



Effects of season, bottom substrate and population dynamics on fish communities in shallow subarctic northeast Atlantic waters

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ABSTRACT

Fish communities in the shallow waters (9–20 m depth) of outer Malangen (69° N), Northern Norway was studied to investigate effects of season, bottom substrate associations and population dynamic parameters on the fish assemblages. In four fieldtrips during one year at four locations, fish were sampled by trammel nets and bottom substrate composition was monitored by underwater video. A total of 16 species of fish were caught, including four species from Pleuronectidae and six from the Gadidae family. Cod (*Gadus morhua* Linnaeus, 1758) was the most numerous species followed by plaice (*Pleuronectes platessa* Linnaeus, 1758), lemon sole (*Microstomus kitt* Walbaum, 1792) and halibut (*Hippoglossus hippoglossus* Linnaeus, 1758). Cod dominated the catches in all months except March, in which plaice and other flatfishes were most dominant. On a community scale, fish species richness was highest in October and lowest in March. Furthermore, the species richness and diversity were generally higher at locations with greater bottom substrate evenness. Cod showed a positive association with large macroalgae coverage and were less numerous at locations dominated by sand and pebble. Plaice and common dab (*Limanda limanda* Linnaeus, 1758) showed positive associations with sand and pebble coverage, while lemon sole was more associated with maerl beds, cobble and low algae coverage. Only halibut younger than 8 years of age were observed, and the sampling areas are suggested to be nursery area for this species. Von Bertalanffy growth functions were estimated for cod, plaice and lemon sole, and the growth coefficient K of cod and plaice were higher than for populations from adjacent fjords or the North Sea populations. Total mortality rates of cod and plaice were lower than for areas further south, and this may contribute to high and relative stable biomasses in the shallow Malangen area.

1. Introduction

Fish assemblages in shallow waters are affected by many biogenic factors, such as macroalgae coverage, predation and competition (Auster, 1988; Fahrig, 2003; Fraser et al., 1996; Gratwicke and Speight, 2005; Sissenwine, 1984). Macroalgae habitats can function as shelter for juvenile fish species (Demartini and Roberts, 1990), thereby influencing the predator-prey dynamics (Sivertsen, 2006). Physical factors such as bathymetry, currents, wave exposure, temperature, salinity, light, turbidity and bottom substrate also affect fish communities (Buhl-Mortensen et al., 2012; Claireaux and Dutil, 1992; Ruppert et al., 2009), and it is more likely that several rather than a single factor decide how a species use a habitat (Gili and Petraitis, 2009). The bottom substrate is a result of biogenic factors as well as physical factors, especially current and exposure levels (Buhl-Mortensen et al., 2012; Rinde et al., 2014;

Sivertsen, 1997) and many of the mentioned physical factors have high seasonal variation in subarctic areas.

The shallow exposed subarctic areas of the Norwegian coast (< 50 m depth) are important areas for a variety of commercially exploited species such as cod (*Gadus morhua* Linnaeus, 1758), European plaice (*Pleuronectes platessa* Linnaeus, 1758) saithe (*Pollachius virens* Linnaeus, 1758) and Atlantic halibut (*Hippoglossus hippoglossus* Linnaeus, 1758) as well as crabs (*Cancer pagurus* Linnaeus, 1758) and many other species (Bakketeig et al., 2016; Mann, 2000; Sundby et al., 2013). There are few studies of fish communities in these areas and knowledge of population and community dynamics for species in these shallow areas are important for proper coastal resource and ecosystem management. Furthermore, it can give us an indicator of how the fish assemblages reacts to human externalities. It is however impossible to survey these shallow waters with conventional survey bottom trawls due

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to bathymetric and biogenic structure complexity, and alternative sampling gears such as gill-nets or fyke nets have to be used.

The bottom substrate associations of cod (Fraser et al., 1996; Meager and Utne-Palm, 2008; Persson et al., 2012) and flatfishes (Hinz et al., 2006; Gibson and Robb, 2000; Jennings et al., 1993) have been studied. Studies from more temperate marine habitats conclude that species richness, diversity and densities are positively related with substratum complexity (Gratwicke and Speight, 2005; Macpherson, 1995; Mesa et al., 2006). This was also shown for benthic communities at deeper water (40–2200 m depth) in Northern Norway (Buhl-Mortensen et al., 2012). We aim to study whether this is also the case for fish communities in a subarctic coastal area. The fish community is also expected to be affected by seasonality in physical factors such as temperature and day duration.

The present study will focus on demersal fish species in the sublittoral zone at different bottom habitats in the outer part of Malangen fjord (69°N, 18°E) in Troms, Northern Norway. The outer part of Malangen has local areas with high natural kelp production, while sea urchins have grazed large areas in the less exposed and shallow inner parts of the fjord (Filbee-Dexter and Wernberg, 2018). Most of the natural kelp production in exposed areas is not grazed on directly, but transformed to detritus which is available for microorganisms and higher animals (Filbee-Dexter and Wernberg, 2018), making kelp forests important habitats for adjacent ecosystems (Vilas et al., 2020).

At high latitudes, the seasonal amplitude of light and temperature is high and the most important commercial demersal fish stocks like coastal cod, saithe and halibut spawn in deeper waters during winter and early spring (Haug and Tjemland, 1986; Heino et al., 2012; Jakobsen, 1987). It is therefore expected that the abundance of large individuals of these species will be lowest during winter and early spring. Individual growth and mortality rates also influence the stability and magnitude of biomass at different locations. Fishery strongly affect mortality rates of potentially long-lived fishes (Pauly, 1980) and we expect that conditions with low or moderate individual growth and mortality rates may promote higher biomass stability in time and space. Despite its northern location at 69°N, the outer Malangen study area is dominated by relatively warm coastal water compared to adjacent colder inner fjords (Mankettikkara and Eilertsen, 2013). Growth rates of boreal fish species in the subarctic regions are generally positively related to temperature, as their temperature optimum for growth often exceeds the observed temperatures in the area (Pedersen and Jobling, 1989). Therefore, within each species we expect higher length at age and a higher von Bertalanffy growth coefficient (K) value compared to inner colder fjord habitats at similar latitude.

There are clear population genetic differentiation between the coastal cod and the Northeast Arctic cod in the Barents Sea and between coastal cod in Malangen and neighbour fjords (Fevolden et al., 2015) which are in accordance with large scale isolation by distance gradients along the Norwegian coast (Dahle et al., 2018). The population structure for other fish species are more uncertain. Populations in the colder part of the species range often reach a larger maximum size and are more long-lived than at southerly and warmer conditions (Beverton, 1992), and we expect a lower K and higher asymptotic length (L_{∞}) than in areas further south. We also expect lower mortality rates than in southerly more intensively exploited areas.

The main objectives were; i) to identify and characterize potential drivers; seasonality, bottom substrate composition, growth and mortality rates, for a shallow water fish community, and ii) identify if there were spawning and nursery habitats within area.

2. Material and methods

2.1. Approach

To identify seasonal and spatial patterns, four locations were sampled with trammel nets four times from November 2016 to October

2017. Spatial patterns were investigated by studying the different catch compositions at the different locations. The species catch compositions were used to identify how community parameters such as species richness, diversity and evenness varied with season and location. By quantifying bottom substrate coverage and habitat heterogeneity, or evenness, specific species-habitat interactions were identified (Boström et al., 2011). Multivariate analysis of spatial habitat metrics will aid to identify how indices and single species are related to habitat type. The single species variables: body length, age, length at age and mortality rate were also estimated for species with sufficient catch data.

2.2. Study area

Malangen is a 60 km long subarctic fjord in Troms county, Norway (Fig. 1), that stretches from Hekkingen lighthouse in the west and 60 km south-eastward (Sælen, 1950). The fjord has a maximum depth of ca 450 m and west of the study area, the fjord has a deep sill at ca 200 m depth and the fjord is fed from west by a high influx of warm Atlantic 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). 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). The temperature in the deep basin at ca 400 m depth is stable around 6.5–7.0 °C (Mankettikkara, unpublished data). Bottom trawling or dredging is not allowed in the area and fish are commercially exploited using gill-nets, long-lines, hand-lines and fishing rods.

The four locations were selected to include locations with varying degree of exposure but with similar bottom slope over a sufficiently large area so that two net-sets could be deployed 200–300 m apart. Two of the locations, Hekkingen and Edøya, were in the outer exposed part of Malangen, and two locations, Molvika and Skårliia, were positioned further into the fjord (Fig. 1). Hekkingen is the most exposed location due to its limited protection from winds and swells. 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 deep basin where Molvika is facing it to the west and Skårliia to the

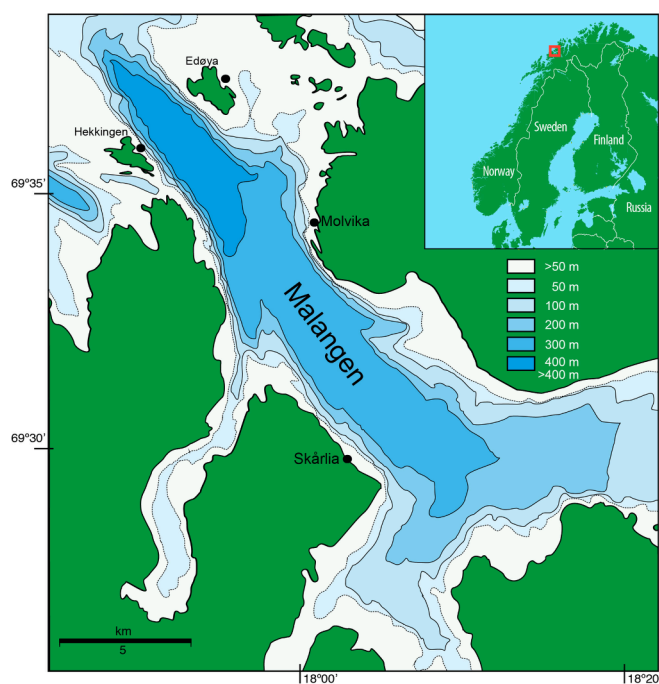


Fig. 1. Positioning of the sample locations in Malangen. Hekkingen, Edøya, Skårliia and Molvika. Landmasses southwest of Malangen belongs to the Senja island.

northeast (Fig. 1).

2.3. Sampling

Data for this study were gathered by fishing with trammel nets and underwater video recording at all four locations (Table S1). Surveys were performed in November 2016, March 2017, August 2017 and October 2017. The nets were deployed at the same locations every time using a handheld Garmin Global Positioning System (GPS). Each net-set had two trammel nets and two net-sets were used at each location, positioned 200–300 m apart (Fig. S1). The nets fished between 14 and 22 h at depths between 9 and 20 m (Table S1). The depth range used is ideal for net-fishing and as light decline 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 bad weather. The bottom substrate at the different locations was expected to vary due to level of exposure.

Each trammel net was 28 m long and 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 was tied to the end of the net-set, and a weight was also attached to the other end of the net-sets. Trammel nets are generally considered to be less species and size selective than gill-nets and long lines, with fish length distributions frequently skewed to the right (Erzini et al., 2006). 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 (Erzini et al., 2006; Salvanes, 1991).

The catches were sorted on the deck of the main vessel at all surveys. The catch was sorted to species and placed in individual bins for each net-set. The fishes, crabs and other invertebrates were counted, individually length measured and weighted. Otoliths were dissected out from cod, halibut, lemon sole and plaice using tweezers after making a cross section between the snout and neck of the fish. Cod otoliths were stored in dry envelopes and flatfish otoliths were stored in fresh water in glass vials. Fish total length was measured from the snout tip to the end of the caudal fin downwards to the nearest centimetre.

2.4. Age determination

Otoliths were analysed at a laboratory at UiT The Arctic University of Norway in Tromsø. Fishes at high latitude (45–70°N) often start to form opaque zones in spring (April–May) and translucent winter zones in October–November (Beckman and Wilson, 1995; Rollefson, 1933). 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, plaice and lemon sole were expected to be hatched in March to May and halibut in February (Falk Petersen, 1982; Haug, 1990). Age was calculated using expected hatching month as zero age.

In the present study, flatfish otoliths were not cut or broken, but glazed with a thin layer of glycerol before reading growth zones under reflective light at magnification of 16× with a dark background. Otoliths from cod were broken transversely, placed in clay leaving the cut end visible from above (Rollefson, 1933). The cod otoliths were illuminated from the side and zones could then be studied and counted.

Fish caught in October and November had a thin translucent zone at the edge. Cod otoliths that were sampled in August had a prominent opaque zone in the outer part. A fish with 7 opaque zones caught in August was therefore identified as 6+ years old specimen (depending on the species). Age reading reliability was categorized to (1) reliable, (2) uncertain and (3) low reliability (Mjanger et al., 2011). All cod otoliths with low reliability (category 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 age.

2.5. Video survey

The video survey was conducted with R/V Hyas in August. One person was controlling the depth (1–2 m above the bottom) of the video rig by lowering and pulling the wire while another person read out the coordinates and depth, using a hand-held GPS and the boat echosounder. Towing speed varied around 0.8 m sec⁻¹. Three to four transects were recorded at each of the four locations following the depth contours in the area, starting at the shallowest depth of ca 9 m. In total 24 min and 4 s were filmed at Edøya, 17 min and 2 s at Hekkingen, 22 min and 9 s at Molvika and 28 min and 17 s at Skårliia.

Bottom substrate composition was assessed by reviewing the footage from the built-in underwater camera. Ten seconds intervals were analysed, and visually assessed values for proportions of various bottom substrate categories and abundance of sea urchins were recorded onto an Excel spreadsheet. Bottom substrate coverage was allocated into seven categories; sand/pebble, cobble, bedrock, low algae, high algae, shell fragments and other. Muddy bottom substrate were included in sand/pebble. Coralline algae and maerl were included in the “cobble” category. Bedrock was defined as hard bottom with little or no algae cover. Algae cover was categorized into either low algae (<30 cm height) or high algae (>30 cm height). In general, high algae cover was present in areas with kelp such as *Laminaria hyperborea* and *Saccharina latissima*, while low algae consisted mostly of Dulce (*Palmaria palmata*) and *Desmarestia aculeata* as well as other unidentified clusters of turf algae. The “Other” category mostly comprised 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. The abundance of sea urchins, mainly *Strongylocentrotus droebachiensis* (Müller, 1776), was assessed and ranked to 0 for “none”, 1 for “some” and 2 for “many”. Sea urchin abundance index was the average rank at each location. The percentage coverage of each category of bottom substrate was noted for a ten second interval corresponding to ca 8 m distance, summing up to 100% for each ten second interval. Totally, 145 individual ten second clips were recorded at Edøya, 99 for Hekkingen, 133 for Molvika and 156 for Skårliia. For each location, average percentages of each substrate category were calculated.

2.6. 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 Hekkingen data were excluded when analysing spatial patterns for flatfishes. Hekkingen was excluded from seasonal pattern analysis. These selections were done to achieve balanced data sets for the statistical analysis. The seven species with sufficient material in focus were cod, common dab (*Limanda limanda* Linnaeus, 1758), halibut, lemon sole, saithe, plaice and thorny skate (*Amblyraja radiata* Donovan, 1808). Figures include all catch data unless otherwise indicated in figure text.

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 a non-parametric test that was employed when more than two sample distributions were tested. In these tests the actual measurements are converted to ranks before the test-statistics are calculated (Zar, 1998).

ANOSIM is a non-parametric test of similarities that was used to test if the catch composition at the different months and locations were similar. A SIMPER (Similarity Percentage) test was used to identify which taxa contributed the most to the dissimilarity. A Bray-Curtis similarity index were used with 9999 permutations (Clarke, 1993).

We estimated von Bertalanffy growth functions which describes the growth of fishes. The parameters 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. Both sexes were pooled in length at age figures for halibut as studies show similar growth rates up to sexual maturity (Karlson et al., 2013). The growth performance index $\Theta' = \log_{10} K + 2\log_{10} L_\infty$ (Moreau et al., 1986) was used to compare growth performances of species between areas.

Mortality rate was estimated applying the Chapman-Robson method (Chapman and Robson, 1960) by using the free statistical software R version 3.5.3 (<http://www.r-project.org>) and applying the FSA package (Fisheries Stock Assessment methods). The method is based on the numbers at age in each age class above age at recruitment. Annual mortality rates assume constant recruitment each year, and the function is expressed as:

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

where Z is the total mortality rate (year^{-1}), n the sample size and \bar{a} is the average age of the individuals above recruitment age.

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 analysing 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 significances of the axes.

The proportional coverage data were arcsine-square root transformed prior to the canonical correspondence analysis to meet assumptions of normality (Zar, 1998). The CCA data set was a matrix with values for each net-set given in rows with associated values for sample location, month, five environmental variables (sand/pebble, cobble, low algae, high algae cover and sea urchin abundance index) and catch in numbers of eight species in columns (Table S2).

For each net-set location and sampling month, we calculated mean species richness (mean number of observed species; S), Shannon-Wiener diversity index (H'), and evenness (J) as well as species catch proportions by number and biomass. The Spearman's rank coefficient (r_s) (Zar, 1998) was used to identify associations between bottom substrates and the community indices or abundance of various fish species.

The Shannon-Wiener diversity index (H') formula is:

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

where p_i is the proportion by numbers of individuals of species i found divided by the total number of species at the location or season, \ln is the natural logarithm, 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 representing the diversity at the location or season where the trammel nets were used. The higher the H' value the higher the 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) was then calculated as $J = H'/H'_{\max}$ where H'_{\max} is the natural logarithm of species richness (S). The evenness of substrate composition (J_{sub}) was calculated from

the Shannon Wiener substrate diversity calculated from proportions of substrate categories at the various locations.

SYSTAT (2017) 13 Version 13.2.01 was used when applying the non-parametric tests Kruskal Wallis H-test (KW) and Mann Whitney U test (MW) to test if a variable were equal in different groups. The test-statistics H for KW and U for MW and the degrees of freedom (df) of the tests were reported. PAST V3 was used for the multivariate analysis applying CCA (Hammer et al., 2001). PAST V3 was also used for correlation tests and the following permutation tests. For all tests, a P -value < 0.05 was considered significant.

3. Results

3.1. Catch composition

A total of 337 individuals from 16 species of fish and one crab species were caught and analysed. 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). Additionally, 39 edible crabs (*Cancer pagurus*) were caught.

3.2. Community structure

Mean species richness (S) and diversity (H') displayed highest scores in October and lowest in March (Fig. 2), but only S had a significant variation between months (KW, $H = 9.1$, $df = 3$, $P = 0.028$). Both species richness and diversity differed significantly between the four locations (KW, $H = 8.02$, $df = 3$, $p = 0.046$ and $H = 10.1$, $df = 3$, $p = 0.018$, respectively). Species richness (S) and diversity (H') were highest at Skårli and lowest at Hekkingen (Fig. 2). The species evenness (J) showed no clear seasonal or spatial patterns.

According to a two-way ANOSIM, the fish species composition differed significantly between locations ($R = 0.24$, $p = 0.04$) but not between months ($R = 0.18$, $p = 0.09$). On a seasonal scale cod

Table 1

Total trammel net fish catches. Numbers caught (No.), average length and weight and ± 1 standard deviation (SD) are given.

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

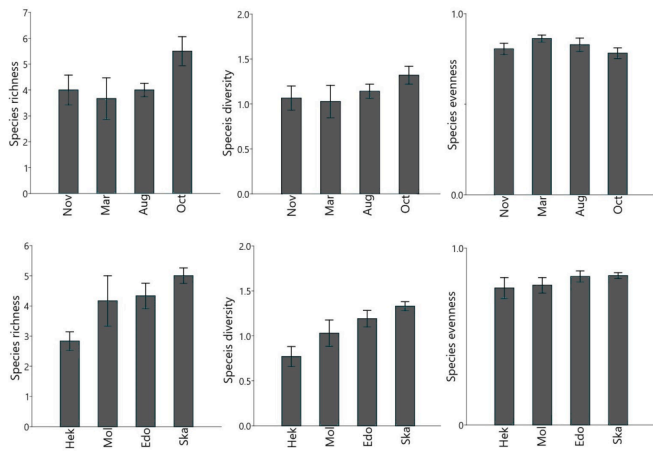


Fig. 2. Mean (\pm SE) species richness, species diversity and species evenness for the net-sets at the different months in outer Malangen excluding samples from Hekkingen (upper panel). Mean (\pm SE) species richness, diversity and evenness for the net-sets at all four locations; Hekkingen (Hek), Edøy (Edo), Molvik (Mol) and Skårliia (Ska), excluding samples from March (lower panel).

contributed to most of the group difference followed by plaice then lemon sole (Table 2), the ranks did not change when testing on a spatial scale.

Cod had the highest proportion of catch numbers at all months except March, in which plaice was the most dominant species followed by lemon sole and common dab (Fig. 3). Both plaice and lemon sole had relatively high catch rates in March and August and low rates in October and November. On the contrary, halibut and thorny skate showed higher proportion in October and November compared to March and August (Fig. 3).

3.3. Substrate associations

Coverage of various substrate categories showed large variability between locations (Fig. 4). Hekkingen had the highest coverage of high algae (93%), due to dominance of kelp (*Laminaria hyperborea*). Molvika and Edøya had similar bottom coverage distributions with sand and pebble dominating, however there were more low algae and shell fragments and less cobble and bedrock coverage at Molvika. Skårliia had high coverage of cobble and low algae as well as some patches with sand (Fig. 4). Skårliia had highest substrate evenness ($J_{sub} = 0.79$), while Molvika ($J_{sub} = 0.67$) and Edøya ($J_{sub} = 0.65$) were lower and Hekkingen ($J_{sub} = 0.20$) had very low evenness due to the homogenously coverage of high algae.

Both mean species richness (S) and diversity (H') were positively correlated with substrate evenness (J_{sub} ; $r_s = 0.50$, $p = 0.004$ and $r_s = 0.52$, $P = 0.003$, respectively). Substrate evenness was significantly positively correlated with catch numbers of halibut ($r_s = 0.40$, $p = 0.03$) and lemon sole ($r_s = 0.37$, $p = 0.04$). Plaice ($r_s = 0.34$), saithe ($r_s = 0.33$) and cod ($r_s = 0.08$) catch numbers were also positively but non-significantly correlated to J_{sub} .

The species-environment ordination diagram display the canonical

Table 2
Contribution to dissimilarity by species (SIMPER).

Taxon	Av. dissimilarity	Contrib. %	Cumulative %
Cod	21.1	30.6	30.6
Plaice	15.0	21.7	52.2
Lemon sole	8.5	12.3	64.5
Halibut	7.7	11.2	75.7
Common dab	5.8	8.5	84.2
Saithe	5.5	8.0	92.2
Thorny skate	5.4	7.8	100.0

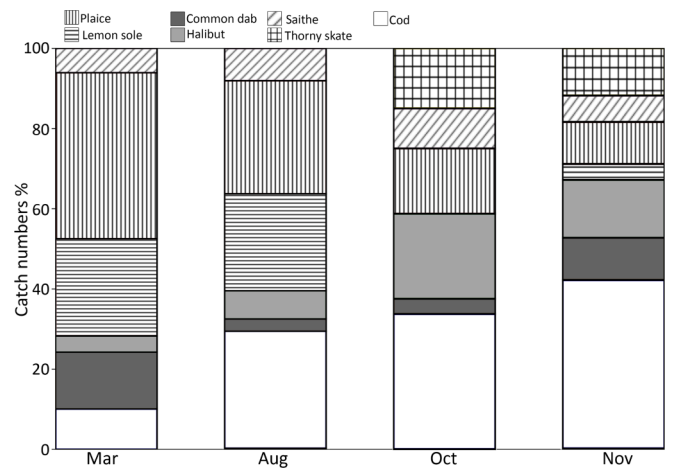


Fig. 3. Species composition (% of catch numbers) in net-sets by seasons (March, August, October and November) for all locations at shallow water in outer Malangen. Percentages were calculated with the seven species summing up to 100%.

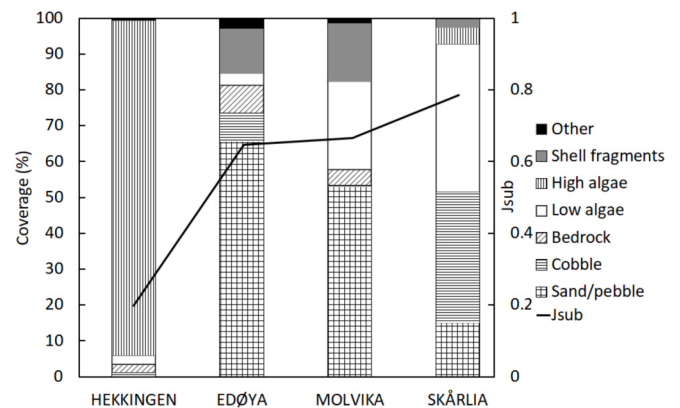


Fig. 4. Coverage of various bottom substrate categories observed with video survey at different locations in outer Malangen in August 2017. Black line represents the calculated substrate evenness (J_{sub}).

correspondence analysis (CCA) resulted from eight species and five environmental variables (Fig. 5). The CCA explained 43.3% of species variance at all four locations and seasons, and the first three axes accounted for close to 100% of this variation and were all significant (Permutation test, $p < 0.05$). Axis 1 explained 62.2% of the variance while axis 2 explained 24.4% with eigenvalues of 0.269 and 0.106 respectively. Axis 3 had an eigenvalue of 0.058 and explained 13.4% of the species-environmental variance.

The first axis of the ordination plot separated the benthopelagic gadids cod and saithe associated with high algae coverage (high axis value) from the flatfish plaice and common dab which were associated with sand/pebble and high sea urchin abundance (low axis value; Fig. 5A). In support of this, cod abundance was significantly positively correlated with high algae ($r_s = 0.53$) and negatively related with sand/pebble ($r_s = -0.58$) as well as with urchin coverage ($r_s = -0.54$; Table 3). The location “Hekkingen” was positively related with the first axis while “Edøya” was negatively related. Plaice catch numbers were significantly positively correlated to both sand/pebble ($r_s = 0.36$) and with cobble ($r_s = 0.50$), but not to urchin coverage ($r_s = 0.07$; Table 3). Common dab was the species with the highest negative relationship to the first axis (Fig. 5A), and had a significant positive correlation with sand/pebble ($r_s = 0.50$) and urchin coverage ($r_s = 0.44$) and a significant negative correlation ($r_s = -0.44$) to high algae coverage (Table 3).

The second axis separated lemon sole (positively related) and halibut

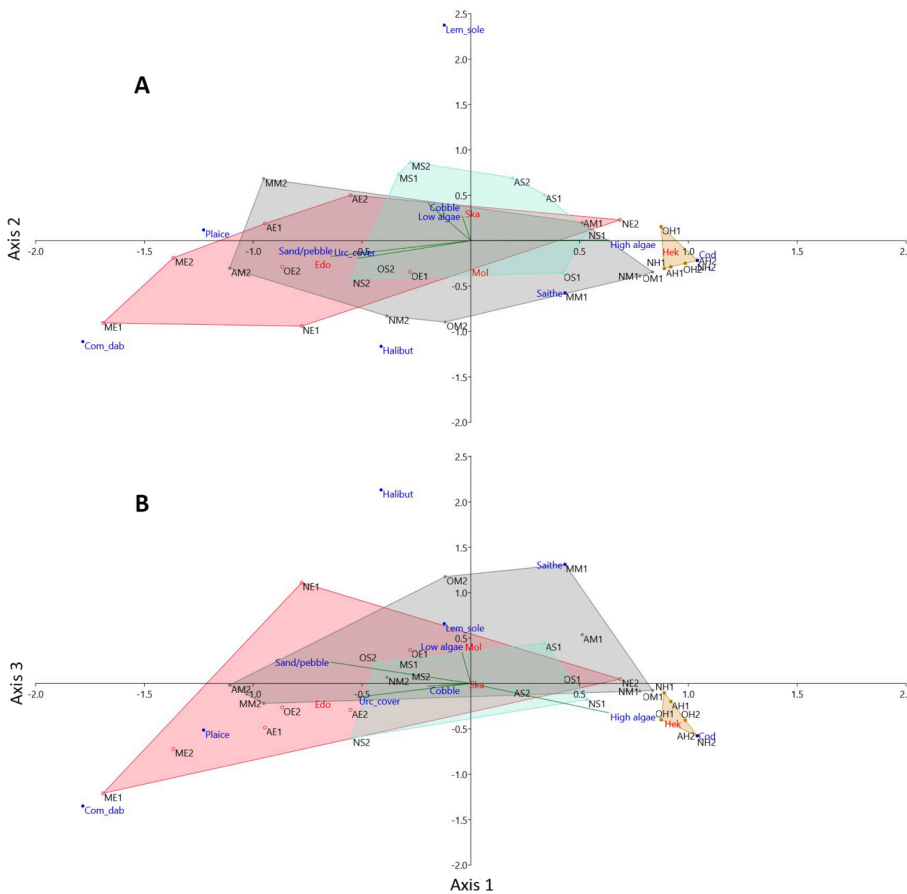


Fig. 5. Ordination diagram of Axis 1 (horizontal) and 2 (vertical) (A) and Axis 1 and 3 (B) from the canonical correspondence analysis (CCA). Species points represent the centroid (weighted average) of the site points in which it occurs, and vectors represent the regression relationships of environmental variables with the canonical axes (Braak and Verdonschot, 1995). The sites are abbreviated with first letters of month then first letter of location name and net-set 1 or 2. Hekkingen (Hek) is represented by six points as there were no sampling in March. Edøya (Edo) is marked as polygon with open circles, Molvika (Mol) with asterisk, Skårliia (Ska) with triangle and Hekkingen with filled squares. Individual scores are shown in table S3.

Table 3

Spearman rank correlations for species catches in numbers and substrate coverage categories, with net-set catches as observation units ($n = 30$). Values in bold indicate significant correlations and p -values are given in brackets.

Species	Substrate coverage categories				
	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	-0.24	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	0.12	-0.34
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

(negatively related), and cobble coverage was the most influential substrate category. Lemon sole were positively correlated to cobble coverage (Table 3). The third axis however grouped lemon sole and halibut closely as explained by low algae coverage (Fig. 5B), and both lemon sole and halibut catch numbers were significantly correlated with low algae coverage (Table 3).

3.4. Population dynamics

Generally, species length frequency distributions were similar in various seasons and between locations. However, lemon sole median length were significantly longer in March (36 cm) than in August (30 cm) and November (24 cm) and the length frequency distributions differed between seasons (KW, $H = 13.6$, $df = 2$, $p = 0.001$). Saithe were significantly larger in November (42 cm) than in the other months and saithe in March had the lowest median length of 25 cm (KW, $H = 7.8$, $df = 3$, $p = 0.047$). On a spatial scale, the flatfishes plaice and common dab were smaller at the location “Molvika”, than at the three other locations

(KW, $H = 6.043$, $df = 2$, $p = 0.049$) and (H = 19.2, $df = 2$, $p < 0.001$) respectively.

Age frequency distributions based on otolith readings were not significantly different between months for most species, but in line with the length distributions, the lemon soles caught in March were older than in August (MW, $U = 20$, $df = 1$, $p = 0.005$; Fig. 6). Spawning individuals of lemon sole and plaice were observed in March.

Length at age for cod, lemon sole and plaice, displayed an asymptotic pattern whereas halibut had a more linear pattern (Fig. 6). Von Bertalanffy growth function parameters (L_{∞} and K) and total mortality rate (Z) were estimated for plaice, cod and lemon sole. Separate and pooled parameters were estimated for each sex for plaice and cod (Table 4). Too few lemon sole were caught to estimate parameters for separate sexes. Cod and lemon sole had the same value for growth coefficient for pooled sexes ($K = 0.30 \text{ year}^{-1}$), while plaice had a lower K (0.22 year^{-1} ; Table 4). For plaice and cod, females had higher L_{∞} and lower K than males (Table 4). Plaice, cod and lemon sole had growth performance index (Θ) of 2.79, 3.26, and 2.67, respectively (Table 4). Cod had higher

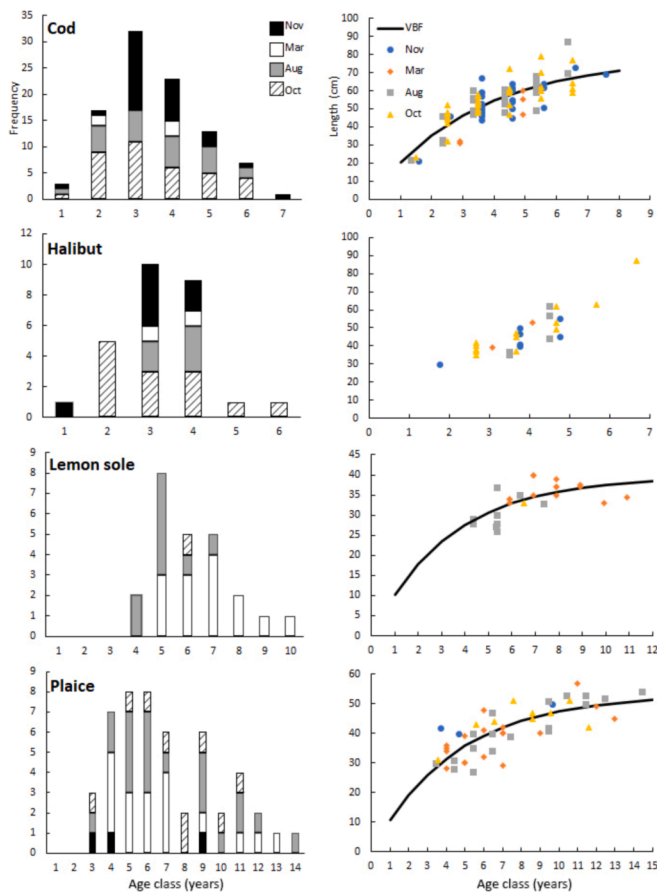


Fig. 6. Age class distribution (left panel) and length at age (right panel) for cod, halibut, lemon sole and plaice from trammel net catches in outer Malangen. Continuous lines in right panel show fitted von Bertalanffy growth functions. Note that age is calculated according to sampling month and expected hatching month, setting age at hatching to zero thereby displaying age more precisely within an age class. Cod, plaice and lemon sole were assumed to be hatched in March–April and halibut in February. Note different axis values. All trammel-net data are included.

Table 4

Von Bertalanffy growth function parameters L_{∞} (cm) and K (year^{-1}), and total mortality (Z , year^{-1}) estimates for plaice, cod and lemon sole. 95% Upper and lower 95% confidence interval (CI) are shown in brackets.

Species	Sex	L_{∞} (95% CI)	K (95% CI)	Θ'	Z (95% CI)
Plaice	Female	53.2 (47.3, 59.2)	0.24 (0.16, 0.32)	2.79	0.31 (0.22, 0.41)
	Male	42.8 (37.0, 48.6)	0.40 (0.18, 0.62)		
	Pooled	53.1 (47.8, 58.4)	0.22 (0.17, 0.28)		
Cod	Female	83.9 (61.5, 106.2)	0.26 (0.13, 0.39)	3.26	0.69 (0.50, 0.89)
	Male	71.2 (61.4, 81.1)	0.36 (0.25, 0.47)		
	Pooled	78.1 (68.8, 87.4)	0.30 (0.23, 0.37)		
Lemon sole	Pooled	39.5 (34.4, 44.6)	0.30 (0.18, 0.43)	2.67	0.52 (0.38, 0.65)

total mortality rate ($Z = 0.69 \text{ year}^{-1}$), than lemon sole ($Z = 0.52 \text{ year}^{-1}$) and plaice ($Z = 0.31 \text{ year}^{-1}$; Table 4).

4. Discussion

4.1. Seasonal patterns

Most fish species caught in this study are boreal species near their northern distribution limit (Wienerroither et al., 2011). The seasonal variation in fish communities in more temperate waters are generally explained by spawning migrations, temperature and prey abundance (Salvanes and Nordeide, 1993). We could hypothesize that all three reasons could explain the low species richness observed in March in our study. 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) and it is possible that fishes migrate to deeper waters in winter and spring as the temperature is higher at depths. Spawning migrations from the shallow water during spring and winter is likely for saithe and cod. Saithe generally spawn in offshore waters in winter (Salvanes and Nordeide, 1993) and cod spawn in deeper water further inside Malangen between March and April (Fevolden et al., 2015).

That fish diversity (H') was similar across seasons may be surprising for a subarctic environment, but may be related to high abundance of non-migratory local prey and also that some species such as lemon sole and plaice used the shallow water as spawning habitats during winter and spring. Fish activity level and turbidity may also affect catchability of trammel nets, thereby affecting the seasonal variation in catch rates (Villegas-Ríos et al., 2014).

That flatfishes dominated the spring and summer whereas cod and thorny skate were the most prominent species during autumn and winter months show that the different groups of species differ in seasonal use of the area. The patterns for cod with high catch numbers for all months except March and for saithe with highest occurrence during summer and autumn is similar to observations from Masfjorden (60°N) in southwestern Norway (Salvanes and Nordeide, 1993). This suggests that the observed cod populations and saithe have similar seasonal distribution patterns in fjord areas.

4.2. Community and species-habitat associations

That species richness and diversity were strongly correlated with habitat evenness was in accordance to our expectations that complex habitats with evenly distributed biotopes function as preferable habitats for various species. Fishes utilize habitat types differently, e.g. as feeding or resting habitats (Hinz et al., 2006), which is why species-specific habitat utilization could explain why species richness and diversity increase with habitat evenness. Certain bottom substrates might have a higher prey abundance than other (Able et al., 2005), thereby attracting more predatory fish species. The location Skårli had the highest substrate evenness, and species-specific utilization of different substrate types may therefore have led to the high species diversity observed at this location. Furthermore, the correlations of species richness and diversity to habitat evenness are also in line with studies on habitat complexity and bottom fauna in adjacent deeper waters (Buhl-Mortensen et al., 2012) as well as for fish communities in other areas (Gratwicke and Speight, 2005; Huang et al., 2019). Importantly, in our study habitat complexity had a more prominent effect than whether the location was an outer or inner location. Additionally, flatfishes were absent at the kelp dominated location Hekkingen.

The canonical correspondence analysis (CCA) and the supportive spearman's rank correlations displayed that some biotas had high influence on the catch compositions. Cod catches were uniquely positively associated to high algae coverage and CCA-axis one, and this kelp habitat was largely found at Hekkingen, where most of the other species were less abundant, especially flatfishes. The importance of kelp beds/

forest as areas for primary production, nursery grounds, ecosystem services and biological diversity has been emphasized (Mann, 2000; Norderhaug and Christie, 2009; Steneck et al., 2003). Kelp forests are therefore important for other reasons than fish species richness or diversity, of which neither were significantly correlated with high algae coverage in this study. An earlier study in a nearby area could not identify bottom substrate preferences for cod older than one year (Sundby et al., 2013), which makes our observations somewhat novel. Furthermore, we found that cod catches were significantly negatively correlated to sand/pebble coverage. It could be that cod of smaller size utilizes these sand/pebble habitats to avoid larger predatory cod as explained by Fraser et al. (1996).

That plaice and common dab were both positively related with sand/pebble and urchin abundance on the negative side of the first CCA-axis, could be explained by their resting and burying behaviour at these substrates. Adult plaice feed on polychaetes, small fish and epibenthic crustaceans, which are more abundant and diverse at benthic habitats with complex emergent epifauna (Hinz et al., 2006). In addition, we observed a relatively large proportion of the stomach content of plaice to be small sea urchins (unpublished obs.). This further support that prey abundance also indirectly influence habitat use for some of the observed species. Cobble substrate in this study included maerl beds and cobble rocks. Lemon sole displayed a significant correlation with this substrate as well as low algae, both of which were prominent at the Skårliia location. It could therefore be hypothesized that lemon sole use this type of habitat exclusively, whereas other flatfishes such as halibut and plaice come to forage in these complex habitats.

Halibut were caught at all locations except the kelp-dominated Hekkingen. All the observed halibuts were immature, which could indicate that halibut use these areas as nursery grounds. This provides arguments to include more shallow water areas in coastal fish resource surveys.

4.3. Patterns in population dynamics

Length at age for the cod found in the present study was similar to values for coastal cod from Berg and Albert (2003) for the same outer coastal area but generally higher than found by Berg and Pedersen (2001) in two adjacent colder fjords at 70°N. The faster growth in outer Malangen is probably explained by higher temperature in the area in summer and autumn which is within the optimal temperature range of

9–12 °C for growth in large cod (Pedersen and Jobling, 1989). The von Bertalanffy growth coefficient K for cod observed in outer Malangen (0.30 year⁻¹) was higher than for Northeast Arctic cod in the Barents Sea and for the southern Masfjorden (0.21 year⁻¹; Heino et al., 2012; Table 5). Thus, our expectations of a low K value in Malangen compared to more southern populations were contradicted. This could be explained by the relatively high temperature found in the outer Malangen area. The growth index (Θ') suggested high growth in Malangen for cod compared to further south (Table 5).

The observed cod age distribution peaked at age three, and as age distributions for trammel net catches were skewed to the right we can assume that the estimate of total mortality (Z) was relatively representative for the population of three year and older cod in the area. The estimated Z in the present study (0.69 year⁻¹) was similar to an earlier estimate of 0.7 year⁻¹ for cod from the inner part of Malangen (Table 5). Our mortality estimate is higher than for the inner and colder fjord area Sørkjord (69.5°N) but is lower than the mortality rate estimates for coastal cod in mid and Southern Norway (58–64 °N) that were in the range of 0.95 to 1.8 year⁻¹ (Table 5).

The asymptotic length L_∞ of 53 cm for plaice in outer Malangen was similar to values from the North Sea and Kattegat & Skagerrak (Table 5). In contrast, the growth coefficient value K of 0.22 year⁻¹ for outer Malangen is higher than for plaice in Barents Sea, the North Sea and Kattegat & Skagerrak (Table 5; Cardinale et al., 2010; Jennings et al., 1998), thereby contradicting our expectations of a low K in Malangen. The relative high growth performance index (Θ') for plaice in Malangen compared to North Sea populations suggest good growth conditions in Malangen.

The total mortality estimated for plaice in the present study (0.31 year⁻¹) was low compared to total mortality rates found for North Sea plaice from 1990 to 2007 (0.6–0.8 year⁻¹; Cardinale et al., 2010; Table 5). For North Sea plaice, there probably was a fishery induced decrease in L_∞ and an increase in K for 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, but our estimates for K of 0.24 year⁻¹ for females and 0.40 year⁻¹ for males were similar to the values for the 2000' in the North Sea (van Walraven et al., 2010). 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

Table 5

Comparison of von Bertalanffy parameters L_∞, growth coefficient (K), growth index Θ', and total annual mortality rate (Z) for the present study in Malangen and other areas.

Species	Area & period	L _∞ (cm)	K (year ⁻¹)	Θ'	Z (year ⁻¹)	Reference	
Cod	Barents Sea (72 °N; Northeast Arctic cod)	129	0.13	3.32		Trout (1954)	
		134	0.10	3.25		Taylor (1958)	
	Malangen (69.4 °N)	78	0.30	3.26	0.69		This study
					0.7		Larsen and Pedersen (2002)
		Inner Malangen 1988 (69.2 °N)				0.47	Pedersen and Pope (2003)
		Sørkjord (69.5°N) 1990–1996				1.30	Kristiansen et al. (2000)
		Flatanger (64°N)				1.02	Salvanes and Ulltang (1992)
		Masfjorden (60°N) 1986–1988	101	0.13	3.12	1.0	Heino et al. (2012)
		Masfjorden (60°N) 1985–1993	80	0.21	3.13	1.8	Kristiansen et al. (2000)
		Heimarkspollen (60°N)				0.95	Kristiansen et al. (2000)
Øygarden (60°N)				1.39	Olsen and Moland (2011)		
Skagerrak (58°N)					Kuznetsova et al. (2004) ^a		
Plaice	Barents Sea (71 °N) 1970–1976	55	0.151	2.60			
		74	0.102	2.74			
	Malangen	53	0.22	2.79	0.31		This study
		Karmøy (59°N) 1991–1993	51	0.22	2.77	0.46	Albert et al. (1998) ^b
		Kattegat-Skagerrak 1990–2007	54.9	0.11	2.52	0.6–0.8	Cardinale et al. (2010)
		North Sea 1975–1994	54.4	0.11	2.51		Jennings et al. (1998)
Lemon sole	Malangen	40	0.30	2.67	0.52	This study	
		Karmøy (59°N) 1991–1993	36	0.25	2.51		Albert et al. (1998)
		North Sea	40	0.32	2.71		Jennings et al. (1998)

^a Calculated from average of lengths for males and females of 5–14 years of age.

^b Calculated from average length at age and age-distributions.

individuals compared with plaice in the North Sea.

L_{∞} and K for lemon sole observed in the present study were slightly higher than at Karmøy (59°N) in Southern Norway (Albert et al., 1998), but similar to values for the North Sea (Jennings et al., 1998; Table 5). The relatively high confidence interval (0.18–0.43 year⁻¹) for lemon sole K is probably due to the lack of young fish in age material.

For cod, the growth index (Θ) was similar for Malangen and the Barents Sea while for plaice the growth index in Malangen was higher than in the Barents Sea. The relatively high growth index (Θ) in Malangen compared to southern areas for both cod, plaice and lemon sole suggest that the relatively warm shallow waters of outer Malangen is an area with good individual growth for these species. Our expectations of lower values for the growth coefficient K and higher values for asymptotic length (L_{∞}) in outer Malangen compared to more southern areas were not supported for cod, plaice and lemon sole (Table 5). In contrast, our expectations regarding spatial mortality patterns were supported as plaice and lemon sole had low mortality and cod showed a moderate mortality compared to more southern populations (Table 5). These moderate mortality rates are likely to contribute to relatively stable biomass of the species in the Malangen area.

Migration of coastal cod which is the dominating cod stock in Malangen is limited and few coastal cod move more than ca. 20 km away from tagging locations (Larsen and Pedersen, 2002; Pedersen et al., 2008; Nøstvik and Pedersen, 1999). In coastal cod, there are strong spatial gradients in population dynamics at the fjord scale (Berg and Pedersen, 2001; Fevolden et al., 2015). Spawning individuals of lemon sole and plaice were observed in March, showing that both these species use the area a spawning ground. These shallow waters are therefore not only important for growth and survival, but also reproduction and hence the recruitment of these two species. For plaice at the open coast of Northern Norway, there are indications of a southwards counter-current spawning migration while the plaice inside the fjords are less mobile (Devold, 1942). The lengths at age for the sampled halibut in Malangen were similar to those of Karlson et al. (2013) from the coast of Norway north of 62°N. That only immature halibut were caught in this study is in line with the study of Godø and Haug (1988) which indicated that juveniles used the coastal nursery areas until the age of 4–6. This indicate that the shallow areas of in the outer coastal zone may be an important nursery ground for halibut, and the low mortality rates of plaice of similar size as juvenile halibut suggest high survival potential for flatfish.

4.4. Limitations of the study

The relatively large mesh size trammel net was chosen to get robust nets that could fish during rough weather. The backside of this was that very few fish less than 25 cm in length were caught, and we could not assess whether the locations had nursery functions for small bodied fish. The sampling design with one video survey per location resulted in one bottom substrate value for each category, lowering the strength of the correlation analysis. Some filamentous and opportunistic low algae have high seasonality which could induce some seasonality in substrate coverage. This was a limited study with sampling over a year at four locations and should be followed by further investigations in shallow water. Although the number of fish is not very large, we have replicate samples (net-sets) at each location and sampling-period and the trammel-nets sample over a long time compared to trawl sampling so that variability within each-trammel net-set sample was relatively low.

4.5. Conclusions

Fish community compositions in outer Malangen were mainly affected by bottom substrate variability. We showed that fish species richness and diversity were strongly associated with bottom substrate evenness which highlight the importance of complex coastal habitats for many of the investigated species. Contrary to our expectations, cod,

plaice and lemon sole all had a comparatively fast growth when compared with adjacent fjord populations and populations further south. Most fish species were long-lived with relatively low mortality rates which may contribute to stability in biomass. Proper management is important to maintain the complexity of these coastal habitats, and with increased warming, this study could provide a baseline for fish habitat use in a moderately exploited shallow outer subarctic coastal area.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.seares.2021.102136>.

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