


Demersal fish assemblages in the boreo-Arctic shelf waters around Svalbard during the warm period 2007–2014

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Abstract The temporal and spatial resilience of abundance patterns of assemblages of organisms inhabiting transition zones between Arctic and boreal regions is an issue of concern in relation to climate change. The recognition that baseline information spanning such transition zones is required to facilitate future monitoring and assessments of temporal dynamics provided the motivation for the present study. One such transition area is the Svalbard archipelago of the Northeast Atlantic, located between the Arctic and the boreal Atlantic, where significant climate changes occur. The study aimed to utilize an existing data series from Svalbard to analyse and describe demersal fish assemblage structure and distributions. Norwegian bottom trawl surveys sampled the area annually in August–September 2007–2014, and the dataset is the first from this area which is sufficiently comprehensive to carry out assemblage analyses. The survey years analysed represent the recent unprecedented warm period in the Barents Sea–Svalbard region which started around 2004. The new baseline information improves the basis for future studies

of resilience under changing environmental conditions. A key finding was that the major transition in species composition is that between deep Greenland Sea and Arctic Ocean assemblages (upper slope assemblages) and the shelf assemblages. In shallower shelf areas (<500 m depth) structuring is weaker with assemblages having many species in common. The expected association of fish assemblages with regional bathymetric and hydrographic features was confirmed. The observed patterns probably reflect a comparatively extensive Atlantic influence during the warm period.

Keywords Baseline · Fishes · Distributions · Arctic · Atlantic · Svalbard

Introduction

Quantification and characterization of potential future variation and change in marine communities and ecosystems require knowledge of previous states. Well-documented information on variability in distribution and abundance patterns of species and assemblages constitute baselines for assessments and monitoring of impacts of known or anticipated sources of variability. At high latitudes, the significance of updated baseline knowledge on fish communities is especially pronounced as the natural variability is high and comprehensive information on fish diversity is limited (Christensen and Reist 2013). Increasing human uses and the recent pronounced warming trend with associated ice-cover changes may lead to wide-ranging ecosystem impacts potentially altering species composition and abundance patterns. Accordingly, there is an increasing demand for pertinent management advice, and baseline studies contribute significantly to the collective

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science effort required to respond to this societal need. In this study, information is presented on demersal fish assemblages inhabiting an extensive continental shelf area of the Arctic Ocean–Atlantic transition zone, the Svalbard archipelago, based on data collected during the recent warm period.

The fish fauna in the pan-Arctic region, including the Atlantic sector, was reviewed recently by Mecklenburg et al. (2011). Regional analyses using extensive bottom trawl survey data, by Byrkjedal and Høines (2007), Dolgov et al. (2011), Johannesen et al. (2012) and Fossheim et al. (2015), supplemented earlier smaller-scaled investigations by Burgos (1989) and Fossheim et al. (2006) of distribution of demersal fish in the Barents Sea. An atlas of fishes of the Barents Sea has also resulted from joint trawl surveys by Russia and Norway (Wienerroither et al. 2011, 2013). These efforts resulted in extensive baseline knowledge for areas with existing or potential uses.

However, for the Svalbard archipelago (Fig. 1) significant data series are available but these were not fully

analysed in the previous studies. Reports on the fish fauna in that area were based on the Russian autumn–winter surveys (Smirnov et al. 2000; Dolgov 2004), but comprehensive analyses were not conducted. Using a multi-year survey dataset, the current account therefore extends the Barents Sea assemblage analyses (Johannesen et al. 2012) to comprise the shelves around Svalbard, including the Arctic Ocean shelf to the north of 80°N.

The Svalbard is the largest archipelago of the arcto-boreal Barents Sea (Ozhigin et al. 2011), characterized by complex bathymetry and numerous islands, as well as steep and strong environmental gradients between the warm areas of the Norwegian Sea under the influence of Atlantic Water and the Arctic Water to the north and northeast (Loeng 1991; Ozhigin et al. 2011). Circulation features around the archipelago reflect the shallow outflow of relatively low-salinity Arctic Water and the deeper saline and warm Atlantic Water flowing northwards along the shelf break on the western side of the western island Spitsbergen (Ozhigin et al. 2011).

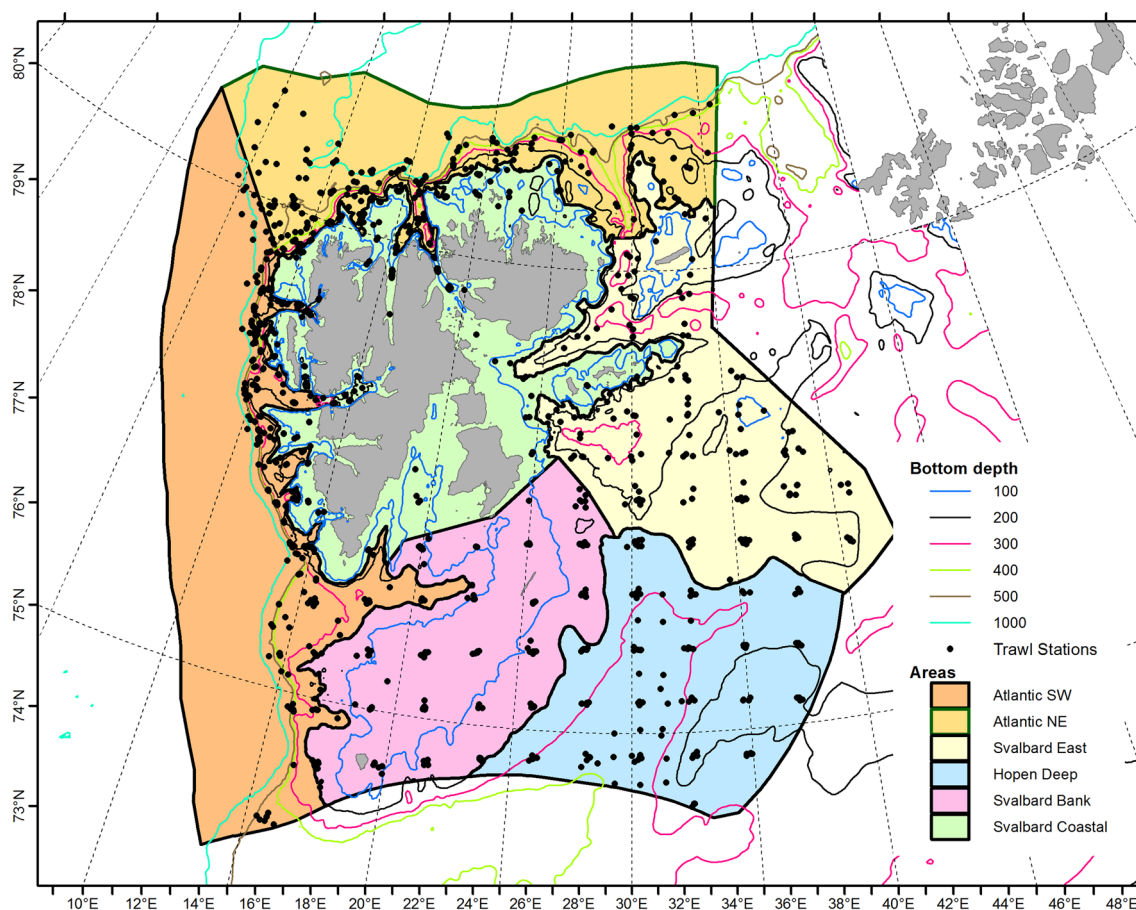


Fig. 1 The Svalbard archipelago and the spatial distribution of trawl sites (black dots) sampled in the 2007–2014 annual bottom trawl surveys used in the analyses of demersal fish assemblages. The multishaded/coloured study area is the Svalbard Fishery Protection

zone managed by Norway. For some of the analyses, the dataset was split into six subareas (shown by different shading/colours), based on bathymetry and information on regional hydrography. The bathymetry used was that provided by the Norwegian Mapping Authority

The main objectives of this study were to identify and characterize demersal fish species assemblages and their geographical patterns. Archived research bottom trawl survey data were used as the source of species-specific abundance information. Our dataset comprised quality-controlled catch data from annual joint Norwegian-Russian ecosystem surveys conducted in August–September 2007–2014. In that period, the Barents Sea was exceptionally warm, i.e. with temperatures in the core of the Atlantic Water entering the Barents Sea, as recorded in the Kola section, on the order of 1 °C above average in all years (Fig. 2c). A comparable increase in temperature has been recorded along the western Spitsbergen shelf during the same period (Walczowski et al. 2012). The last decade (after 2000) was the warmest since the onset of regular measurements in 1900 in the Kola section (Bochkov 1982; Tereschenko 1997; Skagseth et al. 2008; Polyakov et al. 2013), and paleo-records based on foraminifera suggest that the Atlantic Water flowing into the Barents Sea area was at its warmest for the last 2000 years (Spielhagen et al. 2011).

In the earlier analyses of similar trawl survey datasets from Barents Sea (Burgos 1989; Fossheim et al. 2006;

Byrkjedal and Høines 2007; Johannesen et al. 2012; Aschan et al. 2013; Fossheim et al. 2015; Johannesen et al. 2016), spatial patterns at relatively large spatial scales were observed in the demersal fish community. The patterns of distribution were associated with regional hydrography, particularly the geographical position and character of the Polar Front between Atlantic and Arctic water masses (Loeng 1991; Byrkjedal and Høines 2007; Johannesen et al. 2012). In the Svalbard shelf, similar associations were expected with regional hydrography but probably sharper and more localized boundaries between assemblages associated with steep environmental gradients. Diversity was expected to change both with latitude and depth, as well as position around the islands. Generally, it was anticipated that the diversity and abundance in the high-Arctic subarea of the archipelago was low compared with that observed in the warmer south-western shelf areas facing the Norwegian and Greenland Seas being under the influence of Atlantic Water.

The new results from the Svalbard archipelago are discussed in the context of climate change, fisheries and other potential anthropogenic activities in the area.

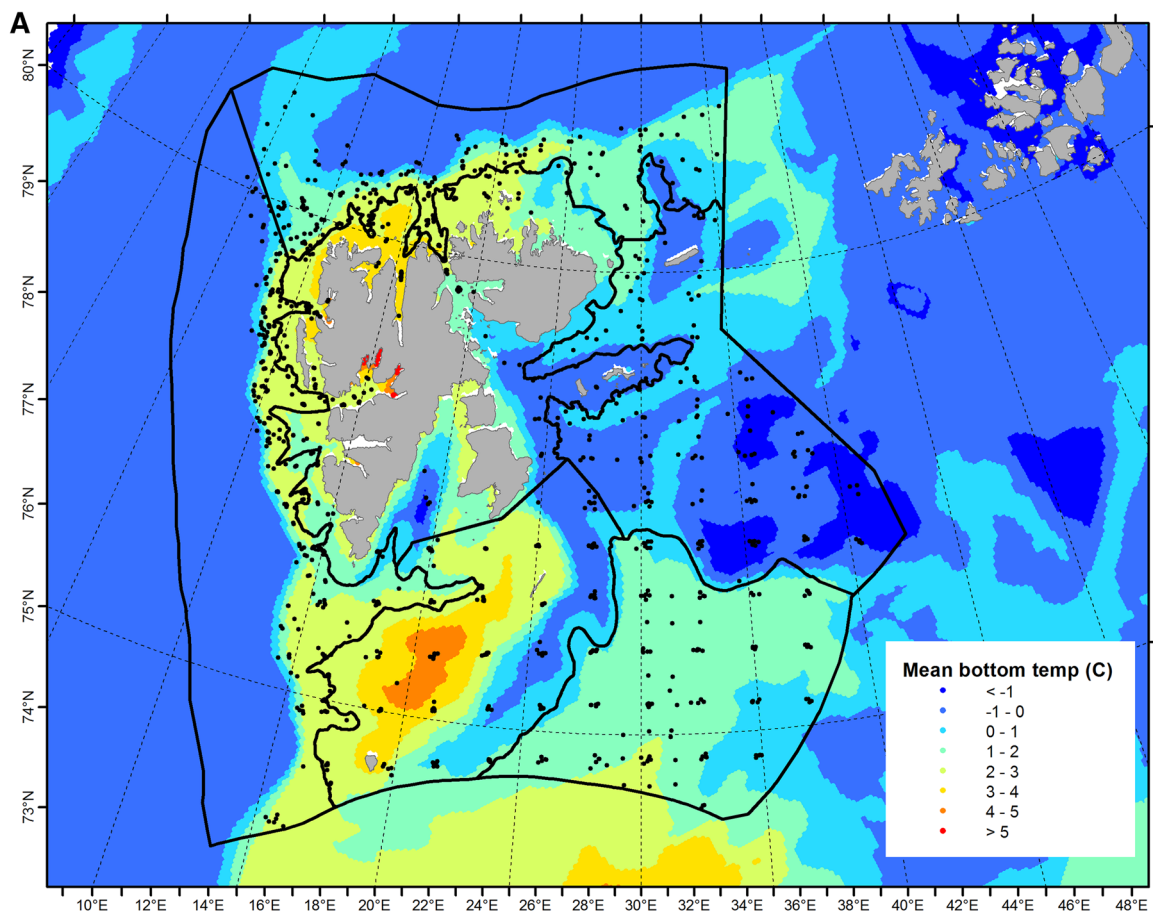


Fig. 2 Modelled average temperature on the Svalbard archipelago across the time series 2007–2014 in **a** August–September and **b** March–April, as well as **c** temperature anomalies from time series

in the Kola section 1950–2014. For details on model set-up and performance, see Lien et al. (2013b; 2014)

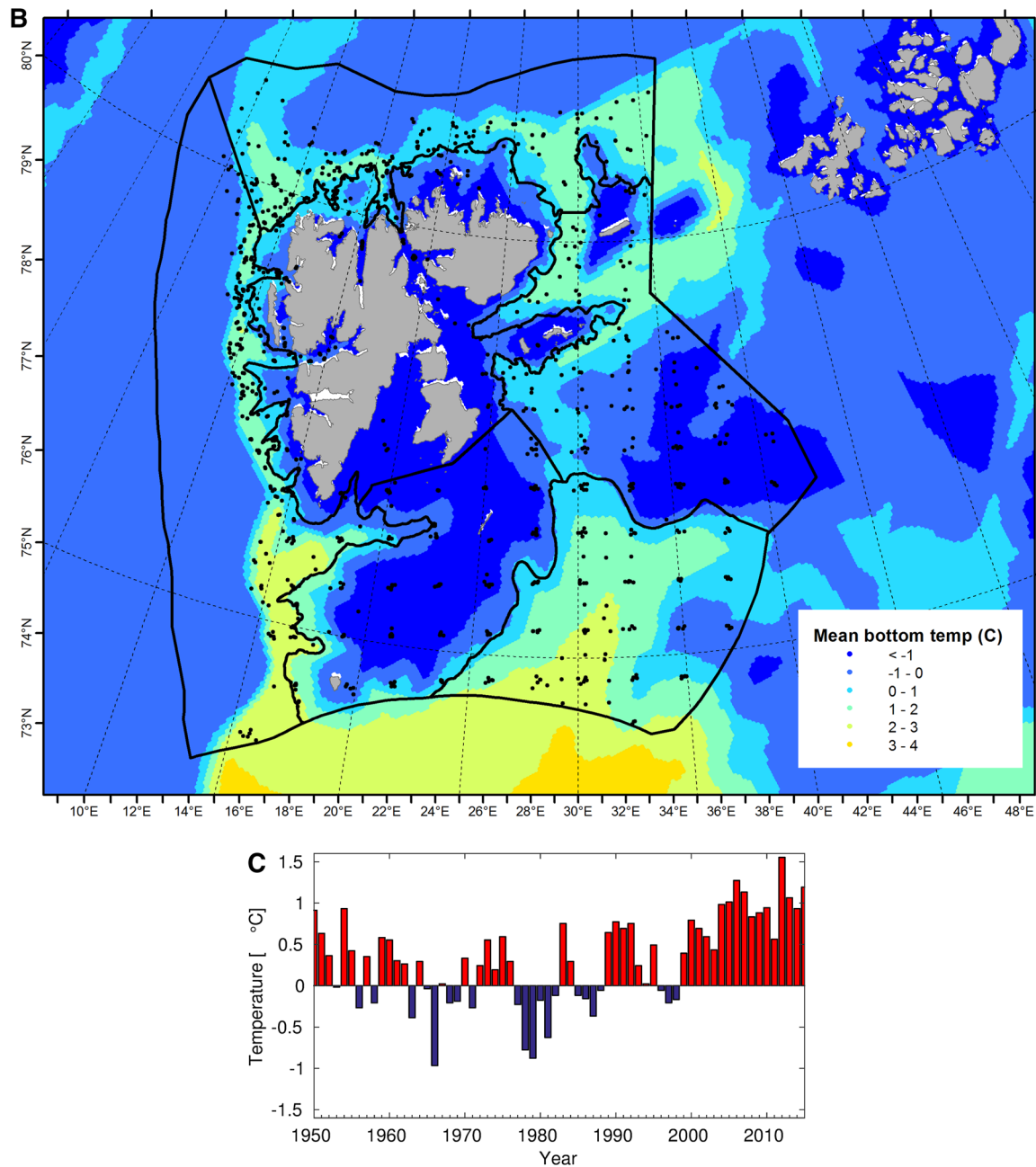


Fig. 2 continued

Study area characteristics

The Svalbard archipelago is located in the north-western part of the Barents Sea (Fig. 1). Towards the west and north the archipelago faces the >3000 m deep basins of the Greenland Sea and Arctic Ocean, respectively, whereas to the east and south there is no deepwater area delineating Svalbard from the shallow and partially ice-covered Barents Sea. During winter, the polar ice cap is extending from the Polar Basin and covers the shallow subareas of our study area (e.g. Onarheim et al. 2014, 2015). During

summer, the polar ice cap retreats and most of the study area is ice-free in an average year. However, the sea-ice extent varies considerably between years. In recent years, with the exception of 2014, the coastal and shelf areas north of Svalbard were ice-free during summer.

The bathymetry in the area is complex. Habitats range from rather deep glacial fjords to coastal shelves extending from the sublittoral to 400 m with wide shallow banks, and to the outer shelf and upper continental slope of 400–1300 m depth.

The hydrographic conditions around Svalbard are dominated by the Polar Front between relatively warm

Atlantic Water advected from the south and regionally generated cold Arctic water masses. The frontal zone generally follows the bathymetric features of the Svalbard archipelago and the Svalbard Bank.

The continental shelf break to the west and north of Svalbard is dominated by the northward flow of Atlantic Water in the West Spitsbergen Current (Beszczynzka-Möller et al. 2012), which continues eastward in the Arctic Ocean on the northern side of Svalbard (e.g. Pnyushkov et al. 2013). To a varying degree, some of this sub-surface Atlantic Water enters the Barents Sea from the north through canyons and troughs (Lind and Ingvaldsen 2012). In addition to the along-path temperature variability, there is considerable cross-slope temperature variability reflecting cross-slope movements of the frontal zone due to temporal changes in the regional atmospheric circulation (Cottier et al. 2007).

The Polar Front is topographically steered and located between the 150 and 200 m isobaths separating colder and relatively low-salinity Arctic-influenced water masses on the shallow Svalbard Bank from warmer and more saline Atlantic-influenced water masses further out on the slope surrounding the bank (Parsons et al. 1996). Although the Polar Front is tightly connected to the topography, the position of the front can vary depending on the strength and position of the Atlantic Water inflow to the Barents Sea (Ingvaldsen 2005; Lien et al. 2013a). The Svalbard Bank is seasonally ice covered, and thus, the temperature is at the freezing point throughout the water column during winter. During summer, the temperature increases due to insolation. The Svalbard Bank is a source of dense, brine-enriched water formed during freezing of sea ice (Sarynina 1969; Årthun et al. 2011). These cold and dense water masses flow at the bottom along the slopes of the bank (Shapiro and Hill 2003; Lien and Ådlandsvik 2014) and slowly descend into the Bear Island Channel and eventually the Norwegian Sea (Blindheim 1989).

Materials and methods

Geomorphology, hydrography and circulation in the study area

Based on bathymetric and hydrographic conditions, the study area was divided into six subareas (Figs. 1, 2) used to provide an initial overview of sampling effort and fish occurrence patterns. The same subareas were subsequently used to interpret results of ordination analyses to which the entire dataset was input. The six subareas were as follows:

Atlantic continental shelf break

The Atlantic continental shelf was split into a south-western (SW) and a north-eastern (NE) subarea at the 1000 m

isobath along the western slope of the Yermack plateau, thereby delineating the two subareas facing the Greenland Sea and Arctic Ocean, respectively.

Hopen Deep

The Hopen Deep forms the northeast extension of the Bear Island Trough and is dominated by Atlantic Water circulating counter-clockwise within the Deep (Skagseth 2008). Intermittently, Atlantic Water flows north-eastward also in the western part along the slope of the Svalbard Bank (Lien et al. 2013a). Despite the Atlantic influence throughout the Hopen Deep, the benthic megafauna here is mainly Arctic, i.e. located north of the “benthic Polar Front”, probably due to intermittent flow of cold bottom water associated with sea ice freezing on surrounding banks (Jørgensen et al. 2015).

Svalbard Bank

The Svalbard Bank is the shallowest of the larger banks within the Barents Sea, with summit depth of 30–50 m. A stationary front governed by the strong tidal currents is surrounding the bank. The front runs approximately along the 50 m isobath, and in areas shallower than 50 m the water column is well-mixed and homogeneous from surface to bottom (Fer and Drinkwater 2014).

Svalbard east

The area to the east of Svalbard exhibits a complex topography comprising several relatively small and shallow bank structures divided by canyons and small basins with depths exceeding 300 m. The banks are dominated by cold Arctic water masses throughout the water column (e.g. Pfirman et al. 1994), whereas the canyons are influenced by inflow of Atlantic Water, typically at depths below 150–200 m (Lind and Ingvaldsen 2012).

Svalbard coastal area

The fjords of Svalbard are dominated by cold Arctic waters, including cold and dense brine-enriched bottom water following sea-ice formation in winter. Along the western side of Svalbard, there is a variable influence from Atlantic Water extending into the fjords, depending on the regional wind pattern (Cottier et al. 2007) and the variable sea-ice production and subsequent interannual variability in density inside the fjords (Nilsen et al. 2008).

Demersal fish survey design and sampling

Species-specific occurrence and abundance data on fishes were available from bottom trawl catches from the Barents

Table 1 Norwegian bottom trawl surveys on the Svalbard archipelago 2007–2014. The number of trawl stations by subarea and year. Stations deeper than 500 m are given in parantheses

Year	Atlantic NE	Atlantic SW	Hopen Deep	Svalbard Coast	Svalbard Bank	Svalbard East
2007	22 (18)	44 (12)	32	24	21	18
2008	16 (13)	32 (13)	8	20	10	12
2009	12 (8)	9 (6)	12	15	8	15
2010	2 (0)	10 (3)	16	8	18	14
2011	16 (6)	21 (3)	7	8	18	25
2012	20 (18)	20 (6)	16	32	15	25
2013	26 (6)	26 (3)	20	33	21	24
2014	11 (1)	14 (8)	20	3	17	7

Sea-Svalbard area in August–September 2007–2014. The effort in the Svalbard area formed part of the Joint annual Norwegian/Russian Ecosystem Survey in the Barents Sea (Anon 2007; Anon 2009a, b; Anon 2010, 2011; Eriksen 2012; Prokhorova 2013; Eriksen 2014). The survey series started in 2004, however, since the quality of species identifications for many taxa were judged unreliable before 2007, it was decided not to include the first three years in the present study of species assemblages and diversity. Although scattered older data exist from the Svalbard area, the selected series was deemed the most suitable for conducting assemblage pattern analyses. The entire area of interest was sampled, and methods were standardized throughout the period selected.

While the full annual survey was and is conducted jointly by the Institute of Marine Research (IMR), Norway, and Polar Research Institute of Marine Fisheries and Oceanography (PINRO), Russia, only Norwegian vessels sampled the Svalbard area and provided data to this study. Data were collected by five vessels and comprised 967 geo-referenced bottom trawl samples (Fig. 1; Table 1). For each sample, bottom depth of the trawl tow was recorded. A full list of samples is provided as Electronic Supplementary Information (Online Resource 1).

Fish were sampled with a Campelen 1800 bottom trawl towed on double warps. The mesh size was 80 mm (stretched) in the front and 16–22 mm in the cod-end, allowing the capture and retention of small-sized fish. The trawl configuration and bottom contact was monitored remotely by Scanmar trawl sensors. The horizontal opening was 17 m, and the vertical opening 4–5 m. A rockhopper ground gear was used throughout. The standard procedure was to tow for 15 min after the trawl had achieved contact with the bottom. Towing speed was 3 knots, equivalent to a towing distance of 0.75 nautical miles (ca. 1400 m) in a 15 min tow. Due to unfavourable bottom conditions or other circumstances, a few (4 out of 967 tows) were interrupted after only 5 min but these were still included as valid. Tows in deep areas (>500 m) usually produced small samples and were extended beyond 15 min, to a maximum of 65 min. This created challenges in the analyses, but only affected the deep areas that were not the primary interest of the study.

Although sampling effort varied somewhat between years due to unforeseen circumstances, such as unfavourable

weather, the bottom trawl sampling comprised the entire shelf and coastal area of the Svalbard archipelago. When samples from all years were pooled, the spatial distribution of the 967 samples (Fig. 1; Table 1, Online Resource 1) was found adequate and sufficient to characterize demersal fish assemblages in the habitats trawled, i.e. the predominant habitats of the mainly soft-substrate shelf and coastal waters beyond the shallowest coastal zone (i.e. beyond the 50 m isobath) to the upper continental shelf depths. Once the design was set and trawl sites selected, the same sites were, if practically possible, visited every year through the time series. A potential shortcoming for the present analysis is that the survey was not originally designed to optimize assemblage analyses. The sites were selected according to a systematic design spanning all habitats rather than to a stratified random design that might have been more appropriate.

Hydrographically the area has strong spatial patterns and pronounced seasonality (Fig. 2a, b), particularly in the shallow subareas where winter cooling and summer warming combined with strong vertical mixing cause bottom temperatures to vary much more than in the adjacent deep shelf waters. The trawl sampling was distributed in all the relevant hydrographic conditions observed or derived from model outputs (Fig. 2a, b). Unfortunately, a limitation in the present study was that environmental data such as near-bottom salinity and temperature and substrate data were not recorded for each trawl tow.

Species identification and data processing

Fish catches were sorted immediately on board by trained technicians to lowest possible taxonomic level. Unidentifiable specimens were frozen on board and subsequently identified by experienced taxonomists. If deemed necessary, voucher specimens were curated by the University Museum Bergen (Online Resource 1). A full account of all species is beyond the scope of this study but further details on the fish records are provided in the Barents Sea Fish Atlas generated from the same and other surveys (Wienerroither et al. 2011).

Only demersal fishes were retained in the dataset (55 species and four genera, Table 2). Predominantly pelagic

species polar cod (*Boreogadus saida*), Arctic cod (*Arctogadus glacialis*), capelin (*Mallotus villosus*), Atlantic herring (*Clupea harengus*), lesser sand-eel (*Ammodytes marinus*), Greenland shark (*Somniosus microcephalus*) as well as mesopelagic species (myctophids, sternoptychids a.o.) were removed. Bottom trawl catches of pelagic species, many which form aggregations or schools in midwater and only occasionally occur near the seabed, were relatively common. However, they were unlikely to reflect the abundance and occurrence of such taxa. Inclusion of such species in, for example, multivariate analyses would rather distort than add valid information to the account of distribution and diversity of truly seabed-associated demersals, i.e. benthic or benthopelagic species. Greenland shark was excluded because it is predominantly pelagic, and also because it is rare in the bottom trawl catches. The species occurs in the area and catches are reported (Wienerroither et al. 2011, 2013), but it is unlikely that the bottom trawl survey catches reflect abundance or distribution. Also pollock (*Pollachius pollachius*) was removed because it was represented by a single possibly misidentified specimen not retained for subsequent confirmation of identity. Furthermore, specimens identified to the genus level were removed (representing <0.51% of the individuals recorded), except for specimens belonging to *Sebastes*, *Icelus*, *Gymnelus* and *Careproctus*. For the three *Sebastes* species Golden redfish (*Sebastes norvegicus*), beaked redfish (*S. mentella*) and Norway redfish (*S. viviparus*) identification uncertainty based on morphology alone persists (especially for juveniles). Up until 2014 the procedure was to only identify specimens >10 cm to the species level. Therefore, not all specimens were identified to species and the decision was made to pool all *Sebastes* records and use the genus as a valid category in the analyses. (However, most of the unidentified specimens were probably *S. mentella* as this species is by far the most common in the Barents Sea. Amongst the *Sebastes* individuals in our dataset identified by skilled personnel, 93% were assigned to *S. mentella*. Only two percent was *S. norvegicus*. The rest were recorded as *S. viviparus* but suspected to be misidentifications as *S. viviparus* is a warmer-water coastal species found along the coast in the south-western Barents Sea of which no records have been confirmed from the Svalbard area).

The two *Icelus* species occurring in the area, *Icelus bicornis* and *I. spatula*, are very difficult to differentiate. The *Gymnelus* and *Careproctus* genera probably have several species in the area but the taxonomy is unresolved.

Data analysis

Prior to exploring the data, the catches were standardized to number of individuals per 15 min tow. All analyses were

done using the software R (R Core Team 2017). Species accumulation curves were produced using the function `Specaccum` in the package `Vegan` (Oksanen et al. 2016). Accumulation curves are built using random permutations of sites (Gotelli and Colwell 2001), and 100 permutations were used to calculate standard errors of estimated species richness. Approximate 95% confidence intervals are calculated using two standard errors. To study changes in species composition and variation amongst sites, correspondence analysis (Jongman et al. 1995) was run using the package `Ade4` (Dray et al. 2016). Correspondence analysis is a multivariate ordination method derived from principal component analysis but adapted to count data (Greenacre 2013). It results in a joint ordination of species and sites, using the relative frequencies (i.e. species and site compositions). The joint ordination is expressed through species and site scores, and the eigenvalues represent the abundance-weighted correlation between these scores. Input to the ordinations were the observed frequencies standardized to a tow duration of 15 min.

Results

Species list, zoogeographical affinity and overall abundance patterns

Table 2 lists the 59 species and higher taxa used in the multivariate analyses, and their zoogeographical affinities. In a first effort to explore the dataset, Fig. 3 presents mean abundances of the 59 taxa for each of the survey years 2007–2014 split by subareas of the Svalbard shelf and slope shown in Fig. 1. For the Atlantic continental shelf break, the records were categorized into south-western and north-eastern subareas shallower than 500 m, and an additional group of stations deeper than 500 m.

Albeit to varying degree, the species accumulation curves for most subareas approach asymptotes, suggesting that the sampling was probably adequate to observe patterns for the major taxa occurring in the different subareas (Fig. 4). In general, the Atlantic sector subareas (SW and NE) had 40–45 taxa, and around 10 more taxa than the Arctic subarea denoted Svalbard East. For the deepest stations (i.e. the upper continental slope deeper than 500 m), the species accumulation curve was not asymptotic. At this depth, catches were generally small and sampling probably also too limited to provide the full taxon list. Similarly, the Svalbard Bank subarea curve did not reach an asymptote. This subarea is a shallow bank with strong seasonal variability in temperature (Fig. 2a, b). These conditions apparently produced rich samples with more variable species composition than adjacent subareas where seasonal temperature variation is less.

Table 2 Demersal fish data from Norwegian bottom trawl surveys on the Svalbard archipelago 2007–2014. Species list with abbreviations used in the figures and zoogeographical groups according to Andriyashev and Chernova (1995) and Mecklenburg et al. (2011). Where the zoogeographical classification differs amongst the two, the group according to Mecklenburg et al. (2011) is given in parenthesis

Family	Species	Abbreviation	Zoogeographical affinity
Arhynchobatidae	<i>Bathyraja spinicauda</i>	Bat.spi	MB
Rajidae	<i>A. hyperborea</i>	Amb.hyp	A
	<i>A. radiata</i>	Amb.rad	MB
	<i>Rajella fyllae</i>	Raj.fyl	MB (B)
Argentinidae	<i>Argentina silus</i>	Arg.sp	B
Macrouridae	<i>Coelorinchus labiatus</i>	Coe.lab	–
	<i>Macrourus berglax</i>	Mac.ber	B (MB)
Gadidae	<i>Gadus morhua</i>	Gad.mor	MB
	<i>Melanogrammus aeglefinus</i>	Mel.aeg	MB
	<i>M. poutassou</i>	Mic.pou	MB
	<i>Pollachius virens</i>	Pol.vir	MB (B)
	<i>T. esmarkii</i>	Tris.esm	B
Lotidae	<i>Brosme brosme</i>	Bro.bro	MB (B)
	<i>Enchelyopus cimbrius</i>	Enc.cim	B
	<i>Gaidropsarus argentatus</i>	Gai.arg	A (AB)
	<i>Molva molva</i>	Mol.mol	B
Sebastidae	<i>Sebastes</i> spp.	Seb.spp	MB
Cottidae	<i>Arteidiellus atlanticus</i>	Art.atl	MB (AB)
	<i>Gymnocanthus tricuspidus</i>	Gym.tri	MA (A)
	<i>Icelus</i> spp.	Ice.spp	AB and MA
	<i>Myoxocephalus scorpius</i>	Myo.sco	MB (AB)
	<i>T. murrayi</i>	Tri.mur	B (MB)
	<i>T. nybelini</i>	Tri.nyb	A
Psychrolutidae	<i>T. pingelii</i>	Tri.pin	AB
	<i>Cottunculus microps</i>	Cott.mic	MA (AB)
Agonidae	<i>Leptagonus decagonus</i>	Lep.dec	AB
Cyclopteridae	<i>Eumicrotremus derjugini</i>	Eum.der	A
	<i>Eumicrotremus spinosus</i>	Eum.spi	MA
Liparidae	<i>Careproctus</i> spp.	Car.spp	MA, A and AB
	<i>Liparis bathyarticus</i>	Lip.bat	MA
	<i>Liparis fabricii</i>	Lip.fab	A
	<i>Liparis tunicatus</i>	Lip.tun	A
	<i>Paraliparis bathybius</i>	Par.bat	A
	<i>Rhodichthys regina</i>	Rho.reg	A
Zoarcidae	<i>Gymnelus</i> spp.	Gym.spp	A and AB
	<i>Lycenchelys kolthoffi</i>	Lyc.ado	A
	<i>Lycenchelys muraena</i>	Lyc.esm	A
	<i>Lycenchelys sarsii</i>	Lyc.eud	B
	<i>L. adolfi</i>	Lyc.fla	A
	<i>L. esmarkii</i>	Lyc.fri	MB
	<i>L. eudipleurostictus</i>	Lyc.gra	A
	<i>L. frigidus</i>	Lyc.lut	A
	<i>L. gracilis</i>	Lyc.paa	MB
	<i>L. luetkenii</i>	Lyc.pall	A
	<i>L. paamiuti</i>	Lyc.ret	(A)
	<i>L. pallidus</i>	Lyc.ros	A (AB)
	<i>L. reticulatus</i>	Lyc.sem	A

Table 2 continued

Family	Species	Abbreviation	Zoogeographical affinity
	<i>L. rossi</i>	Lyc.squ	A
	<i>L. seminudus</i>	Lyce.kol	A
	<i>L. squamiventer</i>	Lyce.mur	A
	<i>Lycodonus flagellicauda</i>	Lyce.sar	A
Stichaeidae	<i>Anisarchus medius</i>	Ani.med	B (AB)
	<i>Leptoclinus maculatus</i>	Lep.mac	MB (AB)
	<i>Lumpenus lampretaeformis</i>	Lum.lam	MB
Anarhichadidae	<i>A. denticulatus</i>	Ana.den	MB (AB)
	<i>A. lupus</i>	Ana.lup	MB
	<i>A. minor</i>	Ana.min	MB
Pleuronectidae	<i>Hippoglossoides platessoides</i>	Hip.pla	MB
	<i>Reinhardtius hippoglossoides</i>	Rei.hip	MA (AB)

A Arctic, MA mainly Arctic, AB Arcto-Boreal, MB mainly Boreal, B Boreal

The five first taxa listed in Fig. 3 were essentially ubiquitous and common in all years of the series, i.e. Atlantic cod (*Gadus morhua*), long rough dab (*Hippoglossoides platessoides*), redfish (*Sebastes* spp.), *Arteidiellus atlanticus*, and Greenland halibut (*Reinhardtius hippoglossoides*). There was substantial similarity in species composition between the six subareas.

However, single species/genera create dissimilarity by either being prominent or almost absent in individual subareas. The group of stations from the deep Atlantic, essentially the shelf break and upper slope deeper than 500 m, was clearly different from the six subareas. This deep group had low abundances of the more typical shelf species, and in contrast, for example, a range of, Arctic eelpouts that were absent from or uncommon in shallower waters was prominent. This was also the only area in which the sub-Arctic macrourid roughhead grenadier (*Macrourus berglax*) and the Arctic skate (*Amblyraja hyperborea*) were consistently present.

Distribution and abundance patterns

Patterns across entire sampling area

The patterns shown in Fig. 3 pre-supposes patterns associated with the selected subareas. Therefore, using correspondence analyses, we explored patterns of variation inherent to the dataset, disregarding the subareas selected. In a preliminary correspondence analyses (CA) of the entire dataset (i.e. samples from all years and all depths pooled, result not shown), it was observed that the samples from depths >500 m tended to dominate the analysis and hide patterns in shallower shelf waters. This confirmed the

patterns observed in the overview plot of the distribution and abundance of all species (Fig. 3) that the deep stations had a species composition distinctly different from all shallower subareas. This contrasting shelf versus upper slope pattern was an obvious main result of the study.

To gain further insight, two further correspondence analyses were carried out. In the first, the >500 m depth samples were omitted in order to explore patterns in the Svalbard shelf area. In the second, only the shelf break areas (Atlantic SW and Atlantic NE) were considered, including also the stations from depths >500 m. Thus three separate CAs were carried out: the one mentioned above on the entire dataset and two on subsets of the data.

Patterns on the shelf (<500 m)

Scores on Axis 1 and 2 resulting from the CA run with all stations shallower than 500 m depth are shown in Fig. 5. In the six plots shown in Fig. 5, scores for all stations are provided and those for stations within individual subareas (Fig. 1) are highlighted (black dots and lines). The eigenvalue distribution suggested that main patterns of variation would be explained by Axis 1 and 2, each explaining roughly equal proportions of the total variation (Eigenvalue Axis 1: 0.67, explained variation 10.6%; Axis 2: 0.64; 10.2%). Most samples (and species) are concentrated in the centre of the plot confirming the above suggestion of a degree of homogeneity amongst samples across the entire Svalbard shelf. There is, however, also a dispersion of samples along three gradients suggesting a spatial pattern (Fig. 5).

The major pattern (i.e. separation along Axis 1) is that of Hopen Deep and Atlantic SW tending to have negative

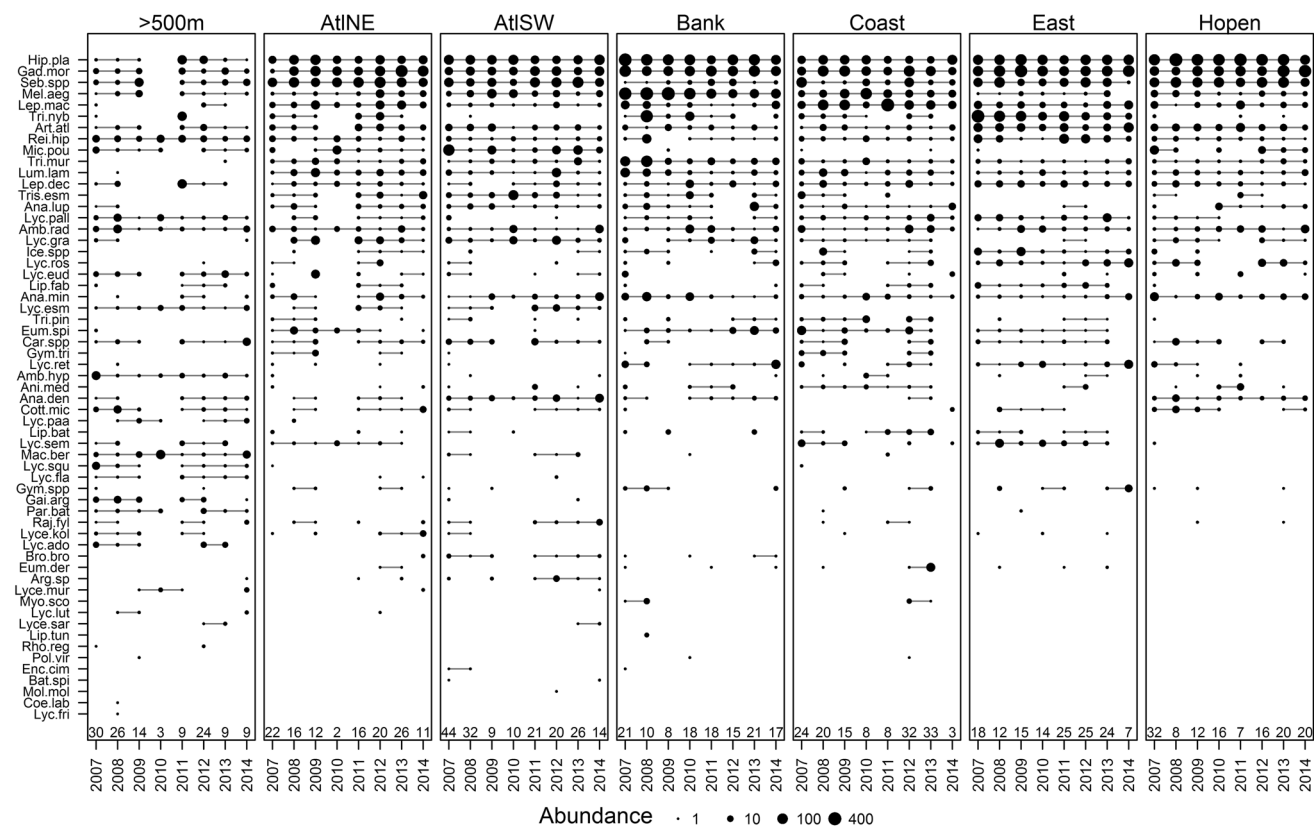
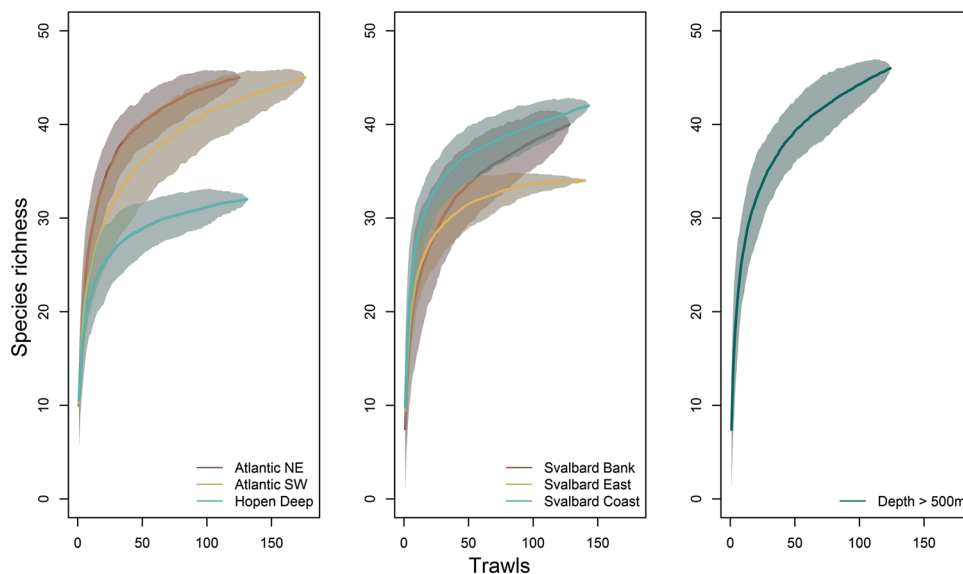


Fig. 3 Demersal fish abundance in Norwegian bottom trawl surveys on the Svalbard archipelago 2007–2014. Overview of distribution and abundance (number of individuals sampled by a 15 min trawl tow) for all species for each sampling year for six subareas of the Svalbard archipelago shown in Fig. 1, and for the group of stations deeper than 500 m. The taxa are listed in ascending order according to overall

abundance in the pooled dataset, and symbol sizes reflect mean abundance levels given in legend beneath the graph. *Horizontal lines* connect symbols in the cases where a species occurs in two or more subsequent years. Numbers of trawl hauls by subarea and year are shown as numbers above the *horizontal axis*

Fig. 4 Demersal fish data from Norwegian bottom trawl surveys on the Svalbard archipelago 2007–2014. Species accumulation curves for all trawl samples from individual subareas of the Svalbard archipelago shown in Fig. 1. Accumulation curves and associated 95% confidence intervals derived by 100 random permutations



scores and Svalbard Bank and Svalbard Coast tending to have positive scores. Taking also Axis 2 into account, the Atlantic SW samples are placed in the upper left quadrant

opposite Svalbard East samples in the lower left quadrant, hence it is suggested that Axis 2 represents a gradient from cold Arctic shelf areas to warm Atlantic waters.

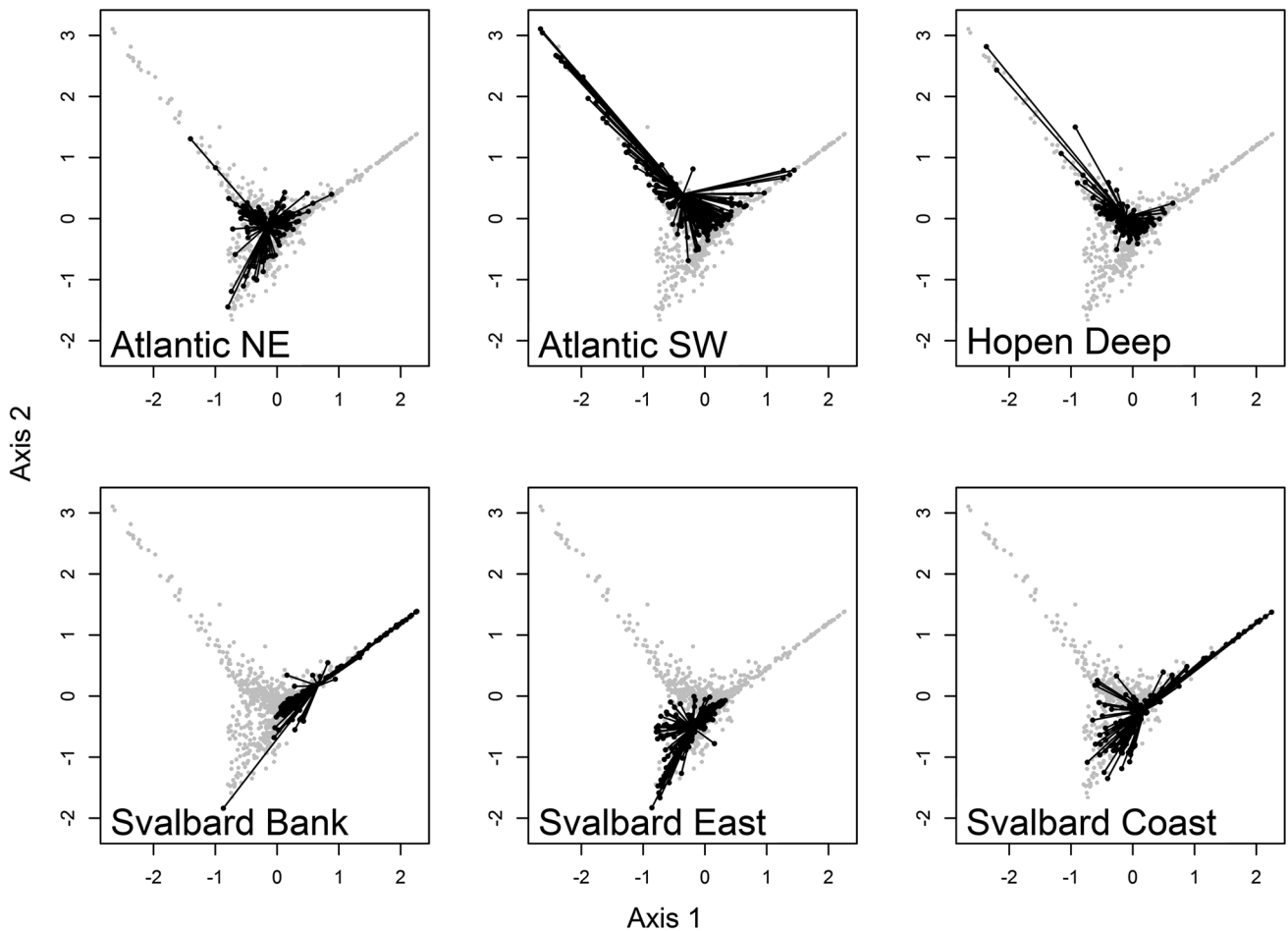


Fig. 5 Correspondence analysis (CA) of demersal fish data from all the trawl sites shallower than 500 m depth of the 2007–2014 Norwegian bottom trawl survey on the Svalbard archipelago. Sampling site scores on Axis 1 versus 2 are given for all stations

(grey dots). All plots show the entire output, but individual panels highlight the score patterns of the sites in the six subareas as black lines and dots

As examples of species providing comparatively clear patterns, we selected 16 abundant species with contrasting score patterns on Axes 1 and 2 (positive, negative and close to 0). For these species, CA site scores on Axis 1 versus 2 were plotted with symbol sizes reflecting abundances in individual trawl samples (Fig. 6). Amongst these 16 selected species were examples of ubiquitous species showing no pattern, and in contrast, species showing clear associations with the three gradients revealed by the CA. Since the input data were not log-transformed, it is likely that abundant species tend to have a comparatively strong influence on the results. Haddock, Atlantic wolffish (*Anarhichas lupus*), and to a lesser extent *Triglops murrayi* and Norway pout (*Trisopterus esmarkii*) are species associated with the ‘Svalbard Bank-gradient’, whereas blue whiting (*Micromesistius poutassou*), *Lycodes esmarkii* and *L. gracilis* are associated with the ‘Atlantic SW-gradient’. *Lycodes pallidus*, *Liparis fabricii*, *T. nybelini*, *Icelus* spp. and to some extent *L. eudipleurostictus* are abundant along the

‘Svalbard East-gradient’. Other species, such as, Atlantic cod, redfish, long rough dab and *Artediellus atlanticus* are distributed across the entire Svalbard shelf.

Atlantic shelf break and upper slope

A further CA was run for samples from the Atlantic subareas supposedly most influenced by Atlantic water masses, i.e. from subareas referred to as Atlantic SW and Atlantic NE in Fig. 1, the latter representing the subarea facing the Arctic Ocean. The deepest stations in the dataset derived from upper slope waters were also included in that analysis.

The results suggested that Axis 1 (Eigenvalue = 0.71; explained variation = 9.5%) essentially represented a depth gradient. The species scores formed a continuum from the deep-living species associated with the upper continental slope with high positive scores to a range of

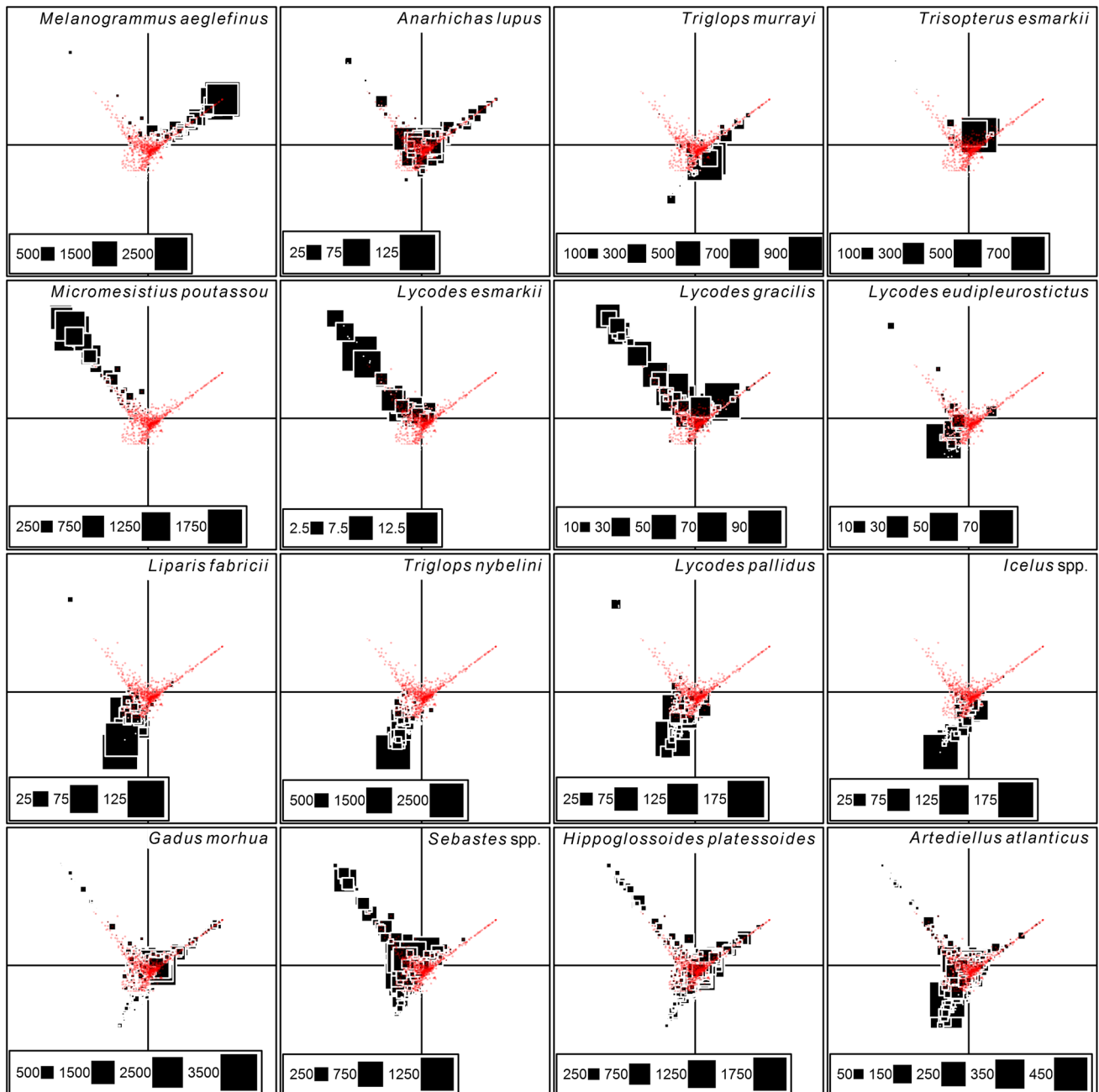


Fig. 6 Correspondence analysis (CA) scores on Axis 1 versus 2 and abundance (standardized to 15 min trawling time) of 16 selected fish species observed during the 2007–2014 Norwegian bottom trawl

survey on the Svalbard archipelago. *Sizes of squares* indicate abundance at individual sites, and small *dots* represent absences (zero observations)

shelf species clustering near the origo. On Axis 2 (Eigenvalue = 0.62; explained variation = 8.3%), blue whiting, a benthopelagic species known to be associated with Atlantic water, was prominent with a low score compared with other species. In Fig. 7a, the two graphs for Atlantic SW and NE, respectively, show CA site scores on Axis 1 versus 2 represented by symbols of depth. In both subareas, Axis 1 is clearly a depth gradient. In the SW, there is considerable variation on Axis 2, independent of depth.

This is not the case in the NE, where blue whiting was virtually absent.

In these two subareas, also Axis 3 (eigenvalue = 0.53; explained variation = 7.1%) and 4 (eigenvalue = 0.48, explained variation = 6.4%) of the CA appeared informative (Fig. 7b), particularly in the Atlantic NE subarea. In Atlantic NE, a group of 7 relatively deep stations form a loose cluster in the lower part of the graph, suggesting a relatively pronounced difference in species composition

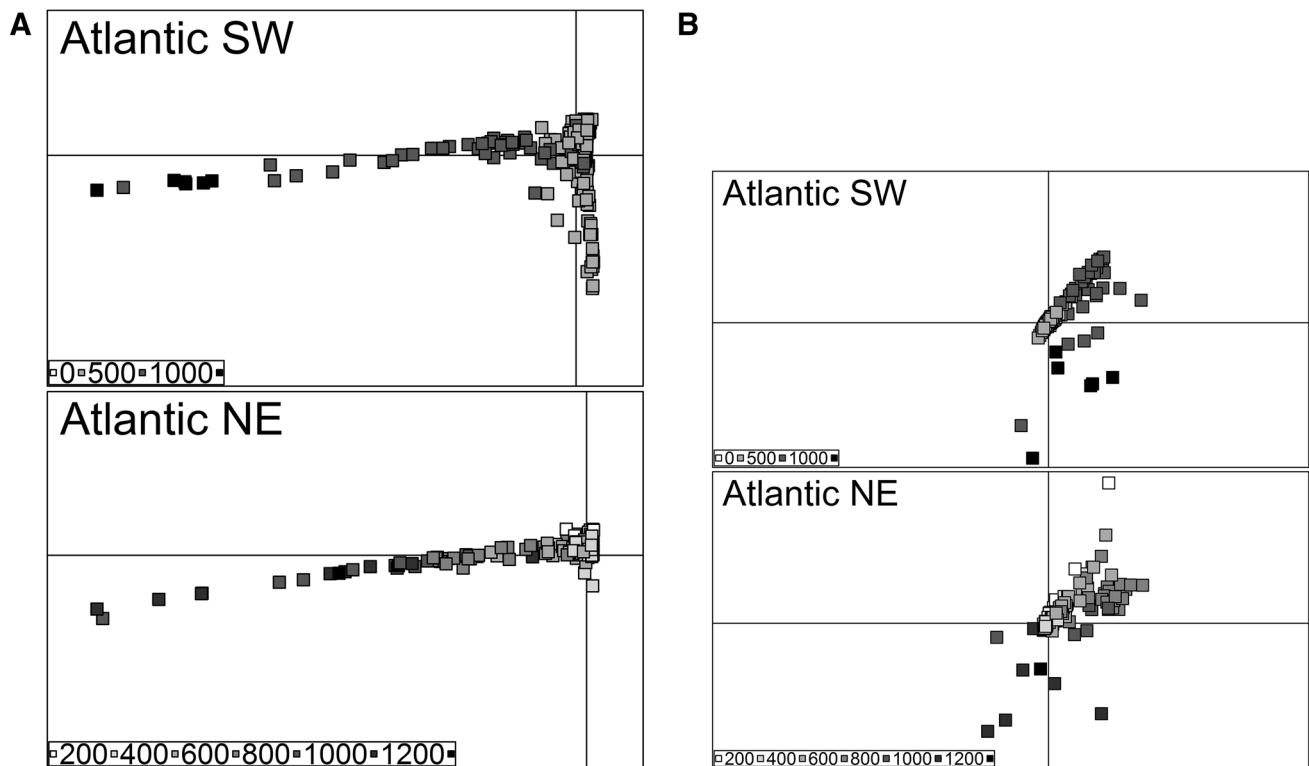


Fig. 7 Correspondence analysis (CA) of demersal fish data from the 2007–2014 Norwegian bottom trawl survey on the Svalbard archipelago, using only the subset of data from the Atlantic SW and NE subareas (Fig. 1). From those subareas, all stations from the

entire depth range are included. **a** Site scores on Axis 1 and 2, and **b** site scores on Axis 3 and 4. Grey scale of symbols indicate site depth

compared with other stations. The species composition for those 7 species and the remainder of the stations (Fig. 8) showed that the seven stations have exclusively Arctic species (*A. hyperborea*, *Lycodes* spp. and *Rhodichtys regina*). The remaining stations have greater richness, and include also many boreal species.

These observations suggest that compared with the Atlantic SW there is greater structuring in the Atlantic NE into a truly deep Arctic assemblage and a shelf assemblage (including also some deep stations) with more boreal species composition. The Atlantic NE is hydrographically complex being a transition area between the Greenland Sea and the Arctic Ocean with a significant inflow of Atlantic water at shelf depths.

Discussion

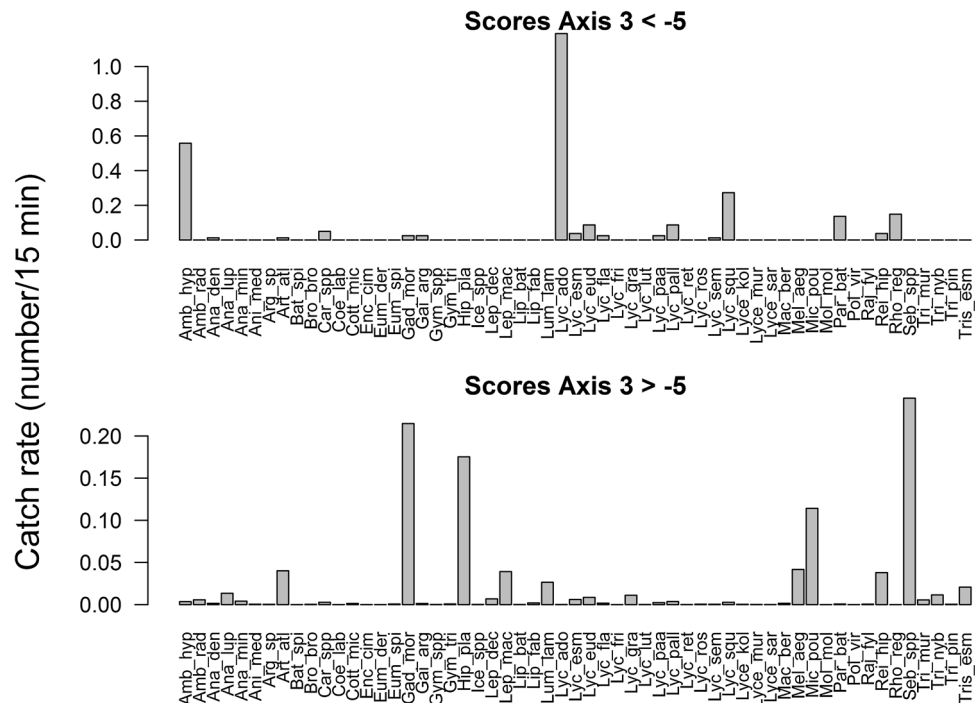
Appropriateness of input data

Although the surveys were not originally designed for assemblage studies, rather for monitoring abundance of key species of commercial interest, the dataset generated was sufficiently comprehensive to carry out such analyses. The

sampling was apparently too limited at depth exceeding 500 m to obtain a full species list, and the results may be weaker for that subarea than for the remainder of the Svalbard area. The identification of species was consistent, and it was a benefit to future validation that voucher specimens were submitted to the University Museum Bergen collection. The number of samples by year was not sufficient to study interannual variation, and a significant shortcoming limiting the scope of the analyses was the lack of temperature, salinity and substrate data for individual samples and trawl tows.

The species accumulation curves were approaching asymptotes for several subareas, suggesting that the sampling was adequate to observe the majority of taxa occurring in each subarea. However, it is premature to make firm subarea-comparisons of richness based on these results. The apparent lower species numbers in the Svalbard East subarea are likely affected by identification problems (for the genus *Icelus*) and the unresolved taxonomy of certain genera (e.g. *Gymnelus*, *Careproctus*). The latter is an issue of concern that requires more taxonomic research. The species accumulation curve for the deepest slope areas >500 m was not asymptotic and this may be attributed to the lower sampling levels at these depths but could

Fig. 8 Correspondence analysis (CA) of demersal fish data from the 2007–2014 Norwegian bottom trawl survey on the Svalbard archipelago, using only the subset of data from the Atlantic NE subarea (Fig. 1). Comparison of species compositions in tows (sites) from the Atlantic NE subarea with CA site scores on Axis 3 > -5, and sites scores on Axis 3 < -5 (7 sites occurred in this range)



also reflect greater heterogeneity of habitats across the wider depth range in those areas compared with the shelf. On the shelf break and upper slope >500 m the tow duration was increased to obtain larger samples, but the number of tows was comparatively low.

Species occurrence and assemblages

The descriptive data by individual subareas and the results of the exploratory multivariate analyses fill a major gap in the understanding of fish assemblage patterns in the north-east Arctic, complementing earlier studies in the Barents Sea (Burgos 1989; Fosshem et al. 2006; Byrkjedal and Høines 2007; Johannesen et al. 2012). The Svalbard region is a transition zone between the Atlantic water masses from the boreal Norwegian Sea and South-western Barents shelf Sea and the Arctic waters to the north. Northern parts of the archipelago have extensive seasonally varying ice cover, even in the recent warm period. There are no apparent topographical or other obstacles to preventing distributional overlap between the Barents Sea and Svalbard, hence it is not unexpected that the Svalbard archipelago and the remainder of the Barents Sea shelf have species lists with most species in common (Wienerroither et al. 2011). A full comparison between species compositions in the two neighbouring areas is beyond the scope of this study, but some features are noteworthy. Species occurring at Svalbard associated with deeper colder water (*Paraliparis bathybius*, *Rhodichthys regina*, *Lycenchelys muraena*, *L. adolfi*, *L. frigidus*, *L. luetkenii* and *L. paamiuti*) are not

found in the main shelf area of the Barents Sea but have been observed in deeper trenches between Franz Josef's Land and Novaya Zemlya (Johannesen et al. 2017). One difference from the entire Barents Sea shelf is that the Svalbard archipelago is partly surrounded by cold deep oceans and thus has marginal deep fish assemblages. The Svalbard area lacks some species associated with shallow soft bottom brackish waters found in the southeastern Barents Sea such as flatfishes *Limanda limanda*, *Liopsetta glacialis* and European plaice (*Pleuronectes platessa*), a few cold-water coastal species (*Lumpenus fabricii* and *Asidophoroides olrikii*), found in the eastern Barents Sea only and a few coastal boreal species reaching their northern distribution limit in the south-western Barents Sea (e.g. Atlantic halibut *Hippoglossus hippoglossus*, Wienerroither et al. 2011).

The major transition in species composition was that between deep Greenland Sea and Arctic Ocean assemblages (shelf break and upper slope assemblage) and the shelf assemblages. Different shelf assemblages could be distinguished, but they had many species in common and were not very different. On the shelf, there appeared to be a clear difference between the Atlantic SW and Svalbard Bank and Svalbard East. The expected association of fish assemblages with regional bathymetric and hydrographic features was thus confirmed. An interesting finding was indication of high richness on the Svalbard Bank, in the subarea experiencing the more pronounced seasonal variation in hydrographic conditions. The varying conditions may facilitate occurrence of comparatively many species

with different zoogeographical affinities in this shallow subarea.

Assemblage patterns and environmental conditions

Prevailing hydrographic conditions may underlie the relatively small differences in the species composition of fishes across the Svalbard shelf areas. Notwithstanding seasonality, during the recent and present warm period it is likely that a greater hydrographic homogeneity across the archipelago occurred as Arctic water masses retract from shallow areas of the shelf, and Atlantic water inflows are more prominent. The change from the Atlantic SW to an Arctic assemblage on the Svalbard Bank and in the Svalbard East subarea contrasts somewhat with the corresponding sharper transition observed in the Barents Sea where an association with the Polar Front was observed in earlier studies (Burgos 1989; Fossheim et al. 2006; Byrkjedal and Høines 2007; Johannesen et al. 2012; Fossheim et al. 2015; Johannesen et al. 2016).

The Atlantic subareas to the southwest and northeast are characterized by the strongest influence of the Atlantic Water influx from the south and also by the prominent deep front against the Norwegian Sea Deepwater with sub-zero temperature. In these subareas, the analyses suggest strong depth-related patterns which probably also reflect the depth-related hydrographical structure. This has been observed also in shelf-break studies further south in the Norwegian Sea (Bergstad et al. 1999). There are also some differences between fish assemblage pattern in the subareas facing the Norwegian/Greenland Sea (SW) and the Arctic Ocean (NE). Supposedly, the Atlantic influence is weaker in the latter area, especially in deep shelf waters.

The Barents Sea and Svalbard region has in recent years experienced an unprecedented warming trend, and a further warming may cause an abrupt northward shift of the Polar Front (Wassmann et al. 2015). Under continued warming, our hypothesis is therefore that the entire Svalbard shelf and coastal waters will be inhabited by an Atlantic species assemblage, leading to a “borealization” of the Svalbard shelf (Fossheim et al. 2015). Since Arctic and Atlantic food webs have different properties (e.g. connectivity) (Kortsch et al. 2015), the dynamic properties of the ecosystem in the region is likely to change. Arctic species will likely retract to northern and eastern waters of the high Arctic. Deep assemblages on the upper continental slope, however, will likely be maintained because deep oceanic waters will remain of Arctic origin (Fossheim et al. 2015).

In contrast, if a cooling trend should occur, or even cooling events during the general warming trend, the Polar Front would probably be stable. This was observed in earlier decades prior to the recent warming. A productivity decline in pelagic system due to cooling and increasing ice

cover may be expected. Some boreal species may retract (e.g. Atlantic cod). However, the hypothesis is that the main distribution and species assemblage patterns will be maintained as suggested in this study.

Utility of results and future work

The results generated in this study represent an improved baseline that will contribute to facilitating future evaluations of states and trends in fish distributions and spatial abundance patterns. As such it is a contribution to regional biodiversity analyses and assessments underlying management advisory processes. It will also benefit the generation of testable hypothesis on structuring processes for this prominent and complex hydrographical frontal zone.

Shortcomings in terms of sampling levels and design that prevented more thorough analyses of assemblage patterns for the entire area as well as those specific to subareas should be taken into account in future efforts. In order to facilitate temporal studies, the sampling design and level (the number of stations and their position) should not change from year to year. If a systematic strategy is retained, a regular grid on the shelf should be continued, but along the shelf break transects following the depth gradient with a shorter interstation distance should be applied. This will allow for finer resolution of the study of species–depth composition relationship and how this relationship varies with time. Also, continued effort is recommended to reduce uncertainty by improving species identification. The use of temperature sensors attached to the sampling gear (the trawl) is suggested for future surveys.

Apart from assessing impacts of climate variation and change, future studies using the new baseline may facilitate investigations of the influence of fisheries as well as increasing petroleum and mineral extraction activity. The Svalbard archipelago has been the subject of commercial fisheries for at least 85–90 years (Boitsov et al. 2004; Townhill et al. 2015). The present species composition in a major part of the Svalbard archipelago is probably already affected by past exploitation and therefore not in a virgin state. There is a continued need for monitoring and assessing fishing activities and to follow up new developments and potential northward shifts in fishing effort during the recent warming trend (Haug et al. 2017). Based on the current regulation practices, however, the expectation is that there will be limited effects of fisheries on the demersal fish community in the Svalbard archipelago. All fisheries are regulated (Total Allowable Catches, technical regulations, Marine Protected Areas) to maintain productivity and habitats, hence major changes may not be very likely. Bycatch rates are assumed small under current move-on-rules and technical regulations. The trend in the recent 15 years is rather declining than increasing shrimp trawling activity around Svalbard (ICES 2014). The possible

expansion in fisheries for Atlantic cod and pot fisheries that may happen will probably be possible without significant additional impact on non-target species. If shrimp trawling and pot fishing for crabs become substantial and venture into northern unexploited subareas, it is however relevant to consider what areas and assemblages will be affected by an increased target and bycatch mortality. Impacts of oil and gas activity as well as mining will naturally depend on scale, geographical distribution and technological approach of such activity. Currently, the only permissions granted are exploratory licenses in the Hopen Deep. It is difficult to develop scenarios, but a growing extractive industry is an issue of concern and enhances the need for monitoring and assessments.

Future work should include continued and improved monitoring and assessments of fish assemblages and their environment, and targeted monitoring of human activity and impacts. For most fish species that are not targeted by current fisheries, i.e. ca. 90% of the species list, essential habitats, spawning and nursery areas are largely unknown, hence there are limited data to make risk evaluations. To facilitate further monitoring and advisory activity, there is thus a need for studies of essential habitats of different life stages of fishes, especially non-target species.

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References

- Andriyashev AP, Chernova NV (1995) Annotated list of fish-like vertebrates and fishes of the Arctic Seas and adjacent waters. *J Ichthyol* 34:435–456
- Anon (2007) Survey report from the joint Norwegian/Russian ecosystem survey in the Barents Sea August–October 2007 (vol.1). IMR/PINRO Joint Report Series, No. 4/2007
- Anon (2009a) Survey report from the joint Norwegian/Russian ecosystem survey in the Barents Sea August–October 2008 (vol.1). IMR/PINRO Joint Report Series, No. 1/2009
- Anon (2009b) Survey report from the joint Norwegian/Russian ecosystem survey in the Barents Sea August–October 2009. IMR/PINRO Joint Report Series, No. 2/2010
- Anon (2010) Survey report from the joint Norwegian/Russian ecosystem survey in the Barents Sea August–September 2010. IMR/PINRO Joint Report Series, No. 4/2010
- Anon (2011) Survey report from the joint Norwegian/Russian ecosystem survey in the Barents Sea August–October 2011. IMR/PINRO Joint Report Series, No. 3/2011
- Årthun M, Ingvaldsen RB, Smedsrud LH, Schrum C (2011) Dense water formation and circulation in the Barents Sea. *Deep-Sea Res I* 58:801–817
- Aschan M, Fossheim M, Greenacre M, Primicerio R (2013) Change in fish community structure in the Barents Sea. *PLoS ONE* 8:e62748. doi:10.1371/journal.pone.0062748
- Bergstad OA, Bjelland O, Gordon JDM (1999) Fish communities on the slope of the eastern Norwegian Sea. *Sarsia* 84:67–78
- Beszczynzka-Möller A, Fahrbach E, Schauer U, Hansen E (2012) Variability in Atlantic water temperature and transport at the entrance to the Arctic Ocean, 1997–2010. *ICES J Mar Sci* 69:852–863
- Blindheim J (1989) Cascading of Barents Sea bottom water into the Norwegian Sea. *Rapports et procès-verbaux des réunions. Conseil permanent international pour l'Exploration de la mer* 188:49–58
- Bochkov YA (1982) Water temperature in the 0–200 m layer in the kola-meridian section in the Barents Sea, 1900–1981. *Sbornik Nauchnyx Trudov PINRO* 46:113–122 (in Russian)
- Boitsov VD, Drevetnyak KV, Seliverstova EI, Smirnov OV, Tereschchenko VV, Ushakov NG, Shevelev MS, Shleinik VN (2004) History of Russian fishery investigations and fisheries of biological resources of Spitsbergen archipelago. In: Shevelev MS (ed) *Investigations by PINRO in the Spitsbergen archipelago area*. PINRO Press, Murmansk pp 28–36 (in Russian)
- Burgos GE (1989) The bottom fish community of the Barents Sea in the winters 1984 to 1987. Dissertation, University of Bergen
- Byrkjedal I, Høines Å (2007) Distribution of demersal fish in the south-western Barents Sea. *Polar Res* 26:135–151
- Christensen JS, Reist JD (2013) Fishes. In: Meltote H (ed) *Arctic biodiversity assessment status and trends in Arctic biodiversity*. Akureyri, Iceland, pp 192–245
- Cottier FR, Nilsen F, Inall ME, Gerland S, Tverberg V, Svendsen H (2007) Wintertime warming of an Arctic shelf in response to large-scale atmospheric circulation. *Geophys Res Lett* 34:L10607
- Dolgov AV (2004) Non-target fishes and skates. In: Shevelev MS (ed) *Investigations by PINRO in the Spitsbergen archipelago area*. PINRO Press, Murmansk, pp 229–274 (in Russian)
- Dolgov AV, Johannesen E, Høines Å (2011) Main species and ecological importance. In: Jakobsen T, Ozhigin VK (eds) *The Barents Sea - ecosystem, resources and management. Half a century of Russian-Norwegian cooperation*. Tapir Academic Press, Trondheim, pp 193–200
- Dray S, Dufour A-B, Thioulouse J (2016) Analysis of ecological data: exploratory and euclidean methods in environmental sciences. <https://cran.r-project.org/web/packages/ade4/ade4.pdf>. Accessed 20 June 2017
- Eriksen E (ed) (2012) Survey report from the joint Norwegian/Russian ecosystem survey in the Barents Sea August–October 2012. IMR/PINRO Joint Report Series, No. 2/2012
- Eriksen E (ed) (2014) Survey report from the joint Norwegian/Russian ecosystem survey in the Barents Sea and adjacent waters, August–October 2014. IMR/PINRO Joint Report Series, No. 1/2015
- Fer I, Drinkwater K (2014) Mixing in the Barents Sea Polar Front near Hopen in spring. *J Mar Syst* 130:206–218
- Fossheim M, Nilssen EM, Aschan M (2006) Fish assemblages in the Barents Sea. *Mar Biol Res* 2:260–269
- Fossheim M, Primicerio R, Johannesen E, Ingvaldsen RB, Aschan M, Dolgov AV (2015) Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature Clim Change* 5:673–677
- Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol Lett* 4:379–391
- Greenacre M (2013) The contributions of rare objects in correspondence analysis. *Ecology* 94:241–249
- Haug T, Bogstad B, Chierici M et al (2017) Future harvest of living resources in the Arctic Ocean north of the Nordic and Barents Seas: a review of possibilities and constraints. *Fish Res* 188:38–57

- ICES (2014) Report from NAFO/ICES Pandalus Assessment Working Group Meeting, 83 pp. ICES CM 2014/ACOM:14
- Ingvaldsen RB (2005) Width of the North Cape current and location of the Polar Front in the western Barents Sea. *Geophys Res Lett* 32:L16603
- Johannessen E, Høines ÅS, Dolgov AV, Fossheim M (2012) Demersal fish assemblages and spatial diversity patterns in the Arctic-Atlantic transition zone in the Barents Sea. *PLoS ONE* 7:e34924. doi:10.1371/journal.pone.0034924
- Johannessen E, Jørgensen LL, Fossheim M, Primicerio Raul, Greenacre Michael, Lubin P, Dolgov AD, Ingvaldsen RB, Anisimova N, Manushyn I (2016) Joint response to environmental gradients by Barents Sea mega-benthos and demersal fish communities. *Polar Biol*. doi:10.1007/s00300-016-1946-6
- Johannessen E, Mørk HL, Korsbrekke K et al. (2017) Arctic fishes in the Barents Sea 2004-2015: Changes in abundance and distribution. *IMR/PINRO Joint Report Series*, No.1/2017
- Jongman RHG, ter Braak CJF, van Tongeren OFR (1995) Data analysis in community and landscape ecology, 2nd edn. Cambridge University Press, Cambridge, p 292
- Jørgensen LL, Ljubin P, Skjoldal HR, Ingvaldsen RB, Anisimova N, Manushyn I (2015) Distribution of benthic megafauna in the Barents Sea: baseline for an ecosystem approach to management. *ICES J Mar Sci* 72:595–613
- Kortsch S, Primicerio R, Fossheim M, Dolgov A, Aschan M (2015) Climate change alters the structure of Arctic marine food webs due to poleward shifts of boreal generalists. *Proc R Soc B* 282:20151546
- Lien VS, Ådlandsvik B (2014) Bottom water formation as a primer for spring-blooms on Spitsbergenbanken? *J Mar Syst* 130:241–247
- Lien VS, Vikebø FB, Skagseth Ø (2013a) One mechanism contributing to co-variability of the Atlantic inflow branches to the Arctic. *Nat Commun* 4:1488
- Lien VS, Gusdal Y, Albreten J, Melsom A, Vikebø FB (2013b) Evaluation of a Nordic Seas 4 km numerical ocean model archive. *Fisken og Havet* 7
- Lien VS, Gusdal Y, Vikebø FB (2014) Along-shelf hydrographic anomalies in the Nordic Seas (1960-2011): locally generated or advective signals? *Ocean Dyn* 64:1047–1059
- Lind S, Ingvaldsen RB (2012) Variability and impacts of Atlantic Water entering the Barents Sea from the north. *Deep-Sea Res I* 62:70–88
- Loeng H (1991) Features of the physical oceanographic conditions of the Barents Sea. *Polar Res* 10:5–18
- Mecklenburg CW, Møller PR, Steinke D (2011) Biodiversity of arctic marine fishes: taxonomy and zoogeography. *Marl Biodivers* 41:109–140
- Nilsen F, Cottier F, Skogseth R, Mattsson S (2008) Fjord-shelf exchanges controlled by ice and brine production: the interannual variation of Atlantic Water in Isfjorden, Svalbard. *Cont Shelf Res* 28:1838–1853
- Oksanen J, Guillaume Blanchet F, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2016) Ordination methods, diversity analysis and other functions for community and vegetation ecologists. <https://cran.r-project.org/web/packages/vegan/index.html>. Accessed 20 June 2017
- Onarheim IH, Smedsrud LH, Ingvaldsen RB, Nilsen F (2014) Loss of sea ice during winter north of Svalbard. *Tellus A* 66:23933
- Onarheim IH, Eldevik T, Årthun M, Ingvaldsen RB, Smedsrud LH (2015) Skillful prediction of Barents Sea ice cover. *Geophys Res Lett* 42:5364–5371
- Ozhigin V, Ingvaldsen RB, Loeng H, Boitsov V, Karsakov A (2011) Introduction to the Barents Sea. In: Jakobsen T, Ozhigin V (eds) *The Barents Sea ecosystem, resources, management. Half a century of Russian-Norwegian cooperation*. Tapir Academic Press, Trondheim, pp 39–76
- Parsons AR, Bourke RH, Muench RD, Chiu CS, Lynch JF, Miller JH, Plueddemann AJ, Pawlowicz R (1996) The Barents Sea Polar Front in summer. *J Geophys Res* 101:14201–14221
- Pfirman SL, Bauch D, Gammelsrød T (1994) The northern Barents Sea: water mass distribution and modification. In: Johannessen OM et al (eds) *The polar oceans and their role in shaping the global environment*. American Geophysical Union, Washington DC, pp 77–94
- Pnyushkov AV, Polyakov IV, Ivanov VV, Kikuchi T (2013) Structure of the Fram Strait branch of the boundary current in the Eurasian Basin of the Arctic Ocean. *Polar Sci* 7:53–71
- Polyakov IV, Bhatt US, Walsh JE, Abrahamsen EP, Pnyushkov AV, Wassmann PF (2013) Recent oceanic changes in the Arctic in context of long-term observations. *Ecol Appl* 23:1745–1764
- Prokhorova T (ed) (2013) Survey report from the joint Norwegian/Russian ecosystem survey in the Barents Sea and adjacent waters, August-October 2013. *IMR/PINRO Joint Report Series*, No. 4/2013
- R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>. Accessed 20 June 2017
- Sarynina RN (1969) Conditions of origin of cold deep-sea waters in the Bear Island Channel. Paper presented at the Symposium on Physical Variability in the North Atlantic. 23-27 September, Dublin, Ireland
- Shapiro GI, Hill AE (2003) The alternative density structures of cold/saltwater pools on a sloping bottom: the role of friction. *J Phys Oceanogr* 33:390–406
- Skagseth Ø (2008) Recirculation of Atlantic Water in the western Barents Sea. *Geophys Res Lett* 35:L11606
- Skagseth Ø, Furevik T, Ingvaldsen RB, Loeng H, Mork KA, Orvik KA, Ozhigin V (2008) Volume and heat transports to the Arctic Ocean via the Norwegian and Barents Seas. In: Dickson R, Meincke J, Rhines P (eds) *Arctic Subarctic ocean fluxes: defining the role of the Northern Seas in climate*. Springer, New York, pp 45–64
- Smirnov OV, Dolgov AV, Guzenko VV, Lepesevich YuM, Ozerov YuB (2000) New data on hydrological regime and ichthyofauna of the archipelagos Spitsbergen and Franz Josef Land. In: *Materials of reporting session of the PINRO Scientific council on results of investigations from 1998 to 1999. Part 1*. PINRO Press, Murmansk, pp 79-92 (in Russian)
- Spielhagen RF, Werner K, Sørensen SA, Zamelczyk K, Kandiano E, Budeus G, Husum K, Marchitto TM, Hald M (2011) Enhanced Modern Heat Transfer to the Arctic by Warm Atlantic Water. *Science* 331:450–453
- Tereschenko VV (1997) Seasonal and year-to-year variation in temperature and salinity of the main currents along the Kola section in the Barents Sea. *Knipovich Polar Research Institute of Marine Fisheries and Oceanography, Murmansk (In Russian)*
- Townhill BL, Maxwell D, Engelhard GH, Simpson SD, Pinnegar JK (2015) Historical arctic logbooks provide insights into past diets and climatic responses of cod. *PLoS ONE* 10(9):e0135418. doi:10.1371/journal.pone.0135418
- Walczowski W, Piechura J, Goszczko I, Wieczorek P (2012) Changes in Atlantic water properties: an important factor in the European Arctic marine climate. *ICES J Mar Sci* 69:864–869
- Wassmann P, Kosobokova KN, Slagstad D, Drinkwater KF, Hopcroft RR, Moore SE, Ellingsen I, Nelson RJ, Carmack E, Popova E, Berge J (2015) The contiguous domains of Arctic Ocean advection: trails of life and death. *Prog Oceanogr* 139:42–65
- Wienerroither R, Johannessen E, Dolgov A, Byrkjedal I, Bjelland O, Drevetnyak K, Eriksen KB, Høines Å, Langhelle G, Langøy H,

Prokhorova T, Prozorkevich D, Wenneck T (2011) Atlas of the Barents Sea Fishes. IMR/PINRO Joint Report Series 1/2011
Wienerroither R, Johannesen E, Dolgov AV, Byrkjedal I, Aglen A, Bjelland O, Drevetnyak K, Eriksen, KB, Høines Å, Langhelle G,

Langøy H, Murashko P, Prokhorova T, Prozorkevich D, Smirnov O, Wenneck T (2013) Atlas of the Barents Sea Fishes based on winter survey data. IMR/PINRO Joint Report Series 2/2013