

Fish communities on the slope of the eastern Norwegian Sea

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Bottom trawl data from the depth interval 300-2050 m on the slope off Norway were analysed to study distribution of fish biomass and the associated species assemblages. It is hypothesised that the pronounced hydrographic front between the warm Atlantic Watermass and the cold Norwegian Sea Deep-water, combined with a declining food supply with depth and distance from the shelf, structure the assemblages on the continental slope of the eastern Norwegian Sea.

From a high level at the shelf edge and upper slope, the fish biomass declined abruptly at about 720 m when crossing the 0 °C-isotherm associated with the hydrographic front. Beneath the frontal zone, the fish biomass was only 11 % of that above it and decreased further with increasing depth. In upper slope waters, the fish biomass increased with increasing latitude.

Arctic species such as *Lycodes frigidus* and *Paraliparis bathybius* were dominant in the deep cold slope waters. The high fish biomass associated with the steep temperature gradient at 600-720 m was mainly attributable to a few large and/or abundant boreo-arctic species, i.e. Greenland halibut *Reinhardtius hippoglossoides*, redfishes *Sebastes mentella* and *S. marinus*, roughhead grenadier *Macrourus berglax*, and *Raja hyperborea*. In the shallower and warmer upper slope waters a species assemblage occurred which resembled that associated with adjacent deep shelf areas strongly influenced by the Atlantic Watermass.

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INTRODUCTION

This paper concerns demersal and benthopelagic fishes inhabiting the continental slope of the eastern Norwegian Sea, i.e. the slope off western Norway. Many fishes occurring in this area have been studied extensively in the past. Attention was focused on pelagic species that support commercial fisheries or may have a fishery potential, e.g. herring *Clupea harengus* L., blue whiting *Micromesistius poutassou*, and mackerel *Scomber scomber*, but also some demersal species such as Greenland halibut *Reinhardtius hippoglossoides* (Godø & Haug 1989, Albert & al. 1997), the redfishes *Sebastes* (Templeman 1959; Trout 1961; Nedreaas & Nævdal 1991), and the roughhead grenadier (*Macrourus berglax*) (Eliassen 1983 a, b; Eliassen & Jobling 1985; Eliassen & Falk-Petersen 1985; Savvatimsky 1985, 1986). Most previous work concerned single species and species-specific spatial and temporal distributions, population dynamics or biology. In this study, however, we focused on communities, i.e. the assemblages of fish species inhabiting different areas and habitats. The most compre-

hensive previous description of communities was the pioneer account of the Norwegian Sea fish fauna included in *The Depths of the Oceans* by Murray & Hjort (1912). A more recent fish assemblage study was conducted in 1974 by Bakken & al. (1975).

Our study formed an element of the research programme Mare Cognitum focusing on the ecosystems of the Nordic Seas. Our aim was to provide updated analyses of distribution patterns and community characteristics, not only to supplement existing knowledge on Norwegian Sea fishes but also to strengthen the basis of descriptive and analytical food-web studies conducted by other projects of the programme. We were interested in aspects such as species composition, integrity and spatial distribution of assemblages in relation to the physical environment, and abundance and diversity of the slope assemblages. An additional aim was to compare demersal fish community patterns in the Norwegian Sea with those in adjacent deep-water areas, particularly the slope waters south of the Scotland-Iceland ridges. Extensive community-orientated studies were conducted in these areas (Ehrich 1983; Rätz 1984; Gordon & Duncan

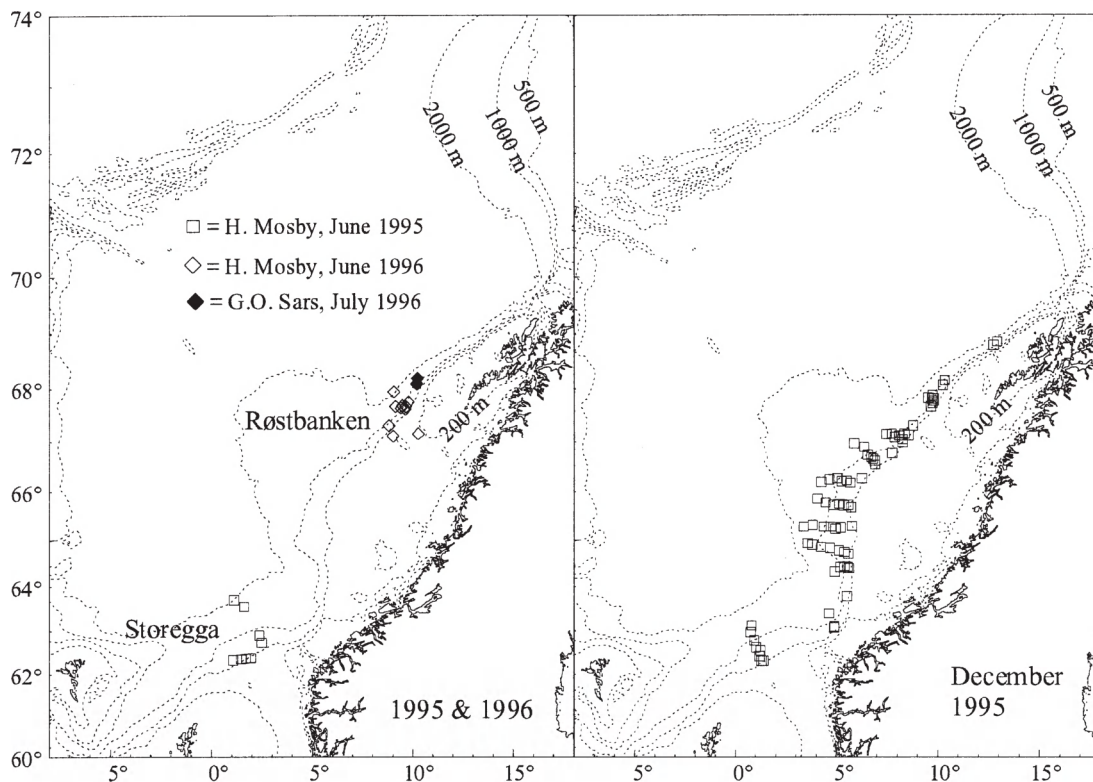


Fig. 1. The study area and locations of bottom trawls stations along the continental slope in 1995 and 1996.

1985; Gordon 1986; Mauchline 1986) and in other parts of the North Atlantic (see Haedrich & Merrett (1988) for an overview).

MATERIAL AND METHODS

SAMPLING

The primary source of data for analyses of species composition and distribution of demersal fishes on the slope were bottom trawl catches from two cruises on the RV *Håkon Mosby* in June of 1995 and 1996. Supplementary data, i.e. two trawl catches, were obtained from a collaborative cruise on the RV *G.O. Sars* in August 1996. Two localities, Storegga-Tampen at approx. 62°N, and Røstbanken at 67–68°N were sampled (Fig. 1) where the sampling effort was distributed within the depth range 430 to 2050 m. Because of rugged terrain and coral beds, it was difficult to locate trawlable areas, and several hauls were classified as unsuccessful and omitted from further analyses. Details on the 17 stations included in the analyses are given in Table 1.

Two different otter trawls were used (Table 1). The primary gear used by the RVs *Håkon Mosby* and *G.O. Sars* was the Campelen 1800 sampling trawl (Engås &

Godø 1989) with 40 mm meshes in the belly and bag and 9 mm mesh cod-end liner. The trawl had a heavy “Rockhopper” ground gear. However, since the *Håkon Mosby* had a limited two-wire capacity, the smaller semi-balloon trawl (OTSB, Stein 1985; Haedrich & Merrett 1988) towed on a single warp was used at depths > 630 m. This trawl had a light ground gear and could only be used on soft substrate. Its wing-end spread is 8.6 m and the mesh-size is 25.4 mm. The headline height was not measured, but was lower than that of the Campelen 1800 trawl.

In addition to the 17 trawls considered above, another 78 bottom trawl catches (Fig. 1) from November–December 1995 were available (courtesy of K. Nedreaas, Institute of Marine Research, Bergen). These catches were not always sorted satisfactorily to species, but could be used to analyse distribution by depth and latitude of easily identified species, entire families (e.g. Zoarcidae, Rajidae), and overall fish biomass. This data set was collected by a chartered commercial trawler investigating the abundance and distribution of the Greenland halibut along the slope between 62 and 69°N. The depth range sampled on this cruise was 491–1390 m, and the same commercial trawl was used throughout (Alfredo

nr. 5 with two bags, mesh width in cod-end liner 60 mm, rockhopper ground gear, 4.5 × 2.55 m MALO otter boards). Trawl performance and geometry was monitored by the SCANMAR gear control system. The distance between the otter boards was 170–175 m, the effective fishing width approximately 80 m, and the headline height 4 m. The catches were standardised to a towing distance of 3 nautical miles based on distance data recorded by the vessel.

ANALYSES

Multivariate ordination and classification techniques were used to reveal patterns in the bottom trawl data for demersal fishes on the slope. Only the June 1995 and 1996 data were included in the analyses. For the classification a divisive clustering techniques, TwoWay Indicator Species Analysis (TWINSPAN)(Hill 1979) was adopted (see Jongman & al. 1987 for details). Input data were catches of individual species by trawl in terms of numbers, standardised to 1 hour tow duration, but the program rescales the catches in accordance with preselected “pseudospecies cut-levels”. The cut-levels found to reflect observed catch levels were 0, 10, 100 and 1000 individuals/standard tow. Output from the analysis was a two-way table showing the result of a simultaneous classification of species and sites (in our case trawls) in a binary notation.

For the ordination analysis, Detrended correspondence analysis (DCA) (Hill & Gauch 1980; Jongman & al. 1987) was used applying the program CANOCO (ter Braak 1991). In DCA the species response curves are assumed to be unimodal which is considered particularly useful in ecological studies (ter Braak & Prentice 1988). Both TWINSPAN and DCA are based on corre-

spondence analysis and it is possible to compare results directly. Input to DCA were $\ln(n+1)$ transformed catches in terms of numbers (n) for each species, and detrending by second order polynomials was applied. All species were given equal weight in the analysis.

Despite the possible differences in fishing power and selection characteristics, the C1800 and OTSB data from the summer cruises were pooled in the ordination and classification analyses. Unfortunately it was impossible to undertake extensive parallel trawling with the two trawls at the same location, and we had no means of correcting for selection differences. Differences in catch rate affecting all species, i.e. reflecting the difference in area swept, should be much reduced by the logarithmic transformation used in the DCA and by the use of pseudospecies rather than original catch figures in the TWIA.

HYDROGRAPHY

On the 1995 and 1996 cruises on the *Håkon Mosby*, salinity, temperature and depth was measured at stations along cross-slope transects in the areas selected for bottom trawling (Fig. 1). In this paper, only the near-bottom observations were used, i.e. the measurement taken 10–20 m off the seabed at a given station. The CTD casts were made with a calibrated Neil-Brown profiler.

RESULTS

The study of demersal fishes extended from the shelf-break at about 300 m down the slope to about 2050 m, with most extensive sampling in the upper half of the range. The maximum depth of the adjacent abyssal basins, i.e. the Norwegian and Lofoten Basins are 3000–

Table 1. Bottom trawl stations used in the analyses of demersal fish communities of the upper continental slope off west Norway, 1995 and 1996. Localities are shown in Fig. 1.

Year	Month	Vessel	St.	Locality	Depth (m)	Gear
1995	June	<i>Håkon Mosby</i>	10	Storegga	2051	OTSB
1995	June	"	11	"	1521	OTSB
1995	June	"	12	"	812	OTSB
1995	June	"	13	"	650	OTSB
1995	June	"	14	"	585	C1800
1995	June	"	15	"	530	C1800
1995	June	"	16	"	482	C1800
1995	June	"	17	"	428	C1800
1996	June	"	1	Røstbanken	2015	OTSB
1996	June	"	2	"	1498	OTSB
1996	June	"	3	"	1000	OTSB
1996	June	"	8	"	562	C1800
1996	June	"	9	"	638	C1800
1996	June	"	11	"	428	C1800
1996	June	"	19	"	217	C1800
1996	Aug	<i>G.O. Sars</i>	622	"	730	C1800
1996	Aug	"	623	"	1020	C1800

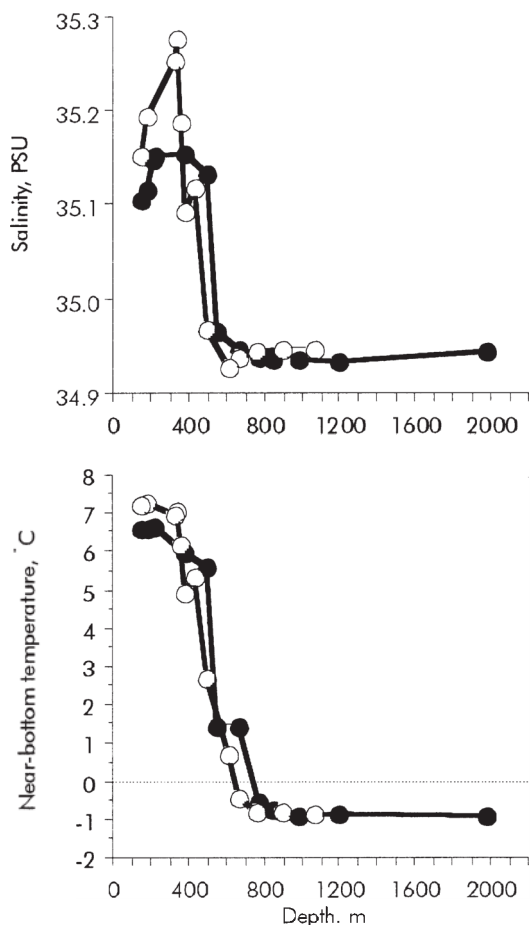


Fig. 2. Near-bottom temperature and salinity along transects crossing the continental slope. Data from June 1995 at Storegga (circles) and June 1996 at Røstbanken (dots).

3800 m. The shelf-break and upper slope shallower than about 500 m is flushed by relatively warm and saline Atlantic Water (temperature 5–10°C, salinity > 35.0 psu) below which is found the cold Norwegian Sea Deepwater with temperature of 0 to –0.9 °C and salinity of 34.9 psu (Helland-Hansen & Nansen 1909; Blindheim 1986). There is a pronounced permanent temperature and salinity front associated with the transition zone between the two watermasses, and this was reflected in the steep gradient of the measured near-bottom temperature and salinity in the two study areas (Fig. 1). The depth of the 0 °C isotherm, i.e. the upper boundary of the Norwegian Sea Deepwater, increases slightly with latitude, but is generally found at about 600 m along the shelf off southern Norway (Blindheim 1986). In our two study areas the temperature fell below zero at approximately 620 and 720 m depth, respectively (Fig. 2).

The geographical and bathymetrical distribution of fish biomass may be illustrated by data from the Greenland halibut cruise in December 1995 (Fig. 3). Each bar in the figure represents a single trawl catch of all species pooled (top left plot) or selected characteristic species, genera and families. The catches were grouped by latitude. There was a steep decline in the fish biomass with depth, but an increasing trend from south to north. Shallower than about 700 m, catches were highly variable, but generally much higher than in the deeper areas of the slope. The median catch below 720 m was 11 % of that above that depth. The decline in fish biomass with depth seemed abrupt at about 700–720 m (Fig. 4), whereas towards deeper slope waters there was a further but more even decline to a very low level at 1300–1400 m. The drop in fish biomass was closely associated with the hydrographical front. The biomass was highest in the transition zone, i.e. in temperatures ranging from 0 to 7 °C, but declined to a low level in waters with negative temperature.

The biomass patterns reflected the abundance of a few characteristic species, in particular Greenland halibut, the redfishes (*Sebastes marinus* and *S. mentella*), and to a lesser extent the roughhead grenadier (*Macrourus berglax*) (Fig. 3). These species appeared especially abundant in the hydrographical transition zone. Below the front, the Rajidae and Zoarcidae were the groups contributing most to the biomass.

The data from the two areas investigated in June 1995 and 1996 (Fig. 1) showed the same general patterns as described above but were analysed in greater detail to study community structure. The number of successful trawls was too low to conduct meaningful area-specific analyses, and trawls from both areas were pooled. The eigenvalues of Axis 1–4 of the correspondence analysis (DCA) were 0.83, 0.44, 0.35 and 0.11, respectively. Axis 1 and 2 explained 36.5 % of the variance in the species data and the first four axes together about 50 %. The length of Axis 1 was 4.6 standard deviation units (SD) (Fig. 5), showing that the species composition of the stations at the ends of the range was entirely different. Axis 2 was 4.8 SD long, mainly due to a single high score station that appeared as an outlier (Fig. 5, upper). There was no clear separation of stations from the two study areas, hence the pooling of the catches seemed justified. The station scores along Axis 1 were strongly positively correlated with depth (Spearman's rank correlation, $r = 0.94$, $p = 0.0002$, $n = 17$), hence depth or depth-related factors explained most of the variation in species composition. Fig. 5 (lower) shows the species plotted according to scores on Axis 1 and 2 of the DCA.

The rearranged species-station matrix resulting from the Two-Way Indicator Analysis revealed tentative

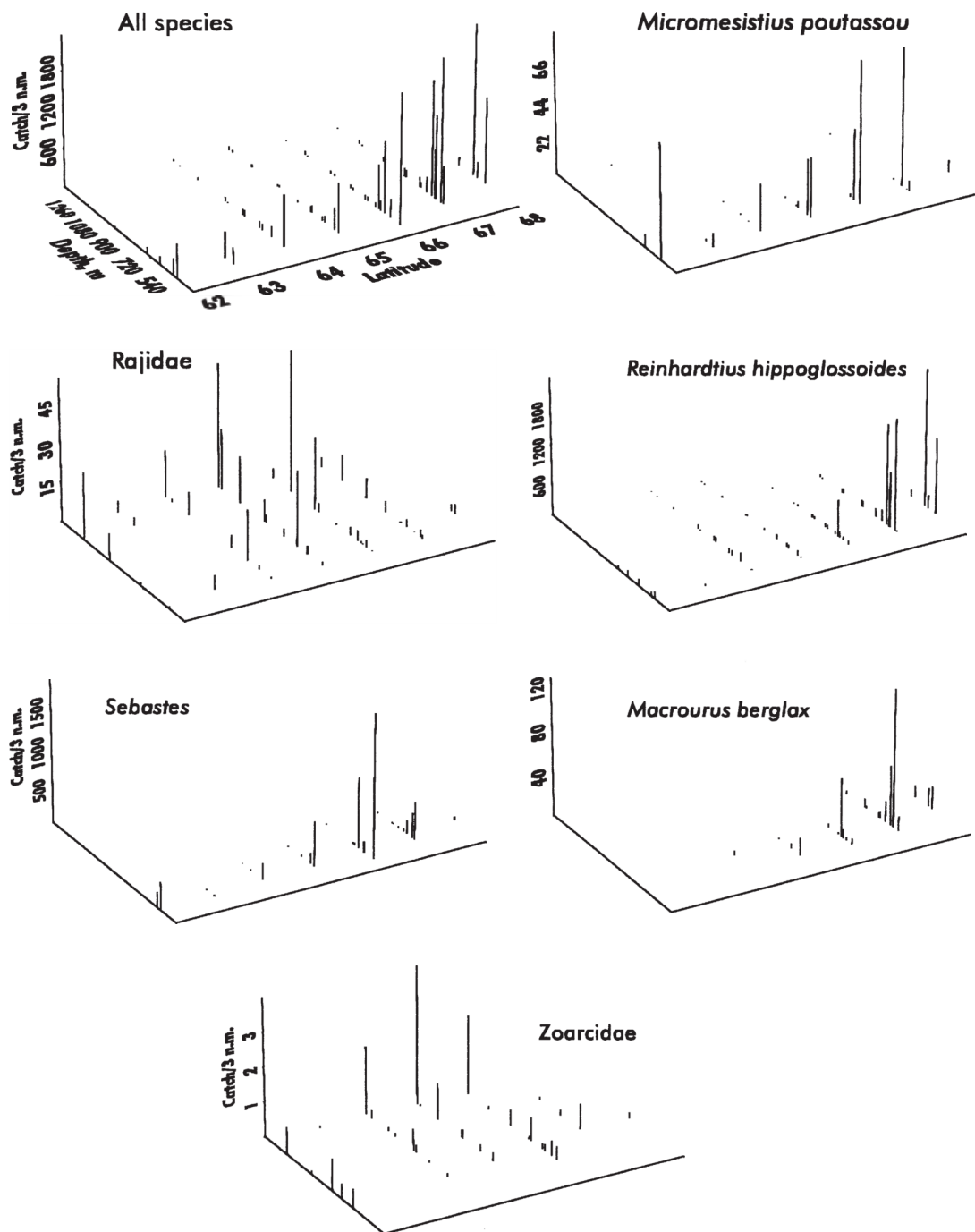


Fig. 3. Bottom trawl catches (kg/3 n.m. tows) from the continental slope off Norway in December 1995 versus depth and latitude. Data from a chartered commercial trawler. Note varying scale on catch axis.

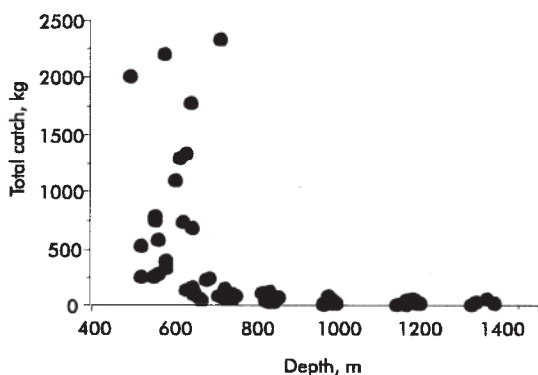


Fig. 4. Total catch (kg/3 n.m.) versus depth on the continental slope off western Norway in December 1995. Dots represent single trawl catches.

groups of species and stations (output from TWINSPAN, Fig. 6). The first division separated stations from the very deepest areas sampled, i.e. the depth range 1498–2051 m, from those in shallower areas. The second division suggested a difference between upper slope stations (217–638 m, Cluster A1) and mid-slope and cold-water stations (585–1020 m, Cluster A2). The positions of the different station clusters in the DCA-plot are indicated in Fig. 5 (upper).

A corresponding pattern resulted from the classification of the 34 species included. The species groups resulting after 3 divisions suggested that four species assemblages might be defined in the area and depth range sampled (Fig. 6). A “Norwegian Sea Deepwater” assemblage with only 3 species had no species in common with the assemblage called “Atlantic water (shelf-edge)” comprising 16 species. The remaining groups “Upper slope 1” and “Upper slope 2” consisted of species that primarily inhabited the transition zone between the Warm Atlantic and cold Norwegian Sea Deepwater, and the two groups probably represented species preferring the relatively warm and cold ends of the temperature gradient, respectively.

The species composition was very different in the three station clusters (Fig. 7). As also illustrated by species abundance plots (Fig. 8), the shallower station group A1 had the most diverse catches, with *Sebastes mentella*, *S. viviparus*, *Reinhardtius hippoglossoides* and *Micromesistius poutassou* as the most abundant species. In the mid-slope stations (Cluster A2), the number of species was slightly lower, and the two most abundant species were *Reinhardtius hippoglossoides* and *Macrourus berglax*. *Onogadus argenteus* and *Lycodes pallidus* were also prominent species. In the very deepest catches, i.e. from the Norwegian Sea Deepwater, the diversity and richness was low, and *Lycodes frigidus* and *Paraliparis bathybius* were strongly dominating species.

DISCUSSION

We aimed at sampling from the shelf edge at approximately 300 m to at least 2000 m. In the two sampling areas this depth interval represents all but the very deepest parts of the slope (Eggvin 1963). On the RV *Håkon Mosby* cruises we unfortunately had to apply two quite different otter trawls when fishing shallower and deeper than 650 m, respectively, i.e. the C1800 towed on double warps and the OTSB towed on a single warp. The number of successful trawls became less than planned because of rugged terrain and coral beds, particularly at intermediate depths. The area swept by the OTSB was much less than that of the C1800, and there may also have been selection differences between the two gears. We were unable to conduct extensive parallel trawling with the two gears, and thus had no satisfactory correction factors to adjust for differences in fishing power or selection characteristics. We therefore only adjusted the catches for differences in tow duration.

The differences in area swept precluded comparisons of catch rate between areas and depth ranges sampled by the two trawls. For such studies we therefore used the more extensive December 1995 data series from the chartered commercial vessel that used the same gear for the entire study period and all depths. Unfortunately, some important families and genera, e.g. *Zoarcidae*, *Rajidae* and *Sebastes*, were not sorted consistently into species on that cruise, and this precluded more detailed analyses.

Despite the possible differences in fishing power and selection characteristics, we pooled the C1800 and OTSB data from the summer cruises in the ordination and classification analyses. Major selection differences would cause the gravest problems in these analyses, whereas differences in catch rate affecting all species, i.e. reflecting the difference in area swept, would be much reduced by the logarithmic transformation used in the DCA and by the use of pseudospecies rather than original catch figures in the TWIA. If consistent differences in species selection occurred, stations where both trawls were used in the same location and depth would be expected to appear at different locations in the DCA plot (Axis 1 vs. Axis 2). No such segregation was found in the result, e.g. comparing the two deep hauls with the C1800 trawl by RV *G.O. Sars* with OTSB hauls in the same depth range. Therefore, we concluded that the species selection patterns of the two trawls were similar, and that pooling data from them would be acceptable for analyses of species composition and distribution patterns.

The most comprehensive of the very few recent studies of fishes inhabiting the Norwegian Sea slopes was that carried out by Bakken & al. (1975). The depth range 300–1000 m in three sub-areas off Norway was sampled

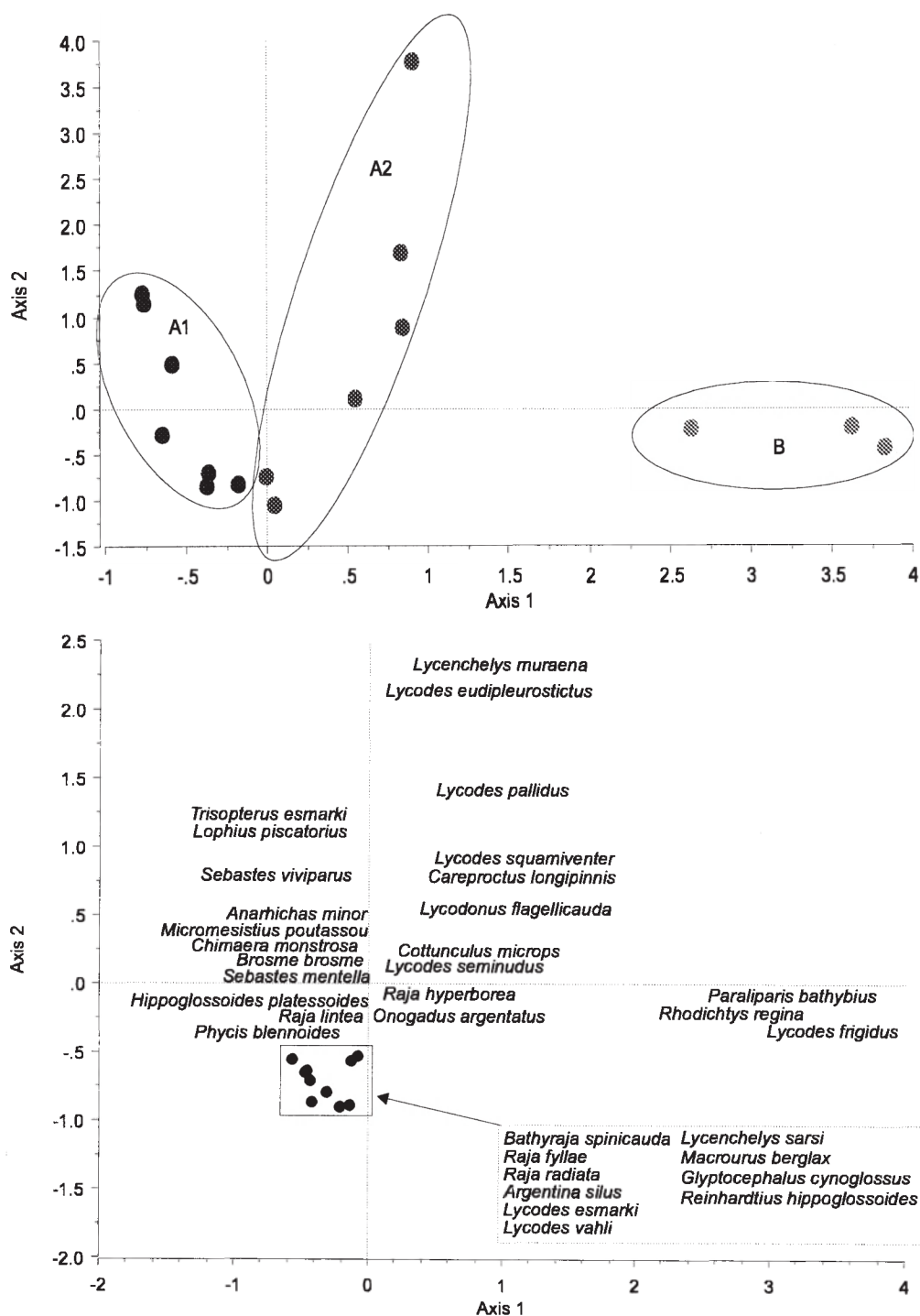


Fig. 5. Scores of stations (upper) and species (lower) on the two first axes of the Detrended Correspondence Analysis (DCA) of the 17 trawl catches from June 1995 and June & August 1996. In the upper figure the encircled stations represent the Station clusters (A1, A2 and B) from the TWINSpan (see Fig. 6).

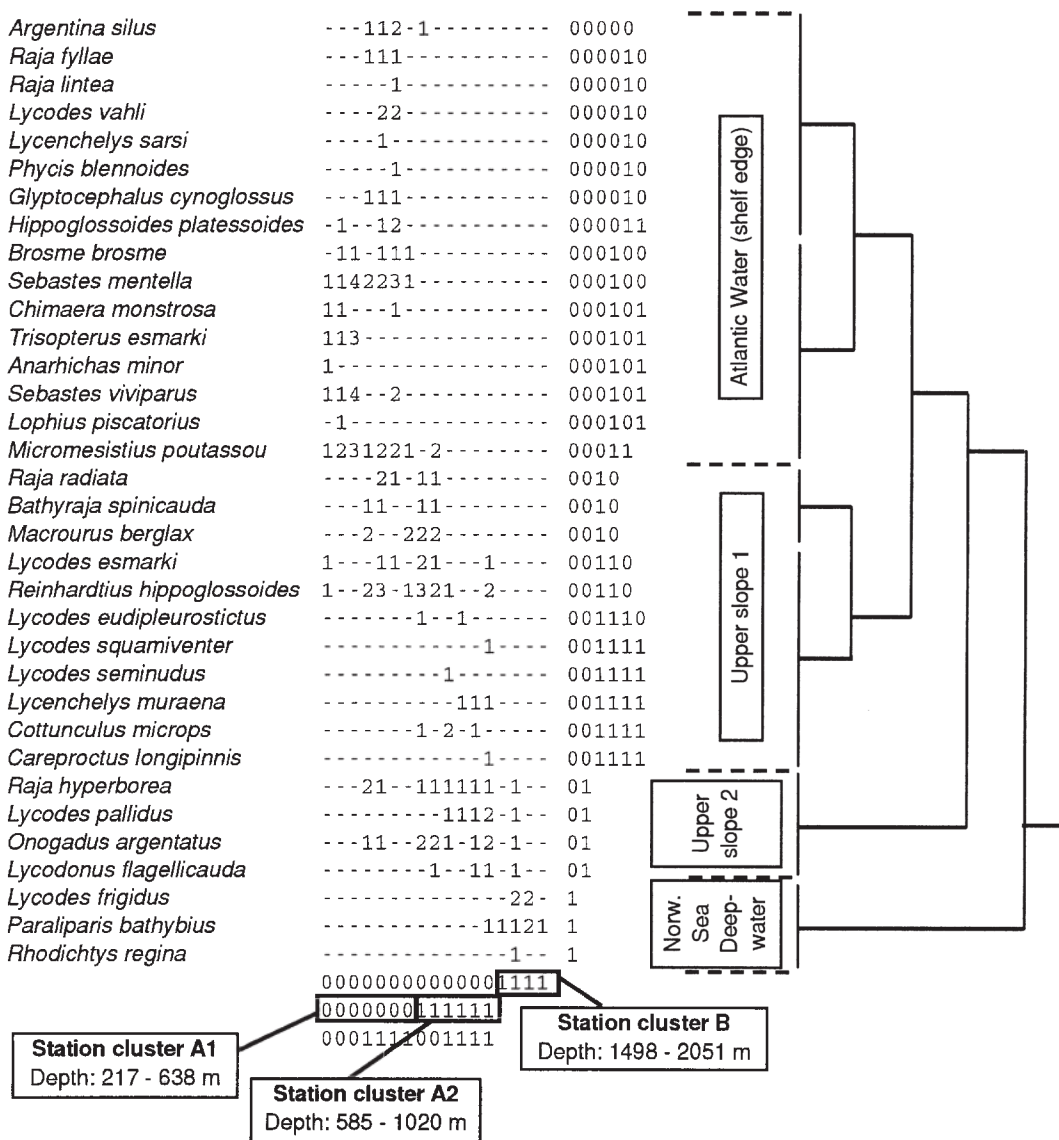


Fig. 6. Results of classification by TWINSpan of the 17 trawl catches from June 1995 and June & August 1996. Two-way table (TWINSpan) output and species and station clusters described in the text.

by bottom trawl (48 tows) and longline (3 sets). Bergstad & Isaksen (1987) and Bergstad (1990) reported data for 7 trawls from the depth range 455-640 m in the same area as sampled in June 1995 in the present study.

Bakken & al. (1975) listed 36 species from their bottom trawl catches. Despite the fact that they included pelagic species (e.g. *Notolepis rissoi*, *Benthoosema glaciale*, *Maurolicus muelleri*) and *Myxine glutinosa* which we excluded, this number is probably an underestimate of the true number of species occurring on the

Norwegian Sea slope. Firstly, catches of *Lycodes* were not sorted into species, and we suspect that some of these actually belonged to other Zoarcid genera. We identified 11 Zoarcids from our 17 trawls. Secondly, we caught 7 non-zoarcid species not listed by Bakken & al. (1975). Together these additions would increase the total number of slope species to 54. The primary reason why our species list only includes 34 species is that, compared with Bakken & al. (1975), few shallow samples from 200-400 m were collected. All the 16 species caught by

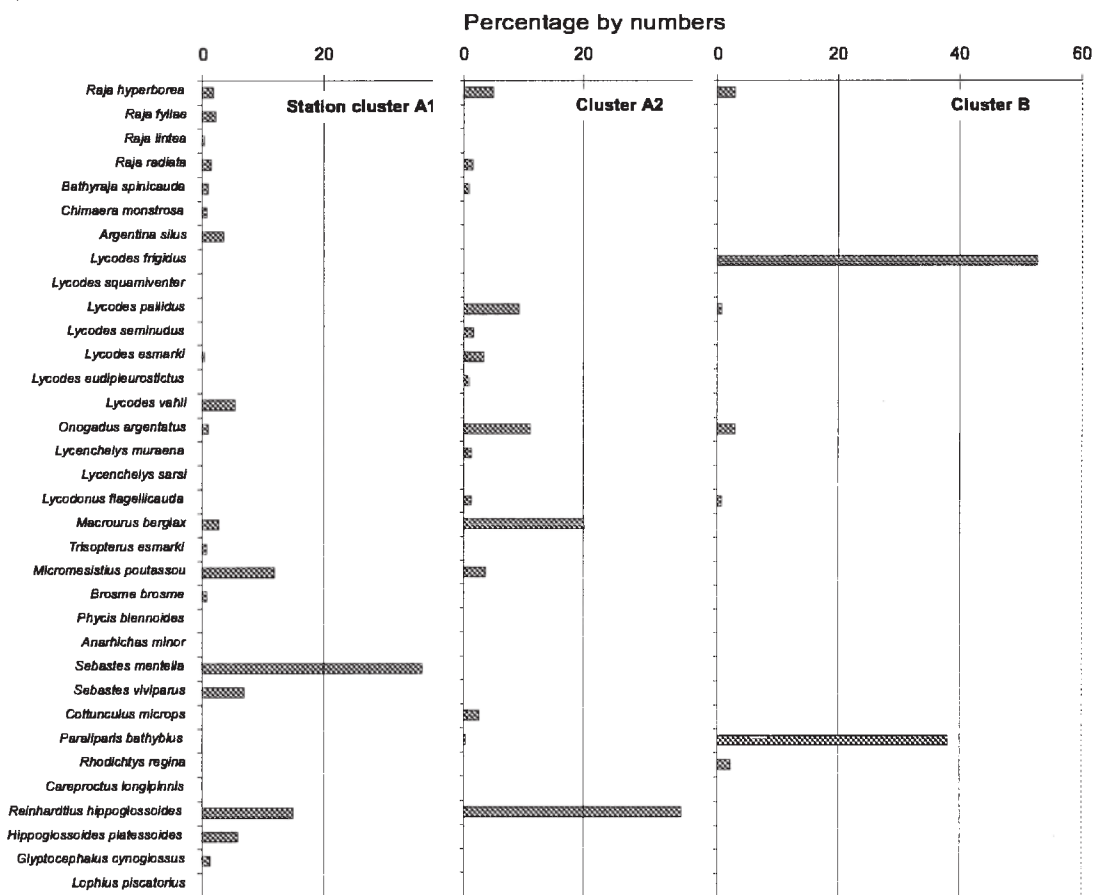


Fig. 7. Species composition, in terms of numbers, in the trawl catches of Station clusters A1, A2 and B resulting from the classification by TWIA (see Fig. 6).

Bakken & al. (1975) and not in this study were listed by Bergstad (1990) as occurring in nearby deep shelf areas of comparable depth, i.e. in the Norwegian Deep.

The true number of Eastern Norwegian Sea slope species may thus be at least 54. This is rather low compared with the 296 species listed by Haedrich & Merrett (1988) as deep-water demersals for the slopes of the North Atlantic Basin to the south of the Scotland-Iceland-Greenland ridges. More interesting than the total number of species, however, is the observation that 11 of the species recorded in our study did not occur on the North Atlantic Basin list. These species may be restricted to the Norwegian Sea and more northerly areas. The only study which has shown some penetration of Arctic species into the North Atlantic Basin slopes was that from the Denmark Strait reported by Haedrich & Krefft (1978), but Haedrich & Merrett (1988) concluded that few of the Norwegian Sea slope species ranged far outside that

area, a view supported by our observations.

Colonization in the opposite direction, i.e. from the North Atlantic Basin to the Norwegian Sea seems primarily restricted to the upper slope waters influenced by Atlantic Water masses. Many of the Norwegian Sea upper slope and shelf-break inhabitants are also common on the upper slope of the Rockall Trough shallower than 750 m (Gordon & Duncan 1985). Among the top ranking species of the 250 and 500 m depth strata in the Rockall Trough *Chimaera monstrosa*, *Etmopterus spinax*, *Coryphaenoides rupestris*, *Micromesistius poutassou*, *Gadiculus argenteus thori*, *Molva molva*, *Phycis blennoides*, *Brosme brosme*, *Helicolenus dactylopterus* and *Glyptocephalus cynoglossus* were also found in the Norwegian Sea or adjacent deep areas by us, Bakken & al. (1975) or Bergstad (1990). In our study most of these were classified together in the "Atlantic Water, shelf edge" assemblage. Of the 16 species in-

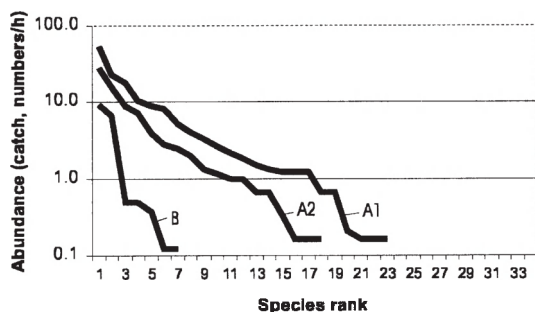


Fig. 8. Abundance plots for the three Station clusters A1, A2 and B (Figs 6 and 7).

cluded in that assemblage, 11 also occurred on the upper slope of the Rockall Trough (Gordon & Duncan 1985).

There is thus some similarity between the two areas but the differences are equally pronounced. Many species that are abundant on the upper slope of the adjacent North Atlantic Basin were not found on the Norwegian Sea upper slope. Notable abundant species on the North Atlantic Basin slopes are *Lepidion eques*, *Coelorhynchus coelorhynchus* and *Halargyreus johnsonii*. In addition there are many others listed by Gordon & Duncan (1985) from the Rockall Trough and by Haedrich & Merrett (1988) for a larger area. Kotthaus & Krefft (1967) studied demersal fish distribution on the Iceland-Faroe Ridge, an area where inter-change of species between the North Atlantic Basin and the Norwegian Sea would be expected. Some southerly slope species, e.g. *Lepidion eques*, *Notacanthus phasganorus*, *Aphanopus carbo*, were found in that area but only in the western relatively warm parts. Of these only a single specimen of *Aphanopus carbo* was caught by us, at Storegga in December 1995. Similar observations were made by Haedrich & Krefft (1978) in the Denmark Strait.

The deeper living species assemblages denoted "Upper slope 1" and "Upper slope 2", and "Norwegian Sea Deep-water" had no species in common with the Rockall Trough (Gordon & Duncan 1985; Gordon & Bergstad 1992). This observation further supports the conclusion already reached by Murray & Hjort (1912) based on several of the early trawling expeditions, that exchange of species across the ridges are restricted to the shelf-break waters.

No more than 7 species occurred in the cold Norwegian Sea deep-water beyond about 1500 m (Station cluster B), and the diversity was low due to the numerical dominance of two species. All were Arctic or Boreo-Arctic species, and with the exception of *Macrourus berglax*, they were secondary deep-sea species *sensu* Andriyashev (1953). This low number of species contrasts sharply with the numbers listed for the same depths

of the Rockall Trough where the expected number of species is 20 at 2000-2220 m (Gordon 1986). The slope areas influenced by the cold Norwegian Sea Deep-water appears to be habitable for only a few cold-adapted secondary deep-water species and *Macrourus berglax*. At 2050 m, the greatest depths sampled, only 2 species were recorded (but it is probable that also *Rhodichthys regina* occurs at that depth). This corresponds with the findings of extensive relatively recent studies of the benthic communities of the Norwegian Sea basins where only 3 species, 2 Liparids and 1 Zoarcid, were caught by trawls and several benthic samplers (Dahl & al. 1978). No fish were caught deeper than 3000 m in that study.

The low number of Macrourids in the Norwegian Sea contrasts with the 12 species recorded in the Rockall Trough (Mauchline & Gordon 1984). *Macrourus berglax* is the only abundant slope species, primarily found near the hydrographic front. Several studies of this species were made previously on the slope off Norway (Eliassen 1983 a, b; Eliassen & Jobling 1985; Eliassen and Falk-Petersen 1985; Savvatimsky 1985, 1986). The only other Macrourid found in abundance in the Norwegian Sea is *Coryphaenoides rupestris*. This species was not caught on the slope in this or any of the previous comprehensive slope studies (Bakken & al. 1975; Bergstad 1990) but seems rather to prefer deep shelf basins and the fjords in this area (Eliassen 1983; Bergstad 1990).

The catches of the three station clusters (Fig. 7) illustrate what seems to be typical for the Norwegian Sea slope: The relatively diverse shelf-edge association (Cluster A1) changes with increasing depth and decreasing temperature to an upper slope association found in the vicinity of the hydrographic front (Cluster A2). At greater depth the deeper-living cold-water slope association is found (Cluster B). The biomass distribution data from the December 1995 cruise showed two main patterns, 1) a pronounced and sudden decline in fish biomass associated with the temperature gradient between Atlantic Water and the Norwegian Sea Deep-water, and 2) an increasing fish biomass from south to north along the shelf. Bakken & al. (1975) suggested that the biomass decreased exponentially with depth, whereas our data rather suggested an abrupt decline at around the depth of the 0 °C isotherm at about 700 m. Both data sets show that the fish biomass is concentrated along the shelf-break and upper slope and primarily on the warm side of the hydrographic front. The bulk of this biomass can be attributed to the dominant species of the Clusters A1 and A2 catches. New data from commercial fishing in the Faroe-Shetland Channel suggest the same main biomass pattern (Bullough & al. 1998). A temperature recorder was fitted to the headline of the trawl, and the subsequent analyses showed that the richest catches were made

on the warm side of the frontal zone while little fishing time was used in water with negative temperatures.

The biomass pattern found in the Norwegian Sea is very different from that of waters to the south of the Scotland-Iceland-Greenland ridges. At the slopes of the Rockall Trough there is a considerable fish biomass at much greater depths than in the Norwegian Sea, and a pronounced mid-depth maximum at around 1000–1200 m (Gordon 1986; Gordon & Mauchline 1990; Merrett & Haedrich 1997). Impingement of micronektonic prey onto the slope at that depth range seems to explain this mid-slope maximum in demersal fish biomass (Mauchline & Gordon 1991). In the Rockall Trough, the temperature declines with depth to about 2 °C, but there is no steep temperature and salinity gradient as that found along the Norwegian Sea slope and no areas with sub-zero temperature.

In conclusion, the temperature gradient seems to be a strong structuring force along the Norwegian Sea slope, both influencing the identity and distribution of species assemblages. We hypothesize that a second structuring factor is the spatial distribution of prey to demersal fishes, probably primarily nekton like euphausiids, amphipods and meso- and epipelagic fish. A detailed discussion of this aspect is beyond the scope of this paper. Recent stud-

ies have shown deep scattering layers of vertically migrating nekton along the shelf-break and off the shelf (Torgersen & al. 1997). Hydroacoustic observations show diurnal migrations between about 50 and 450 m. In addition to comparatively high local pelagic production, there is evidence of advective production of nekton and plankton in the northeasterly Atlantic current (Mauchline 1986). This may provide a steady food supply to demersal fish along the upper slope, and may also lead to a certain accumulation of nekton in the northerly areas of the slope. Both these processes may primarily benefit the species living above the hydrographic front. Deeper-living species may depend to a much larger degree on benthic production and/or food falls from the overlying pelagic layers.

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REFERENCES

- Albert OT, Nilssen EM, Nedreaas KH, Gundersen AC. 1997. Recent variations in recruitment of Northeast Atlantic Greenland halibut (*Reinhardtius hippoglossoides*) in relation to physical factors. *ICES Council Meeting 1997/EE:06*. 10 p.
- Andriyashev AP. 1953. Ancient deep-water and secondary deep-water fishes and their importance in a zoogeographical analysis. In: *Notes on Special Problems in Ichthyology*. Akademiya Nauk SSSR, Ikhtologicheskaya Komissiya, Moscow. p 58–64. (English translation by A.R. Gosline. Issued by Bureau of Commercial Fisheries, USNM, Washington D.C. p 1–9)
- Bakken E, Lahn-Johannessen J, Gjosæter J. 1975. Demersal fish on the continental slope off Norway. *ICES Council Meeting 1975/F:29*. 15 p.
- Bergstad OA. 1990. Ecology of the fishes of the Norwegian Deep: distribution and species assemblages. *Netherlands Journal of Sea Research* 25:237–266.
- Bergstad OA, Isaksen B. 1987. Deep-water resources of the Northeast Atlantic: distribution, abundance and exploitation. *Fisken og Havet* 3:1–56.
- Blindheim J. 1989. Ecological features of the Norwegian Sea. In: Rey L, Alexander V, editors. *Proceedings of the Sixth Conference of the Comité arctique international 13–15 May*. New York: K.J. Brill. p 366–401.
- Bullough LW, Turrell WR, Buchan P, Priede IG. 1998. Commercial deep water trawling at sub-zero temperatures – observations from the Faroe-Shetland Channel. *Fisheries Research* 39:33–41.
- Dahl E, Laubier I, Sibuet M, Strömberg J-O. 1976. Some quantitative results on benthic communities of the deep Norwegian Sea. *Astare* 9:61–79.
- Eggvin J. 1963. *Bathymetric chart of the Norwegian Sea and adjacent areas*. Bergen, Norway: A/S Johan Grieg.
- Ehrich S. 1983. On the occurrence of some fish species on the slopes of the Rockall Trough. *Archiv für Fischereiwissenschaft* 33:105–150.
- Eliassen J-E. 1983a. Occurrence, gonad development and age distribution of the roughhead grenadier (*Macrourus berglax* Lacepède) (Gadiformes, Macrouridae) along the continental slope of northern Norway. *ICES Council Meeting 1983/G:41*. 19 p.
- Eliassen J-E. 1983b. Depth distribution of roughhead grenadier (*Macrourus berglax* Lacepède) in relation to hydrographical conditions along the continental slope of northern Norway. *ICES Council Meeting 1983/G:42*. 17 p.
- Eliassen J-E, Jobling M. 1985. Food of the roughhead grenadier, *Macrourus berglax*, Lacepède in North Norwegian waters. *Journal of Fish Biology* 26:367–376.



- Eliassen J-E, Falk-Petersen I-B. 1985. Reproductive biology of the roughhead grenadier (*Macrourus berglax* Lacepède) (Pisces, Gadiformes) from the continental slope of northern Norway. *Sarsia* 70:59-67.
- Engås A, Godø OR. 1989. Escape of fish under the fishing line of a Norwegian sampling trawl and its influence on survey results. *Journal du Conseil* 45:269-276.
- Helland-Hansen B, Nansen F. 1909. The Norwegian Sea. *Reports of Norwegian Fisheries and Marine Investigations* 2:1-390.
- Godø OR, Haug T. 1989. A review of the natural history, fisheries, and management of Greenland halibut (*Reinhardtius hippoglossoides*) in the eastern Norwegian and Barents Seas. *Journal du Conseil* 46:62-75.
- Gordon JDM. 1986. The fish populations of the Rockall Trough. *Proceedings of the Royal Society of Edinburgh* 88b:191-204.
- Gordon JDM, Duncan JAR. 1985. The ecology of the deep-sea benthic and benthopelagic fish on the slopes of the Rockall Trough, Northeastern Atlantic. *Progress in Oceanography* 15:37-69.
- Gordon JDM, Mauchline J. 1990. Depth-related trends in diet of a deep-sea bottom-living fish assemblage of the Rockall Trough. In: Barnes M, Gibson RN, editors. *Trophic relationships in the marine environment*. *Proc. 24th Europ. Mar. Biol. Symp.* Aberdeen University Press, UK. p 439-452.
- Gordon JDM, Bergstad OA. 1992. Species composition of demersal fish in the Rockall Trough, north-eastern Atlantic, as determined by different trawls. *Journal of the Marine Biological Association of the United Kingdom* 72:213-230.
- Haedrich RL, Krefft G. 1978. Distribution of bottom fishes in the Denmark Strait and Irminger Sea. *Deep-Sea Research* 25:705-720.
- Haedrich RL, Merrett NR. 1988. Summary atlas of deep-living demersal fishes in the North Atlantic Basin. *Journal of Natural History* 22:1325-1362.
- Hill MO. 1979. *TWINSPAN A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes*. Ithaca, N.Y.: Cornell University. 90 p.
- Hill MO, Gauch HG. 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42:47-58.
- Jongman RHG, ter Braak CJF, van Tongeren OFR, editors. 1987. *Data analysis in community and landscape ecology*. Wageningen, The Netherlands: Pudoc. 299 p.
- Kotthaus A, Krefft G. 1967. Observations on the distribution of demersal fish on the Iceland-Faroe ridge in relation to bottom temperatures and depths. *Rapport et Procès-Verbaux des Réunions Conseil International pour l'Exploration de la Mer* 157:238-274.
- Mauchline J. 1986. A review of the ecology of the deep-water pelagic fauna of the Rockall Trough. *Proceedings of the Royal Society of Edinburgh* 88b:145-157.
- Mauchline J, Gordon JDM. 1984. Diets and bathymetric distributions of the macrourid fish of the Rockall Trough, northeastern Atlantic Ocean. *Marine Biology* 81:107-121.
- Mauchline J, Gordon JDM. 1991. Oceanic pelagic prey of benthopelagic fish in the benthic boundary layer of a marginal oceanic region. *Marine Ecology Progress Series* 74:109-115.
- Merrett NR, Haedrich RL. 1997. *Deep-sea demersal fish and fisheries*. London: Chapman & Hall. 282 p.
- Murray J, Hjort J. 1912. *The Depths of the Ocean*. London: Macmillan. 821 p.
- Nedreaas K, Nævdal G. 1991. Genetic studies of redfish (*Sebastes* spp.) along the continental slopes from Norway to East Greenland. *ICES Journal of Marine Science* 48:173-186.
- Rätz J-J. 1984. Qualitative und quantitative Untersuchungen der Ichthyozonose an der archibenthischen Zone des Rockall-Grabens und umliegender Banke (Westbritische Gewässer). *Mitteilungen aus dem Institut für Seefischerei* 34.
- Rottingen I. 1992. Recent migration routes of Norwegian spring spawning herring. *ICES Council Meeting* 1992/H:18. 6 p.
- Savvatimsky PI. 1985. Features of spawning concentrations of roughhead grenadier *Macrourus berglax* L. at the Norwegian coast. *ICES Council Meeting* 1985/G:6. 34 p.
- Savvatimsky PI. 1986. Ecological characteristics of the roughhead grenadier *Macrourus berglax* near the Lofoten Islands. *Journal of Ichthyology* 25:23-29.
- Stein DL. 1985. Towing large nets by single warp at abyssal depths: methods and biological results. *Deep-Sea Research* 32:183-200.
- Templeman W. 1959. Redfish distribution in the North Atlantic. *Bulletins of the Fisheries Research Board of Canada* 120:1-173.
- ter Braak CJF. 1991. *CANOCO Version 3.12*. Wageningen, The Netherlands: Agricultural Mathematics Group, DLO.
- Trout GC. 1961. A bibliography of the North Atlantic redfish. *Rapport et Procès-Verbaux des Réunions Conseil International pour l'Exploration de la Mer* 150:300-311.
- Torgersen T, Kaartvedt S, Melle W, Knutsen R. 1997. Large scale distribution of acoustical scattering layers at the Norwegian continental shelf and the eastern Norwegian Sea. *Sarsia* 82:87-96.

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