rates at sand bottom habitats, as sand habitats are the least profitable habitat for cod compared with more complex bottom substrates where prey density is higher. Molvika was mostly covered by sand / pebble, which larger cod had a negative association with, which could explain why foraging efficiency was found highest for juvenile cod at sand bottom substrates compared with more complex habitats (Persson et al., 2012). There were also a relatively high proportion of shell fragments and low algae at Molvika – providing shelter if predators were present (Fraser et al., 1996).

It was expected that adult fish would be more dispersed than juvenile fish, which to some degree is supported by the observations at Molvika. Larger individuals of plaice and common dab were less abundant and catch numbers of halibut were highest at this location. Molvika therefore also stands out as an important location for smaller halibut. Is to be noted that only three common dabs were observed at Molvika, so certain conclusions are to be interpreted with care. These observations do however highlight that bottom substrate, and perhaps indirectly predator/prey interactions, influence the length distribution patterns of common dab and plaice, while seasonal vertical migration could be more important for lemon sole. This is further supported by Albert et al. (1998) which did not find any clear bathymetric patterns for the length distribution of plaice (excluding juveniles) but did so for lemon sole. The edible crab had highest catch rate in numbers at Molvika. This observation was not clearly explained by any environmental variables in the first ordination plot, but more so by the second CCA through strong associations with October and November. Literature suggest that the sexual spatial distribution is affected by level of exposure (Woll et al., 2006), the limited catch numbers of the present study could not however identify such an effect.

Fishes might utilize habitat types differently, e.g. feeding or resting habitats (Bergmann et al., 2006). This theory could offer some explanation to why species richness and diversity increase with habitat complexity and evenness. Skårlia was the location with the highest degree of substrate evenness, with large patches maerl beds (cobble), sand / pebble and a low algae coverage. Perhaps different species utilize different substrate types at the location differently, leading to the high species diversity at Skårlia. Roughly 80 % of all lemon soles were caught at Skårlia which suggest a more specific habitat association for this species compared to the other flatfishes. Plaice on the other hand had high abundance at all locations but Hekkingen. Adult plaice feed on epibenthic crustaceans, polychaetes, small fish and echinoderms, which are more abundant and diverse at benthic habitats with complex emergent epifauna (Bergmann et al., 2006), hence the high abundance at Skårlia. Specifically, the CCA found that lemon sole was highly related to cobble and low algae coverage, whereas plaice and common dab were more positively related with sand / pebble and urchin coverage. Both common dab and plaice were observed to have small sea urchin in their stomachs (my pers. obs.), further supporting the theory that bottom substrate types indirectly influence habitat use for some of the observed species, especially common dab which was positively correlated with urchin coverage.

4.5 Implications for management

In many contexts, the traditional single species fisheries management have failed to address ecosystem interactions when managing fish stocks. Furthermore, fisheries do not only affect the targeted species. Habitat damage by gear, bycatch or cascading effects such as the mesopredator release process are all important factors for fisheries management (Eriksson et al., 2011), which is why an ecosystem approach (EA) to fisheries management has been developed. Coastal shallow water habitats and their fish species are especially vulnerable to exposure to anthropogenic impact, e.g. oil spills, aquaculture or infrastructure development. Since 2002, an EA has been the goal when managing marine areas and activities in Norway, where the overall goal is to lay down the foundations for a clean and rich sea through sustainable activities from the stakeholders (White paper, nr. 10, 2001-2002). The municipalities are expected to implement these policies through area-based management (Johnsen and Hersoug, 2012). However, Johnsen and Hersoug (2012) argue that the municipalities lack resources and capturability for proper management. In the Tromsø region, an inter-municipal coastal plan was implemented in March 2015. With the EA policies, an important goal for the area-based management should therefore be to protect pristine marine habitats and their associated fauna (Buhl-Mortensen et al., 2012). Studies such as the present one could be of great support for decision makers, especially on a municipality level where local coastal management is taken place.

The edible crab was present in the study, whereas the invasive Red King crab (*Paralithodes camtschaticus* Tilesius, 1815) was absent. However, the red king crab has its' southernmost distribution area close to Tromsø (Christie et al., 2019). How these species may interact in the future is of great importance, as both species have a strong impact on kelp and sea urchin interactions (Christie et al., 2019). Many species are now moving northwards, and this rapid "Borealization" of species into the Arctic is outpacing the previous expected patterns (Christiansen et al., 2016). It should therefore be of interest to continue to survey shallow waters and identify possible expansions of other species more common in shallow waters further south, such as the pollack, which was observed in low catch rates for the present study.

Many tourist fishing lodges and local recreational fishing in the area selectively target cod and halibut. Most of this catch data is not registered, but only estimated. Underestimation of any type of fisheries, be it recreational or commercial, can have devastating effect on fish recruitment (Beverton and Holt, 1957). In the late 1980s an apparent near collapse in the North East Arctic cod stock led to the immediate cease of fishing from the coastal fleet north of 62°N. To quote a former fisheries director, Viggo Jan Olsen – "*En dau torsk er en dau torsk uansett hvilket redskap den er tatt med*" (A dead cod is a dead cod regardless of what gear it was fished with) (Nordlys, 2019).

Plaice, lemon sole and common dab fisheries are in general low in Northern Norway, whereas halibut fisheries have grown from just under 500 tonnes in 2000 to 2500 tonnes in 2016 (Havforskningsinstituttet et al., 2016). Fishing pressure from tourist, recreational and commercial fisheries could affect the population to the extent of a collapse, as seen in the North Sea, where commercial fisheries greatly affected the population (Devold and Eggvin, 1938; Havforskningsinstituttet et al., 2016). To avoid recruitment overfishing on halibut, passive gear fishing at certain coastal areas, such as the in the present study, should be avoided due to the higher catch rate of undersized (< 80 cm) individuals.

5 Conclusions

The coastal shallow waters in the present study contain various habitats from kelp forests, sand bottom to complex habitats. The present study highlights seasonal and spatial variations for various species in these shallow coastal waters. Fish community compositions were largely affected by season, location and bottom substrate. In general, the flatfishes dominated the shallow waters in March whereas cod were the most numerous the rest of the year. Indirectly, the catches could be explained by bathymetric migrations, temperature, prey abundance or habitat structures such as bottom substrate. As the Arctic warms up and climate change is imminent, we should expect to see changes in the marine fauna, especially in shallow waters. Which highlights the importance of shallow water studies to identify spatial distribution of boreal species moving into the Arctic.

Species richness and diversity showed a strong association with bottom substrate evenness. Complex coastal habitats are therefore of great importance for many of the investigated species. Anthropogenic activity such as aquaculture, mining or fishing can impact the bottom fauna and flora, changing it to a more homogenous habitat, which has been proven to negatively affect species richness and diversity. Proper management is therefore key to maintain the complexity of these coastal habitats, and ecosystem-based fisheries and coastal management should aim to protect pristine habitats. Further studies should be done to include more habitats and species and develop tools to predict effects of human and environmental impacts on coastal habitats.

Growth of the observed cod populations investigated here is comparably high with inner fjord or North Sea populations. Plaice and lemon sole in these waters consists of long-lived individuals, with a relatively low annual mortality rate. Shallow coastal waters were identified as nursery ground for halibut, which suggests that surveys from shallow waters should be included when monitoring the development of juvenile halibut.

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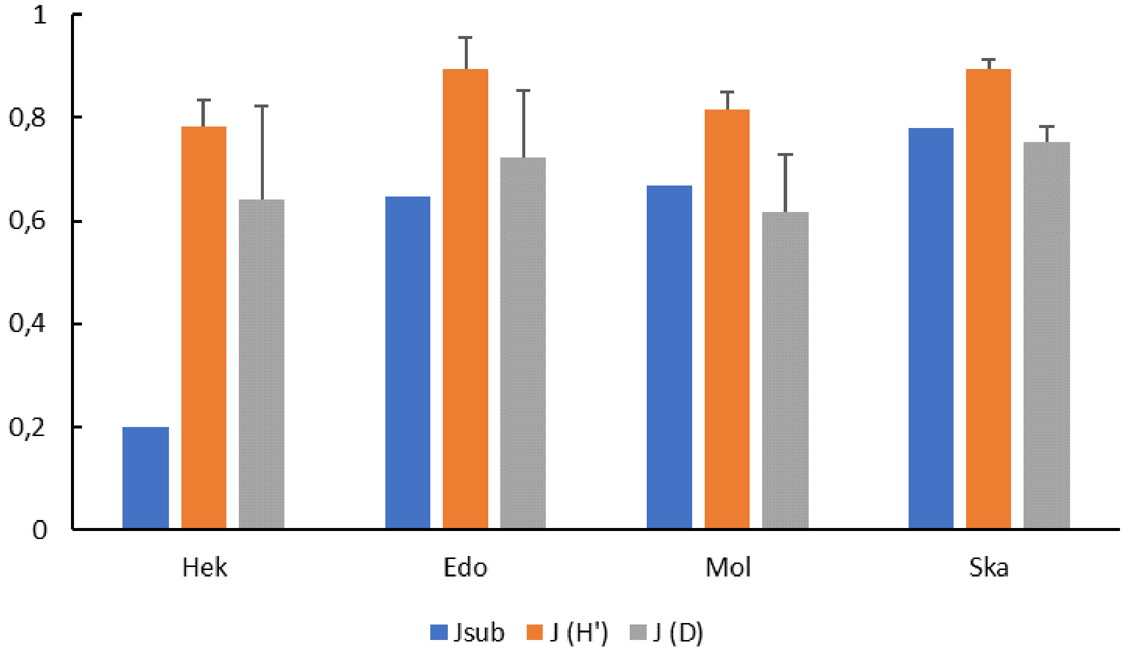
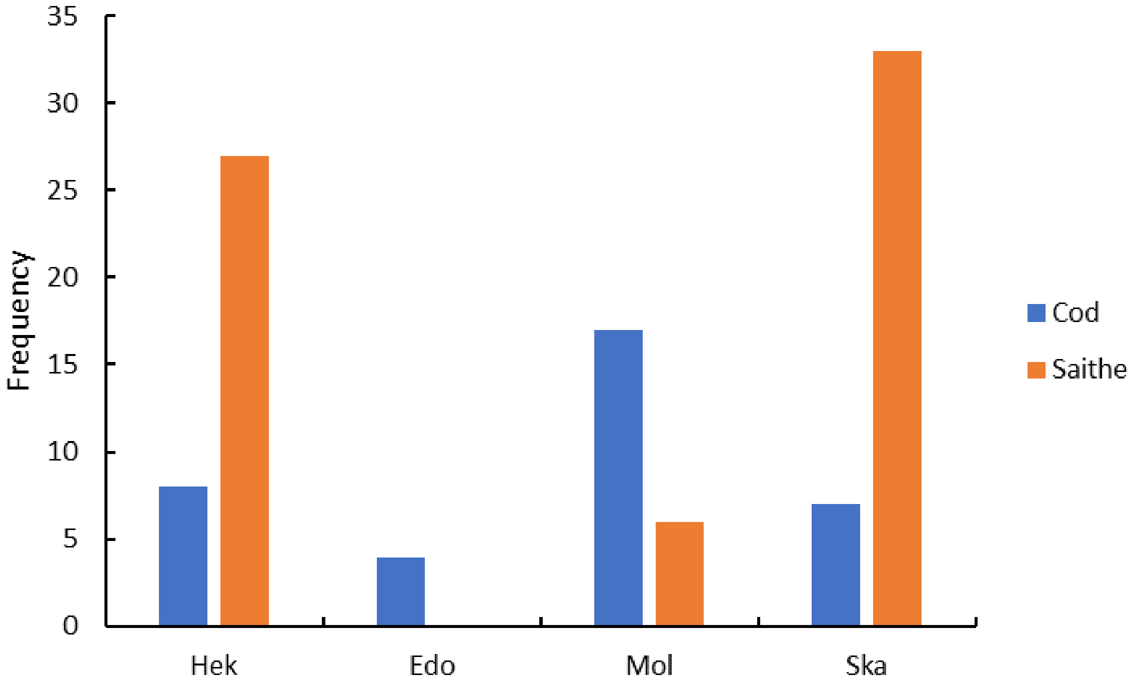
7 Appendix

Appendix table 1: Overview of trammel net locations in Malangen, the coordinates are displayed as degrees, minutes and decimal seconds. “Mol” is short for Molvika, “Ska” is Skårlia. “Hek” is Hekkingen and “Edo” is Edøya. There were two trammel net-sets, 1 and 2 at each location. Depth-values in bold are estimated from maps (Kartverket, 2019), as no depth were recorded during those samplings.

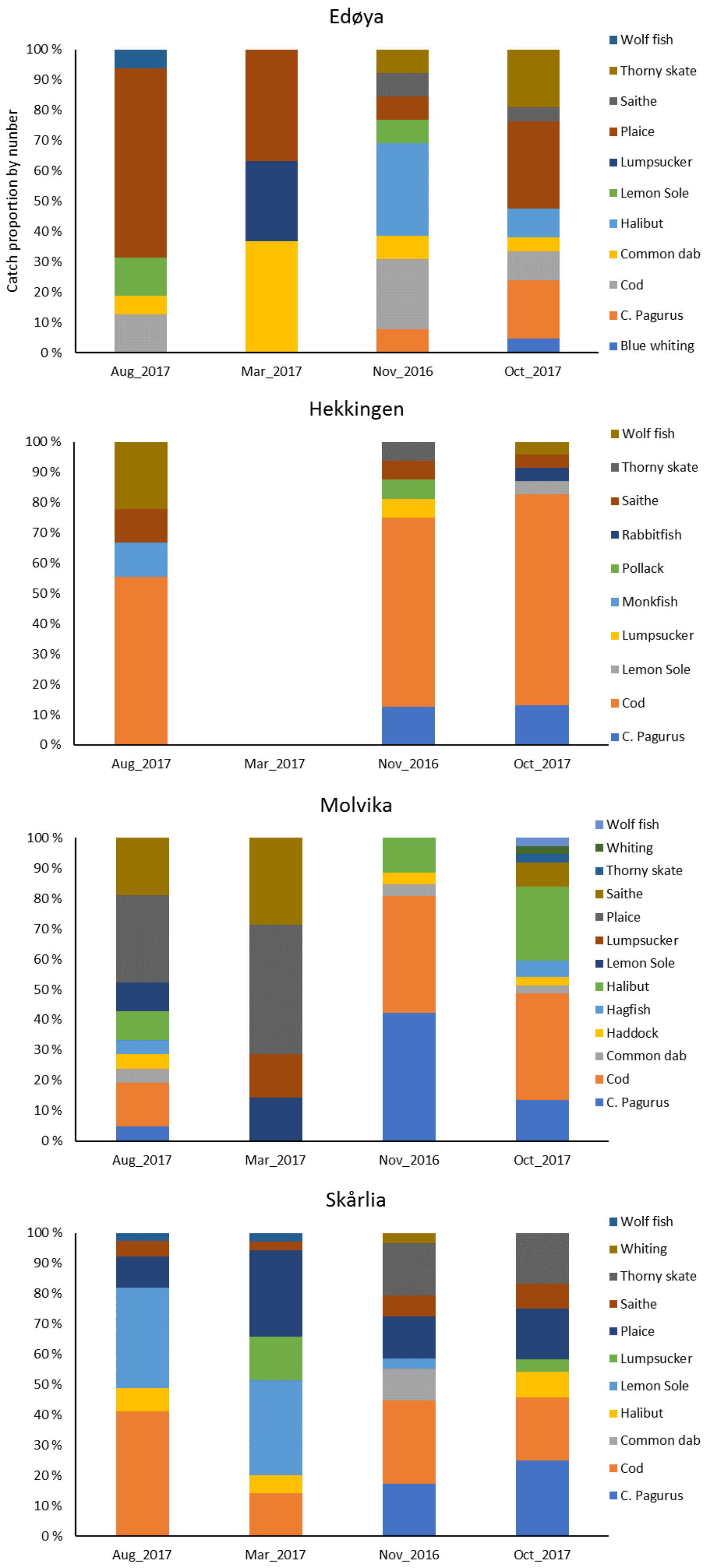
Season	Loc	Set	Start pos (N°)	Start pos (E°)	End pos (N°)	End pos (E°)	Fishing time (hs/m)	Depth start (m)	Depth end (m)
Nov_2016	Hek	1	69’35.884	17’50.553	69’35.901	17’50.478	21:48:00	17	9
Nov_2016	Hek	2	69’35.959	17’50.400	69’35.986	17’50.343	21:43:00	16	13
Nov_2016	Edo	1	69’37.225	17’55.500	69’37.313	17’55.420	14:02:00	13	17
Nov_2016	Edo	2	69’37.451	17’55.406	69’37.443	17’55.294	13:50:00	19	13
Nov_2016	Mol	1	69’34.458	18’00.439	69’34.476	18’00.400	20:00:00	13	17
Nov_2016	Mol	2	69’34.534	18’00.480	69’34.540	18’00.435	20:17:00	12.1	15.4
Nov_2016	Ska	1	69’29.681	18’03.403	69’29.700	18’03.460	18:26:00	13.6	19.8
Nov_2016	Ska	2	69’29.783	18’02.884	69’29.776	18’02.976	18:45:00	12.3	14.5
Mar_2017	Edo	1	69’37.313	17’55.420	69’37.255	17’55.495	19:10:00	11.60	13.00
Mar_2017	Edo	2	69’37.452	17’55.333	69’37.415	17’55.453	19:10:00	14.00	16.00
Mar_2017	Mol	1	69’34.477	18’00.400	69’34.460	18’00.467	15:00:00	17.00	12.50
Mar_2017	Mol	2	69’34.540	18’00.435	69’34.535	18’00.480	15:00:00	13.40	15.30
Mar_2017	Ska	1	69’29.682	18’03.403	69’29.697	18’03.430	15:15:00	13.10	16.70
Mar_2017	Ska	2	69’29.783	18’02.885	69’29.796	18’03.011	15:15:00	13.20	18.30
Aug_2017	Hek	1	69’35.882	17’50.451	69’35.934	17’50.476	19:10:00	17	10
Aug_2017	Hek	2	69’35.988	17’50.310	69’35.961	17’50.404	18:54:00	10	17
Aug_2017	Edo	1	69’37.303	17’55.393	69’37.360	17’55.467	18:02:00	14	10
Aug_2017	Edo	2	69’37.481	17’55.258	69’37.458	17’55.389	18:06:00	10	17
Aug_2017	Mol	1	69’34.458	18’00.459	69’34.477	18’00.324	20:42:00	**10**	**26.4**
Aug_2017	Mol	2	69’34.530	18’00.491	69’34.492	18’00.303	21:01:00	**10**	**28**
Aug_2017	Ska	1	69’29.675	18’03.373	69’29.709	18’03.332	20:48:00	**11**	**15**
Aug_2017	Ska	2	69’29.787	18’02.907	69’29.824	18’02.941	20:14:00	**13**	**18**
Oct_2017	Hek	1	69'35.880	17’50.584	69’35.900	17’50.513	20:50:00	**19**	**11**
Oct_2017	Hek	2	69'35.963	17’50.420	69’35.983	17’50.356	20:50:00	**9**	**9**
Oct_2017	Edo	1	69'37.227	17’55.508	69’37.255	17’55.495	20:45:00	**9**	**9**
Oct_2017	Edo	2	69'37.457	17’55.400	69’37.449	17’55.319	20:45:00	*17*	*12*
Oct_2017	Mol	1	69'34.481	18’00.396	69’34.461	18’00.441	19:30:00	15	12
Oct_2017	Mol	2	69'34.542	18’00.433	69’34.533	18’00.501	19:30:00	16	16
Oct_2017	Ska	1	69'29.693	18’03.338	69’29.719	18’03.326	22:00:00	14	16
Oct_2017	Ska	2	69'29.780	18’02.983	69’29.784	18’02.877	22:00:00	15	12



Appendix 1: Evenness parameters at the different locations for bottom substrate (Jsub) and mean evenness (±SE) (J) calculated from Shannon-Wiener (H') and Simpsons (D) indices.



Appendix 2: Small cod and saithe frequency at different locations, data from gill-net used in August 2017.



Appendix 3: Catch proportion of each species at location and month.

Appendix table 2: Scores for species, net-set values and environmental variables with the corresponding axis (Axes 1-3) for the ordination diagram shown in Figure 20A&B.

	Axis 1	Axis 2	Axis 3
Cod	1.11	0.13	-0.81
Halibut	-0.33	-1.49	1.60
Plaice	-1.34	0.05	-0.48
Lem_sole	-0.26	2.2	1.39
Saithe	0.52	-0.64	0.95
Ed_crab	0.39	-0.93	0.85
Com_dab	-1.88	-1.08	-1.70
Skate	-0.83	1.23	-0.42
NovHek1	0.60	0.20	-0.38
NovHek2	0.95	-0.11	-0.44
NovEdo1	-0.62	-0.84	0.58
NovEdo2	0.72	0.39	-0.02
NovMol1	0.70	-0.40	0.01
NovMol2	0.13	-0.89	0.46
NovSka1	0.21	0.32	-0.14
NovSka2	-0.42	-0.24	-0.42
MarEdo1	-1.78	-0.89	-1.49
MarEdo2	-1.47	-0.23	-0.78
MarMol1	0.52	-0.64	0.95
MarMol2	-1.07	0.60	-0.01
MarSka1	-0.40	0.68	0.39
MarSka2	-0.35	0.83	0.34
AugHek1	0.99	-0.02	-0.46
AugHek2	1.11	0.13	-0.81
AugEdo1	-1.04	0.17	-0.45
AugEdo2	-0.63	0.50	-0.17
AugMol1	0.54	0.25	0.46
AugMol2	-1.02	-0.46	-0.05
AugSka1	0.33	0.53	0.49
AugSka2	0.16	0.77	0.07
OctHek1	0.80	0.13	-0.20
OctHek2	1.01	-0.02	-0.53
OctEdo1	-0.25	-0.09	0.19
OctEdo2	-0.77	-0.21	-0.27
OctMol1	0.84	-0.22	-0.19
OctMol2	-0.022	-0.87	0.69
OctSka1	0.10	-0.02	0.035
OctSka2	-0.24	-0.46	0.25
Sand/pebble	-0.61	-0.32	0.21
Cobble	-0.25	0.40	0.09
Low algae	-0.04	0.17	0.52
High algae	0.61	0.17	-0.38
Urc_cover	-0.52	-0.21	-0.28

Appendix table 3: Grouping data for CCA in PAST. Environmental values are arcsine square root transformed and catch data are total catches for each net-set.

Name	Location	Month	Sand/pebble	Cobble	Low_algae	High_algae	Urc_cover	Cod	Halibut	Plaice	Lem_sole	Saithe	Ed_crab	Com_dab	Skate
NovHek1	Hek	Nov16	0.00	0.10	0.15	1.31	0.17	3	0	0	0	1	0	0	1
NovHek2	Hek	Nov16	0.00	0.10	0.15	1.31	0.17	7	0	0	0	0	2	0	0
NovEdo1	Edo	Nov16	0.94	0.29	0.19	0.00	0.72	0	4	1	0	0	1	1	1
NovEdo2	Edo	Nov16	0.94	0.29	0.19	0.00	0.72	3	0	0	1	1	0	0	0
NovMol1	Mol	Nov16	0.81	0.05	0.52	0.00	0.20	9	2	0	0	0	5	0	0
NovMol2	Mol	Nov16	0.81	0.05	0.52	0.00	0.20	1	1	0	0	0	6	1	0
NovSka1	Ska	Nov16	0.40	0.65	0.70	0.22	0.09	5	0	1	1	1	2	0	3
NovSka2	Ska	Nov16	0.40	0.65	0.70	0.22	0.09	3	0	3	0	1	3	3	2
MarEdo1	Edo	Mar17	0.94	0.29	0.19	0.00	0.72	0	0	1	0	0	0	5	0
MarEdo2	Edo	Mar17	0.94	0.29	0.19	0.00	0.72	0	0	6	0	0	0	2	0
MarMol1	Mol	Mar17	0.81	0.05	0.52	0.00	0.20	0	0	0	0	2	0	0	0
MarMol2	Mol	Mar17	0.81	0.05	0.52	0.00	0.20	0	0	3	1	0	0	0	0
MarSka1	Ska	Mar17	0.40	0.65	0.70	0.22	0.09	2	1	5	5	1	0	0	0
MarSka2	Ska	Mar17	0.40	0.65	0.70	0.22	0.09	3	1	5	6	0	0	0	0
AugHek1	Hek	Aug17	0.00	0.10	0.15	1.31	0.17	4	0	0	0	1	0	0	0
AugHek2	Hek	Aug17	0.00	0.10	0.15	1.31	0.17	1	0	0	0	0	0	0	0
AugEdo1	Edo	Aug17	0.94	0.29	0.19	0.00	0.72	1	0	7	1	0	0	1	0
AugEdo2	Edo	Aug17	0.94	0.29	0.19	0.00	0.72	1	0	3	1	0	0	0	0
AugMol1	Mol	Aug17	0.81	0.05	0.52	0.00	0.20	3	0	0	2	4	0	0	0
AugMol2	Mol	Aug17	0.81	0.05	0.52	0.00	0.20	0	2	6	0	0	1	1	0
AugSka1	Ska	Aug17	0.40	0.65	0.70	0.22	0.09	7	3	0	6	1	0	0	0
AugSka2	Ska	Aug17	0.40	0.65	0.70	0.22	0.09	9	0	4	7	1	0	0	0
OctHek1	Hek	Oct17	0.00	0.10	0.15	1.31	0.17	6	0	0	1	0	2	0	0
OctHek2	Hek	Oct17	0.00	0.10	0.15	1.31	0.17	10	0	0	0	1	1	0	0
OctEdo1	Edo	Oct17	0.94	0.29	0.19	0.00	0.72	1	1	2	0	1	3	0	3
OctEdo2	Edo	Oct17	0.94	0.29	0.19	0.00	0.72	1	1	4	0	0	1	1	1
OctMol1	Mol	Oct17	0.81	0.05	0.52	0.00	0.20	10	1	0	0	2	2	0	0
OctMol2	Mol	Oct17	0.81	0.05	0.52	0.00	0.20	3	8	0	0	1	3	1	1
OctSka1	Ska	Oct17	0.40	0.65	0.70	0.22	0.09	4	1	1	0	1	4	0	4
OctSka2	Ska	Oct17	0.40	0.65	0.70	0.22	0.09	1	1	3	0	1	2	0	0