

Identification of fish communities in the Barents Sea: Is there a faunal discontinuity across the Polar Front?

MARIA FOSSHEIM & EINAR M. NILSSEN

(Norwegian College of Fishery Science, University of Tromsø, N-9037 Tromsø, Norway. Email: mariaf@nfh.uit.no)

Abstract

Fish species inhabiting the Barents Sea display great seasonal and between-year variation in abundance and distribution. This study describes the assemblages and distributions of fish species in the south-western part of the Barents Sea which includes the Polar front. The area has an unpredictable environment due to variable inflow of Atlantic water and assemblages and distributions of fish species differ between Arctic and Atlantic water masses. These assemblages can be identified as distinct groups corresponding to the different environments. In the period 1997 – 1999, 57 fish species and shrimp were identified and 32 species/species groups were used in the statistical analyses. Cluster and Correspondence analyses (CA) showed that the fish community consists of four different assemblages: A Northern, a Southern, a Deep and a Central group. In the Northern assemblage, species composition and spatial distribution varied least. The Central assemblage was the most variable. The Northern group included Polar cod, Atlantic poacher, spotted snake blenny and two species from the sculpin family. The Southern group included haddock and Norway pout. The Deep group included northern wolffish and long rough dab. Temperature explained 22% of the variation in the species data, and depth 12% of the variation. The assemblages are coherent with previous zoogeographic studies from the Barents Sea.

Key Words: zoogeography, correspondence analysis, assemblages, distributions, unpredictable environment

Introduction

The Barents Sea is a highly productive ecosystem and an important nursery and nourishment area for several important commercial and non-commercial fish stocks. Great season and between-year variation in abundance and distribution of fish species have been observed (Loeng, 1989; Murawski, 1993; Nilssen and Hopkins, 1992; Shepherd *et al.*, 1984; Shevelev *et al.*, 1987). A comprehension of this dynamic is a matter of necessity for a sustainable development of the area. The commercial fish species have hitherto caught most attention, especially cod (*Gadus morhua*), herring (*Clupea harengus*) and capelin (*Mallotus villosus*), but also haddock (*Melanogrammus aeglefinus*), redfish (*Sebastes marinus* and *S. mentella*), Greenland halibut (*Reinhardtius hippoglossoides*) and to a limited extent Polar cod (*Boregadus saida*) (Loeng, 1989; Nakken, 1998; Shevelev *et al.*, 1987). The non-commercial fish stocks can be equally important from an ecological point of view, either as prey for commercial species or as indicators of the environment (Horn, 1980). The biology of non-commercial species are less known and a zoogeographic study that addresses the species assemblages and distributions while including these species, may give an indication of the extent and significance of this ignorance.

Exploitation of most marine resources is intrinsically of multispecies nature and it is therefore important to know whether some groups of species can be considered ecological entities comprising the same response to the environmental regime (Burgos, 1989; Overholtz and Tyler, 1985; Tyler *et al.*, 1982). If different fish communities can be identified in the Barents Sea this information may help the authorities in monitoring and managing the area. Surveys are costly and labour-intensive and by identifying distinct assemblages of species and the distribution of these assemblages one might be able to reduce the number of stations on surveys and thus minimise costs, or in practicality get more research for a limited amount of money (Weslawski and Kwasniewski, 1983). Identifying assemblages of species that can be managed adaptively as similar entities of production has also been suggested to alleviate overfishing in the trawl fishery (Jay, 1996; Tyler *et al.*, 1982).

To manage such ecological entities they need to be stable (in the sense of ‘resilience’ used by Grimm and Wissel (1997)). Especially the assemblages need to consist mainly of the same species between years even if their joint geographical distribution varies considerably. It is also important to know where faunal discontinuity between assemblages arise and off course why. In the Barents Sea it is expected that a faunal discontinuity area will be concurrent with the position of the Polar Front since it is the major transition area of the physical environment (Fig. 1) (Loeng, 1991; Loeng *et al.*, 1997).

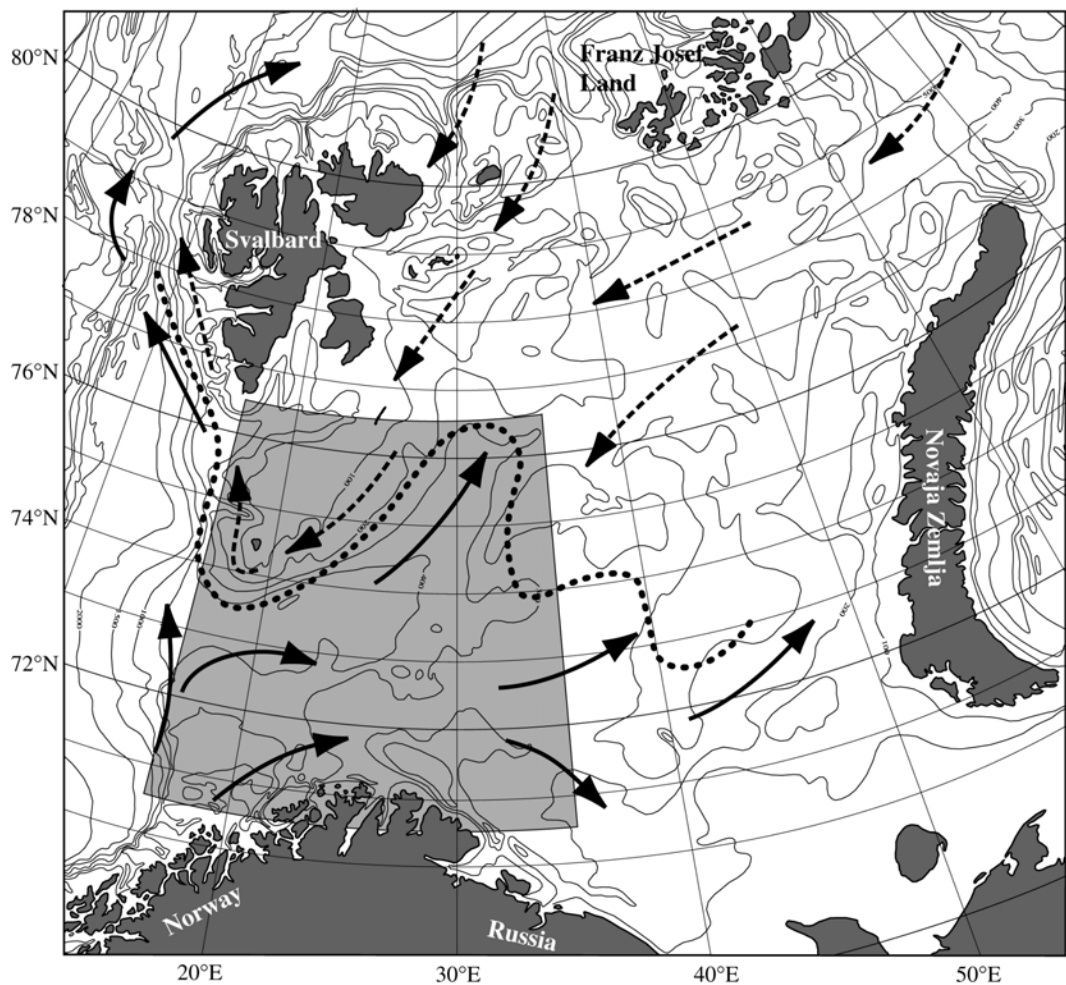


Fig. 1 The Barents Sea with main surface currents. Atlantic currents (—>), Arctic currents (--->) and the mean position of the Polar Front (•••). The study area is indicated by the grey square.

In a zoogeographical analysis of the Barents Sea fauna Zenkevich (1956) demonstrated three geographical areas with different environmental properties. (i) The main, central part of the sea is considered a subarctic area of the Arctic region and (ii) the south-westernmost part of the sea is a section receiving most of the Atlantic heat with the bottom water temperature being above +1°C and the fauna belonging to the boreal type. (iii) The northernmost part of the sea is characterised by a severe temperature regime and drift ice during a lengthy period and is considered a deep Arctic area of the Arctic region. Ekman (1953) equally classified the fish fauna into four zoogeographical groups: Arctic, Arctic-Boreal, Boreal and warmwater-Boreal (not included by, but south of the area described by Zenkevich (1956)).

Since the middle of the 20th century more data on several species have emerged and the computer has offered an important tool in exploring community data of multivariable nature. Multivariate methods such as cluster analysis and ordination has proved very helpful in exploring patterns in large data sets from community sampling (Farina *et al.*, 1997; Gaertner *et al.*, 1998; Gomes *et al.*, 1995; Greenstreet and Hall, 1996; Jacob *et al.*, 1998; Ungaro *et al.*, 1998). Ordination is also able to explore complex environmental gradients in an intelligible way. Burgos (1989) uses cluster analysis and ordination to explore the fish community of the southern part of the Barents Sea, but does not include the area of the Polar Front. Our study area comprises the Polar Front and the data set includes both commercial species, previously explored by (Nilssen and Hopkins, 1992), as well as non-commercial species.

Our main objectives are thus:

- 1) Can the fish community in the south-western Barents Sea be divided into different assemblages?
- 2) Is there a faunal discontinuity across the Polar Front?
- 3) Are the assemblages stable?
- 4) Can this pattern be explained by abiotic factors such as temperature and different watermasses with certain characteristics?
- 5) Can the assemblages be considered entities suitable for management?

Materials and methods

Data on fish assemblages and distributions were collected during three surveys in the south-western Barents Sea in spring 1997 – 1999 (Fig. 1). The area corresponds to grids ranging from 70°35'N to 76°24'N and 16°52'E to 35°36'N and varies somewhat between the years. Depth varied between 167 to 495 meters. Data was collected with a bottom trawl at 3 knots and the fishing distance was 1 nautical mile. The trawl is a modified commercial shrimp trawl (Campelen Super 2000) adjusted for scientific purposes (Aschan and Sunnanå, 1997). Total number of used trawl hauls ended 317 stations corresponding to 101 stations in 1997, 116 stations in 1998 and 100 stations in 1999.

The main purpose of the surveys was to map biomass and distribution of shrimp (*Pandalus borealis*), but all bycatch of fish were species identified, counted and weight measured. We identified 57 species of fish belonging to 19 families and one species of shrimp (Table 1). Due to uncertain identification some species were merged in groups of lowest taxonomic level. Rare species (less than six individuals in total or represented on less than five stations each year) were excluded from the analysis because they represented less than 5% of the station catch (Høines *et al.*, 1998). We ended with 32 species/species groups in the final analyses (Table 1).

Abundance data was standardised to 20 min trawl hauls (or 1 nautical mile) when necessary and $\log_{10}(a+1)$ - transformed prior to cluster and correspondence analyses with the purpose of downscaling very abundant species and reducing skewness (ter Braak, 1997).

Table 1 Species identified in the south-western Barents Sea in spring 1997 – 1999 (n = 317 stations). += Species identified all three years. * = Species excluded from statistical analyses due to low abundance. spp = several species.

Family	Scientific name	Abbreviation	Common name	
Anarhichadidae	<i>Anarhichas denticulatus</i>	<i>An de</i>	Northern wolffish	+
Anarhichadidae	<i>Anarhichas lupus</i>	<i>An lu</i>	Atlantic wolffish	
Anarhichadidae	<i>Anarhichas minor</i>	<i>An mi</i>	Spotted wolffish	+
Agonidae	<i>Leptagonus decagonus</i>	<i>Le de</i>	Atlantic poacher	+
Argentinidae	<i>Argentina silus</i>	<i>Ar si</i>	Greater argentine	*
Argentinidae	<i>Argentina sphyraena</i>	<i>Ar sp</i>	Lesser argentine	*
Chimaeridae	<i>Chimaera monstrosa</i>	<i>Ch mo</i>	Rabbit fish	*
Clupeidae	<i>Clupea harengus</i>	<i>Cl ha</i>	Herring	+
Cottidae	<i>Arctiellus atlanticus</i>	<i>Ar at</i>	Atlantic hookear sculpin	+
Cottidae	<i>Myoxocephalus scorpius</i>	<i>My sc</i>	Shorthorn sculpin	*
Cottidae	<i>Triglops murrayi</i>	<i>Tr spp</i>	Moustache sculpin	+
Cottidae	<i>Triglops pingelii</i>	<i>Tr spp</i>	Ribbed sculpin	+
Cottunculidae	<i>Cottunculus microps</i>	<i>Co mi</i>	Polar sculpin	*
Cyclopteridae	<i>Careproctus reinhardti</i>	<i>Cy spp</i>	Longfin seasnail	+
Cyclopteridae	<i>Cyclopterus lumpus</i>	<i>Cy lu</i>	Lumpsucker	+
Cyclopteridae	<i>Eumicrotremus spinosus</i>	<i>Eu sp</i>	Atlantic spiny lumpsucker	*
Cyclopteridae	<i>Liparis fabricii</i>	<i>Cy spp</i>	Gelatinous seasnail	+
Cyclopteridae	<i>Paraliparis bathybi</i>	<i>Pa ba</i>	Black seasnail	
Gadidae	<i>Boreogadus saida</i>	<i>Bo sa</i>	Polar cod	+
Gadidae	<i>Brosme brosme</i>	<i>Br br</i>	Tusk	*
Gadidae	<i>Ciliata mustela</i>	<i>Ci mu</i>	Fivebeard rockling	*
Gadidae	<i>Gadiculus argenteus thori</i>	<i>Ga at</i>	Silvery pout	*
Gadidae	<i>Gadus morhua</i>	<i>Ga mo</i>	Cod	+
Gadidae	<i>Melanogrammus aeglefinus</i>	<i>Me ae</i>	Haddock	+
Gadidae	<i>Micromesistius poutassou</i>	<i>Mi po</i>	Blue whiting	+
Gadidae	<i>Pollachius virens</i>	<i>Po vi</i>	Saithe	+ *
Gadidae	<i>Trisopterus esmarkii</i>	<i>Tr es</i>	Norway pout	+
Macrouridae	<i>Macrourus berglax</i>	<i>Ma be</i>	Onion-eye grenadier	*
Myctophidae	<i>Benthoosema glaciale</i>	<i>Be gl</i>	Glacier lanternfish	+
Osmeridae	<i>Mallotus villosus</i>	<i>Ma vi</i>	Capelin	+
Pandalidae	<i>Pandalus borealis</i>	<i>Pa bo</i>	Shrimp	+
Paralepididae	<i>Notolepis rissoi krøyeri</i>	<i>No rk</i>	White barracudina	+
Pleuronectidae	<i>Glyptocephalus cynoglossus</i>	<i>Gl cy</i>	Witch flounder	*
Pleuronectidae	<i>Hippoglossoides platessoides</i>	<i>Hi pl</i>	Long rough dab	+
Pleuronectidae	<i>Reinhardtius hippoglossoides</i>	<i>Re hi</i>	Greenland halibut	+
Rajidae	<i>Breviraja spinicauda</i>	<i>Br sp</i>	Spinetail ray	*
Rajidae	<i>Raja batis</i>	<i>Ra ba</i>	Blue skate	*
Rajidae	<i>Raja clavata</i>	<i>Ra cl</i>	Thornback ray	*
Rajidae	<i>Raja fyllae</i>	<i>Ra fy</i>	Round ray	*
Rajidae	<i>Raja hyperborea</i>	<i>Ra hy</i>	Arctic skate	*
Rajidae	<i>Raja radiata</i>	<i>Ra ra</i>	Thorny skate	+
Scorpaenidae	<i>Sebastes marinus</i>	<i>Se ma</i>	Golden redfish	+
Scorpaenidae	<i>Sebastes mentella</i>	<i>Se me</i>	Deepwater redfish	+
Scorpaenidae	<i>Sebastes viviparus</i>	<i>Se vi</i>	Norway redfish	*
Scorpaenidae	<i>Sebastes spp</i>	<i>Se spp</i>	Redfish (spp)	
Sternoptychidae	<i>Maurolicus muelleri</i>	<i>Ma mu</i>	Pearlsides	*
Stichaeidae	<i>Leptoclinus maculatus</i>	<i>Le ma</i>	Spotted snake blenny	+
Stichaeidae	<i>Lumpenus lampraetaeformis</i>	<i>Lu la</i>	Snake blenny	+
Zoarcidae	<i>Gymnelus retrodorsalis</i>	<i>Gy re</i>	Eelpout sp. 1	*
Zoarcidae	<i>Lycenchelys kolthoffi</i>	<i>Ly ko</i>	Eelpout sp. 2	*
Zoarcidae	<i>Lycenchelys sarsii</i>	<i>Ly sa</i>	Sars' wolf eel	*
Zoarcidae	<i>Lycodes esmarkii</i>	<i>Ly es</i>	Greater eelpout	+
Zoarcidae	<i>Lycodes eudipleurostictus</i>	<i>Ly eu</i>	Doubleline eelpout	+

Zoarcidae	<i>Lycodes frigidus</i>	<i>Ly fr</i>	Eelpout sp. 3	*
Zoarcidae	<i>Lycodes pallidus</i>	<i>Ly pa</i>	Pale eelpout	
Zoarcidae	<i>Lycodes reticulatus</i>	<i>Ly re</i>	Arctic eelpout	
Zoarcidae	<i>Lycodes rossi</i>	<i>Ly ro</i>	Threespot eelpout	*
Zoarcidae	<i>Lycodes seminudus</i>	<i>Ly se</i>	Longear eelpout	
Zoarcidae	<i>Lycodes spp</i>	<i>Ly spp</i>	Eelpout (spp)	
Zoarcidae	<i>Lycodes vahlii</i>	<i>Ly va</i>	Vahl's eelpout	+

Cluster analysis was used to give information on the concurrence of species and a hierarchical method was chosen, exploring the results as a dendrogram. The cluster analysis was based on a Spearman ranking correlation matrix and Ward's method was chosen to minimise the variance within clusters. Groupings of species with similar distribution and their correspondence to some environmental parameters were explored by correspondence analysis (CA) (Greenacre, 1984). CA 'extracts' the ordination axes from the species data alone. Species appearing close to one another in the ordination diagram has a more similar distribution than species further apart. The environmental variables are added afterwards and are represented as arrows that point in the direction of maximum change. The fraction of variance accounted for by the regression indicates whether the environmental variable is sufficient to predict the variation in species composition that is represented by the first ordination axis (ter Braak, 1997).

Results

The cluster analyses resulted in a four-group pattern where especially the species known to have a northern distribution were separated from the remaining species as a distinct group (Fig. 2). Also species known to have southern, deep and central distributions seemed to form groups but they were less distinct than the northern group. The groupings were somewhat variable between the three years, but conformed to a clear pattern.

The results from the correspondence analyses of the species – environment data in axes I and II are presented in Fig. 3 and shows that latitude is negatively correlated with temperature and the major determinants of the first axes, while depth is the major determinant of the second axes. Approximately 40 % of the variance in the species distribution is explained by axes I and II, which is adequate for the analyses to have explanatory power. The species – environment correlations for axes I and II are strong (>0.7 , Table 2) (Fowler *et al.*, 1998).

Table 2 Percentage of species distribution explained by four axes in Correspondence analyses (CA) and correlations between species distribution and the environment. Only the two first axes are considered adequate for visual presentation (see Fig. 3).

Year	Axis (Percentage explained)				Species-environment correlation				Figure 3 (Axis I and II)
	1	2	3	4	1	2	3	4	
1997	28.0	14.3	8.5	6.3	0.94	0.76	0.54	0.50	top
1998	26.2	14.5	6.5	5.5	0.93	0.78	0.61	0.33	middle
1999	22.3	12.4	11.1	6.6	0.90	0.73	0.55	0.25	bottom

Species with a northern, southern and deep distribution can be identified as distinct groups in the correspondence analysis corresponding to the same groups as in the cluster analyses. The grouping of species is largely sustained and especially the northern group is persistent, with the same species assemblage (for species occurring all three years) throughout the whole three-year period. This group is located towards the northeast of the study area (positively correlated with the latitude and longitude vectors) and is negatively correlated with the temperature vector. The Southern and Deep group show positive correlations with the latitude and depth vectors, respectively.

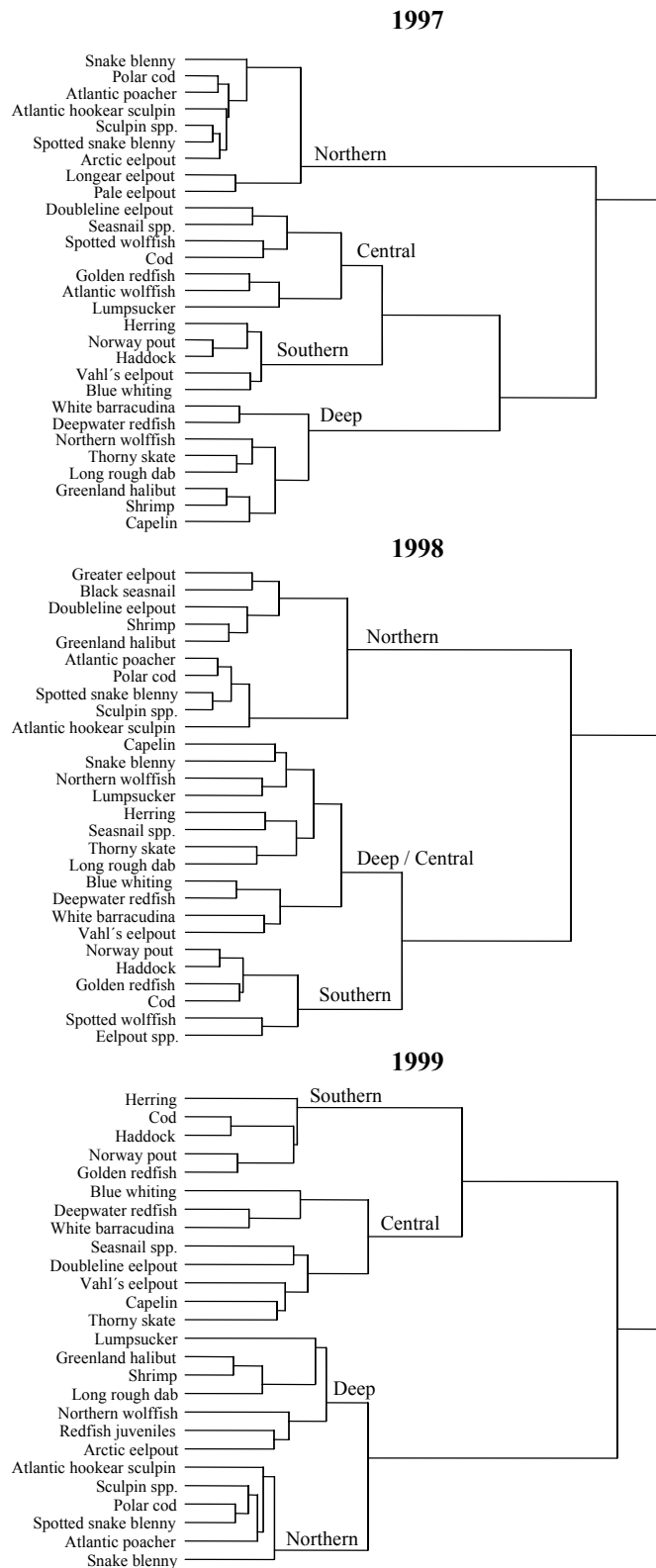


Fig. 2 Species data from cruises in the south-western Barents Sea in spring 1997, 1998 and 1999. Hierarchical cluster analyses (using Ward's method and based on a Spearman ranking correlation matrix) by grouping species with similar distributions. (n=91 (1997), n=116 (1998) and n=101 (1999) stations.) (Sculpin spp. = *Triglops murrayi* + *T. pingelii*, Seasnail spp. = *Careproctus reinhardtii* + *Liparis fabricii*, Eelpout spp. = *Lycodes* spp., Redfish juveniles = Juveniles of (*Sebastes marinus* + *S. mentella*).

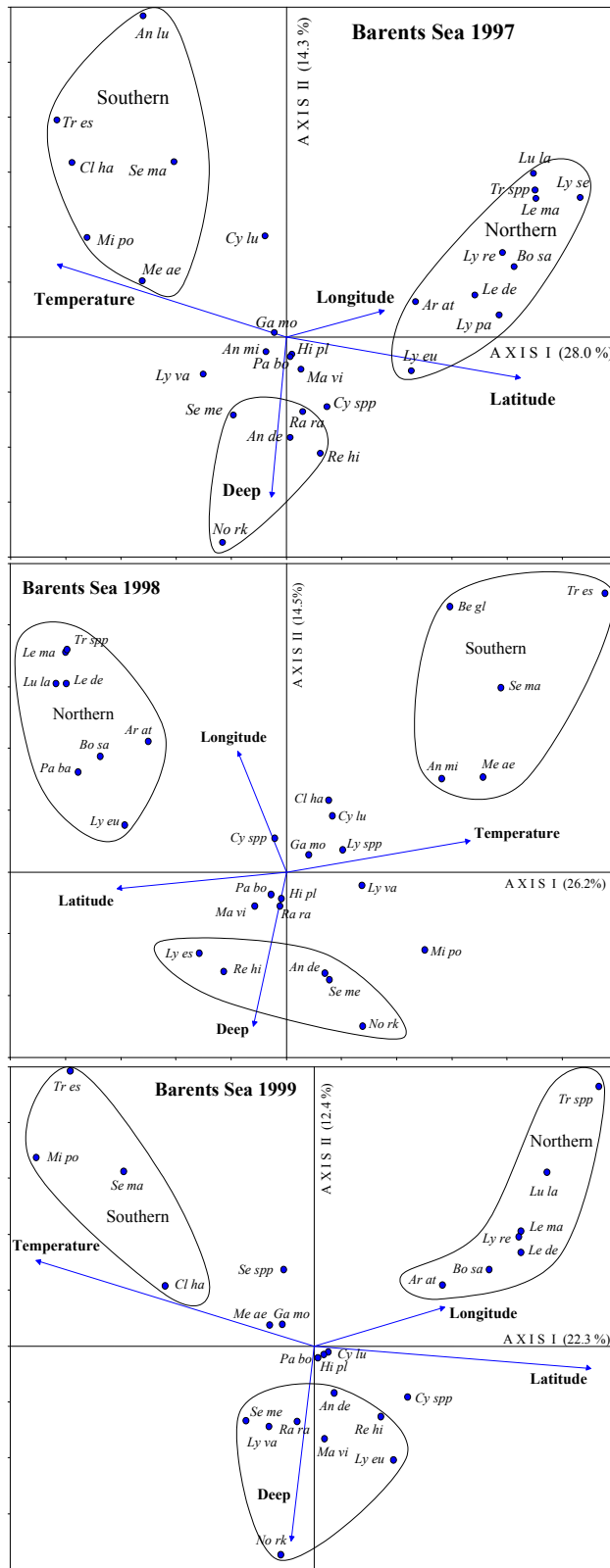


Fig. 3 Data on species assemblages and distribution from the south-western Barents Sea in spring 1997 – 1999. Correspondence analysis (CA) ordination plot of axis I and II relating abundance variations in species to environment (temperature, depth, latitude and longitude). (n = 101 (1997), 116 (1998) and 100 (1999) stations). Scientific abbreviations explained in Table 1.

Discussion

Given that there are some subjectivity in the assemblage analyses, e.g. where to conclude groups in cluster analysis and which species to include in the correspondence analysis groups, consistency among different approaches would enhance credibility. Species occurring in a cluster group usually fell within the same group in the correspondence analysis. This indicates that the multivariate methods produced results consistent with the obvious major distribution patterns. The resulted groups also correspond well to the historical evidence and are consistent with distributions of single species, for gadoids (Bergstad *et al.*, 1987), and several non-target fish species (including eelpouts, blennies, sculpins, snailfishes and others) (Dolgov, 1994).

Species that are commonly known to inhabit a certain area and to co-occur with other known species seem to be reflected in the assemblages produced by both the cluster and correspondence analyses. A few consequences of the analyses are nevertheless worth mentioning. Assemblages are determined by i) species that tend to co-occur primarily together, and not by widespread species that co-occur with many other species and ii) by species that tend to co-occur at unusually high frequencies, even if they are not particularly abundant overall. Rare species may be given more weight since it is the covariation with other species that are considered important and not abundance. Core species may actually be less abundant than other species. Discriminate analysis (not presented) showed that the core species for the different assemblages fits this theory well, giving Norway pout (*Trisopterus esmarkii*) as the core species for the Southern group and Atlantic hookear sculpin (*Artediellus atlanticus*) for the Northern group (Fossheim, 2000).

The Polar Front may represent a transitional area with faunal discontinuity since many species seem to be restricted to areas north or south of this area. On the contrary several species seem to be distributed both north and south of this area and may in fact constitute an assemblage by itself, then being the Central group in this study. The Central group is the most variable assemblage both in composition and distribution, which supports the anticipation of the Polar Front as a

transitional area. The Polar Front represents an area of high primary production and it is therefore expected that many species will take advantage of this larder.

Assemblages are fairly stable entities, their development and distribution may vary through time as species distributions and abundances fluctuate. (Mahon *et al.*, 1998). The data studied here are all from years considered relatively ‘warm’ years (Dickson *et al.*, 2000), and as such high productive years (Sakshaug, 1995). It might therefore be that assemblages from ‘cold’ years would have given assemblages with other species compositions, but we do not believe this to be the case. When our assemblages are compared with the zoogeographical grouping by Ekman (1953) and Burgos (1989) (Table 3), the consistency of assemblages seems substantiated because the different groupings can be recognised in the three different studies. Our Northern assemblage seems to be concurrent with Ekman’s (1953) Arctic group and Burgos’ (1989) East/arctic group and our Southern assemblage seems concurrent with the Boreal (Ekman, 1953) and Southern/boreal group (Burgos, 1989). One species exception is worth mentioning though; the capelin (*Mallotus villosus*) can not be classified as an arctic species in our study, a conclusion also reached by Nilssen and Hopkins (1992). Capelin is traditionally thought to be arctic (Dragesund and Gjøsæter, 1988; Ekman, 1953).

Table 3 Comparison of zoogeographical grouping of fish species in the Barents Sea by Ekman (1953), Burgos (1989) and Fossheim (2000). Only species that are found in two or three studies are included.

Species	Ekman (1953)	Burgos (1989)	Fossheim (2000)
Polar cod	Arctic	East (arctic)	Northern/arctic
Atlantic poacher	-	East (arctic)	Northern/arctic
Atlantic hookear sculpin	-	East (arctic)	Northern/arctic
Capelin	Arctic	-	Central
Snake blenny	Arctic-boreal	-	Northern/arctic
Seasnail spp.	Arctic-boreal	East (arctic)	Central
Long rough dab	Arctic-boreal	Central	Deep
Golden redfish	Boreal	Vest/Central	Southern/boreal
Cod	Boreal	Central	Southern/boreal
Haddock	Boreal	Central	Southern/boreal
Herring	Boreal	-	Southern/boreal
Saithe	Boreal	Vest/Central	-
Norway pout	-	Vest/Central	Southern/boreal
Greenland halibut	Boreal	Northeast	Deep
Deepwater redfish	Boreal	Northeast	Deep
Blue whiting	Warmwater-boreal	Vest/Central	-

The assemblages might be considered stable entities if they can be considered restricted according to different spatial scales. Burgos (1989) divided his assemblages according to an east-west axis while the assemblages in our study can be described according to a north-south axis. In addition we should expect a similar pattern to emerge along the depth axis, since species inhabiting cold areas in the north are known to submerge in deeper areas further south (Ekman, 1953). The Barents Sea is a neritic ocean with few depths below 500 meter, but if we compare our assemblages to the assemblages identified on the slope of the eastern Norwegian sea (Bergstad *et al.*, 1999), the deepest assemblages (Upper slope and Norwegian Sea Deepwater) includes many of the same species (e.g. eelpouts) as our Northern assemblage. Bergstad *et al.* (1999) also conclude that the temperature gradient seems to be a strong structuring force along the Norwegian Sea slope, as well as in the south-western Barents Sea (Burgos, 1989; Nilssen and Hopkins, 1992).

The water mass distribution and characteristics have a major influence on the production processes and the current patten largely determines the zoogeographical boundaries in the area (Bergstad *et al.*, 1987), but the assemblage and distribution patterns can not be solely explained by abiotic factors included in this study. Temperature explains 22% of the variation in the species data and depth 12 % of the variation (Fig. 3), but the data set lacks information on bottom topography as well as biotic information on primary production and important non-fish prey or predator organisms. Whether the assemblages represent biologically functional entities or merely consist of species with similar responses to environmental gradients can not be determined by this study, but the consistency of the assemblages suggest that monitoring and managing these entities might be justified.

Conclusions

- 1) This study shows that the fish community in the south-western Barents Sea can be divided into different assemblages.
- 2) The Polar Front probably represents a transitional area of faunal discontinuity.
- 3) The consistency of the assemblages through different approaches, including historical literature shows that the assemblages remain continuous through time and space.
- 4) The assemblage and distribution patterns can partly be explained by the measured environmental factors, but this study lacks important abiotic and biotic variables.
- 5) Monitoring and management of entities consisting of different assemblages might be justified.

This paper is in part based on my master thesis in resource biology at the Norwegian College of Fishery Science, University of Tromsø, December 2000.

Acknowledgement

I want to thank the Norwegian Institute of Fisheries and Aquaculture A/S for providing me with the data underlying this study and Eggvins fond for financial support during my master study.

References:

- Aschan, M. and Sunnanå, K. (1997). Evaluation of the Norwegian shrimp surveys conducted in the Barents Sea and the Svalbard area 1980-1997. *ICES C.M. 1997 Y:7*, 23.
- Bergstad, O. A., Bjelland, O. and Gordon, J. D. M. (1999). Fish communities on the slope of the eastern Norwegian Sea. *Sarsia* **84**, 67-78.
- Bergstad, O. A., Jørgensen, T. and Dragesund, O. (1987). Life history and ecology of the gadoid resources of the Barents Sea. *Fisheries Research* **5**, 119-161.
- Burgos, G. E. (1989). The bottom fish community of the Barents Sea in the winters 1984 to 1987. In *Department of fisheries biology*, pp. 76. Bergen: University of Bergen.
- Dickson, R. R., Osborn, T. J., Hurrell, J. W., Meincke, J., Blindheim, J., Adlandsvik, B., Vinje, T., Alekseev, G. and Maslowski, W. (2000). The Arctic Ocean response to the North Atlantic oscillation. *J. Clim.* **13**, 2671-2696.
- Dolgov, A. V. (1994). Some aspects of biology of non-target fish species in the Barents Sea. *ICES C.M. O:12*, 23.
- Dragesund, O. and Gjørseter, J. (1988). The Barents Sea. In *Continental Shelves*, vol. 27 (ed. H. Postma and J. J. Zijlstra), pp. 339-361. Amsterdam: Elsevier.
- Ekman, S. (1953). The boreal fauna of the North Atlantic. In *Zoogeography of the sea.*, pp. 100-141. London: Sidgwick & Jackson.
- Farina, A. C., Freire, J. and GonzalezGurriaran, E. (1997). Demersal fish assemblages in the Galician continental shelf and upper slope (NW Spain): Spatial structure and long-term changes. *Est. Coast. Shelf Sci.* **44**, 435-454.
- Fossheim, M. (2000). Sammensetting og fordeling av fisk i det sørvestlige Barentshavet i perioden 1997 - 1999. In *Norwegian College of Fishery Science*, pp. 54. Tromsø: University of Tromsø.
- Fowler, J., Cohen, L. and Jarvis, P. (1998). The strength and significance of a correlation. In *Practical statistics for field biology.*, pp. 132. West Sussex: John Wiley & Sons.
- Gaertner, J. C., Chessel, D. and Bertrand, J. (1998). Stability of spatial structures of demersal assemblages: a multitable approach. *Aquat. Liv. Res.* **11**, 75-85.
- Gomes, M. C., Haedrich, R. L. and Villagarcia, M. G. (1995). Spatial and temporal changes in the groundfish assemblages on the north-east Newfoundland/Labrador Shelf, north-west Atlantic, 1978-1991. *Fish. Ocean.* **4**, 85-101.
- Greenacre, M. J. (1984). Theory and applications of correspondence analysis., pp. 364. London: Academic Press Inc.
- Greenstreet, S. P. R. and Hall, S. J. (1996). Fishing and the ground-fish assemblage structure in the north-western North Sea: An analysis of long-term and spatial trends. *J. Anim. Ecol.* **65**, 577-598.
- Grimm, V. and Wissel, C. (1997). Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* **109**, 323-334.
- Horn, M. H. (1980). Diversity and ecological roles of noncommercial fishes in California marine habitats. *Calif. Coop. Oceanic Fish. Invest. Rep.* **21**, 37-47.
- Høines, A. S., Bergstad, O. A. and Albert, O. T. (1998). The structure and temporal stability of the fish community on a coastal bank utilized as a spawning ground by herring. *ICES J. Mar. Sci.* **55**, 271-288.
- Jacob, W., McClatchie, S., Probert, P. K. and Hurst, R. J. (1998). Demersal fish assemblages off southern New Zealand in relation to depth and temperature. *Deep Sea Res. I* **45**, 2119-2155.
- Jay, C. V. (1996). Distribution of bottom-trawl fish assemblages over the continental shelf and upper slope of the US west coast, 1977-1992. *Can. J. Fish. Aquat. Sci.* **53**, 1203-1225.

- Loeng, H. (1989). The influence of temperature on some fish population parameters in the Barents Sea. *J. Northw. Atl. Fish. Sci.* **9**, 103-113.
- Loeng, H. (1991). Features of the physical oceanographic conditions of the Barents Sea. *Pol. Res.* **10**, 5-18.
- Loeng, H., Ozhigin, V. and Ådlandsvik, B. (1997). Water fluxes through the Barents Sea. *ICES J. Mar. Sci.* **54**, 310-317.
- Mahon, R., Brown, S. K., Zwanenburg, K. C. T., Atkinson, D. B., Buja, K. R., Claffin, L., Howell, G. D., Monaco, M. E., O'Boyle, R. N. and Sinclair, M. (1998). Assemblages and biogeography of demersal fishes of the east coast of North America. *Can. J. Fish. Aquat. Sci.* **55**, 1704-1738.
- Murawski, S. A. (1993). Climate change and marine fish distributions: Forecasting from historical analogy. *Tran. Am. Fish. Soc.* **122**, 647-658.
- Nakken, O. (1998). Past, present and future exploitation and management of marine resources in the Barents Sea and adjacent areas. *Fish. Res.* **37**, 23-35.
- Nilssen, E. M. and Hopkins, C. C. E. (1992). Regional variability in fish-prawn communities and catches in the Barents Sea, and their relationship to the environment. *ICES mar. Sci. Symp.* **195**, 331-348.
- Overholtz, W. J. and Tyler, A. V. (1985). Long-term responses of the demersal fish assemblages of Georges Bank. *Fish. Bull.* **83**, 507-520.
- Sakshaug, E. (1995). A synopsis of the biomass distribution and energetics of the pelagic ecosystem of the Barents Sea. *ICES C.M. 1995/Mini:3*, 11.
- Shepherd, J. G., Pope, J. G. and Cousens, R. D. (1984). Variations in fish stocks and hypothesis concerning their links with climate. *Rapp. P.-v. Réun. Cons. int. Explor. Mer* **185**, 255-267.
- Shevelev, M. S., Tereshchenko, V. V. and Yaragina, N. A. (1987). Distribution and behaviour of demersal fishes in the Barents and Norwegian Seas, and the factors influencing them. In *The effect of oceanographic conditions on distribution and population dynamics of commercial fish stocks in the Barents Sea*. (ed. H. Loeng), pp. 181-190. Bergen: Inst. of Mar. Res.
- ter Braak, C. J. F. (1997). Ordination. In *Data analysis in community and landscape ecology*. (ed. R. H. G. Jongman, C. J. F. ter Braak and O. F. R. van Tongeren), pp. 91-173. Cambridge: Cambridge University Press.
- Tyler, A. V., Gabriel, W. L. and Overholtz, W. J. (1982). Adaptive management based on structure of fish assemblages of northern continental shelves. *Can. Spec. Publ. Fish. Aquat. Sci.* **59**, 149-156.
- Ungaro, N., Marano, G., Vlora, A. and Martino, M. (1998). Space-time variations of demersal fish assemblages in the South-Western Adriatic sea. *Life Envir.* **48**, 191-201.
- Weslawski, M. and Kwasniewski, S. (1983). Application of biological indicators for determination of the reach and origin of sea currents within the region of Spitsbergen. *Pol. Arch. Hydrobiol.* **30**, 189-197.
- Zenkevich, L. A. (1956). The Barents Sea. In *Seas of the USSR, their fauna and flora.*, pp. 240-273. Washington D. C.: U.S. Navy Hydrographic Office.