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Fish assemblages at the Yermak Plateau and in northern Svalbard waters during the period 2012–2020

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ABSTRACT

During several surveys covering the north-western and northern Svalbard waters, and the deeper Yermak Plateau north of Svalbard during the period 2012–2020, 291 standardized hauls with a demersal trawl were made. All fishes in the catches were identified to the lowest possible taxonomic level, mostly to species. In addition to the data generated from the trawl catches, bottom temperature, salinity, and depth were recorded at each trawl station. The eelpouts were the most species rich family, with 15 species, followed by codfishes and sculpins with six species each. The other 13 families were represented with one to four species each. Atlantic cod (*Gadus morhua*) dominated by weight in the catches, while polar cod (*Boreogadus saida*) dominated by numbers. In the deeper areas including the Yermak Plateau, Greenland halibut (*Reinhardtius hippoglossoides*) dominated by weight. Zoogeographically, 23 species were Arctic, 5 were Mainly Arctic, 4 Arctoboreal, 25 Mainly Boreal, 9 Boreal, and 2 Widely Distributed. The Arctic species dominated in the deeper areas (Yermak Plateau and slope > 500 m) and on the shallow eastern shelf, whereas the Mainly Boreal species dominated along the slope and on the western and northern shelves < 500 m. A hierarchical cluster analysis revealed three prominent station clusters consistent with the zoogeographical classifications which reflected the oceanographic conditions, water masses and sea ice. The hierarchical cluster analysis additionally separated the cold-water species into two groups consistent with the bathymetry of the region. Diet studies of Atlantic cod revealed that it mainly fed on hyperiids, and that its preferred food further south, capelin, was not prominent in the diet.

Regional index terms: Northeast Atlantic, Fram Strait, Svalbard, Yermak Plateau.

1. Introduction

The coastal area to the west and north of Svalbard (Fig. 1) has been utilized for sealing and whaling since about 1610 (Molaug, 1968), and for commercial fishing at least since 1874 (Iversen, 1934), when catches of Atlantic cod (*Gadus morhua*) were reported from this area for the first time. Human activities in these remote areas, especially in the early period when boats were small and had sails as propulsion, were dependent on favourable weather and sea-ice conditions. Consequently, the level of activity varied considerably over the years and decades.

Apart from sporadic expeditions like for instance the Swedish expeditions of Torell in 1858, of Nordenskjöld in 1864 and of Nathorst in 1898 (Nathorst, 1899), or the Norwegian North Atlantic Expedition (Mohn, 1878), that all visited the areas to the west and north of Svalbard, no systematic mapping of fishes was carried out there in the 19th century. In the 20th century fisheries and research interest gradually

increased and monitoring of the groundfish community around Svalbard became a regular undertaking from about 1970 (Hylen et al., 1972). Since 2004, ecosystem surveys covering the whole Barents Sea, including the coastal areas around Svalbard, have been conducted every autumn (Eriksen et al., 2018). While these surveys include stations on a regular grid along the coast of Svalbard (and in recent years also depth-stratified stations and increased research effort especially to the north of Svalbard), the research project SI_ARCTIC, lasting from 2014 to 2017, provided the opportunity to undertake more in-depth studies of these areas, including in ice-covered waters.
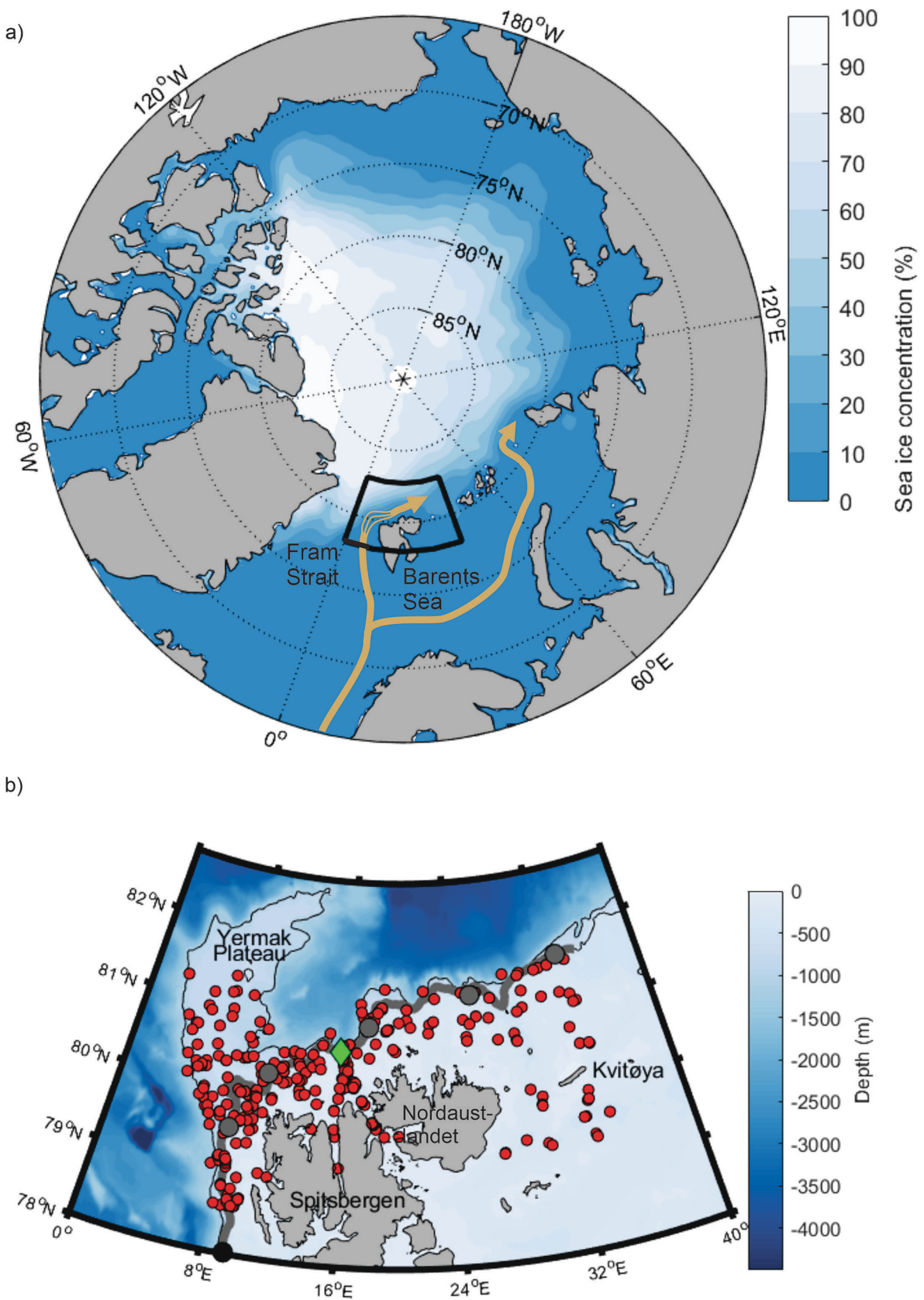
1.1. Physical characteristics of the area

A substantial amount of Atlantic Water is transported into the northern Fram Strait with the West Spitsbergen Current (Fig. 1 a). When encountering the Yermak Plateau (Fig. 1 b) at the north-western corner

Fig. 1. Study area and stations. a) Sea ice concentration in September averaged over 2012–2020. The yellow arrows show the general flow of Atlantic Water, and the black box denotes the study area. b) Study area and demersal trawl stations included in this study (red dots). The along-track contour which was used to calculate along-slope distance from 78°N is shown in dark grey, and every 100 nmi of the contour is shown by dark grey dots. The green diamond shows the Hinlopen Trough region, which is about the mid-point on the along-track contour. The 500 and 1000 m depth contours are shown with black lines.

of Svalbard, this slope current splits into three branches; a narrow and shallow branch following the 200-m isobath, a branch crossing the Yermak Plateau slightly further north (near approximately 80.5°N), and a third branch flowing along the western rim of the Plateau (Menze et al., 2020 (this issue); Athanase et al., 2021). After passing the Plateau, the Atlantic Water flow continues eastwards in a narrow band along the slope forming a continuous flow encircling the Arctic Basins (Aagaard, 1989; Bluhm et al., 2020).

Atlantic Water is also brought onto the shelf by e.g., episodes of wind driven upwelling (Cottier et al., 2007; Goszczko et al., 2018), and by the general circulation in trenches such as the Hinlopen Trough (Menze et al., 2020 (this issue)) and the trench northwest of Kvitøya (Pérez-Hérnandez et al., 2017), as well as into the northern Barents Sea (Lind and Ingvaldsen, 2012). Less is known about the circulation on the shelf, but it is influenced by colder and fresher coastal waters, freshwater from seasonal freezing and melting of sea ice and glaciers, and exchange with the fjords. Moreover, Atlantic Water is brought onto the shelf by the general circulation in the trenches such as Isfjorden, the Hinlopen Trough and the trench northwest of Kvitøya (Nilsen et al., 2016; Pérez-Hérnandez et al., 2017; Menze et al., 2020 (this issue)), and episodes of wind-driven upwelling (Cottier et al., 2007; Goszczko et al., 2018).

On its northward journey, the Atlantic Water is substantially cooled by heat loss to the atmosphere (e.g., Renner et al., 2018), transforming it into the colder but still salty Arctic Intermediate Water. This is the dominant water mass found below the modified Atlantic Water, at about 700 m depth and deeper (Våge et al. 2016; Pérez-Hérnandez et al., 2017; Jones et al., 2021 (this issue)). The shallow shelves east of Svalbard are dominated by fresh Polar Surface Water originating in the Arctic Basin as mixture of melt/freeze water, Atlantic Water, precipitation, and river runoff (Rudels et al., 2005; Jones et al., 2021 (this issue)).

The sea ice cover varies greatly within the region. The western and northern shelves are currently free-of ice most of the year (Fig. 1a), while the slope and the shallow shelves east of Svalbard is more variable from year to year. The Yermak Plateau is usually ice-covered throughout winter and large parts of the summer in the northern and central parts (Fig. 1a).

1.2. Biological characteristics of the area

Catches of Atlantic cod (*Gadus morhua*) were reported from this area for the first time in 1874, together with other boreal species like saithe (*Pollachius virens*), haddock (*Melanogrammus aeglefinus*), tusk (*Brosme brosme*) and Atlantic halibut (*Hippoglossus hippoglossus*) (Iversen, 1934). The fishery in this area was carried out regularly from 1874 to 1882, but then dwindled. Although 18 Norwegian fishing vessels visited the area in 1883, they did not catch any cod. A new period with rich cod fisheries in Svalbard waters came in 1925–1935.

There is thus reason to believe that the presence of typical boreal fish species in fishable concentrations west and north of Svalbard followed periods of higher water temperatures in the area (Haug et al., 2017). In the more recent period, fisheries for deep sea prawn (*Pandalus borealis*) have dominated, but both trawl and longline fisheries for Atlantic cod, haddock, and other species were also conducted and there was an increased trend in landings in the Svalbard area during the period 1980–2013 (Misund et al., 2016). Small Atlantic cod, haddock, Greenland halibut (*Reinhardtius hippoglossoides*) and redfish (*Sebastes* sp.) in the size range of 5–25 cm are also caught as by-catch in the shrimp fisheries (Hvingel and Thangstad, 2018; ICES, 2021).

Especially in late 1960 s to early 1970 s, targeted trawl catches of young Greenland halibut were high in ICES area 2b (Godø and Haug, 1989). This ICES area includes the study area, but it also overlaps with the main fishing grounds that are further south along the slope between 68°N and 74°N (Bowering and Nedreaas, 2000). Greenland halibut have been regularly caught in deeper water along the slope.

While information about the distribution of commercial fish and shellfish along the western and northern coasts of Svalbard has been available for a long time (see for instance Misund et al. (2016)), less is known about non-commercial demersal fishes from this area. This is particularly true for the Yermak Plateau, where ice is normally present for several months in a year (Fig. 1), and for the deeper arctic areas north of the shelf (Bergstad et al., 2018).

As sea temperatures in these areas are increasing and sea ice cover is decreasing, the living conditions for demersal fishes are changing rapidly (Ingvaldsen et al., 2021; Brandt et al., 2023), and we may foresee further changes in fish distribution, fisheries, and feeding habits (Haug et al., 2017). The aims for the paper are to describe how demersal fish species in the area northwest and north of Svalbard were geographically distributed during 2012–2020, and to discuss whether the borealization reported from before 2010 (Bergstad et al. 2018) has continued during our study period. Additionally, we study whether the food and feeding of Atlantic cod are influenced by an increased occurrence of Arctic species, where Arctic species and boreal species now overlap. Increased predation from Atlantic cod, together with increasing water temperatures, have been postulated to be a threat to Arctic fish species (Fossheim et al., 2015).

An overarching goal is to establish a baseline for future investigations by describing the assemblages of demersal fish, to describe the biological characteristics of dominant species, and to analyse connections between the fish assemblages and environmental factors in the study area. The study area being the area covered by the cruises in the SI_ARCTIC research project, which took place annually in the period 2014 to 2017 supplemented by data from the annual Barents Sea ecosystem surveys in 2012 and 2018–2020.

Some of the areas we include have not been well described previously with regards to fish species assemblages. The Yermak Plateau, which is a deep (mean depth 650 m) plateau northwest of Svalbard (Fig. 1 b), has normally been ice-covered year-round. However, in some years, including 2012 and some of the years in the SI_ARCTIC project period and after, the central parts of it were accessible and visited in September. Additionally, the relatively shallow shelf area northeast of Svalbard, is more seldom visited and has been poorly described with regard to benthic fish assemblages due to varying sea ice conditions.

2. Materials and methods

2.1. Cruises

The material for this study came from a set of nine cruises conducted during the period 2012–2020 (Table S1). Four of these formed parts of the research project "SI_ARCTIC" (Ingvaldsen et al., 2016a, b; Ingvaldsen et al., 2017a, b), the others were the "Arctic" parts of the annual autumn Norwegian-Russian Barents Sea ecosystem surveys "BESS" (Eriksen et al., 2018). While the SI_ARCTIC surveys were restricted to the Fram Strait and the areas north of Svalbard, the ecosystem surveys cover the entire Barents Sea. We defined the study area to be north of 78°30'N and west of 35°E and excluded stations outside this area. The data from the 2012 ecosystem survey are included because that year, the survey included the Yermak Plateau northwest of Svalbard, and this area was revisited during some of the SI_ARCTIC surveys. Including these data allowed us to give a better description of the Yermak Plateau.

These cruises were all multi-purpose surveys including studies in physical and chemical oceanography, phytoplankton, zooplankton, demersal and pelagic fish, sea mammals, and birds, applying a variety of sampling gears and instruments. Here, we use data from hauls with a demersal trawl, and measurements from CTD-casts in the same positions, or near to, where the trawl hauls were made. The number of trawl hauls included in our material was 291, after a few hauls had been excluded due to damages on the trawl or other circumstances that might have rendered the catches non-representative.

2.2. Survey design and catch sampling

The design of demersal trawling during the BESS surveys is mainly a regular grid with distance 30–35 nautical miles between stations. However, in the Svalbard region this design has been altered, to include depth-stratification along the steep slope west and north of Svalbard (Michalsen et al., 2011; Eriksen et al., 2018). The SI_ARCTIC surveys on the other hand, were different and more adaptive, since each of the surveys included some special studies that demanded non-regular survey grids (for instance observations of sea mammals in ice-covered waters, detailed oceanographic characterisation of various locations etc.). In these surveys, some transects from the coast across the shelf and slope and into deep water were conducted, when the ice conditions allowed. Otherwise, demersal trawl hauls were conducted at regular intervals and at various depths, see the cruise reports for further details (Ingvaldsen et al., 2016a, b; Ingvaldsen et al., 2017a, b). In the Hinlopen area, stations at predetermined positions along a transect from the coast to beyond the shelf break were visited every year from 2014 to 2020.

The demersal trawl used was a Campelen 1800 with mesh size 80 mm in the front panels gradually decreasing to 16 mm in the cod end, allowing for retention of small-sized fish. The typical vertical trawl opening of this trawl is 3.5–4.5 m and the trawl geometry and bottom contact is monitored with acoustic censors on the trawl doors and the trawl. Standard trawling implies 15 min of trawl contact with bottom during each haul, and the standard towing speed is 3 knots. For the deeper stations, the trawl contact with bottom was extended to 30 min. The trawl is designed for catching fish but depending on bottom substrate and other local conditions, a by-catch of whole, or fragments of benthic organisms are normally also retained in the trawl (Johannesen et al., 2017a; Jørgensen et al., 2022 (this issue)). In the present study, only the catch of fish is considered and benthic organisms, including prawns, were excluded from the material. Since the trawl will to some degree catch organisms from the pelagic zone during setting and heaving, a small amount of the catch may stem from the water column. It is not possible to discern among this part of the catch and that taken at the bottom, other than by judging from the types of fish caught. Since many species of demersal fish spend parts of their time above the bottom, and many species of pelagic fish may spend parts of their time near the bottom, such judgements are arbitrary. Consequently, we have not excluded species based on these criteria, as was done for instance by Bergstad et al. (2018), who described demersal fish in the Svalbard area based on the BESS surveys prior to 2015. Note though, that when analysing catch biomass, we excluded a few specimens of Greenland shark caught in 2012 and 2016. With each individual weighing several hundred kg, this species was one of the dominants by weight. However, because only some of the Greenland sharks were weighed before they were released live to sea, the weights were not included in our study.

The catch was sorted to lowest possible taxonomic level, weighed, and counted. An experienced taxonomist took part in most of the surveys and checked all species that were difficult to identify. On the remaining surveys unidentified species were frozen on board and subsequently identified by experienced taxonomists. The genera Sebastes, Icelus and Careproctus caused special problems. Small individuals of Sebastes are not possible to identify to species in the field and these were identified to genus level. Two species of Icelus were identified, but these need careful examination to tell them apart, and in some cases, these were identified only to genus level. Consequently, we lumped these together as Icelus spp. in our analysis. The various species in genus Careproctus is also very difficult and time consuming to discern among, and these were all identified only to genus level. Samples were taken of all fish species according to prescribed procedures (Mjanger et al., 2020). This includes length measurements of all species and more detailed measurements (individual weights, sex, maturity stage, age, stomach content analysis etc.) of selected species.

In our material, six specimens were marked as questionable in the database: silvery pout (*Gadiculus argenteus*), poor cod (*Trisopterus minutus*), pollock (*Pollachius pollachius*), witch (*Glyptocephalus cynoglossus*), and striped seasnail (*Liparis liparis*). These species have not been observed in Svalbard waters and may have been misclassified when included in the database after sampling. They were excluded from our material.

2.3. Preparation of dataset

The dataset extracted from the IMR survey database contains information about the surveys, the individual trawl hauls (position, depth, time etc.), the catches of various species (weight and number of specimens caught, and which samples were taken), and the measurements taken on each individual (length, weight, age, sex, maturity stage, stomach filling degree, prey species in the stomachs etc.). We added some environmental data pertaining to the geographical position of each trawl haul to this dataset, viz. bottom temperature, days covered with sea ice since last summer, water masses, and along-slope distance from 78°N.

During the SI_ARCTIC and BESS surveys a CTD cast was made for most trawl hauls, and the bottom temperature and salinity was extracted from these casts. For a few trawl hauls CTD data were missing, and bottom temperature and salinity from the nearest CTD station was used if within 20 nautical miles from the trawl position. In 2012, the temperature sensor of the CTD was not working properly, and no temperature/salinity measurements were included from that survey. Water masses were defined using the same characteristics as Jones et al. (2021 (this issue)) for the 2014–2017 SI_ARCTIC data set; Atlantic Water (AW) by $T > 0\ °C$, $S > 34.9$, Arctic Intermediate Water (AIW) by $27.97\ kg/m^3 < \sigma$, $T < 0\ °C$, Polar Surface Water (PSW) by $\sigma \leq 27.97\ kg/m^3$, $T \leq 0\ °C$ and the warmer variety of this mixture, called warm Polar Surface Water (PSWw) by $T > 0\ °C$, $S < 34.9$.

We also included in our dataset the number of days with ice cover during the last year in the positions where the trawl hauls were made. To compute days covered with sea ice, we used daily sea ice concentrations from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave. Data were received from NSIDC (Cavalieri et al., 1996). The total number of days with >15 % ice concentration within the period 1 September the year before to 31 August was thereafter assigned to each trawl station.

The pronounced bathymetry and strong topographic steering of the Atlantic Water flow along the slope in our study region, facilitate gradients and changes in the demersal communities to occur along the slope rather than directly northwards. Therefore, all stations (except for the stations south of Kvitøya on the Eastern shelf) were projected onto the 500 m isobath and then sorted according to their distance from the southernmost part (78° N) (see Fig. 1b). With this approach we traced the Atlantic Water along its poleward pathway towards north and northeast to reveal transition regions where the demersal community structure changes.

2.4. Subdivision of data and selection and characterisation of species

To characterize the species' zoogeographic affinity, we used the zoogeographical groups described by Andriyashev and Chernova (1995). However, for a few species not classified there, and for Greenland halibut, we used zoogeographic affinity from Mecklenburg et al. (2018).

2.5. Analysis methods

All biological analyses were undertaken using R statistical software (R core Team, 2022), while all oceanographic analyses were undertaken in Matlab (2021). Based on the total catch of each species and the distance of trawling, we calculated standardized catch rates in weight and numbers per nautical mile trawled. To compare feeding habits across size, age, and area for Atlantic cod and polar cod, we calculated the frequency of occurrence of 17 prey categories following Holt et al.

(2019).

We grouped the stations by fish species composition using a hierarchical cluster analysis (R package vegan, Oksanen et al., 2020). The fish abundance data were square root transformed before clustering using the Bray-Curtis distance metric and the Ward clustering method.

As the survey design varied among the years, abundance estimates for the total area or subareas were not calculated, and we did not focus on inter-annual variation.

3. Results and discussion

3.1. Number of species

The total number of species recorded was at least 68 (Table 1). More species were probably in the catches since the species recorded in the genus *Careproctus* has unresolved taxonomy but could include more than one species. The family Zoarchidae (eelpouts) dominated with 15 species, followed by Gadidae (codfishes) and Cottidae (sculpins) with six species each. The other 13 families were represented with one to four species each (Table 1). Three species (polar cod, Atlantic cod, and Greenland halibut) where found in over 70% of the stations, and ten species were found in>30% of the stations, most of which are abundant in other parts of the Barents Sea like haddock, capelin, long rough dab and deepwater redfish. Eight species were found in<1% of the stations (1–2 stations, Table 1). The average number of species found per station was 12.4, median 12, range 1–23. We note that the species list in Table 1 is not directly comparable to the species list in Bergstad et al., (2018) since that study excluded pelagic and mesopelagic species from the trawl data and covered a larger area.

Despite our study having a better coverage of the northern part of the Svalbard area than earlier studies, including Yermak, we did not record any species not previously recorded in the region, or in the Barents Sea as a whole (Wienerroither et al., 2011; Johannesen et al., 2017a; Bergstad et al., 2018). This implies that northward range extensions associated with warming (e.g., Fossheim et al., 2015) had occurred prior to 2012, consistent with Bergstad et al. (2018) who argued that their observed patterns probably reflect an extensive Atlantic influence starting in 2004.

However, range extensions only constitute one part of the borealization process, which probably starts with a few stray individuals occupying areas where the species was not previously present, but which continues, possibly over a long period, when the species become established more permanently and increase in abundance and biomass. The processes involved in the borealization observed in the Barents Sea primarily has been driven by species like cod and haddock extending their distribution and seasonal feeding migrations (e.g., Johannesen et al., 2020) due to increasing stock size (e.g., Kjesbu et al., 2014; Landa et al., 2014). Both cod and haddock peaked in biomass in the Barents Sea around 2012, as a result of reduced fishing and high recruitment, and have declined in biomasses and retreated further south within the Barents Sea after that (ICES, 2021). Nevertheless, while range extensions or shifts are relatively easy to observe, the gradual increase or decrease in abundance and biomass within a region is a lot harder to prove, since that is dependent on quantitative studies, which are rare in such regions. Furthermore, borealization may imply that arctic species become less common or leave the area (Fossheim et al., 2015). Two arctic species; *Liparis tunicatus* (Liparidae) and *Lycodes frigidus* (Zoarchidae) were not found in our material but have been caught in the region earlier (Bergstad et al., 2018). However, these species were also extremely sparce in the material of Bergstad et al. (2018), the latter were only found at one station, so these differences could be caused by chance alone. Based on the above it is not possible to conclude that borealization has continued over the period 2012–2020, if borealization is taken to mean that species move into or out of specific areas that are not considered boreal areas.

3.2. Abundance and biomass

The catch rates varied considerably across years, but some features were common to the whole period (Table S2). Polar cod had the highest catch rates by number and Atlantic cod ranked next (disregarding the 0-group of *Sebastes* sp.). In addition to these, beaked redfish, long rough dab, and capelin were also found among the top ten species every year in the series. Catches of polar cod were removed from the material reported by Bergstad et al. (2018) because it was considered to be a pelagic fish that might have been caught when the trawl was set and hauled. According to Mecklenburg et al. (2018) however, the polar cod is one of the most numerous species caught in bottom trawl surveys at appropriate depths on continental shelves in the whole Arctic. Norcross et al. (2013), sampling close to the seabed by beam trawls, concluded that polar cod was abundant throughout their study area in the Northeastern Chukchi Sea. However, this species is also often found pelagically, and huge polar cod schools can extend from the bottom to near-surface depths for instance in the Barents Sea (Ajiad et al., 2011). The polar cod may thus be regarded a semipelagic species. Consequently, the catches in demersal trawl does not tell the whole story about its distribution, but it is likely that the polar cod caught in our bottom trawl hauls were caught at near-bottom depth.

Judged by catch weight, Atlantic cod dominated in all years (except for the Greenland shark that was excluded from the catch biomass). The species that had catch rates by weight among the top ten each year were Atlantic cod, long rough dab, and spotted wolffish. Although a direct comparison is difficult, this seems to correspond well with the results in Bergstad et al. (2018). The average catch rates (in weight) of Atlantic cod were more than ten times higher than that for the next species on the list (polar cod). It may seem surprising that a boreal species like Atlantic cod dominates the biomass of bottom fishes in this region. As mentioned in the introduction, commercial fisheries for Atlantic cod are known to have taken place northwest of Svalbard since the mid-to late 19th century, but on an irregular basis. As shown by Misund et al. (2016), the yield of Atlantic cod has also varied substantially during recent history when detailed catch statistics from the area have been available. Whether or not Atlantic cod is found in large quantities northwest and north of Svalbard is likely connected both to climatic variation and to the size of the Northeast Arctic cod stock, which the Atlantic cod found in these areas belong to. Ingvaldsen et al. (2017c) documented Atlantic cod feeding off shelf over deep waters in the Fram Strait. Their findings suggest that cod can leave the shallower Barents Sea while feeding on a mesopelagic layer of small prey. Snoeijs-Leijonmalm et al. (2022) caught three Atlantic cod further from their previously known distribution area: in the central Amundsen Basin at 86°N and 126°E, at depths 350–400 m over a bottom depth of about 4400 m. During the same expedition, they also caught an additional three Atlantic cod just north of the Yermak Plateau. Genetic studies revealed that all specimens caught belonged to the Barents Sea stock. This clearly shows that Atlantic cod, generally considered a shelf species connected to bottom waters, may sometimes leave their preferred environment e.g., in search of food such as mesopelagic and pelagic fish, squid, and large krill and amphipods (Ingvaldsen et al., 2017c). This may also partly explain why Atlantic cod are found both along the western Svalbard shelf, but also to the north of Svalbard as far east as 34°E where water temperatures are colder. Measurements of $\delta^{18}O$ in otoliths of the Atlantic cod sampled in the Amundsen Basin showed that they had stayed in water with temperatures between 0 °C and 1 °C the year they were caught (Snoeijs-Leijonmalm et al., 2022). In our material adult Atlantic cod were found at stations where the bottom temperature was as low as −0.69 °C. Righton et al. (2010) also found that Atlantic cod in the Barents Sea can enter sub-zero water, probably to feed.

3.3. Zoogeographic distribution

Out of 68 taxons identified to species, (including both *Icelus spatula*,

Table 1

Species caught with zoogeographic affiliation according to Andriyashev and Chernova (1995) A: Arctic, MA: Mainly Arctic, AB: Arcto-Boreal, MB: Mainly Boreal, B: Boreal, and WD: Widely Distributed. The total number of trawl hauls were 291.

Family	Scientific name	Common name	Zoogeo-graphic group	Stations n	Stations %
Somniosidae	*Somniosus microcephalus*	Greenland shark	MB	7	2.4
Arhynchobatidae	*Bathyraja spinicauda*	Spinytail skate	MB	2	0.7
Rajidae	*Amblyraja hyperborea*	Arctic skate	A	73	25.1
	Amblyraja radiata	Thorny skate	MB	127	43.6
	Rajella fyllae	Round skate	B	10	3.4
Clupeidae	*Clupea harengus*	Atlantic herring	MB	11	3.8
Argentinidae	*Argentina silus*	Silver smelt	B	2	0.7
Osmeridae	*Mallotus villosus*	Capelin	MB	147	50.5
Paralepididae	*Arctozenus risso*	Spotted barracudina	WD	47	16.2
Myctophidae	Myctophidae	Family lanternfishes		22	7.6
	Benthosema glaciale	Glacier lanternfish	MB	37	12.7
	Lampanyctus macdonaldi	Rakery beaconlamp	WD	2	0.7
Macrouridae	*Macrourus berglax*	Roughhead grenadier	B	12	4.1
Lotidae	*Brosme brosme*	Tusk	MB	14	4.8
	Enchelyopus cimbrius	Fourbeard rockling	B	1	0.3
	Gaidropsarus argentatus	Arctic rockling	A	49	16.8
Gadidae	*Arctogadus glacialis*	Ice cod	A	11	3.8
	Boreogadus saida	Polar cod	A	253	86.9
	Gadus morhua	Atlantic cod	MB	209	71.8
	Melanogrammus aeglefinus	Haddock	MB	115	39.5
	Micromesistius poutassou	Blue whiting	MB	40	13.7
	Pollachius virens	Saithe	MB	1	0.3
	Trisopterus esmarkii	Norway pout	B	19	6.5
Sebastidae	*Sebastes* genus	Redfish		157	54.0
	Sebastes mentella	Beaked redfish	MB	170	58.4
	Sebastes norvegicus	Golden redfish	MB	53	18.2
	Sebastes viviparus[a]	Norway redfish	B	1	0.3
Cottidae	*Artediellus atlanticus*	Hookear sculpin	MB	146	50.2
	Gymnocanthus tricuspis	Arctic staghorn sculpin	MA	10	3.4
	Icelus spp.[b]	Sculpin genus Icelus	AB and MA	27	9.3
	Myoxocephalus scorpius	Shorthorn sculpin	MB	5	1.7
	Triglops murrayi	Moustache sculpin	B	90	30.9
	Triglops nybelini	Bigeye sculpin	A	53	18.2
	Triglops pingelii	Ribbed sculpin	AB	7	2.4
Psychrolutidae	*Cottunculus microps*	Polar sculpin	MA	58	19.9
Agonidae	*Leptagonus decagonus*	Atlantic poacher	AB	86	29.6
Cyclopteridae	*Cyclopterus lumpus*	Lumpsucker	MB	4	1.4
	Eumicrotremus derjugini	Leatherfin lumpsucker	A	3	1.0
	Eumicrotremus spinosus	Atlantic spiny lumpsucker	MA	13	4.5
Liparidae	*Careproctus* genus[c]	Seasnail	A	98	33.7
	Liparis bathyarcticus	Nebulous snailfish	MA	9	3.1
	Liparis fabricii	Gelatinous snailfish	A	60	20.6
	Paraliparis bathybius	Black seasnail	A	25	8.6
	Rhodichthys regina	Threadfin snailfish	A	1	0.3
Zoarcidae	*Gymnelus retrodorsalis*	Aurora pout	A	11	3.8
	Lycenchelys kolthoffi	Checkered wolf eel	A	18	6.2
	Lycenchelys muraena	Moray wolf eel	A	11	3.8
	Lycenchelys sarsii	Sars' eelpout	B	10	3.4
	Lycodes adolfi	Adolf`s eelpout	A	11	3.8
	Lycodes esmarkii	Greater eelpout	MB	59	20.3
	Lycodes eudipleurostictus	Doubleline eelpout	A	84	28.9
	Lycodes gracilis	Checker eelpout	MB	34	11.7
	Lycodes luetkenii	Lütken's eelpout	A	10	3.4
	Lycodes paamiuti	Paamiut eelpout	A	27	9.3
	Lycodes pallidus	Pale eelpout	A	75	25.8
	Lycodes reticulatus	Arctic eelpout	A	8	2.7
	Lycodes rossi	Threespot eelpout	A	27	9.3
	Lycodes seminudus	Longear eelpout	A	30	10.3
	Lycodes squamiventer	Scalebelly eelpout	A	31	10.7
	Lycodonus flagellicauda	Whiptail scutepout	A	36	12.4
Stichaeidae	*Anisarchus medius*	Stout eelblenny	B	9	3.1
	Leptoclinus maculatus	Daubed shanny	MB	151	51.9
	Lumpenus lampretaeformis	Snakeblenny	MB	74	25.4
Anarhichadidae	*Anarhichas denticulatus*	Northern wolffish	MB	36	12.4
	Anarhichas lupus	Atlantic wolffish	MB	89	30.6
	Anarhichas minor	Spotted wolffish	MB	76	26.1
Ammodytidae	*Ammodytes marinus*	Lesser sandeel	MB	1	0.3
Pleuronectidae	*Hippoglossoides platessoides*	Long rough dab	MB	196	67.4
	Reinhardtius hippoglossoides	Greenland halibut	AB	213	73.2

[a] Bergstad et al. (2018) pooled the *Sebastes* genus, as species identification of the genus was deemed unreliable, including records of *S. viviparous*. However, there now also exists voucher specimens of *S. viviparus* from the Svalbard region.

[b] Two species, (*I. spatula*, and *I. bicornis*) but these are very difficult to distinguish. According to Andriyashev and Chernova (1995) *I. spatula* is arcto-boreal and *I. bicornis* is mainly arctic.

c Chernova (2005) reclassified and described new species of this genus in the Barents Sea. Ongoing genetic work (unpublished) seems to reduce the number of species to three of this genus in the Barents Sea.

and *I. bicornis,* and counting those individuals determined to genus Careproctus as one species) 23 species were Arctic, 5 were Mainly Arctic, 4 Arctoboreal, 25 Mainly Boreal, 9 Boreal, and 2 Widely Distributed. The mainly Arctic and Arctic species dominated in the deeper areas (Yermak Plateau and slope > 500 m) and on the eastern shelf, whereas the Mainly Boreal species dominated along the slope and western and northern shelves < 500 m, Fig. 2 a-b). Arctic species were also found along the entire Hinlopen Trough (Fig. 2a), probably due to the larger depth (300–400 m) compared to the surrounding shelves. However, the Mainly Boreal species dominated in biomass (Fig. 2b), consistent with the trough forming a hybrid habitat between the shelf and shelf-break (Menze et al., 2020 (this issue)).

The zoogeographic classification showed a close correspondence to the distribution of water masses, sea ice and bathymetry of the region (Fig. 2c-d). Most of the Mainly Arctic and Arctic species on the Yermak Plateau and slope at > 500 m depth lived in Arctic Intermediate Water (Fig. 2c) with sea ice present for 9–12 months of the year before sampling (Fig. 2d). A few stations on the Yermak Plateau had Atlantic Water near the bottom, probably due to a crossing Atlantic Water flow (e.g., Athanase et al., 2021), and Arctoboreal and Mainly Boreal species were also present. The Mainly Arctic and Arctic species on the eastern shelf experienced Polar Surface Waters (Fig. 2c) and were covered by sea ice between 3 and 9 months during the preceding year (Fig. 2d).

The pattern of Mainly Boreal species along the slope and on the western and northern shelves (<500 m) closely correspond to the distribution of stations which carried Atlantic Water (Fig. 2c), and which had sea ice present for<3 months or between 3 and 6 months during the preceding winter (Fig. 2d). Moreover, the abundance, and even more so, the biomass was higher in this region than in the deeper areas and the eastern shelf (Fig. 2 a-b). The close correspondence between water mass distribution, sea ice and bathymetry reflect the strong topographic influence of the continental slope on forming the environment and ecosystems of the study region (e.g., Bluhm et al., 2020).

3.4. Species assemblages

Zoogeographical classifications systems differ and using other classification systems could provide a slightly different classification. To investigate species assemblages in more detail without using predefined classification systems, we applied a hierarchical cluster analysis. The analysis revealed three prominent station clusters consistent with the zoogeographical classifications (Fig. 3), but divided the regions dominated by Arctic species (Fig. 2) into two – a deep-water cluster, where Greenland halibut, an Arctoboreal species dominated the biomass, and a cluster with Arctic species associated with the shelf. Both clusters were dominated by polar cod in terms of abundance. Based on their locations,
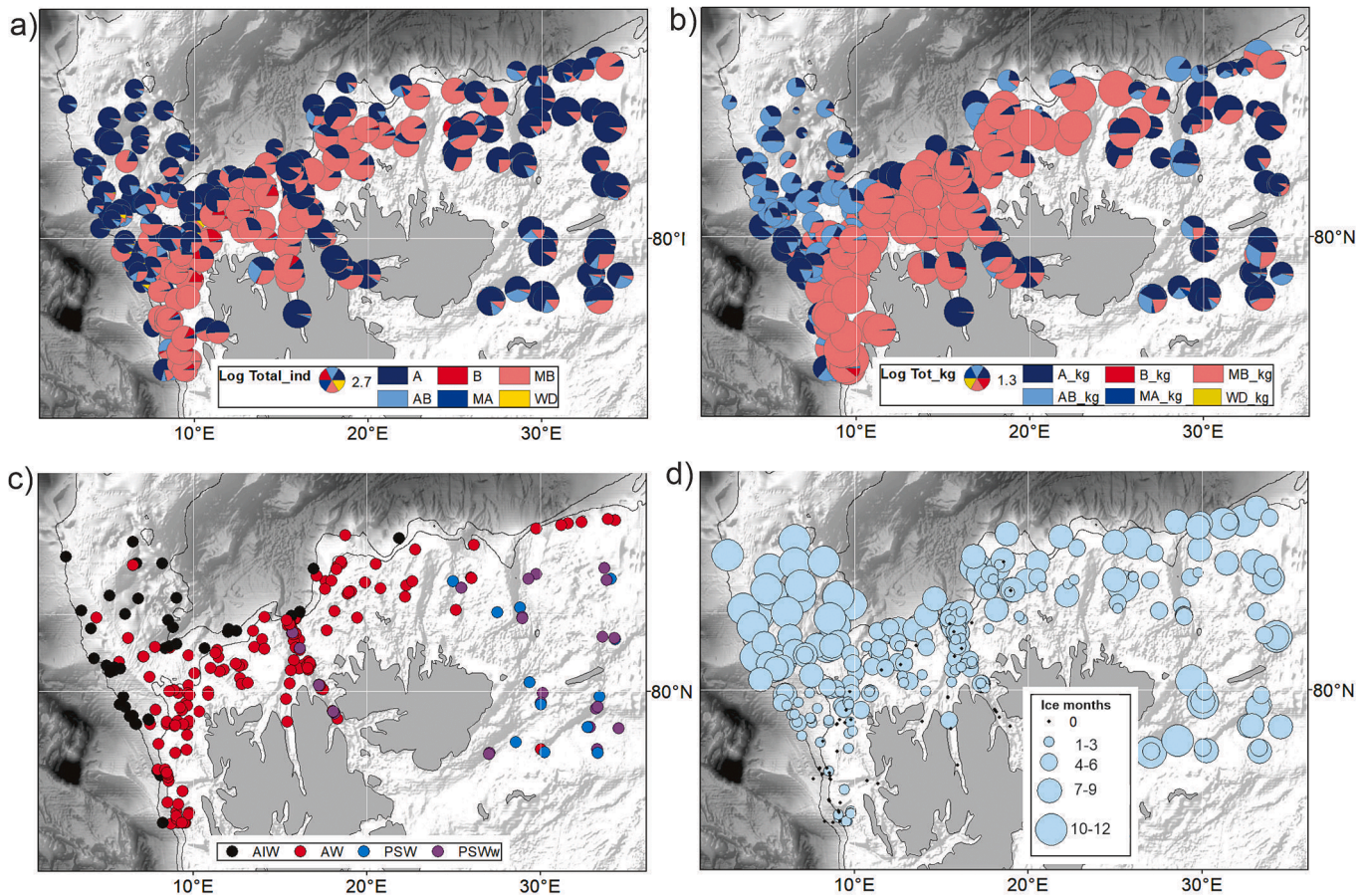
Fig. 2. Top rows show catch rates by zoogeographical category per station all years. a) The size of the pies is proportional to the logarithm of the total number of individuals per nautical miles towed. b) The size of the pies is proportional to logarithm of the catch in kg standardised by the towing distance. The colours represent the zoogeographical groups; dark blue: Arctic (A), blue: Mainly Arctic (MA), light blue: Arctoboreal (AB), pink: Mainly Boreal (MB), red: Boreal (B), yellow: Widely Distributed (WD). Bottom rows show abiotic factors. c) Stations categorized by the water mass present near the seabed. Arctic Intermediate Water (AIW), Atlantic Water (AW), Polar Surface Water (PSW), warm Polar Surface Water (PSWw). d) The number of months in the previous year with sea ice present. Note that only stations with temperature and salinity observations are included in (c).
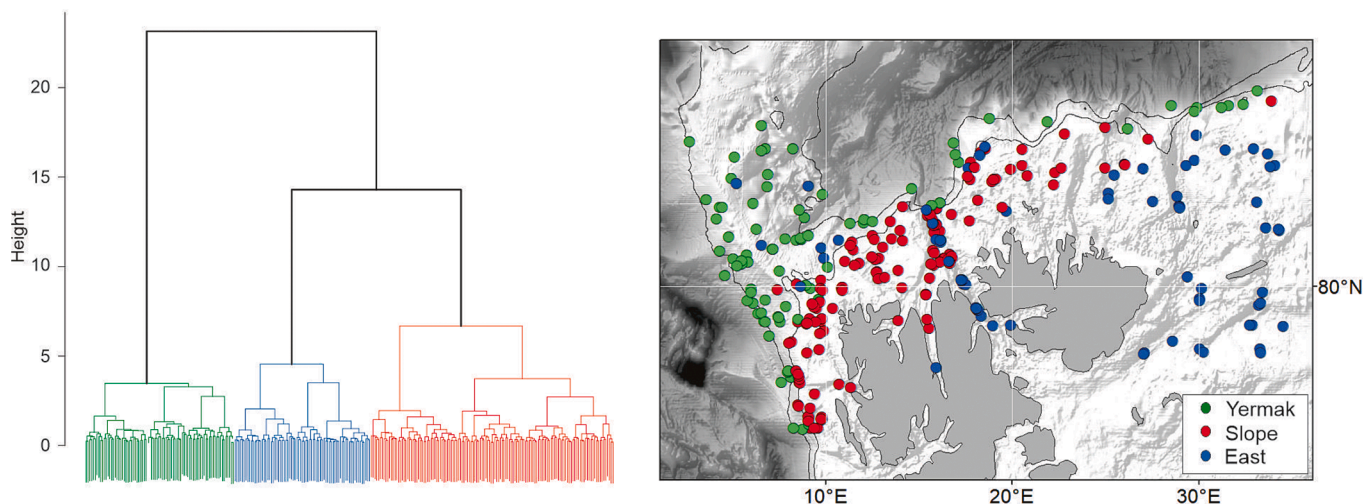
Fig. 3. Result of hierarchical cluster analysis based on the fish diversity data. Left panel: cluster dendrogram. Right panel: map of stations, the colours indicate which of the three main clusters the stations belong to (green: Yermak, red: Slope, blue: East).

we refer to them as "Yermak", even though this also includes deeper stations along the slope, "Slope", which also includes stations on the western and northern shelves, and "East". The Slope cluster was the largest with 138 stations, compared to 86 in the Yermak cluster and 67 in the East cluster. The clustering reflected the bathymetric and oceanographic conditions as well as the zoogeographic distributions (Fig. 2 and Fig. 4).

The Yermak cluster was most clearly separated from the two other clusters by depth (Fig. 4, average depth 823 m) confirming the dominance of depth for species segregation (Fig. 2, Bergstad et al., 2018; Jørgensen et al., 2022 (this issue)). The ambient temperature (-0.4 °C) was lower than for the two other clusters (Fig. 4a), and the ice duration was in general higher with many of the stations having sea ice for >6 months each year (Fig. 4d). Consistent with the abiotic factors, the cluster was dominated by species like flatfishes (including Greenland halibut which dominated by weight), rays, and wolffishes, but polar cod (greatest in numbers) and Atlantic cod (no. three by weight) were also high up on the list (Table 2). Redfishes, eelpouts, lings, and smelts were also represented among the top-ten families. Arctic and Mainly Arctic species were dominating, but Mainly Boreal species were also

represented.

The catch rates in the Yermak cluster were low both in numbers and biomass (Fig. 5a-b), consistent with Bergstad et al. (2018). The number of species caught per tow was also low (<ten on average, Fig. 5c). Low species richness in this region compared to further south has also been documented for benthos (Jørgensen et al., 2022 (this issue)). Low catches and number of species makes it questionable whether the trawl catches are representative for the species occupying the region. Bergstad et al. (2018) found a no-asymptotic species accumulation curve for stations deeper than 500 m and argued that the sampling was probably too limited to provide a full taxon list. However, our additional trawls did not reveal species not already detected by Bergstad et al. (2018), implying that the taxon list in that study was not impaired by low sampling intensity. The deviation in Bergstad et al. (2018) could be due to their study regions spanning from south of Bear Island, thereby including more species than our study. The latter is also consistent with this study revealing higher species richness than our study.

The Slope cluster was separated most clearly from the other two clusters by temperature and salinity (Fig. 4). Average ambient temperature and salinity was 3.3 °C and above 35.0, reflecting that this cluster
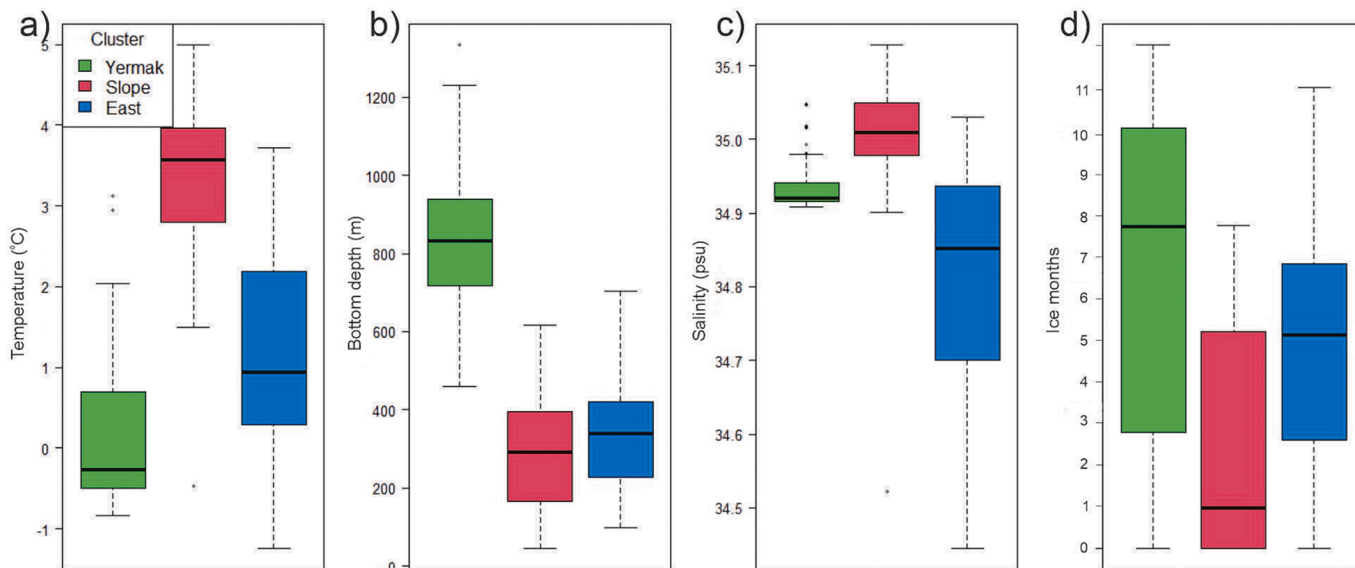
Fig. 4. Boxplot by cluster of a) temperature at the bottom, b) bottom depth, c) salinity at the bottom, and d) number of months with ice coverage.

Table 2
Top ten most common species by weight and by numbers in the catches in the three clusters.

YERMAK Name (zoogeogr.)	hauls	Catch rate N/nmi	Name (zoogeogr.)	hauls	Catch rate kg/nmi
Polar cod (A)	68	17.90	Greenland halibut (AB)	75	4,81
Redfish sp. (MB)	25	16.57	Arctic skate (A)	58	3.74
Doubleline eelpout (A)	59	11.56	Atlantic cod (MB)	30	0.65
Greenland halibut (AB)	75	6.41	Northern wolffish (MB)	8	0.65
Arctic skate (A)	58	3.30	Doubleline eelpout (A)	59	0.45
Greater eelpout (MB)	35	2.90	Thorny skate (A)	17	0.21
Atlantic cod (MB)	30	2.44	Polar cod (A)	68	0.19
Capelin (MB)	11	2.24	Atlantic wolffish (MB)	2	0.19
Pale eelpout (A)	40	2.23	Greater eelpout (MB)	35	0.17
Scalebelly eelpout (A)	29	2.14	Arctic rockling (A)	41	0.14

SLOPE Name (zoogeogr.)	hauls	Catch rate N/nmi	Name (zoogeogr.)	hauls	Catch rate kg/nmi
Atlantic cod (MB)	134	145.13	Atlantic cod (MB)	134	118.97
Polar cod (A)	107	82.91	Beaked redfish (MB)	105	6.27
Redfish sp. (MB)	86	76.09	Long rough dab (MB)	122	6.22
Daubed shanny (MB)	81	74.62	Haddock (MB)	84	5.94
Beaked redfish (MB)	105	69.77	Spotted wolffish (MB)	61	3.28
Long rough dab (MB)	122	52.97	Northern wolffish (MB)	25	2.88
Capelin (MB)	80	26.71	Atlantic wolffish (MB)	74	2.76
Haddock (MB)	84	25.87	Polar cod (A)	108	1.53
Snakeblenny (MB)	55	17.79	Golden redfish (MB)	52	1.17
Hookear sculpin (MB)	96	15.22	Greenland halibut (MA)	74	1.01

| EAST Name (zoogeogr.)	hauls	Catch rate N/nmi	Name (zoogeogr.)	hauls	Catch rate kg/nmi
Polar cod (A)	75	1125.41	Polar cod (A)	75	16.02
Bigeye sculpin (A)	40	172.86	Atlantic cod (MB)	42	10.95
Redfish sp. (MB)	46	80.81	Greenland halibut (AB)	61	5.12
Daubed shanny (MB)	65	64.67	Long rough dab (MB)	60	4.54
Beaked redfish (MB)	49	50.65	Thorny skate (A)	36	1.44
Capelin (MB)	54	47.18	Bigeye sculpin (A)	40	1.28
Gelatinous snailfish (A)	50	37.49	Beaked redfish (MB)	49	0.87
Long rough dab (MB)	60	36.40	Capelin (MB)	54	0.75
Greenland halibut (AB)	61	26.60	Gelatinous snailfish (A)	50	0.74
Atlantic poacher (AB)	48	22.26	Redfish sp. (MB)	46	0.54

was associated with the warm and saline Atlantic Water slope current (Fig. 1) and intrusions of Atlantic Water on the western and northern shelves (e.g., Cottier et al., 2007; Nilsen et al., 2016; Menze et al., 2020 (this issue)). The numerous stations on the shelf gave an average depth of 284 m for this cluster, making it comparable in depth but slightly shallower than the East cluster (Fig. 4b). The species composition in these two clusters was not much different when it comes to dominating families and species, although there were more Arctic species (by weight and numbers) in the East cluster (Table 2). In the Slope cluster, Atlantic cod dominated both in number and biomass, and polar cod and various redfish species were also high up on the list. One notable difference was that haddock was number four by weight and eight by number at the Slope cluster, a species not so common in the two other clusters. In addition to the Atlantic cod, flatfish, and redfish families, pricklebacks, sculpins, smelts, wolffishes and skates were represented among the top ten species in this cluster. Zoogeographically these species belong to the Mainly Boreal and Arctic groups (Table 2).

Due to the wide extent of the Slope cluster, as well as large inter-annual variability in sea ice conditions, the sea ice duration for this cluster varied from free-of-ice year-round to ice covered for almost 8 months (Fig. 4d). Such large variations might indicate that ice presence during the year is not a strong abiotic driver for the species associated with this cluster. A weak relation to sea ice duration can be expected for Mainly Boreal seasonal migrants like Atlantic cod and haddock arriving in summer when the sea ice has gone. Moreover, the fact that part of this region is free-of-ice throughout the year and has on average sea ice present only for about 1 month each year (Fig. 4d), can make it suitable for boreal species that do not go south during winter. Adult Atlantic cod is present on the west coast of Svalbard also during winter (e.g., Mehl, 2019).

The East cluster is separated most clearly from the other two clusters by having lower and more varying salinity (Fig. 4c), likely reflecting the strong influence of Polar Water on the eastern Svalbard shelf (Fig. 2c) rather than salinity being a driver of the cluster. It is colder than the Slope cluster with temperatures mostly below 2 °C (average 0.9 °C) and most of the stations are covered with sea ice between 3 and 7 months each year. The cluster was dominated by codfishes and flatfishes (Table 2). Polar cod dominated the catches by weight and numbers, while the Atlantic cod ranked second by weight. Greenland halibut and long rough dab also showed quite high catch rates. Some representatives from the pricklebacks, eelpouts, and sculpins were also caught in large numbers. The zoogeographic affinity of the species dominating in this cluster was Arctic, Mainly Arctic and Mainly Boreal (Table 2). This is in line with the observed borealization of the region occurring between 2004 and 2012 (Fossheim et al., 2015; Bergstad et al., 2018) followed by a temporary recovery of the Arctic species due to colder conditions during 2014–2017 (Ingvaldsen et al., 2021).

The East cluster had the highest catch rates of individuals (Fig. 5a), while the Slope had the highest catch rates in biomass (Fig. 5b). These differences between the clusters reflect the general pattern of larger, predatory Mainly Boreal species on the slope and smaller, but more numerous Arctic species on the eastern shelf (Fossheim et al., 2015). Since both groups of species were present in both clusters (Table 2), the species richness in the two clusters was similar (Fig. 5c). A high overlap of species between clusters were also evident for megabenthic species in the area (Jørgensen et al., 2022 (this issue)). However, the megabenthos showed a stronger separation between slope and shelf which is likely due to the less motile megabenthic species being more confined by depth and currents. We also note that as for demersal fish, the megabenthic species showed the highest biomass at the slope, due to high aggregations of the filtering *Geodia* sponge utilizing the fast-moving, warm Atlantic Water slope current.

Our analysis confirms earlier studies showing that abiotic factors like water mass distribution, depth and sea-ice cover drive the zoogeographic distribution of fishes in this region (Johannesen et al., 2012, Johannesen et al., 2017b, Bergstad et al., 2018). Similar results have
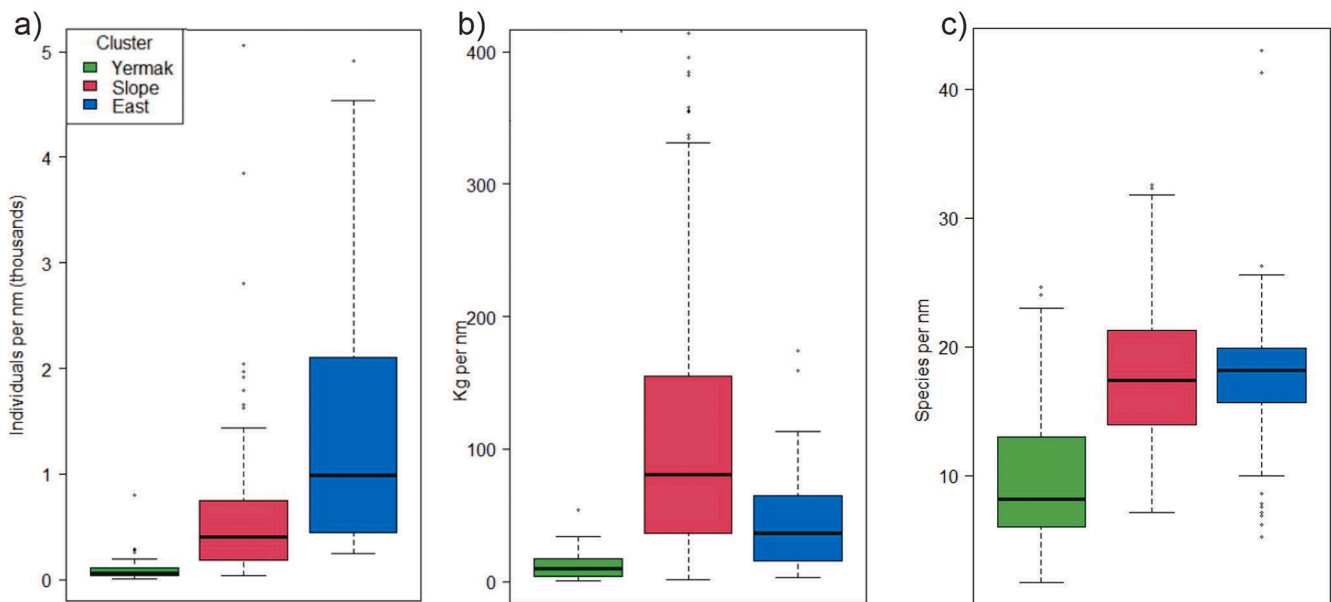
Fig. 5. Catch rates by cluster. a) Individuals per nautical mile, b) kg per nautical mile and c) number of species per nautical mile. The y-axis in a) is cut off at maximum value of 5000 individuals per nautical mile, not showing seven stations with higher catch rates, 2 from the Slope cluster, and five from the East cluster. For readability, the y-axis in b) is cut off at maximum value of 400 kg per nautical mile, not showing 11 stations from cluster 2 with higher catch rates.

also been shown for the demersal fish assemblages in the northern Bering and Chukchi Seas (Nishio et al., 2020) and for megabenthic species in our study region (Jørgensen et al., 2022 (this issue)). A close correspondence between the zoogeographic distributions of demersal fish species and megabenthic species implies distinct patterns across several functional groups in the ecosystem (Johannesen et al., 2017a).

Catch rates in the three clusters were dominated by Greenland halibut (on average 42% of the catches in kg per station) at Yermak, Atlantic cod (53%) at the Slope and polar cod (40%) in the East cluster (Table 2). Atlantic cod was among the three most dominant species by weight in all three clusters. Ranged by catch rate in numbers, the polar cod was among the two topmost species in all clusters. The genus *Sebastes* was also important in all three clusters, the reason is the relatively large catches of 0-group *Sebastes*, not determined to species (but probably mostly *Sebastes mentella*). These are advected into the area by the West Spitsbergen Current and dominate among the juvenile fishes (Gjøsæter et al., 2020 (this issue)).

3.5. Biological characteristics of dominating species in the survey area

3.5.1. Atlantic cod (Gadus morhua)

Atlantic cod was the dominant species (by weight) summed over all three clusters. The number of cod caught (and length measured) was much higher at the Slope (n = 7984) and Yermak (n = 1274) clusters than in the East (n = 53) cluster. The length distribution varied somewhat among the three clusters (Fig. 6). The length distributions in the Slope and Yermak clusters were similar, both in total range and shape, while the few cod sampled in the East cluster were more dominated by the smallest size classes (0-group fish) and no specimens>80 cm were caught. Since age determination of Atlantic cod is stratified according to length (one individual in each 5-cm length group in each sample is aged), age distributions cannot be directly extracted from the samples. Nevertheless, since Atlantic cod from the Barents Sea stock grows roughly 10 cm per year up to age 6–8 years and somewhat less during the rest of their life, the length distributions imply that cod in the Slope cluster have peaks corresponding to 1-, 2-, 3- and 5–6-year-old individuals while cod in the Yermak cluster have peaks corresponding to 1-, 3- and 6–7-year-old individuals. Both clusters also show a fair amount of even older fishes. Due to the few length-measured cod from
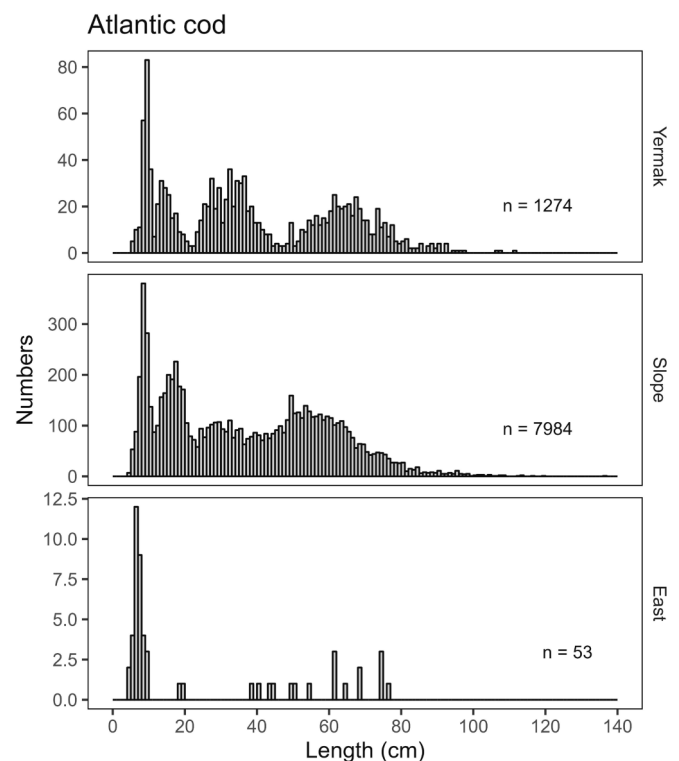
Fig. 6. Length distributions of Atlantic cod within the three clusters. The numbers of samples are shown in the figures.

the East cluster (n = 53), the uncertainty in the data set is large, but it implies a clear dominance of 0-group fish and just a few individuals of older cod.

While some Atlantic cod larvae are dispersed off the continental shelf and into the Norwegian Sea (Strand et al., 2017), considerable amounts of 0-group cod are carried with the West Spitsbergen Current along Svalbard (Gjøsæter et al., 2020 (this issue)). Some of those Atlantic cod 0-group, which live a pelagic life during their first summer and autumn,

probably settle to the bottom and grow up on the western and northern Svalbard shelf and might also return to that region during later feeding migrations. The large proportion of large, old, Atlantic cod found in our material indicates that adult cod actively migrate to this area to feed.

As part of the routine sampling protocol for cod, stomach samples were taken from those individuals where detailed sampling was done. Since the diversity of prey was large, we aggregated prey into 17 prey categories, following Holt et al. (2019). Two of the prey categories defined in that paper were not found in any Atlantic cod stomachs in our material (herring and snow crab), and consequently we used 15 groups in addition to unidentified prey. Frequency of occurrence (FO) for each prey category, per length group of cod (a) and per cluster (b) is shown in Fig. 7.

Prey composition changed with cod length (Fig. 7a), and since cod length varies somewhat with cluster (Fig. 6) this will affect the prey composition by cluster (Fig. 7b). However, since stomach content was analysed only for individuals that were aged, that is one individual per 5 cm length group per sample, the total prey composition was not affected by the proportion of fish in each length group, only by differences in length range. Since the length range was approximately the same in all clusters, the prey composition shown for each cluster in Fig. 7 should be representative. While the smallest length group (mostly 0-group cod) mainly contained other food and unidentified food, the diet was more diverse for larger predators. The larger the predator, the more the diet was dominated by fish. The FO of crustacean plankton decreased with increasing predator length, while the FO of shrimp was high in all length groups of cod.

Holt et al. (2019) published a comprehensive report of Atlantic cod diet in the Barents Sea, based on a 33-year time series from the total distribution area of the stock, presenting prey composition across years and seasons, as well as ontogenetic trends in diet. They found the same general pattern of prey shift with predator length; fish prey becoming increasingly important with increasing predator size. We noted some clear differences between our results and those of Holt et al. (2019). While Holt et al. (2019) showed that capelin constituted a significant component of the cod's diet over much of the predator length range, representing on average 33% of the total prey weight for cod between 20 and 90 cm, this prey, although present in cod larger than 30 cm in our material, had a frequency of occurrence mostly between 10 and 15%. This lower importance of capelin in our material reflects that this prey species is less common in our study area than in the general distribution area of the Barents Sea Atlantic cod stock. An unexpected result of our study was that the prey group Arctic fishes, which one would think could constitute a large part of the diet of Atlantic cod in our study area, was almost non-existent in the diet, only cod in three length groups had eaten this prey group and the frequency of occurrence was below 1% in those length groups. The Atlantic cod sampled by Snoeijs-Leijonmalm et al. (2022) from the Amundsen Deep had almost exclusively hyperiid amphipods of genus *Themisto* in their stomachs, probably reflecting availability of prey in that area. We also found hyperiids to be an important prey group, being present in all length groups > 20 cm.

When compared between clusters (Fig. 7b), the diets in cluster Yermak and Slope were diverse, with a variety of fish prey, in addition to shrimp, that was found in 20–25% of the Atlantic cod stomachs. The diet was more homogeneous in cluster East, where only hyperiids, other fishes and other food were found in the stomachs. However, the number of examined stomachs in this cluster were too few to draw firm conclusions about the diet.

3.5.2. Polar cod (Boreogadus saida)

The species ranking next regarding catch rate was the polar cod. Judged by numbers it dominated in cluster East and ranked second in cluster Yermak and Slope. It also dominated by weight in cluster East and was among the top ten species by weight in the two other clusters
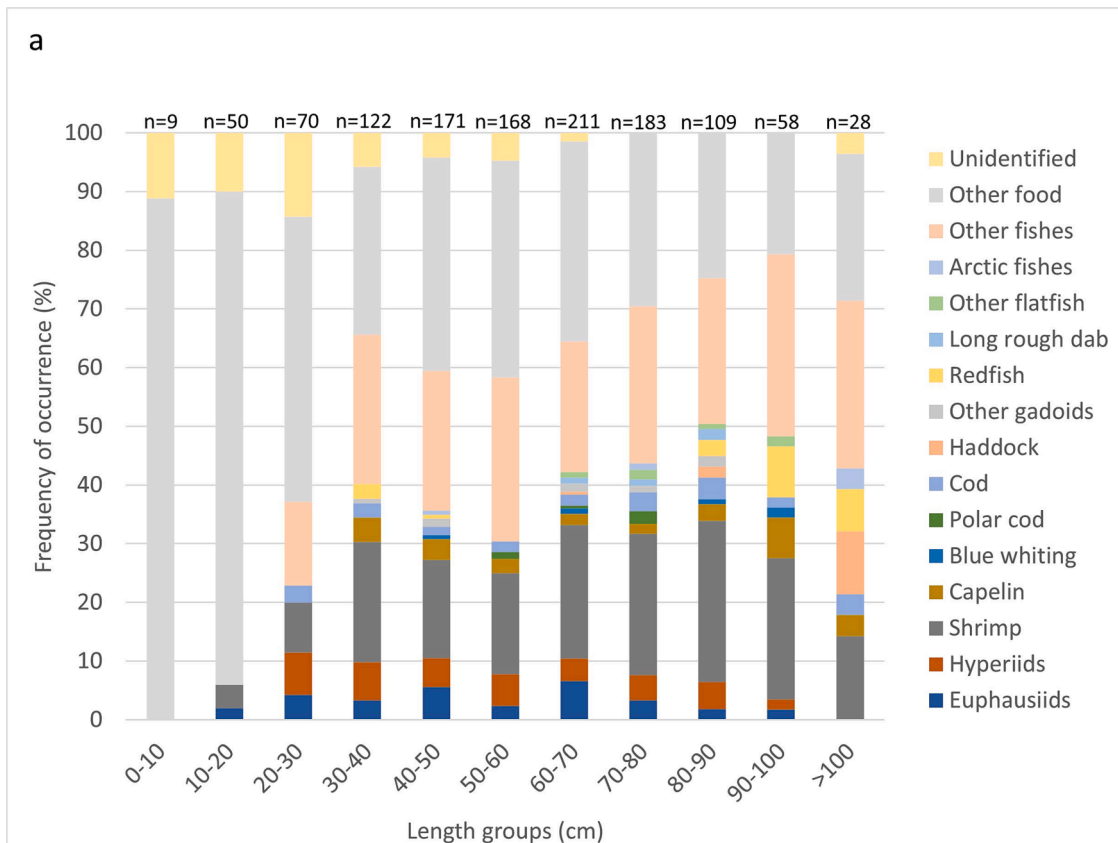

Fig. 7. Frequency of occurrence of each prey category, a) per cod length groups and b) per cluster.
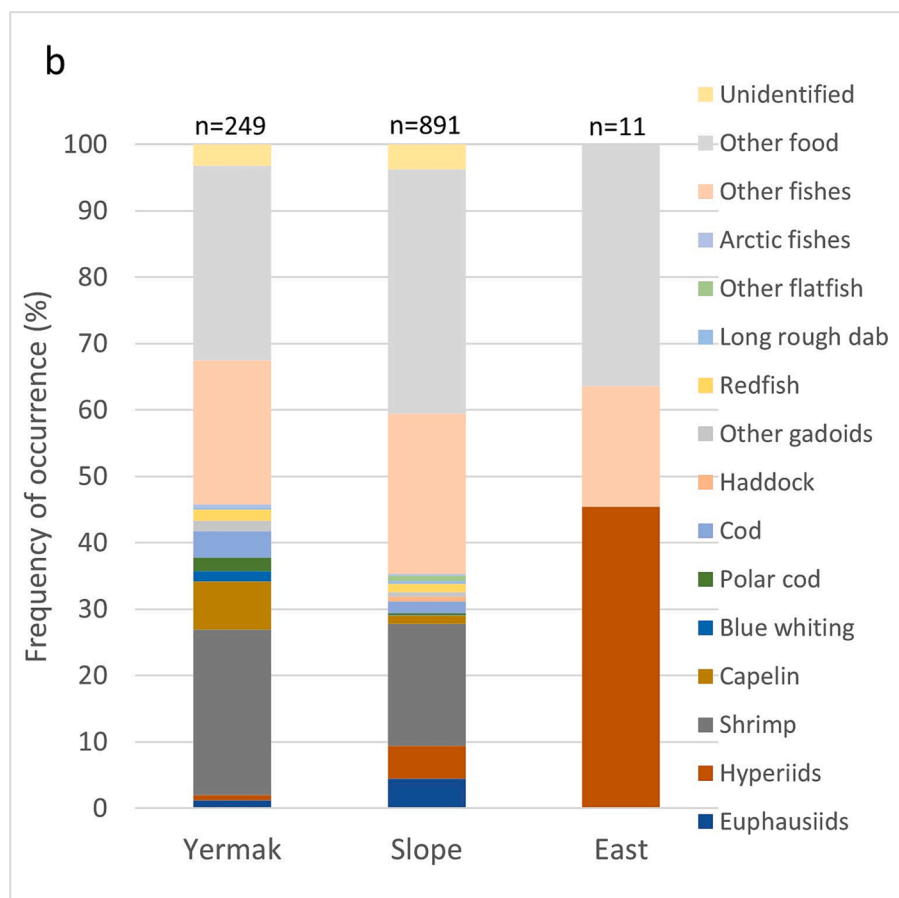
Fig. 7. (*continued*).

([Table 2](#)). This shows that this true Arctic species plays a dominant role in the bottom layer of the whole study area.

The length distribution of polar cod was similar in the three clusters ([Fig. 8](#)), except that the presence of fish over approx. 11 cm was relatively less in the East cluster. The range was from 2 to 3 cm up to about 25 cm and the mode was at about 10–11 cm. The age range was 0–4 years with a mode of 2 years. The shape of the age distributions within each cluster shows that the presence of 0-group was highest in Yermak and lowest in the East, while the presence of 3 years old fish was highest in Slope and lowest in East.

Prey composition based on stomach samples from 1489 polar cod (of which 1413 contained food) showed that only the five prey groups euphausiids, hyperiids, other fishes, and other food and unknown were represented in the stomachs. The group "other fishes" mainly consisted of fish remains that could not be identified to species. The large group "other food" mostly consisted of copepods. Euphausiids were present in stomachs from all length groups. With increasing length of the predator, the frequency of occurrence of hyperiids increased and that for other food decreased ([Fig. 9](#)a). The comparison of prey composition per cluster ([Fig. 9](#)b) showed minor differences, the most striking difference was that the frequency of occurrence of the prey groups euphausiids and hyperiids were smaller in cluster East compared to the clusters Yermak and Slope.

3.5.3. Greenland halibut (Reinhardtius hippoglossoides)

Greenland halibut was highest in catch rate (by weight) in the Yermak cluster, which includes the deep slope west and north of Svalbard and was also high in catch rates in the East cluster. Catch rates of the species were low in the Slope cluster, i.e., the shallow slope areas.

The species has its nursery area north and east of Svalbard and towards Franz Josef Land. The spawning area is south-west of Svalbard, and further south, at the slope below approximately 500 m depth ([Godø and Haug, 1989; Ådlandsvik et al., 2004; Vihtakari et al., 2021](#)). The survey area thus covers important areas for the lifecycle of the population.

Stomach sampling of this species was not conducted in our study. Earlier investigations of feeding of Greenland halibut in the area show that Atlantic cod and polar cod are prominent in the diet, but also other fish species like redfish, long rough dab, sculpins, eelpouts and pricklebacks are found, as well as invertebrates like deep sea prawn, hyperiids, cephalopods and polychaetes ([Haug and Gulliksen, 1982; Vollen et al., 2004](#)).

Greenland halibut shows considerable sexual dimorphism, with males becoming mature at lengths approx. 35–45 cm and females at approx. 55–65 cm ([Vihtakari et al., 2021](#)) and differences in longevity where males die off younger and rarely become longer than 60 cm. For this reason, we show length frequencies by sex for this species. Of those that had been sex determined, mature males and immature females were found in all clusters ([Fig. 10](#)). Mature females (ca > 60 cm) were to lesser degree found in this area, as expected in a nursery area. Greenland halibut measured to be less than 35 cm are predominantly 1–3 years old ([Albert et al., 2009](#)). These recruiting individuals were not numerous in the East cluster but were abundant at both the Slope and noticeably at Yermak. Not much research has been done on Greenland halibut at the Yermak Plateau. Tagging experiments have shown that young specimens of the NEA stock can migrate to Iceland ([Albert and Vollen, 2015, Vihtakari et al., 2021](#)), and it is possible that they take a western route along the coast of East Greenland. The abundance of especially small individuals, found at Yermak in our surveys may give support to that theory.
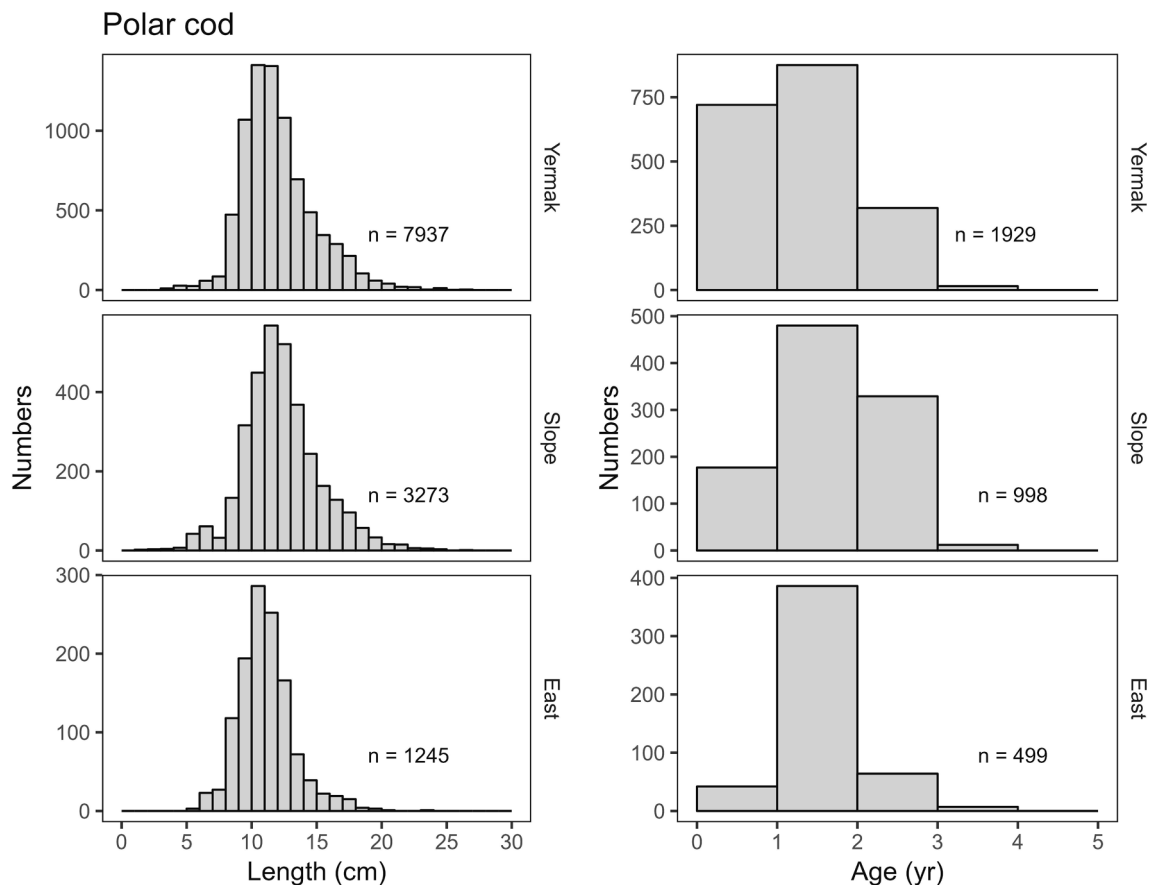
Fig. 8. Length- and age-distributions for polar cod within the three clusters. The number of samples are shown in the figures.

During a survey in ice-covered waters north of Svalbard in September 2021, where a pelagic trawl was operated in the ice-lead, a Greenland halibut larva, about 4 cm long, was caught in the Nansen Basin at about 84°N (Ingvaldsen et al., 2023). It is unknown whether Greenland halibut larvae drift out into the Arctic Ocean on a regular basis.

3.5.4. Transition regions along the Atlantic Water poleward pathway

Northward distribution shifts of marine species (Geoffroy et al., 2018; Leopold et al., 2019; Mańko et al., 2020), including demersal fishes (Fossheim et al., 2015; Haug et al., 2017) are well documented in the northern Barents Sea. However, the strong topographic steering of the Atlantic Water flow along the shelf break causes gradients and changes to occur along the slope rather than northward in our study region. The inflowing Atlantic Water alleviates nutrient and light limitations, leading to increased pelagic primary productivity along the slope (Randelhoff et al., 2018; Vernet et al., 2020). Boreal *Calanus finmarchicus* (Wassmann et al., 2015; Basedow et al., 2018; Hop et al., 2019; Wassmann et al., 2019) and larger boreal organisms, like macrozooplankton (krill and hyperiids) and juvenile and mesopelagic fishes (Knutsen et al., 2017; Geoffroy et al., 2019; Gjøsæter et al., 2020 (this issue)) are advected with the Atlantic Water flow along the shelf-break, making this region more productive and with higher biomass than the deeper basins to the north (Bluhm et al., 2020).

For most demersal fishes, the slope is also a boundary towards the deep (>3000 m) basins to the north. It forms the northern boundary of both the retracting Arctic fish species (Fossheim et al., 2015), and for the feeding migration of the large predatory seasonal migrants like Atlantic cod (Ingvaldsen et al., 2017c). To investigate transition regions along the Atlantic Water poleward pathway, catch rates for Atlantic cod and polar cod were sorted according to their distance from 78°N (Fig. 11).

The investigation was conducted on each cluster separately, as the large difference in numbers and biomass between the clusters (Fig. 5a-b) otherwise would mask any poleward changes.

Atlantic cod in the Slope cluster showed a weak increase in catch rate in numbers towards the Hinlopen region (Fig. 11a), while the catch rate in weight was relatively stable (Fig. 11b). We note, however, that no statistically significant trend lines appear when testing on the original data. Continuing eastwards from the Hinlopen region, both catch rates in Atlantic cod numbers and biomass decreased in the Slope cluster. For Atlantic cod in the deep Yermak cluster, there were no apparent poleward trends except that both catch rates were reduced east of the Hinlopen region (it should be noted that even though these stations are classified within the Yermak cluster they are deep at the slope north of Svalbard (Fig. 3)). The stable catch rate of Atlantic cod from west of Svalbard to the Hinlopen region implies that cod migrate from the Barents Sea or from the spawning areas along the Norwegian coast along the western coast of Svalbard. This is supported by the observation that the cod west and north of Svalbard had a significant portion of 5–7-year-old cod (approx. 50–70 cm, Fig. 6), while cod on the eastern shelf showed both lower catch rates and very few adults.

As opposed to the Atlantic cod, the polar cod catches in the Slope cluster imply a poleward increasing catch rate in both numbers and biomass towards the Hinlopen region (Fig. 11c-d). The high variability in number of individuals challenges firm conclusions on trends, but the numbers of polar cod in the Slope cluster had a statistically significant weak positive linear trend when testing on the original data. Maximum catch rate in numbers and biomass occurred in the easternmost regions (in the East cluster), implying higher abundance, and thus more suitable conditions for this species when going north- and eastwards.

The Hinlopen region seems to reflect a shift from the dominance of Atlantic cod (both in numbers and biomass) to the west of this region
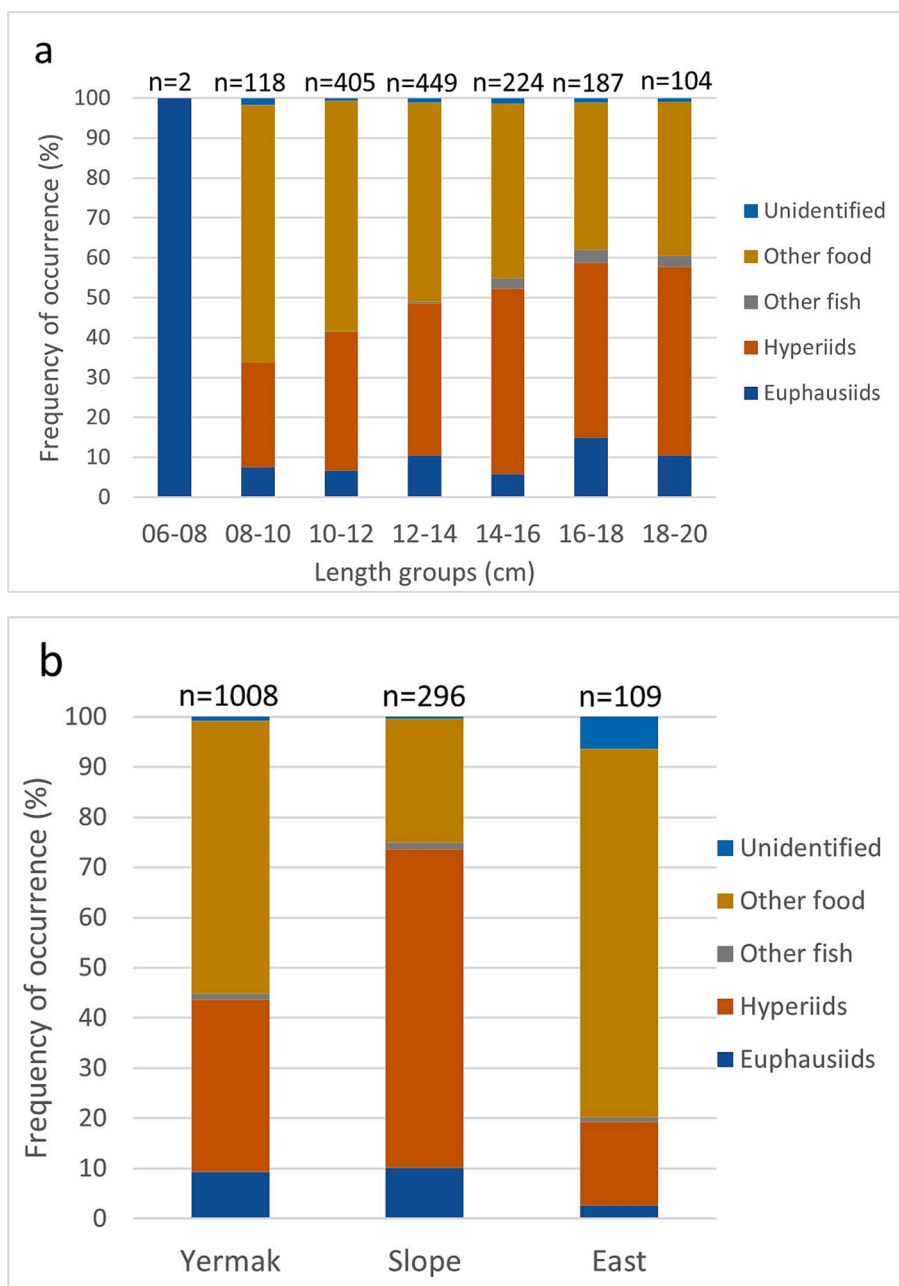
Fig. 9. Prey composition in polar cod stomachs by predator length groups (a) and by cluster (b).

(except at the Yermak Plateau) to a dominance of polar cod (in numbers and biomass) to the east of it. The region is characterized by the Hinlopen Trough channelling Atlantic Water with nutrients and organisms into the shelf (Menze et al., 2020 (this issue)). The circulation makes the region productive (Menze et al., 2020 (this issue)), likely explaining the rich benthic communities (Jørgensen et al., 2022 (this issue)), the frequent occurrence of baleen whales (e.g., Storrie et al., 2018) and the high fishery activity occurring in the region (Misund et al., 2016). Since Atlantic cod and polar cod are dominating our catches, our results imply that the Hinlopen region can be considered as a transition region between boreal and Arctic species, meaning that boreal species decrease in biomass and Arctic species increase in biomass along the slope into the Arctic Ocean.

4. Summary and conclusions

The region west and north of Svalbard showed a strong zoogeographic mix with 34 Mainly Boreal or Boreal species and 28 Arctic or Mainly Arctic species, in addition to 4 Arctoboreal and 2 Widely Distributed species. The Mainly Boreal Atlantic cod dominated in catch biomass while the Arctic polar cod were largest in catch abundance, although the Arctoboreal Greenland halibut was most numerous below 500 m. Greenland sharks was also common in the region. Our analyses showed that abiotic factors like water mass distribution, depth and sea ice cover drove the zoogeographic distribution of demersal fishes in this region.

The Yermak Plateau is poorly described in earlier literature due to the extensive sea ice cover, and our results serve as an important baseline describing the fish species in this region. We found that Arctic and Mainly Arctic species were dominant, but Mainly Boreal species were also represented. The taxa included flatfishes, of which Greenland halibut dominated by numbers, rays, and wolffishes, but also polar cod and Atlantic cod. Other top ten families included redfishes, eelpouts, lings, and smelts.
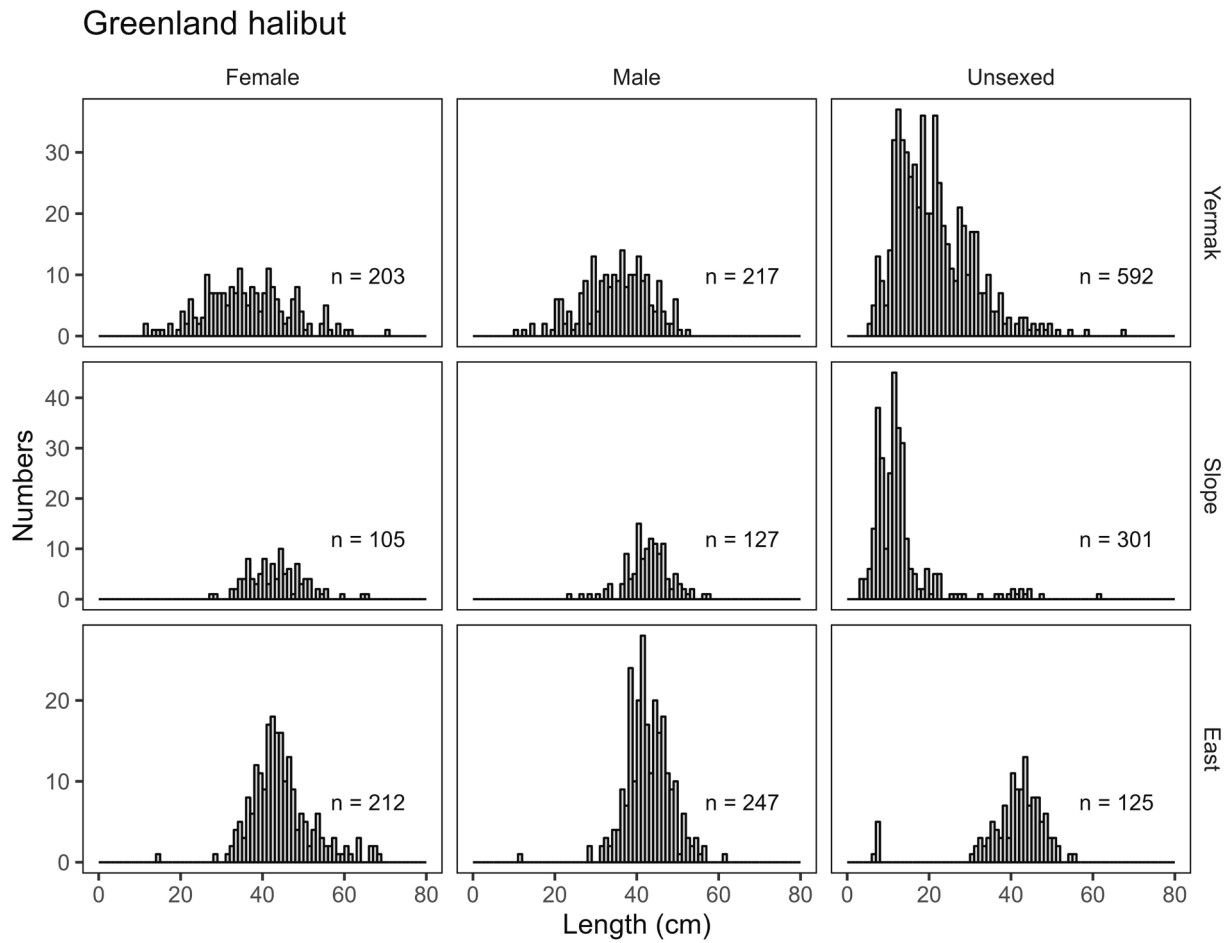
Greenland halibut

Fig. 10. Length distribution of Greenland halibut in the three clusters, divided females, males and unsexed. The number of samples are shown in the figures.
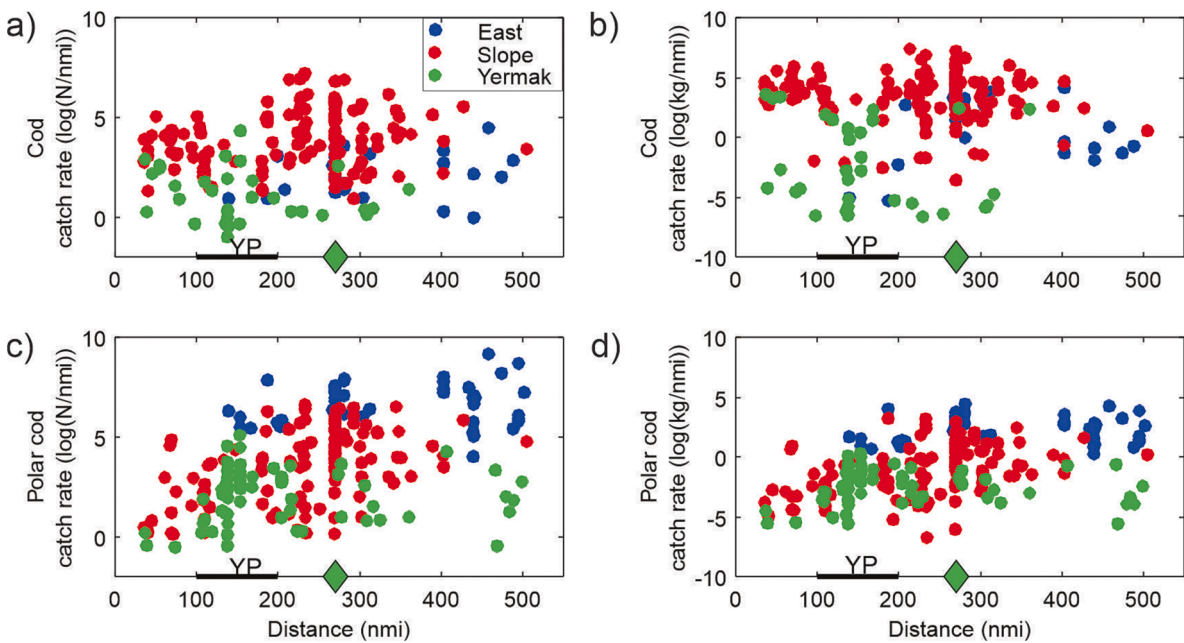

Fig. 11. Catch rate in numbers (a and c) and biomass (b and d) of Atlantic cod and polar cod per station by cluster. X-axis is the distance from 78°N for each station projected onto the 500 m isobath. Catch rates were log-transformed for plotting. The thick black line (and YP) on the horizontal axis shows the location of the Yermak Plateau while the green diamond shows the Hinlopen region.

In the Introduction we listed some research topics that we wanted to study and describe, namely how demersal fish species are geographically distributed, and how the borealization process has affected demersal fishes in the area northeast and north of Svalbard, whether the borealization reported from before 2010 has continued in our study period (2012–2020) and in particular whether the food and feeding of some selected fish species in our study area are characterized by an increased amount of Arctic species compared to other areas.

We conclude that our study area is a boundary region where both boreal and Arctic species are found, but where boreal species decrease and Arctic species increase northwards and eastwards along the slope from the Fram Strait to the Arctic Ocean, and from the continental shelf into deeper water.

We did not find a progression of borealization over the period 2012–2020. The main reason was likely a combination of extensive Atlantic influence starting in 2004 (Bergstad et al., 2018) in combination with a peak in the biomasses of the large predatory seasonal migrants (cod and haddock) involved in the borealization process (e.g., Johannesen et al. 2020) in the beginning of the study period. Increased competition and predation are thought to be one of the main challenges of the Arctic fish community associated with borealization (Fossheim et al., 2015), and two arctic species observed in the region earlier (Bergstad et al., 2018) were not present in our trawl catches. However, due to the sparseness of these species, this could be coincidental.

We did, however, find a transition region between boreal and Arctic species in the Hinlopen region near 20°E. Along the slope east of the transition region, Atlantic cod decreased while polar cod increased in both number and biomass. In the Pacific Arctic, polar cod has shifted northwards during warmer conditions (Wildes et al., 2022). Due to topography and the dominating currents in this region, further warming and borealization of the demersal communities in our region will likely shift this transition zone toward east rather than north.

Finally, we found that despite a substantial overlap in boreal and Arctic fishes, the Arctic fishes constituted only a small fraction of the diet of Atlantic cod. Thus, warming induced increased predation from Atlantic cod may not be a threat to Arctic fish species in the region north and west of Svalbard. However, since our data set (1151 specimens) is relatively small, this topic should be investigated further in future studies.

CRediT authorship contribution statement

Harald Gjøsæter: Conceptualization, Data curation, Writing – original draft, Writing – review & editing. **Randi B. Ingvaldsen:** Data curation, Visualization, Writing – review & editing. **Elvar H. Hallfredsson:** Writing – review & editing, Visualization. **Edda Johannesen:** Data curation, Visualization, Writing – review & editing.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2023.103156.

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