SUMMER DISTRIBUTION PATTERNS AND BIOMASS ESTIMATES OF MACROZOOPLANKTON AND MICRONEKTON IN THE NORDIC SEAS

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The vertical and horizontal distribution patterns of zooplankton and micronekton were mapped during three research cruises in summers 1993, 1994 and 1995 by pelagic trawl and MOCNESS plankton net sampling. The distribution patterns have been related to the distribution of water masses and the distribution of planktivorous fish such as herring, *Clupea harengus*. Zooplankton biomass typically revealed a bimodal vertical distribution with high values in the surface layer and at 200-600 m depth. This subsurface maximum contained, among others, several species of macrozooplankton and micronekton such as krill, pelagic shrimps and mesopelagic fish. The dominant krill species *Thysanoessa inermis, T. longicaudata* and *Meganyctiphanes norvegica* are widely distributed in the Nordic Seas, extending from the coastal areas of southern Norway in the south to the subarctic and Arctic water masses in the northwest. Though widespread, highest abundances of *M. norvegica* were restricted to the warmer Atlantic waters. The pelagic shrimps *Sergestes* and *Pasiphaea* spp., the squid *Gonatus fabricii* and jellyfish *Periphylla periphylla* were distributed throughout the study area. Of the mesopelagic fishes only the lanternfish *Benthosema glaciale* showed a wide distribution whereas *Maurolicus muelleri* and *Notolepis rissoi* were restricted to the warm Atlantic water masses. *Themisto libellula* was the dominant amphipod in the subarctic and Arctic waters of the Nordic Seas. Based on trawl catches in 1994 the total biomass of krill and amphipods was estimated at 50 and 110 million tons wet weight respectively. Biomass estimates of other groups varied from 0.25 to 11 million tons wet weight.

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KEYWORDS: Distribution; biomass; krill; amphipods; jellyfish; squid; shrimps; mesopelagic fish; Nordic Seas.

INTRODUCTION

Water masses of the Nordic Seas (Norwegian, Greenland, Iceland and western-most portion of the Barents Seas) are of Coastal, Atlantic, Arctic, or Polar origin. The circulation and the distribution of these water masses are strongly affected by the bottom topography (JOHANNESSEN 1986; BLINDHEIM 1989).

The dominant components of the zooplankton-micronekton community are krill, amphipods, mesopelagic fish and squids, forming major prey items of many commercially and ecologically important fish species in the Nordic Seas. These include herring (*Clupea harengus* L.), mackerel (*Scomber scombrus* L.), blue whiting (*Micromesistius poutassou* (RISSO)), cod (*Gadus morhua* L.), haddock (*Melanogrammus aeglefinus* (L.)), redfish (*Sebastes* spp.), and salmon (*Salmo salar* L.) (TIMOKHINA 1974; ZILANOV 1982; MAGNUSSON & PALSSON 1988; HOLST & al. 1993; MELLE & al. 1993a; DALPADADO & al. 1996; BJELLAND & MONSTAD 1997). Studies of the distribution of zooplankton and micronekton are therefore important in understanding their role in the ecosystem.

Previous investigations have shown that the dominant krill species *Thysanoessa inermis* (KRØYER, 1846), *T. longicaudata* (KRØYER, 1846) and *Meganyctiphanes norvegica* (M. SARS, 1857) are widespread, occurring in Coastal, Atlantic and Arctic water masses in the Nordic Seas, with the latter species being most abundant in Atlantic waters (EINARSSON 1945; DUNBAR 1964). Of the pelagic amphipods, *Themisto* spp. dominate with *T. abyssorum* (MANDT, 1822) and *T. compressa* being predominantly subarctic and *T. libellula* (BOECK, 1870) predominantly Arctic (DUNBAR 1964). Among the micronekton, jellyfish *Periphylla periphylla* (PÉRON & LESUEUR, 1809), squid *Gonatus fabricii* (Lichtenstein, 1818), and lanternfish *Benthosema glaciale* (REINHARDT, 1837) are distributed throughout the Nordic Seas (GJØSÆTER & KAWAGUCHI 1980; FOSSÅ & al. 1994; BJØRKE 1995). The pearlside *Maurolicus muelleri* (GMELIN, 1788) appears to be the most abundant mesopelagic fish in the Norwegian deep, forming dis-

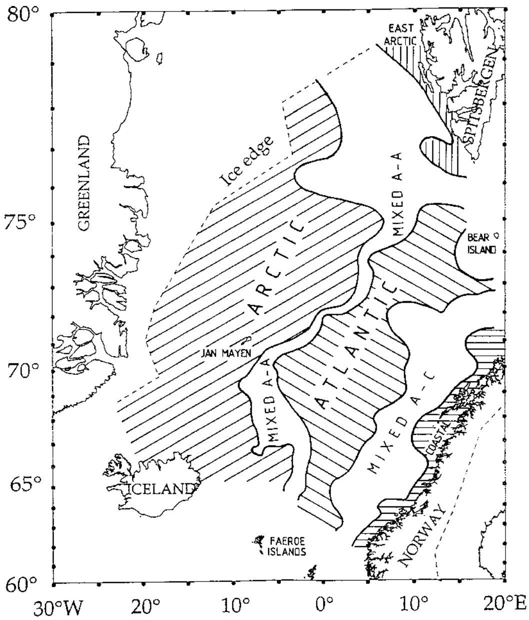

Fig. 1. Schematic presentation of water masses in the Nordic Seas. A-C = Atlantic/Coastal; A-A = Atlantic/Arctic.

tinct scattering layers at 100-200 m (Gjøsæter 1981; Goodson & al. 1995; Kaartvedt & al. 1996; Torgersen & al. 1997). Though the zoogeographical distribution of these organisms is known, there is limited information on the vertical distribution patterns as well as abundance or biomass estimates within the Nordic Seas.

The primary aim of this study was to describe the horizontal and vertical distribution patterns of the major macrozooplankton and micronekton during summer in the Nordic Seas. Investigations were carried out during the summers of 1993, 1994 and 1995. The distribution patterns of krill, amphipods, pelagic shrimps, squids, jellyfish and mesopelagic fish, are discussed in relation to water mass distribution (Coastal, mixed Coastal/Atlantic, Atlantic, mixed Atlantic/Arctic, Arctic, and East Arctic). In addition, attempts were made to estimate the biomass of these organisms in the study area. Finally the distribution of zooplankton in relation to the distribution of planktivorous herring, which has its main feeding grounds in the Nordic Seas is also discussed.

Table 1. Surveys in the Nordic Seas in summers 1993-1995.

Research vessel	1993	1994	1995
Johan Hjort	29Jul-15Aug	5Jul-22Jul	7Jul-2Aug
G.O. Sars	24Jul-16Aug	30May-30Jun	25May-22Jun
Michael Sars	9Jul-31Jul	16Jul-15Aug	

MATERIAL AND METHODS

Surveys in the Nordic Seas were undertaken on board R/Vs *G.O. Sars, Johan Hjort and Michael Sars* (Table 1). The distribution patterns were determined by sampling with a pelagic trawl. We have also used krill data from the MOCNESS plankton sampler (Wiebe & al. 1976, 1985) as the trawl mostly catches the larger sized krill. MOCNESS data for amphipods were not available. No trawl catch data were available for the jellyfish in 1993.

A pelagic trawl (Åkra trawl, see Valdemarsen & Misund 1995) with a 30 x 30 m mouth opening was used to sample the macroplankton and micronekton. The cod end mesh size was 10 mm (stretched). The mesh size in the front of the cod end was 38 mm. Inside the 38 mm mesh net was a 20 m long inner-net with 16 mm mesh size. The trawl was fitted with a Scanmar depth sensor. The towing speed of the vessel was 3-4 knots. In 1993 trawl hauls were taken only at the surface (0-30 m), whereas in 1995 most hauls were taken between 0-30m with only few hauls covering 500-0 m. In 1994 the hauls were usually taken at three depth intervals, 30-0, 200-30, and 600/bottom to 200 m. The present data are based upon 92, 232 and 181 trawl hauls in 1993, 1994 and 1995 respectively (Table 2). The distribution patterns of macroplankton and micronekton presented in this study are mainly based on trawl catches obtained in 1994 because of the higher frequency of catches covering 600-0 m depth range in that year compared to 1993 and 1995. Data on the distribution of krill were supplemented with catches from the MOCNESS in 1994. MOCNESS samples were taken at most trawl stations. Tem-

Table 2. Number of trawl stations in different water masses and depth intervals 0-30, 30-200 and 200-600 m; – = no data.

	1993	1994	1995
Coastal			
0-30 m	2	9	13
Coastal/Atlantic			
0-30 m	30	27	35
30-200 m	–	5	3
200-600 m	–	4	3
Atlantic			
0-30 m	39	35	94
30-200 m	–	9	4
200-600 m	–	8	4
Atlantic/Arctic			
0-30 m	6	43	10
30-200 m	–	11	1
200-600 m	–	9	1
Arctic			
0-30 m	12	37	11
30-200 m	–	13	1
200-600 m	–	12	1
Arctic East			
0-30 m	3	6	–
30-200 m	–	2	–
200-600 m	–	2	–

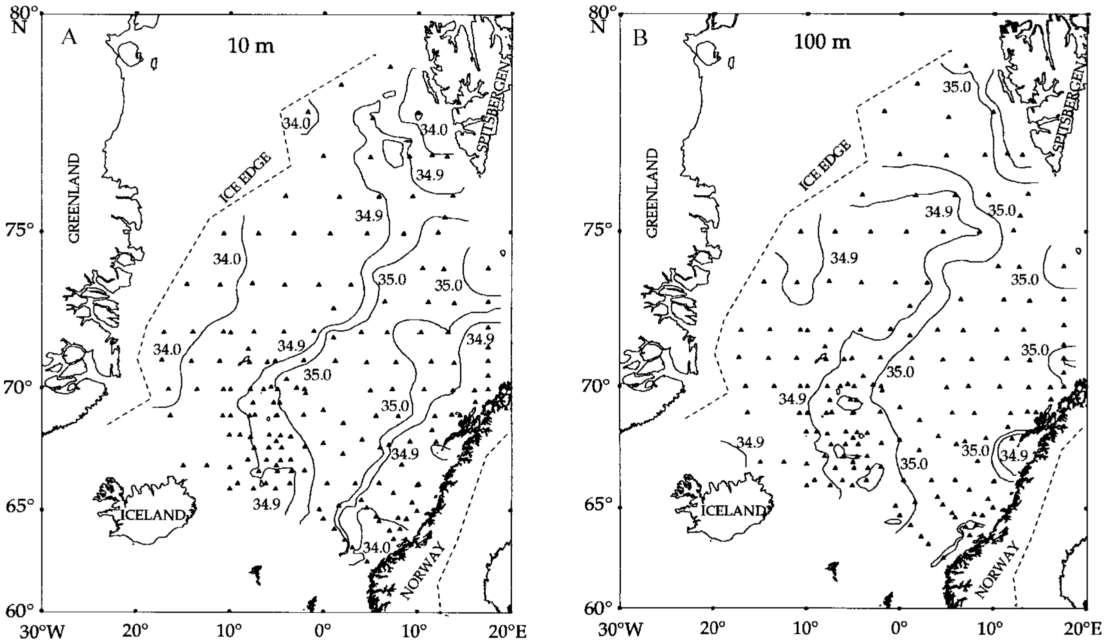

Fig. 2. Salinity at depths 10 m (A) and 100 m (B) in 1994. Locations of trawl stations are indicated by triangles.

perature and salinity data were obtained using a CTD drop sonde at all trawl and MOCNESS stations.

The biomass estimates are based only on trawl catches in 1994 (0-600m). For each trawl haul the wet weight per square meter was calculated based on catch and trawl data (depth interval, effective opening, distance trawled). The total biomass of organisms in the study area was estimated by a computer program using Map-Library developed by Westgard & al. (1988). Map-Library uses the subroutine package GPGS-F (Anon. 1984) which contains all basic functions for geographical presentation of curves and alphanumeric data. The program integrates a variable over an area to estimate the total amount present.

For krill and amphipods the herding effect of the large meshes in front of the trawl is presumably negligible, and the effective mouth opening of the trawl was set to $10m^2$, identical to the mouth opening of the 16 mm mesh inner-net. In a similarly constructed trawl, Godø & al. (1994) found insignificant herding effect on juvenile cod smaller than 65 mm, and Valdemarsen (Institute of Marine Research, Norway, pers. commn) estimates an effective catch opening of $30\ m^2 \pm 10\ m^2$ on the trawl to sample young cod. This $30\ m^2$ effective opening is used in estimating the biomass of larger organisms such as squid, mesopelagic fish and shrimps.

On the basis of temperature and salinity data obtained at different depths (10, 100, 500 m) from all three years and using the description of water masses given by Johannessen 1986 and Blindheim 1989, the Nordic Seas were divided into the following six hydrographic regions: 1) Coastal water, 2) Mixed Coastal/Atlantic water 3) Atlantic water, 4) Mixed Atlantic/Arctic water, 5) Arctic water and 6) East Arctic. A schematic presentation of the water masses in the Nordic Seas is presented in Fig. 1. Salinity and temperature data at individual stations were used to classify into different hydrographic regimes. We have only presented salinity data from 10 and 100 m from 1994 (Fig. 2A, B).

STATISTICAL ANALYSES

Statistical analyses were only performed on biomass data from trawl catches in 1994 as trawl samples from below 30 m depth were few in 1995 and lacking in 1993. The aim of these analyses was to describe the distribution of biomasses in relation to major water masses. The favoured method of analysing the distribution data would have been a multivariate direct gradient analysis (ter Braak & Prentice 1988), relating biomass of the taxa to parameters reflecting links to other trophic levels and advection. The only environmental variables available to us, however, were salinity and temperature. We used salinity and temperature to classify sampling stations according to water masses. Assuming that advection and trophic relationships determining population size vary between water masses, we performed an indirect gradient analysis relating water mass classifications (see description above) to the ordination of trawl stations using detrended correspondence analysis, DCA (ter Braak & Prentice 1988).

Among the indirect methods we preferred ordination techniques (e.g. DCA) over classification by cluster analysis as we believed changes in biomass to occur

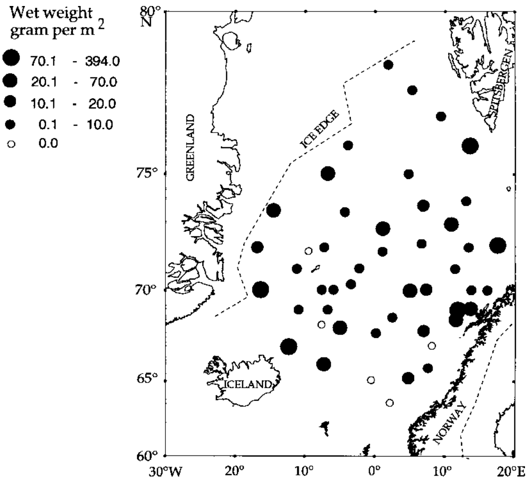

Fig. 3. Horizontal distribution of krill in the Nordic Seas in summer 1994, based on pelagic trawl catches from 600-0 m.

gradually between water masses. If environmental gradients are long the taxa are inclined to show a unimodal rather than a linear response curve (TER BRAAK 1988, 1990; TER BRAAK & PRENTICE 1988). For example, over a long temperature gradient (wide temperature range) biomass of a species does not increase continuously but reaches a local maximum at the optimal temperature, showing a unimodal response curve. The length of the major gradient of the ordination can be used to decide whether response curves are linear or unimodal (TER BRAAK & PRENTICE 1988). In DCA the axes are in standard deviation (SD) units and if gradients are longer than 2 SD units then response curves are probably unimodal and ordination methods using weighted averaging (such as DCA) are preferred to linear least-squares methods such as principal component analysis (TER BRAAK & PRENTICE 1988). In our data the length of the major gradient plotted along the first axis was 3 SD and we chose the DCA.

The DCA was run in CANOCO 3.11 (TER BRAAK 1988, 1990). Prior to the analysis biomasses were log-transformed and within CANOCO rare species were down-weighted (TER BRAAK 1988) to reduce the influence of extreme values on the ordination results. The results were displayed using CanoDraw 3.0 (SMILAUER 1992).

RESULTS

Krill distribution based on trawl data

Krill were widely distributed in the Nordic Seas in 1994 (Fig. 3) covering the entire sampling area ranging from 64°N to 79°N and from 20°W to 20°E. In the Coastal and mixed Coastal/Atlantic waters the biomass of krill was generally low with the highest values of 1.4 and 1.6 g m^{-2}, respectively, in depths of 200-600 m in 1994 and 1995 (Figs 8 & 9). Krill were present in 6 out of the 8 stations taken in Atlantic waters in 1994 between 200-600 m. The highest mean biomass of 8.3 g m^{-2} in 1994 was recorded between 200-600 m (Fig. 10B). In

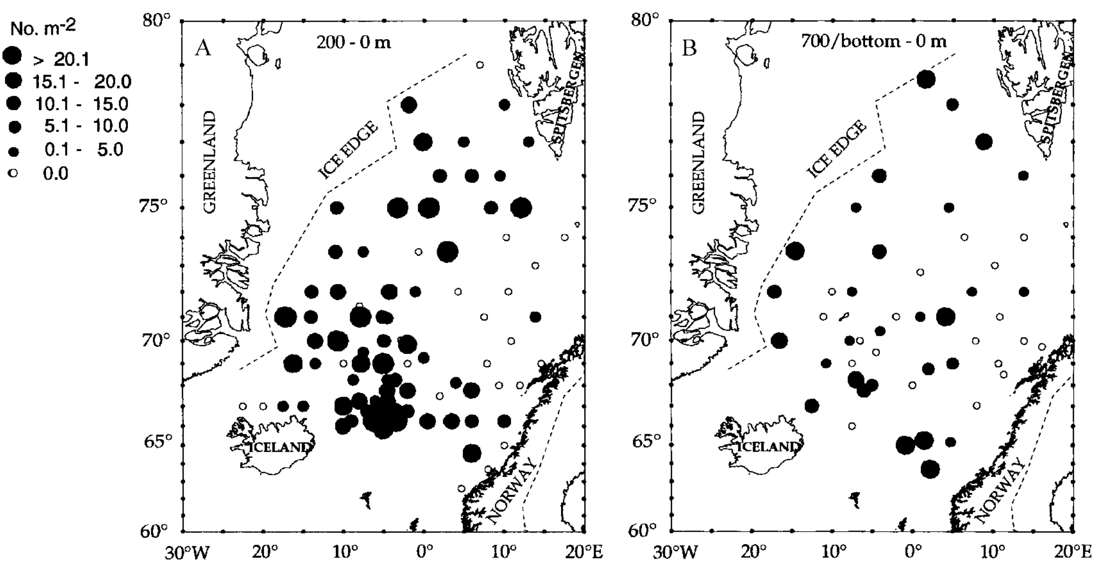

Fig. 4. Horizontal distribution of *T. longicaudata* in the Nordic Seas in summer 1994, based on MOCNESS profiles from 200-0 m (A) and 700m/bottom - 0 m (B).

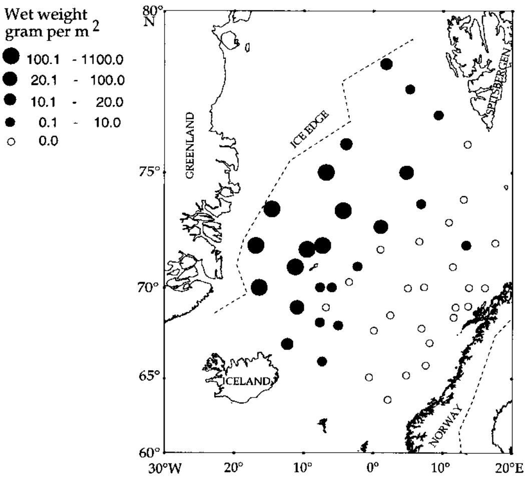

Fig. 5. Horizontal distribution of amphipods in the Nordic Seas in summer 1994, based on pelagic trawl catches from 600-0 m.

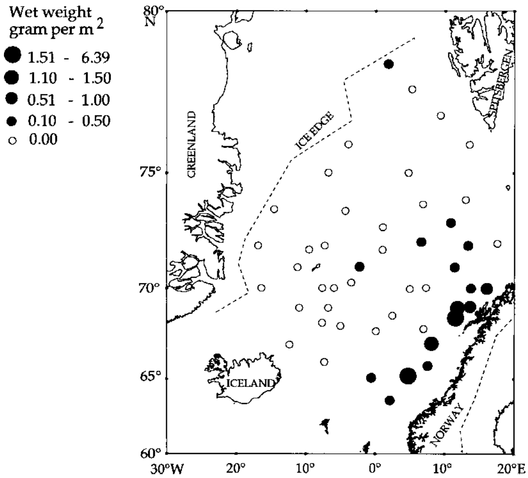

Fig. 6. Horizontal distribution of *Maurolicus muelleri* in the Nordic Seas in summer 1994, based on pelagic trawl catches from 600-0 m.

the mixed Atlantic/Arctic waters the highest biomass was also recorded from 200-600 m (mean 4.3 g m^{-2}; SD = 7.1) (Fig. 11B). Compared to other water masses, the biomass of krill recorded in the cold Arctic waters was high (mean 31.0 g m^{-2}; SD = 41.8) with the greatest biomass values found again between 200 and 600 m (Fig. 12B). In 1994 large krill biomass (210.7 g m^{-2}) was recorded in one out of the two stations between 30-200 m in the East Arctic waters (Fig. 13).

Krill were found sporadically in the 0-30 m trawl hauls in 5.4, 10.2 and 1.2 % of the stations in 1993, 1994 and 1995 respectively. The data give no indication of a day and night variation of their presence in the surface layer.

Krill distribution based on MOCNESS samples from 1994

Though the largest size-fraction of *Meganyctiphanes norvegica* (total length (TL) up to 42 mm) are not caught by the MOCNESS due to net avoidance, the data still indicate that this species is widespread with the highest abundances (above 20 ind. m^{-2}) restricted to the warmer Atlantic and Coastal water masses of the Nordic Seas (not shown). The average abundance of this species recorded from 0-700 m was 4.3 ind. m^{-2} (SD = 11.7). In the 0-200 meter depth range *M. norvegica* was only observed in the southeastern part of the study region in June 1994.

Thysanoessa inermis (TL up to 35 mm) was recorded at fewer stations than *T. longicaudata* and *M. norvegica* (not shown). In the upper 200 m this species was found in the colder water masses between Iceland and Jan Mayen and near the coastal areas of southern Norway. The abundance of this species was lower than those of *M. norvegica* (mean 1.2 ind. m^{-2}; SD = 3.0). In the MOCNESS hauls from 700 m/bottom - 0 m this species was found in areas surrounding Jan Mayen - Greenland and in the central Norwegian Sea.

The smaller krill, *T. longicaudata* (TL up to 19 mm) were found throughout the study area but to a lesser extent in the north-east part of the Atlantic, mixed Atlantic/Coastal and Coastal region (Fig. 4). Abundances of 10 ind. m^{-2} were quite common with abundances as high as 80 ind. m^{-2} observed in the upper 200 m.

Amphipods

The distribution of amphipods collected by the trawl in the upper 600 m in 1994 showed that the highest biomasses were present in the cold Arctic waters (Fig. 5). The larger hyperid amphipod *Themisto libellula* (TL up to 40 mm) dominated (more than 90 %) the trawl catches. In the Arctic waters amphipods were recorded in 41 %, 70 % and 60 % of the stations sampled in 1993, 1994 and 1995 respectively. In these waters they were present at all depths in 1994 and 1995 with the greatest biomass recorded between 30-200 m (Fig. 12B, C). The highest mean biomass of 110 g m^{-2} (SD =265.4) was recorded in 1994 at a depth of 30-200 m.

In the mixed Atlantic/Arctic waters amphipods were observed only in 1994 and 1995. They were found at all depths from 0-600 m, with the largest biomass (mean = 6.7; SD = 9.7) at 200-600 m in 1994 (Figs 11B, C).

Amphipods were not found in Coastal waters in 1993,

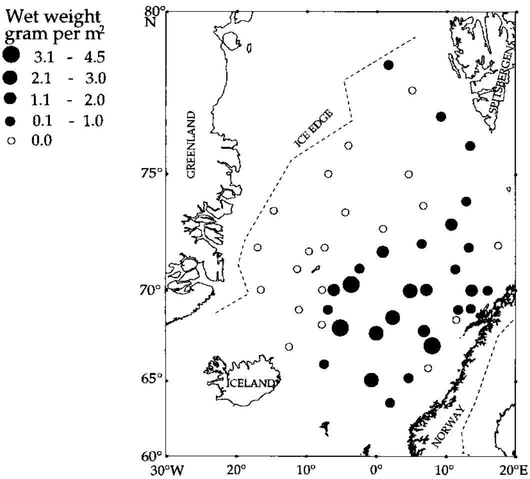

Fig. 7. Horizontal distribution of *Notolepis rissoi* in the Nordic Seas in summer 1994, based on pelagic trawl catches from 600-0 m.

1994 and 1995 (Fig. 8). In the Atlantic and mixed Coastal/Atlantic waters, amphipods were found at only a few stations with mean biomass varying from 0.08-0.50 g m^{-2} (Figs 9 & 10).

Shrimps

Pelagic shrimps, *Sergestes* and *Pasiphaea* spp. (TL up to 55 and 127 mm respectively) were widely distributed in the Norwegian, Iceland and Greenland Seas with the highest biomasses in deeper waters, 200-600 m (Figs 8-13). In the Atlantic waters these organisms were observed at more than 95 % of the stations. The mean biomasses in 1994 and 1995 were similar (1.3 g m^{-2}) and were recorded at 200-600 m depths only. In the mixed Coastal/Atlantic waters the highest biomasses were also observed below 200 m, being 0.8 and 2.2 g m^{-2}, respectively for 1994 and 1995 (Fig. 9). In the Atlantic/Arctic waters the biomass of shrimps was low, with the highest mean biomass (1.3 g m^{-2}) recorded at 200-600 m (Fig. 11). Very low biomasses were also recorded from Arctic waters (Fig. 12).

Shrimps were rarely present in the upper 30 m. Only in 10 of the 505 stations were shrimps recorded with a mean biomass of 0.027 g m^{-2}.

Jellyfish Periphylla periphylla

The jellyfish *P. periphylla* showed a wide distribution (Figs 8-13). In the Coastal waters it was recorded only in 1995 at 0-30 m depths at very low abundances (Fig. 8). In the mixed Coastal/Atlantic waters this species was found at all depths with the highest mean biomass of 1.5 g m^{-2} (SD = 1.6) from 200-600 m in 1994 and 1.0 g m^{-2} (SD = 0.9) between 30-200 m in 1995. In the Atlantic and mixed Atlantic/Arctic waters the biomass of this species was usually higher than in the Coastal and mixed Coastal/Atlantic waters, being highest below 200 m. The mean biomass in the Atlantic and mixed Atlantic/Arctic waters was usually around 6.0 g m^{-2}. The largest biomass of 7.4 g m^{-2} (SD = 4.4) recorded for the jellyfish *P. periphylla* in this study was also between 200 and 600 m in the Arctic waters indicating this species to be deep oceanic (Fig. 12B).

Squid Gonatus fabricii

This species is widely distributed, with lowest biomass in the Coastal, Coastal/Atlantic and Atlantic mixed waters (Figs 8-13). In these water masses the mean biomass varied between 0.16 and 3.5 g m^{-2}.

In the mixed Atlantic/Arctic waters *G. fabricii* was found at more than 70 % of the stations sampled. In these waters the largest biomasses were recorded in the surface waters (0-30 m), 2.5 and 0.2 g m^{-2} respectively in 1994 and 1995 (Fig. 11). Also in the Arctic waters this species was present in more than 70 % of the stations with the highest biomasses in the surface layer. The highest mean biomass (5.5 g m^{-2}; SD= 10.6) recorded for *G. fabricii* in this study was from Arctic waters in 1994.

Mesopelagic fish

Benthosema glaciale. Data from 1994 show that lanternfish *B. glaciale* (TL up to 15 cm) was widely distributed, with the highest mean biomass (2.9 g m^{-2}; SD = 1.2) being observed in the warmer Atlantic waters (Figs 8-13). In 1995 this species was present at all 9 stations covering 200-600 m in different water masses, confirming its wide distribution (Figs 8-12). The largest mean biomass in 1995 was 4.4 g m^{-2} in the Atlantic waters; the second largest was 3.4 g m^{-2} in the mixed Coastal/Atlantic waters (Figs 9 & 10). The biomasses in the colder waters were comparatively lower (0.8 and 0.08 g m^{-2} for 1994 and 1995 respectively). The species was recorded only below 200 m. *B. glaciale* was not recorded between 0-30 m in 1993.

Maurolicus muelleri. In the present study *M. muelleri* (TL up to 6 cm) was largely restricted to the mixed Coastal/Atlantic waters indicating that it is a typical warm water species (Figs 6, 8-13). In 1993 (0-30 m) *M. muelleri* was recorded only at 3 of 30 stations in mixed Coastal/Atlantic waters. This species was present at most stations taken between 30-600 m in the mixed Coastal/Atlantic waters in 1994 with the highest biomass

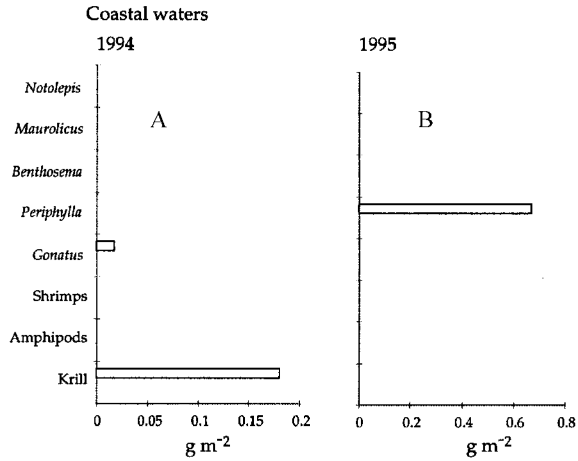

Fig. 8. Vertical distribution of macrozooplankton and micronekton in Coastal water masses based on pelagic trawl catches from 1994 (A) and 1995 (B). Hatching code as in Fig. 9.

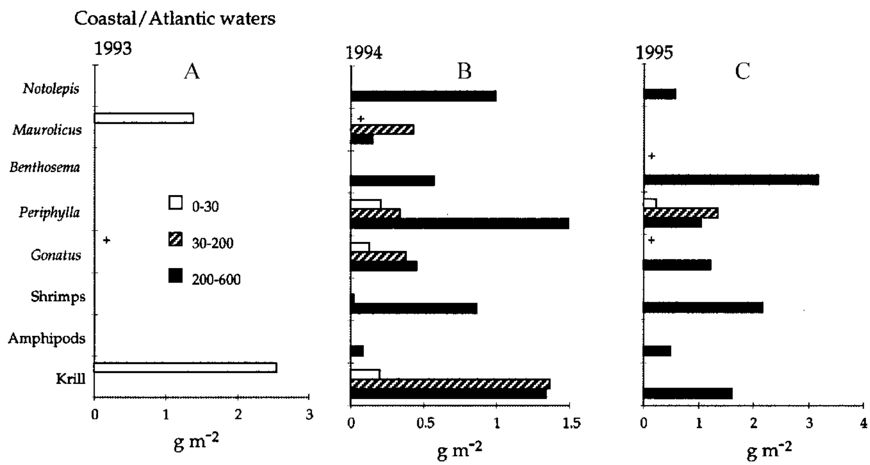

Fig. 9. Vertical distribution of macrozooplankton and micronekton in mixed Coastal/Atlantic waters based on pelagic trawl catches from 1993 (A), 1994 (B) and 1995 (C). In 1993 trawl hauls were taken only at the surface (0-30 m).
+ = low biomass values not evident on scale.

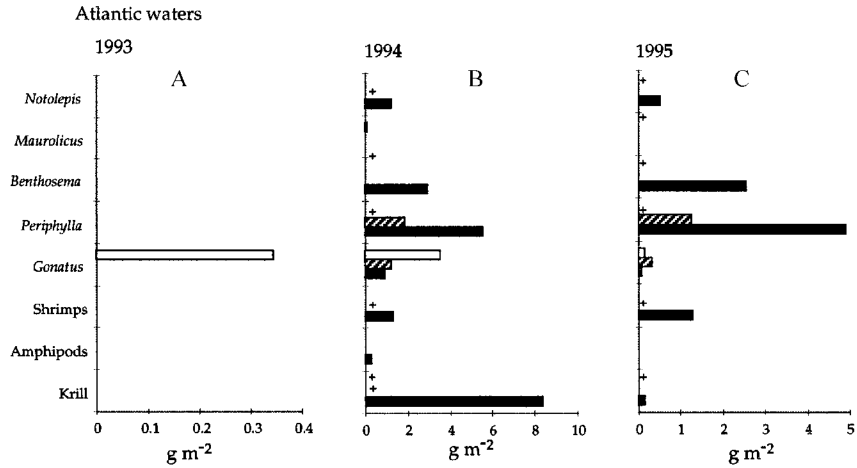

Fig. 10. Vertical distribution of macrozooplankton and micronekton in Atlantic waters based on pelagic trawl catches from 1993 (A), 1994 (B) and 1995 (C). In 1993 trawl hauls were taken only at the surface (0-30 m).
+ = low biomass values not evident on scale. Hatching code as in Fig. 9.

being restricted to 30-200 m (Fig. 9B). In the surface layer this species was present in 1 of 30 stations. In the Atlantic and mixed Atlantic/Arctic waters, low biomasses (< 0.001 g m^{-2}) of *M. muelleri* were observed at only a few stations. In 1995 the pearlside was recorded also in Coastal/Atlantic waters in 1 of 35 stations (0-30 m) and 1 of 3 stations between 200-600 m.

Notolepis rissoi (BONAPARTE, 1840). The horizontal distribution of this species for 1994 is shown in Fig 7. This species was restricted to the warmer Atlantic and mixed Coastal/Atlantic and Atlantic/Arctic waters of the Nordic Seas. *N. rissoi* (TL up to 28 cm) was only recorded at one station with small biomass (0.5 g m^{-2}) in the Arctic waters both in 1994 and 1995. This species was only recorded below 30 m depth with highest biomasses restricted to the deepest waters (200-600 m). In the mixed Coastal/Atlantic waters the mean biomasses recorded for 1994 and 1995 were 1.0 and 0.5 g m^{-2}, respectively. The highest mean biomass of *N. rissoi* was recorded in Atlantic waters in 1994 (1.2 g m^{-2}, SD =1.0) at 200-600 m (Figs 9 & 10). In the mixed Atlantic/Arctic waters the mean biomass was 0.9 g m^{-2} between 200-600 m in 1994, and 0.04 g m^{-2} at 200-30 m and 0.6 g m^{-2} from 600-200 m in 1995 (Fig. 11).

The total biomasses in the study area of krill, amphipods, shrimps, squid *G. fabricii*, jellyfish *P. periphylla*, mesopelagic fish *M. muelleri*, *N. rissoi* and *B. glaciale* are summarized in Table 3.

STATISTICAL ANALYSIS

DCA of the biomasses from all depth layers was dominated by the high biomasses of squid *G. fabricii*, amphipods, and euphausiids caught in the upper 30 m (Fig. 14). The DCA also indicated that the highest biomasses in the upper 30 m of these three taxa were mostly found in Arctic waters. The other taxa included in the analysis were generally not abundant in the upper 30 m catches. The two first axes explained 44.5 % of the total variation in the data. To emphasise the variation among the deeper trawl hauls the samples from the upper 30 m were excluded from the data before the DCA was run again.

The result of the DCA after exclusion of the 0-30 m hauls from the data is shown in Fig. 15. The two first axes explained 49.3 % of the total variation in the data. Symbols used in the ordination diagram are from the non-numerical classification of water masses and the depth of sampling. With some variation, the first axis represents a gradient from Arctic to Atlantic water masses, and the second axis a depth gradient (Fig. 15). Sample score on an ordination axis is the value of the eigenvector in a sample and in DCA a weighted average of species scores (e.g. TER BRAAK 1988). Sample scores of Atlantic stations on the first axis range from 0 to 1.75 and Arctic stations from 1.5 to 3.25. Mixed Atlantic/Arctic stations were generally found between these extremes. The mixed Coast/Atlantic and Eastern Arctic stations did not cluster in separate groups but rather mix with the Atlantic stations (Fig. 15). This was probably related to the vertical distribution of water masses at these stations, with Coastal or Arctic water on top of Atlantic water masses. Thus, samples from 0-200 and especially 200-600 depth should resemble the Atlantic stations in the ordination output.

Species (taxa) score is the eigenvector coefficient and the centre of the unimodal species curve in DCA (e.g. TER BRAAK 1988). In an ordination plot it shows the positions of the biomass maximum on the axes, and the taxa have highest biomass at the stations in the vicinity of the maximum (TER BRAAK 1988). Amphipods and euphausiids were the taxa most closely associated with the Arctic water masses (Fig. 15). In the mixed Atlantic/Arctic waters and towards Atlantic water *P. periphylla*, *G. fabricii*, shrimps and *B. glaciale* displayed maxima in biomass. The most typical Atlantic species were *N. rissoi* and *M. muelleri* (Fig. 15). Taxa far out at

Table 3. Distribution and total biomass of macrozooplakton and micronekton in the Nordic Seas based on trawl catches in summer, 1994.

Group/species	Horizontal distribution	Vertical distribution	Total biomass (Million tons wet weight)
Krill	wide*	mostly < 200 m	50.00
Amphipods	Atlantic/Arctic	600-0 m	110.00
Shrimps	wide*	mostly < 200 m	1.60
Gonatus fabricii	wide*	mostly > 30 m	4.10
Periphylla periphylla	wide*	mostly < 200 m	11.00
Maurolicus muelleri	Atlantic/coastal	30-200 m	0.25
Notolepis rissoi	Atlantic/coastal	mostly < 200 m	1.30
Benthosema glaciale	wide*	mostly < 200 m	2.30

*wide = covering Coastal, Atlantic and Arctic water masses.

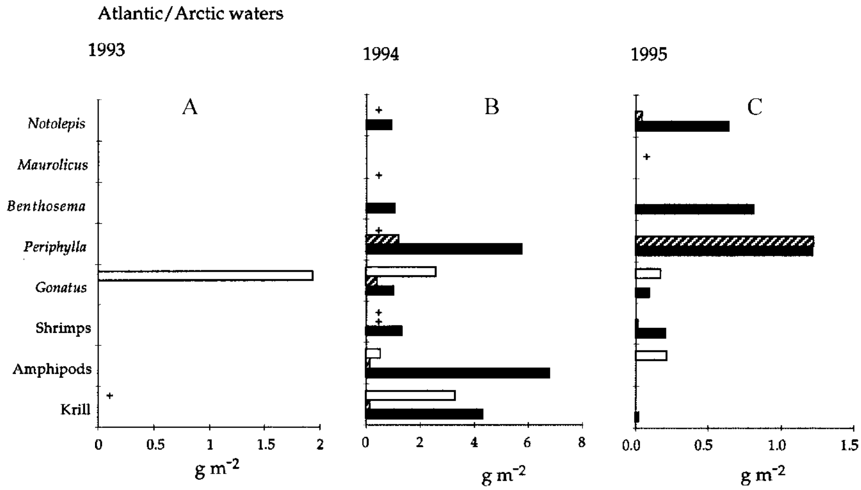

Fig. 11. Vertical distribution of macrozooplankton and micronekton in mixed Atlantic/Arctic waters based on pelagic trawl catches from 1993 (A), 1994 (B) and 1995 (C). In 1993 trawl hauls were taken only at the surface (0-30 m).
+ = low biomass values not evident on scale. Hatching code as in Fig. 9.

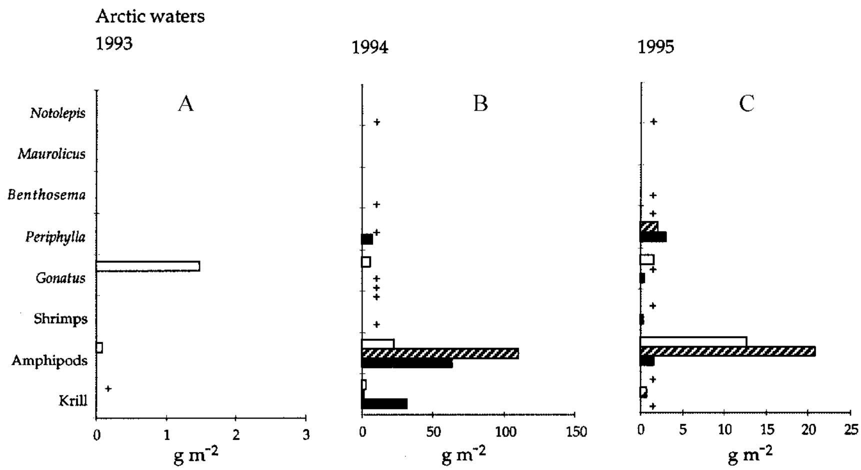

Fig. 12. Vertical distribution of macrozooplankton and micronekton in Arctic waters based on pelagic trawl catches from 1993 (A), 1994 (B) and 1995 (C). In 1993 trawl hauls were taken only at the surface (0-30 m).
+ = low biomass values not evident on scale. Hatching code as in Fig. 9.

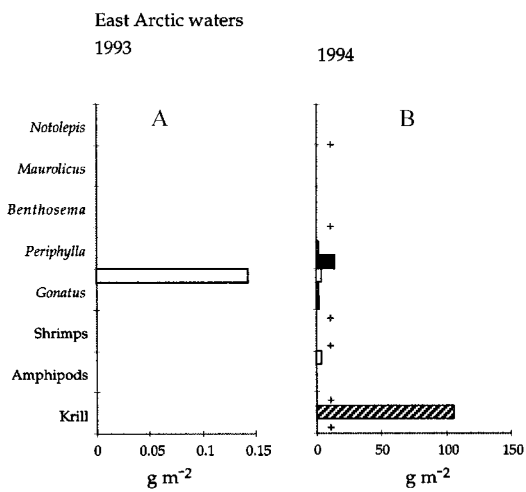

Fig. 13. Vertical distribution of macrozooplankton and micronekton in East Arctic waters based on pelagic trawl catches from 1993 (A), 1994 (B). In 1993 trawl hauls were taken only at the surface (0-30 m).
+ = low biomass values not evident on scale. Hatching code as in Fig. 9.

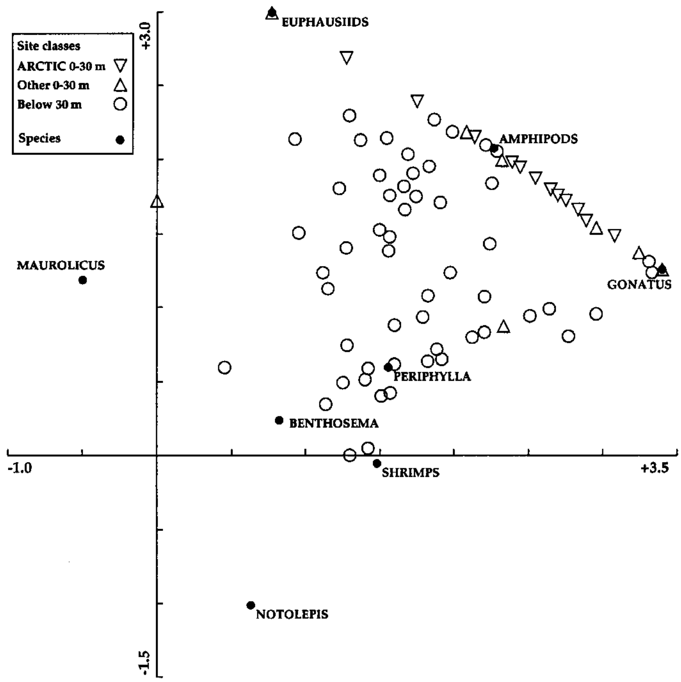

Fig. 14. Ordination of trawl sampling stations in 1994 by Detrended Correspondence Analysis. In the legend 'Species' are taxa in the catches, 'Site classes' are trawl stations classified according to hydrography and sampling depth, 'Other' are hauls from water masses other than the Arctic and 'Below 30 m' are all hauls from below 30 m. Eigenvalues of first and second axis are 0.63 and 0.31, respectively. Length of first axis is 3.4 SD. Note that number of stations shown was reduced, for the sake of clarity, by automated routines in CanoDraw 3.0 (SMILAUER 1992).

the ends of the axes should be interpreted with some care, however, since they contribute less to the ordination (TER BRAAK 1988).

The second axis distinguishes between the shallow hauls 30-200 m at the positive end of the axis and the deeper hauls 200-600 m at the negative end. The mixed Coastal/Atlantic and Eastern Arctic stations showed the greatest discrepancy from this trend, indicating catch of 'deep' taxa in the shallower hauls. The species most associated with the shallow hauls was *G. fabricii*. *P. periphylla*, amphipods and shrimps were in an intermediate position, and the species associated with the deeper hauls were euphausiids, *B. glaciale*, *N. rissoi*, and *M. muelleri* (Fig. 15).

DISCUSSION

Data from both trawl and MOCNESS profiles show that krill (*Thysanoessa inermis*, *T. longicaudata* and *Meganyctiphanes norvegica*) is widely distributed in the Nordic Seas. *M. norvegica* though widespread, is most abundant in the warmer Atlantic and Coastal waters. In the 0-200 meter depth range *M. norvegica* was only observed in the southeastern part of the study region in June 1994. This is the main spawning season of krill (EINARSSON 1945; DALPADADO & SKJOLDAL 1996) and it is likely that *M. norvegica* came to upper waters to spawn. The distribution of *T. inermis* indicates that it is more of a cold water species. The low abundances observed in the Nordic Seas are in contrast to the Barents Sea, where *T. inermis* was the dominant krill species with abundances up to 200 individuals per m^2 (DALPADADO & SKJOLDAL 1996). In the Barents Sea *T. inermis* was largely confined to the boreal and sub arctic. The smallest of the dominant krill species, *T. longicaudata*, was widespread in the Nordic Seas with large abundances in the Arctic waters. Though *T. longicaudata* is regarded as more closely associated with the Atlantic waters than *T. inermis* (EINARSSON 1945; DUNBAR 1964; DROBYSHEVA 1979; DALPADADO & SKJOLDAL 1996) it has been recorded in the Arctic waters in the Barents, Kara and Laptev Seas (ZENKEVITCH 1963; TIMOFEEV 1995; DALPADADO & SKJOLDAL 1996).

The biomass of krill based on pelagic trawl catches was estimated at 50 million tons wet weight in the upper 600 m. In the trawl catches, the larger *M. norvegica*

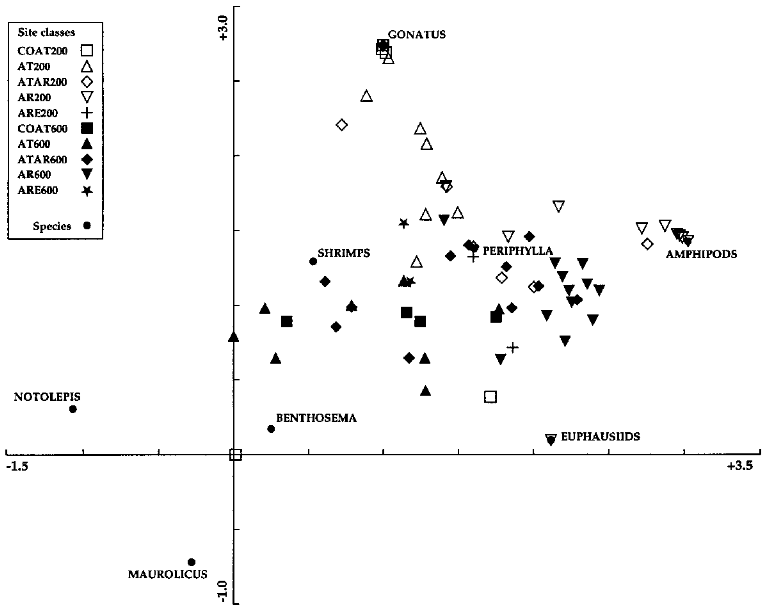

Fig. 15. Ordination of trawl sampling stations in 1994 by Detrended Correspondence Analysis. In the legend 'Species' are taxa in the catches, 'Site classes' are trawl stations (samples) classified according to water masses and sampling depth. Mixed Coastal/Atlantic: COAT, Atlantic: AT, mixed Atlantic/Arctic: ATAR, Arctic: AR, Arctic East: ARE. The numbers 200 and 600 refer to the sampling depths, 30-200 and 200-600 m, respectively. Eigenvalues of first and second axis are 0.47 and 0.21, respectively. Length of gradient revealed by first axis is 3.0 SD.

(TL up to 42 mm) dominated while especially smaller krill as *T. longicaudata* (TL up to 17 mm) were probably underestimated. To our knowledge estimates of krill stocks in the whole Nordic Seas, based on large sampling gears as trawl, are not available in literature. From Hensen and Juday net samples, PAVSHTIKS & TIMOKHINA (1972) estimated the annual production of juvenile krill in the Nordic Seas to vary from 3.3 to 13.0 million tons in wet weight. With the gears used they probably did not sample the larger krill. Given a total area investigated of ca. 1.7 million km^2, we estimated a mean biomass of 29 g m^{-2} or 48 mg m^{-3} in the upper 600m. In the upper layer of the Barents Sea, Zelikman (1958) estimated a krill biomass between 70 and 114 mg m^{-3}. In the Weddell Sea MARR (1962) estimated a *Euphausia superba* biomass of 29.3 g m^{-2} in the upper 5 m.

The large biomass of amphipods in the subarctic and Arctic waters is due to the larger species *T. libellula* (up to 40 mm) which is reported to be a typical cold water species (DALPADADO & al. 1994; DUNBAR 1964). The smaller amphipods, *T. abyssorum* and *T. compressa* (< 20 mm) are most probably not efficiently collected by the trawl and therefore underestimated in this study.

These figures of biomass of euphausiids and amphipods are tentative. The values should be interpreted with caution, as a change in assumed effective trawl opening would have profound effects on the biomass estimates. The annual production of *Calanus finmarchicus* (GUNNERUS, 1770), the most dominant copepod in the Norwegian Sea, was estimated to be 50 million tons (TIMOKHINA 1964). Biomass estimates of krill and amphipods in this study show that these organisms constitute a major fraction of the total biomass of the zooplankton, and thus are important in the ecosystem. From estimations of the biomass of euphausiids in many areas, studies of their food, and the array of predators dependent upon them for nourishment (PAVSHTIKS & TIMOKHINA 1972; MAGNUSSON & PALSSON 1988; DALPADADO & al. 1996; BJELLAND & MONSTAD 1997) it is apparent that euphausiids form a most important link between the primary producers and higher trophic levels in the marine food chain. In the western Norwegian Sea amphipods may be of similar importance.

Herring stocks have increased due to strong year classes in 1983 and in the recent years (1990-1993), and the feeding grounds at present have extended to the western part of the Nordic Seas (RØTTINGEN 1989; DRAGESUND & al. 1997). Herring feeds in different water masses through its feeding migrations in the Norwegian and Iceland Seas. DALPADADO & al. (1996) showed that herring fed almost exclusively on krill in

February-March, in their main spawning period. These authors also showed that krill was important in the diet during the peak feeding period in May and June, especially in the Coastal and mixed Atlantic/Arctic waters, regions of high krill abundance.

Investigations carried out in 1995 and 1996 showed that the herring did not cross the Arctic Front into the deep Arctic waters of the Nordic Seas despite larger zooplankton biomass and thus better feeding conditions in that region (DALPADADO & al. 1996; MISUND & al. 1997). This is presumably due to a preference by herring for water warmer than 2 °C (MISUND & al. 1997). Thus *Themisto libellula*, the Arctic amphipod species, is probably not preyed upon by herring. In contrast, DALPADADO & al. (1996) showed that *T. abyssorum* was a dominant prey of herring in the warmer central Norwegian Sea in the late summer after the peak feeding period. In addition to being important food of adult herring, krill and amphipods may also have a direct predatory impact on herring larvae (BAILEY 1984; HUNTER 1984).

The jellyfish *Periphylla periphylla,* squid *Gonatus fabricii* and pelagic shrimps, *Sergestes* and *Pasiphaea* spp. are widely distributed in the Norwegian, Iceland and Greenland Seas. The distribution pattern of *P. periphylla* recorded in this study is similar to that described by RUSSELL (1970) and FOSSÅ (1992) in that it is a deep oceanic species. The pelagic shrimps had quite a low biomass compared to *G. fabricii* and *P. periphylla.* Pelagic shrimps, *Sergestes* and *Pasiphaea* spp., are food for many commercially and ecologically important fish species in the Nordic Seas such as cod, salmon, and redfish, but seldom for herring (MAGNUSSON & PALSSON 1988; DALPADADO & al. 1996; JACOBSEN & HANSEN 1996; BJELLAND & MONSTAD 1997).

Studies by FOSSÅ & al. (1994) and BJØRKE (1995) show that *G. fabricii* is distributed throughout the Nordic Seas, with highest densities, consisting of juveniles, in the upper 30 m, while the adults live below 300 m. BJØRKE (1995) reported a total biomass of 2.0 million tons wet weight in the upper 30 m, provided a 30 m^2 effective trawl opening. Using the same method of biomass calculation, we estimated a biomass of 4.1 million tons for catches down to 600 m. *Gonatus fabricii* mainly feed upon amphipods, euphausiids and copepods (BJØRKE 1995). RODHOUSE & NIGMATULLIN (1996) assumed a mean feeding rate of 3 % body mass per day in their estimates of global daily consumption by cephalopods. Using the same mean feeding rate in *G. fabricii* the annual consumption in the Nordic Seas is approximately 45 million tons.

Among the mesopelagic fish the lanternfish *Benthosema glaciale* was distributed throughout the study area with the largest abundances in the warmer Atlantic waters. Other studies e.g. BEKKER (1967) and GJØSÆTER & KAWAGUCHI (1980), have also shown *B. glaciale* to be a dominant species in the North Atlantic. This study shows that the pearlside *Maurolicus muelleri* is a typical warm water species. *M. muelleri,* which is usually found at intermediate depths (TORGERSEN & al. 1997) is placed at the deeper end of axis 2 by the DCA (Fig. 15). This is related to the high biomass of this species in the trawl catches from below 200 m in the mixed Coastal and Atlantic waters. This makes the distribution of the species more similar to the deep taxa and will tend to make all samples that the species occurred in more similar to the deep samples. Thus, a deep classification of the mixed Coast and Atlantic samples from above 200 m.

Mesopelagic fish usually perform diurnal vertical migration, staying in deeper waters during daytime and coming up to the surface layers at night to feed on zooplankton and micronekton (BEKKER 1967; GJØSÆTER & KAWAGUCHI 1980; GJØSÆTER 1973; DALPADADO & GJØSÆTER 1988). In the present study, the highest abundances of the mesopelagic fish *Benthosema glaciale* and *Notolepis rissoi* were found below 200 m at stations sampled both during the day and at night indicating that these species remain in deeper waters in summer, forming deep scattering layers. The differences in light intensities between day and night in summer in these high-latitude areas are rather small and they probably stay in the deeper waters to avoid visual predators. *Benthosema glaciale*, *M. muelleri* and *N. rissoi* mainly feed at depths below 100 m during summer (MELLE & al. 1993b). In this study large biomasses of krill, amphipods and shrimps, all of which are major prey of the mesopelagic fish (GJØSÆTER 1981; KAWAGUCHI & MAUCHLINE 1982; KAARTVEDT & al. 1996), were also found in deeper waters. Pelagic fish species as blue whiting and salmon are reported to be major predators of mesopelagic fish (ZILANOV 1982; JACOBSEN & HANSEN 1996; BJELLAND & MONSTAD 1997) whereas herring is found to feed occasionally on *B. glaciale* and *M. muelleri* (DALPADADO & al. 1996).

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