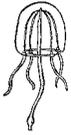


Physical and biological factors influencing the seasonal variation in distribution of zooplankton across the shelf at Nordvestbanken, northern Norway, 1994

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SARSIA



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This paper presents data on species composition, abundance, horizontal and vertical distributions of zooplankton from selected sites across Nordvestbanken, northern Norway, sampled monthly from March to September 1994. The sampling covered three stations: A (closest to shore), C and D (close to the shelf break). There was a distinct succession in species composition over the season, with a shift from a community almost entirely dominated by *Calanus finmarchicus* in May, towards a larger contribution of smaller, neritic species in August and September. Numerically *C. finmarchicus* made up about 70 % of the total zooplankton stock at stations D and C in May (about 90 % if nauplii, which mostly belonged to this species, are included), whereas the proportion of this species was about 50 % at station A this month. The population development of the most common species agreed with earlier findings in the area. A CCA analysis was performed including a total of 18 copepod species and 8 environmental variables. The pattern found demonstrated an inshore-offshore community gradient correlated to temperature, salinity and distance to shore. The most abundant copepod species at Nordvestbanken constituted a group which showed little or no correlation with either of the environmental variables included in the CCA analysis. These species are probably present in the area throughout the season, and are breeding successfully on the shelf. *Temora longicornis*, *Acartia longiremis*, and *Paracalanus parvus* represent the more neritic, shallow water, autumn species, and their presence is probably related to the offshore extension of the coastal water during summer. A third group composed of deep-water species such as *Heterorhabdus norvegicus*, *Chiridius armatus*, *Scolecitricella minor* and *Pleuromamma robusta* could also be distinguished, most likely introduced to the outer shelf area by events of intrusion of deeper slope water.

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INTRODUCTION

The seasonal variation in species composition and abundance of zooplankton is a result of the combined effects of physical and biological structuring of the pelagic community. The succession of the phytoplankton bloom during the productive season varies locally, and is determined by physical factors such as light, mixing, circulation patterns, temperature, and salinity; and on biological factors like competition and grazing (Smayda 1983; Erga & al. 1984; Eilertsen & al. 1989; Ziemann & al. 1991). The flow of energy among lower trophic organisms will to some extent be determined by the degree of "match" between production cycles of phytoplankton and zooplankton. This is expressed in large seasonal variation in abundance and biomass of key species in high latitudes.

The Norwegian Atlantic Current transports Atlantic

water northwards, and thus creates a marine environmental continuum which extends into the Barents Sea and further northwards to the eastern coast of Spitsbergen (Blindheim & Loeng 1981). With these fairly homogeneous physical environmental conditions one would expect to find an offshelf plankton community which is structured and functioning basically in the same way throughout the entire area.

The continental shelf outside Troms county in northern Norway is rather narrow with a steep slope, depths ranging from 70-300 m on the shelf and falling to 2000 m outside the shelf break. Topography (trenches and banks) is an important factor in shaping the detailed current patterns in the area (Sundby 1984). The Norwegian Coastal Current flows along the continental shelf, extending beyond the shelf depending on season and locality (Sundby 1976). The continental shelf outside northern Norway is influenced by both Atlantic

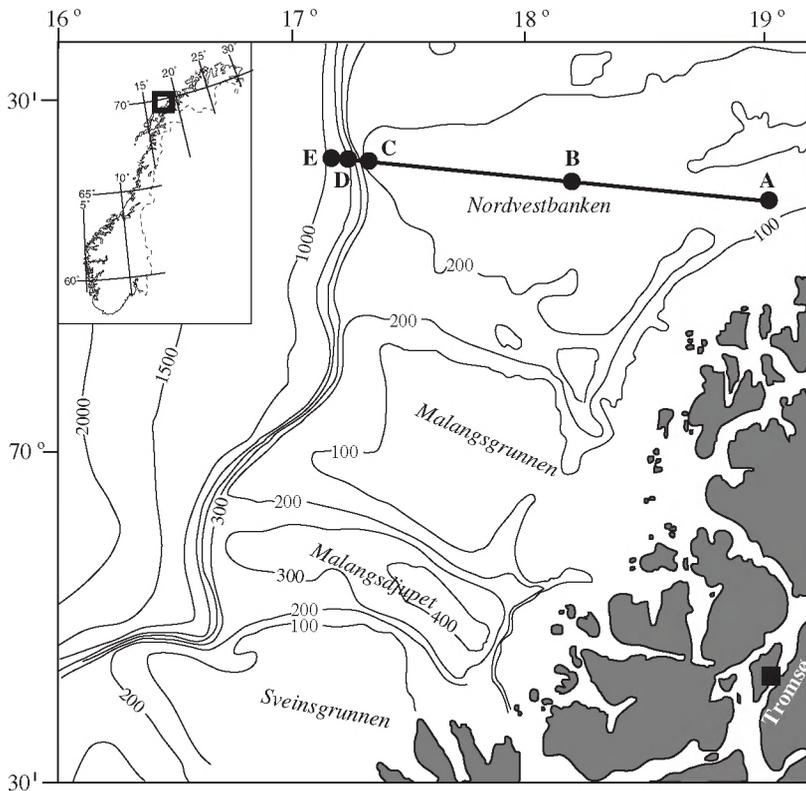


Fig. 1. Map of the study area, showing depth contours and the position of the five stations (A-E) across the shelf at Nordvestbanken, northern Norway.

(> 35 psu) and Coastal (< 35 psu) water (Sundby 1976, 1984), and seasonal changes in the distribution of these water masses are believed to have strong impact on the zooplankton community structure.

Ecological investigations of the plankton community in coastal and oceanic waters in northern Norway (Ruud 1929; Sømme 1934; Wiborg 1954; Hopkins & al. 1985; Tande 1991) have demonstrated that the copepods are by far the most dominant group within the mesozooplankton, and the quantitatively most important herbivorous species is the calanoid copepod *Calanus finmarchicus* Gunnerus. This species breeds during the spring phytoplankton bloom, and the population builds up during May and June (Marshall & Orr 1972; Tande 1982; Diel & Tande 1992). Other copepod species have their maximum biomass in late summer and autumn, and some may be introduced from more southern areas (Wiborg 1954).

Species on the shelf are most likely advected northwards with the Norwegian Coastal Current, but because the continental shelf is rather steep and narrow outside the Troms county, there is also a pronounced mixing

with Atlantic water along the continental slope. Zooplankton species composition will thus give an indication of water mass distribution on the shelf, and could reveal whether this mixing of Atlantic and coastal water influences the entire shelf area, or is restricted to the shelf edge. Many zooplankton species perform vertical migrations (Banse 1964; Williams & Conway 1980; Conover 1988; Osgood & Frost 1994), and the extent and timing of this behaviour in combination with current patterns will influence the horizontal distribution along and across the shelf area. The transport of animals on and off the shelf will thus depend not only on the circulation patterns, but also on the vertical behaviour of the different species.

The EU funded project Ocean Margin EXchange (OMEX) is a multidisciplinary project which aims to reveal the physical and biological processes that influence the flux of carbon along and across the continental margins of the Northeast Atlantic. This study is a contribution to the goal with the following objectives: identify the key zooplankton components involved and describe the seasonality of the exchange of species along

a transect across the shelf outside Troms. This paper presents data on species composition, abundance, horizontal and vertical distributions of zooplankton from selected sites across Nordvestbanken, northern Norway. The sampling occurred monthly from March to September 1994.

MATERIAL AND METHODS

The material was collected during seven cruises with R/V *Jan Mayen*, each following several transects across the continental shelf outside Troms, northern Norway (Fig. 1). The transect at Nordvestbanken covered five stations: A (closest to shore), B (on the bank) C and D (close to the shelf break), and E (slope). Echo depths at the stations are 170 m, 110 m, 200 m, 300 m and 500 m, respectively. The direction of towing at the stations varied between months, so the actual depth might be deeper or shallower depending on whether the tows were made along or across the shelf. The zooplankton distribution is only given for stations A (70°20'N, 18°57'E), C (70°24'N, 17°24'E) and D (70°24'N, 17°13'E). Temperature, salinity, σ_t and fluorescence were measured using an E.G.&G. (Mark IIIB) CTDF, except in August and September, when a Meerestechnik OTS-1200 was used. The fluorometer measures natural fluorescence in the water column, with a range that includes chlorophyll and phaeopigments. Since the measurements have not been calibrated against extracted chlorophyll, the fluorescence gives only a rough estimate of the distribution of chlorophyll in the water column (presented in Nordby & al. 1999).

Zooplankton was sampled with a 1 m² MOCNESS (Wiebe & al. 1985) mesh size 180 μ m, which sampled each depth stratum (0-20 m, 20-50 m, 50-100 m, 100-200 m, 200-300 m) obliquely, at a vertical velocity of ca. 10 m min⁻¹. Time of sampling varied (Table 1).

TREATMENT OF SAMPLES

Zooplankton samples were split at sea using a Motoda splitter (Motoda 1959); one half was immediately frozen in liquid nitrogen for later estimation of biomass (ash free dry weight), the other half was preserved in equal amounts of 4 % formaldehyde and propylene glycol buffered with hexamine, for later species identification and counting. When the sample was large, it was split twice, and only 1/4 kept for identification. The sample was screened through a 180 μ m mesh, diluted to 1000 ml in a beaker, and stirred to get a homogeneous distribution before taking out a 100 ml subsample for counting. The number of subsamples taken out were determined according to the size of the original sample, so that at least 700 individuals were counted.

DATA ANALYSIS

In order to explore the relationship between species abundances and the environmental variables, canonical ordination was applied to the data. The multivariate gradient analysis (Jongman & al. 1987; ter Braak & Prentice 1988) is a combination of ordination and multiple regression, and is designed to identify the observed environmental variables that “best” explain the patterns of variation in the species data. Canonical Correspondence Analysis (CCA) is a technique that selects the linear combinations of environmental variables that maximise the dispersion of the species scores. A test of significance of the first canonical axis and an overall test was made by applying Monte Carlo significance test (ter Braak 1988). The tests are carried out by randomly permuting the sample numbers in the environmental data: the environmental data are randomly linked to the species data, giving rise to a “random data set”. For each random data set, CANOCO calculates a test statistic, namely the first eigenvalue and/or the sum of all eigenvalues (the trace). If the species react to the current environmental variables, then the test statistic calculated from the data-as-observed will be larger than most of the test statistics calculated from the random data.

RESULTS

The species encountered at Nordvestbanken can be divided in three groups, according to whether they were permanent or transient residents on the bank. *Calanus finmarchicus* Gunnerus, *Microcalanus pusillus* (G.O. Sars), *Oithona similis* Claus, *Oithona spinirostris* Claus, *Metricia lucens* Boeck, and *Metricia longa* Lubbock were present throughout the period of investigation. *Pseudocalanus acuspes* Giesbrecht, *P. minutus* (Krøyer), *Acartia longiremis* Lilljeborg, and the pteropod *Limacina* sp. (Fleming) were present in high numbers in the autumn, whereas *Calanus hyperboreus*

Table 1. Date and time of sampling with the MOCNESS at the different stations. (Underlining denotes hauls made during darkness).

Stn D		Stn C		Stn A	
Date	Time	Date	Time	Date	Time
13 Mar	12:35	14 Mar	<u>03:16</u>		
13 Apr	13:58	11 Apr	15:10	11 Apr	09:05
17 May	11:15	17 May	08:55	17 May	00:10
16 Jun	10:45	16 Jun	07:50	14 Jun	05:55
16 Jul	10:05	16 Jul	01:33	15 Jul	18:13
09 Aug	11:03	09 Aug	08:55	09 Aug	<u>00:50</u>
06 Sep	13:40	06 Sep	08:40	05 Sep	<u>01:35</u>

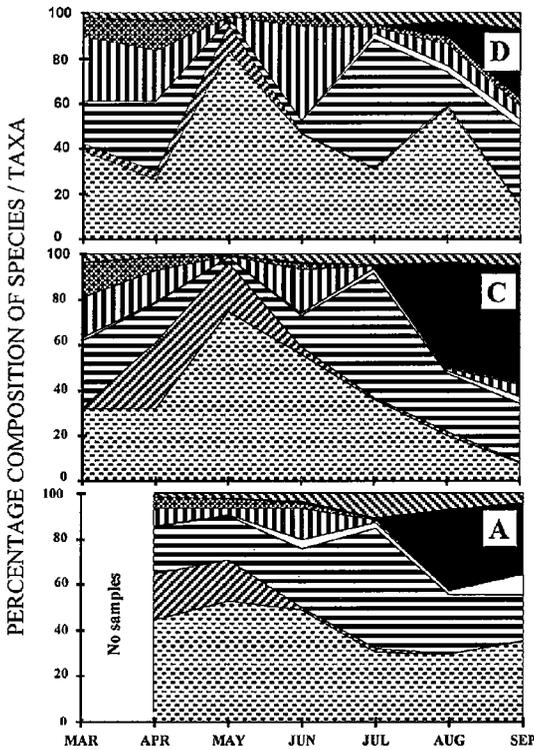


Fig. 2. Seasonal variation in species composition at the three stations, presented as the percentage contribution of the numerically most important species/taxa each month. Symbols: /// *Calanus finmarchicus*, |||| Nauplii, ==== *Oithona* spp., \square *Pseudocalanus* spp., |||| *Microcalanus pusillus*, ■ *Metridia* spp., \blacksquare *Limacina* sp., /// Others.

Krøyer, *Euchaeta norvegica* Boeck, *Paracalanus parvus* Claus, *Pleuromamma robusta* Dahl, *Heterorhabdus norvegicus* Boeck, *Centropages typicus* Krøyer, *Chiridius armatus* Boeck, *Aetideus armatus* Boeck, *Scolecitricella minor* Brady, *Temora longicornis* Hill, the cladocerans *Evadne* sp. Loven and *Podon* sp. Lilljeborg, and the chaetognaths *Sagitta elegans* Verill and *Eukrohnia hamata* Møbius occurred more sporadically on the bank.

SPECIES COMPOSITION

There was a distinct change in species composition over the season at all three stations (Fig. 2), with a shift from a community almost entirely dominated by *Calanus finmarchicus* in May, towards a larger contribution of smaller, neritic species in August and September. Numerically *C. finmarchicus* made up about 70 % of the total zooplankton stock at stations D and C in May (about 90 % if nauplii, which mostly belonged to this species,

are included), whereas the proportion of this species was about 50 % at station A this month. The numerical contribution of *Microcalanus pusillus* was highest in the period March-April and in June, while *Oithona* spp. made up a large part of the zooplankton stock in July. A mesh size of 180 μm may not accurately sample the nauplii and CI-CIII stages of *Microcalanus pusillus* and *Oithona* spp. though, resulting in a possible underestimation of these species. *Pseudocalanus* spp. made a small contribution to the composition of the zooplankton from June onwards, being most abundant at station A. The pteropod *Limacina* sp. appeared in the zooplankton in July, and constituted up to 50 % of the stock in August and September.

The species termed "others" include chaetognaths (*Sagitta elegans* and *Eukrohnia hamata*), appendicularians, cladocerans, euphausiids, different larvae of meroplankton as well as rarer copepod species, and together they make up only about 3-11 % of the total numerical abundance.

SEASONAL VARIATIONS IN ABUNDANCE ON THE SHELF

The abundance of the different species changed with season, and a peak in abundance of *C. finmarchicus* (at most > 1.1 mill ind. m^{-2}) was observed in May at all stations (Fig. 3). From June onward this species was numerically low compared to the previous month. *Oithona similis* and *Microcalanus pusillus* are two other numerically important species, the former peaked in July (ca. 300 000 ind. m^{-2} at station D), while *M. pusillus* attained abundance of > 50 000 ind. m^{-2} at station A in June. *Oithona spinirostris* was present the whole period, but with less clear peaks in abundance (< 15 000 ind. m^{-2}). Of the two *Metridia* species, *M. lucens* was the most numerous, with maximum abundances in May and June (about 12 000 ind. m^{-2}) at the stations A and D, respectively. *M. longa* was present in low numbers during the whole period.

The more neritic forms, such as *Pseudocalanus acuspes* (about 10 000 ind. m^{-2} at station A in September) and *Acartia longiremis* (about 15 000 ind. m^{-2} at station A in August), appeared to build up their populations from June to September. *P. acuspes* was more numerous than *P. minutus*, and the latter seemed restricted to the outermost station. The pteropod *Limacina* sp. totally dominated the upper 20 m in August and September (> 200 000 ind. m^{-2} at station C in August).

The distribution in time and space of other copepod species indicated that some occurred sporadically at the shelf break (C) and on the shelf (A), such as *Calanus hyperboreus*, *Euchaeta norvegica*, and *Paracalanus parvus* (see Tables 2 and 3). Other species occurred only in more oceanic waters at the shelf break. This was the case for *Pleuromamma robusta*, *Heterorhabdus*

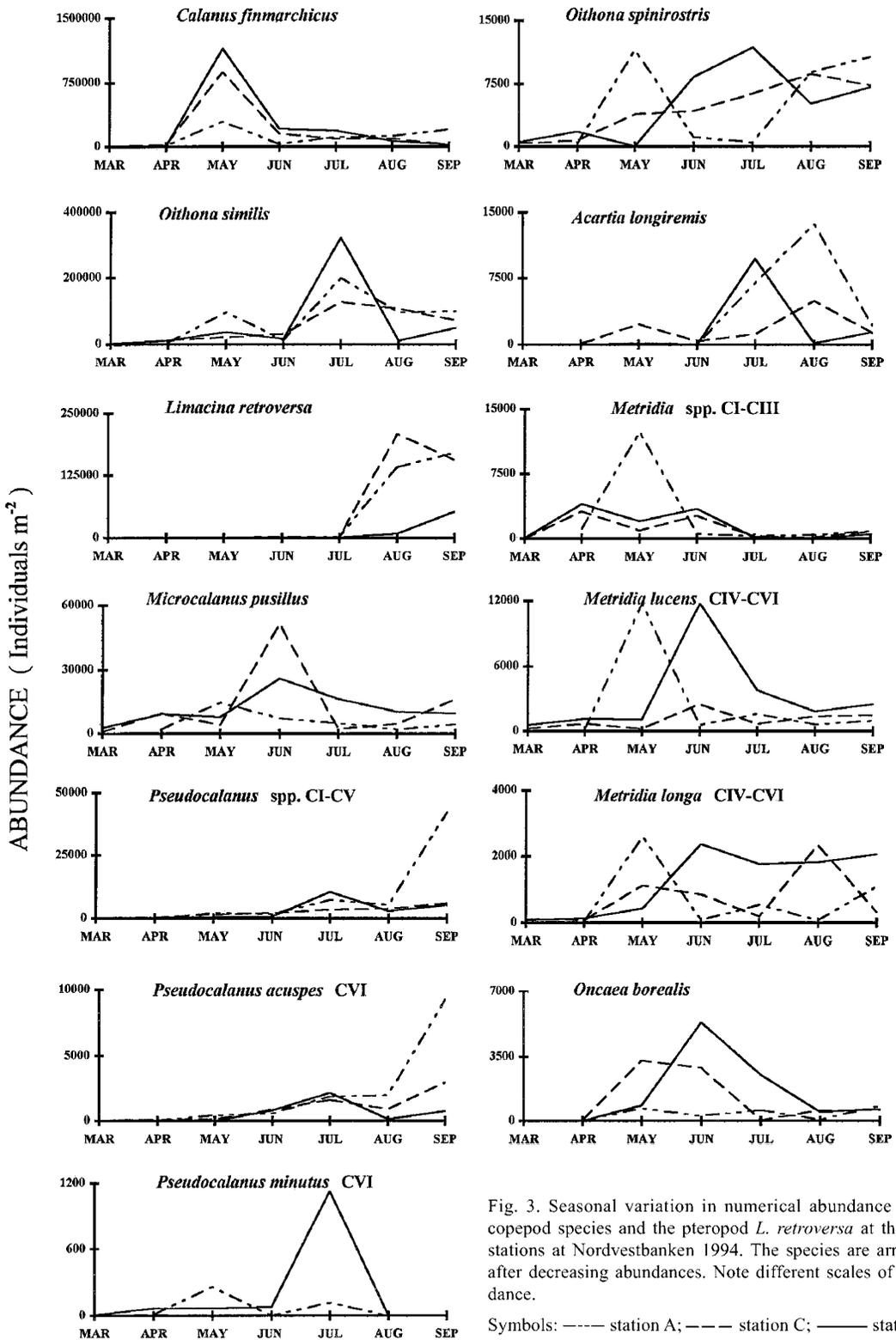


Fig. 3. Seasonal variation in numerical abundance of 10 copepod species and the pteropod *L. retroversa* at the four stations at Nordvestbanken 1994. The species are arranged after decreasing abundances. Note different scales of abundance.

Symbols: ····· station A; - - - station C; — station D

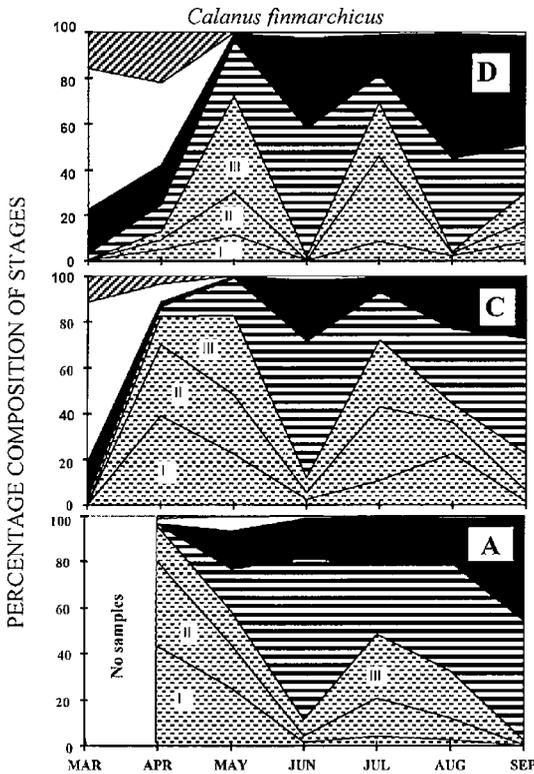


Fig. 4. Population development of *Calanus finmarchicus* at the four stations, presented as the percentage composition of stages each month. Symbols: ▨ CI-CIII, ▨ CIV, ■ CV, □ females, ▨ males.

norvegicus (one exception in September when it did occur at station A), *Centropages typicus*, *Chiridius armatus*, *Aetideus armatus*, and *Scolecitricella minor*. *A. armatus* and *C. hyperboreus* were present in highest

numbers in March-May, whereas *C. typicus*, *Temora longicornis*, *P. parvus* and the cladocerans *Evadne* sp. and *Podon* sp. showed the highest abundances in July-September. For the other species there were no clear temporal patterns in the abundance.

POPULATION DEVELOPMENT

At Nordvestbanken only a small number of species occurred with all copepodite stages present during the periods of investigation. These included *Calanus finmarchicus*, *Pseudocalanus acuspes*, *Pseudocalanus minutus*, *Metridia longa*, *Metridia lucens*, *Microcalanus pusillus*, and *Oithona similis*. For the latter two species, the mesh size was too coarse to quantitatively retain the smaller stages, and the population development is therefore presented only for *C. finmarchicus*, *P. acuspes*, *P. minutus*, *M. longa*, and *M. lucens*.

In *C. finmarchicus*, adults and some CIV-CV made up the population in March, CI-CIII appeared in April followed by a succession of CIV and CV, with the disappearance of adults in June (Fig. 4). CI-CIII had two peaks at all stations during the season, with the largest peak in April/May, and a secondary one in July.

P. acuspes and *P. minutus* CI-CIII peaked in May, resulting in an increase of CV and adults later in the summer (Fig. 5). *M. longa* and *M. lucens* had a similar pattern of stage distribution as *Pseudocalanus*, except for the peaks in CI-CIII being in April (Fig. 5). *M. lucens* stages CIV and CV dominated in May and June, while *M. longa* made a larger contribution to the stock from July to September. Most adults found were *M. lucens*.

VERTICAL DISTRIBUTION

The main patterns in vertical distribution between species are illustrated by data from station C (see Table 1 and Fig. 6). *Calanus finmarchicus* was confined to the upper 50 m in April and May. From June onwards, this species was distributed somewhat deeper, although the

Table 2. The occurrence of species not permanently occurring at station C from March to September 1994, given as number of individuals m⁻².

Station C	Mar	Apr	May	Jun	Jul	Aug	Sep
<i>Calanus hyperboreus</i>	6	6	1414	58	-	121	-
<i>Euchaeta norvegica</i>	86	-	118	-	16	-	107
<i>Pleuromamma robusta</i>	29	-	-	-	-	-	-
<i>Heterorhabdus norvegicus</i>	5	-	2	-	2	-	-
<i>Paracalanus parvus</i>	-	19	-	-	16	360	4111
<i>Centropages typicus</i>	-	-	-	-	-	90	263
<i>Chiridius armatus</i>	-	-	-	-	-	-	-
<i>Aetideus armatus</i>	18	-	-	-	-	-	-
<i>Scolecitricella minor</i>	-	9	-	-	-	-	-
<i>Temora longicornis</i>	-	-	-	-	467	823	481
<i>Evadne</i> sp.	-	28	-	-	943	6771	-
<i>Podon</i> sp.	-	-	-	-	1154	391	49

largest part of the population was found in the upper 50 m from April to September. *Oithona similis* stayed primarily in the upper 50 m throughout the season, but was also found at greater depths in August and September. *Metridia* spp. and *Microcalanus pusillus* were located mainly at depths below 50 m, and *Limacina* sp. occurred mostly in the upper 50 m from June to September.

CCA ANALYSIS

To search for significant differences and patterns within the copepod community at Nordvestbanken during the period of investigation, a CCA analysis was performed. A total of 18 copepod species and 8 environmental variables were included. The environmental variables included echo depth, median depth (midpoint of depth interval sampled), temperature, salinity, density, month, fluorescence and distance from shore, variables that are known to have influence on the temporal and spatial distribution of copepod species. Each depth interval comprised a sample, and a log transformation was applied to the species data.

The species that dominated the zooplankton community throughout the period of investigation were all located near the origin of the ordination diagram, indicating a low correlation with either of the environmental variables (Fig. 7). This was the case for *Calanus finmarchicus*, *Oithona* spp., *Metridia* spp., and *Pseudocalanus* spp. A group consisting of *Temora longicornis*, *Paracalanus parvus*, *Acartia longiremis* and *Centropages typicus* was located to the right in the ordination diagram, relating the build-up of these populations to periods of higher water temperatures towards the autumn. *Calanus hyperboreus*, *Aetideus armatus* and *Pleuromamma robusta* were located to the left in the diagram, which means a stronger correlation with density, salinity and median depth. They were separated along the second axis however, relating *C.*

hyperboreus to higher values of fluorescence and *P. robusta* to increasing median depth. The dispersion of *E. norvegica*, *Scolecitricella minor*, *C. armatus* and *Heterorhabdus norvegicus* along the second axis also indicates a correlation with median depth.

The eigenvalue of the first ordination axis was 0.149, and the cumulative percent variance of species environment relation accounted for by the first two axes was 81.9 (Table 4). The Monte Carlo test gave a P-value of 0.01 for both the first canonical axis (first eigenvalue) and the overall test (trace = sum of all eigenvalues), indicating that the species were significantly related to the environmental variables (Table 5). Temperature ($r = 0.8064$) and density ($r = -0.6352$) showed the highest correlations with the first ordination axis, whereas median depth ($r = -0.4495$) and fluorescence ($r = 0.4043$) best explained the distribution of the species along the second axis (Table 6).

DISCUSSION

HYDROGRAPHY AND ITS IMPACT ON THE PLANKTON

In March 1994, the distinction between the colder (4.5–5 °C), less saline (34.6 psu) coastal water above the shelf at Nordvestbanken, and the warmer (6 °C) and saltier (> 35 psu) Atlantic water offshore was marked by a frontal zone at the shelf break (Nordby & al. 1999). The development of a shelf break front is believed to be enhanced where the topography of the slope is steep and dissected by canyons (Holligan 1981), which is the case in this area. The physical structure and dynamics of frontal systems allows for episodic nutrient enrichments to surface waters (Mann & Lazier 1991), which may result in enhanced primary production (see also Moseidjord & al. 1999).

The spring bloom in 1994 was not detected in the present sampling program as expected based on earlier

Table 3. The occurrence of species not permanently occurring at station A from March to September 1994, given as number of individuals m⁻².

Station A	Mar	Apr	May	Jun	Jul	Aug	Sep
<i>Calanus hyperboreus</i>	-	26	1199	-	33	-	-
<i>Euchaeta norvegica</i>	-	-	169	-	1761	271	-
<i>Pleuromamma robusta</i>	-	-	-	-	-	-	-
<i>Heterorhabdus norvegicus</i>	-	-	-	-	-	-	41
<i>Paracalanus parvus</i>	-	60	169	32	-	496	4906
<i>Centropages typicus</i>	-	-	-	-	-	-	-
<i>Chiridius armatus</i>	-	-	-	-	-	-	-
<i>Aetideus armatus</i>	-	-	-	-	-	-	-
<i>Scolecitricella minor</i>	-	-	-	-	-	-	-
<i>Temora longicornis</i>	-	-	-	-	3810	281	2729
<i>Evadne</i> sp.	-	-	169	-	1761	271	-
<i>Podon</i> sp.	-	-	-	-	794	-	108

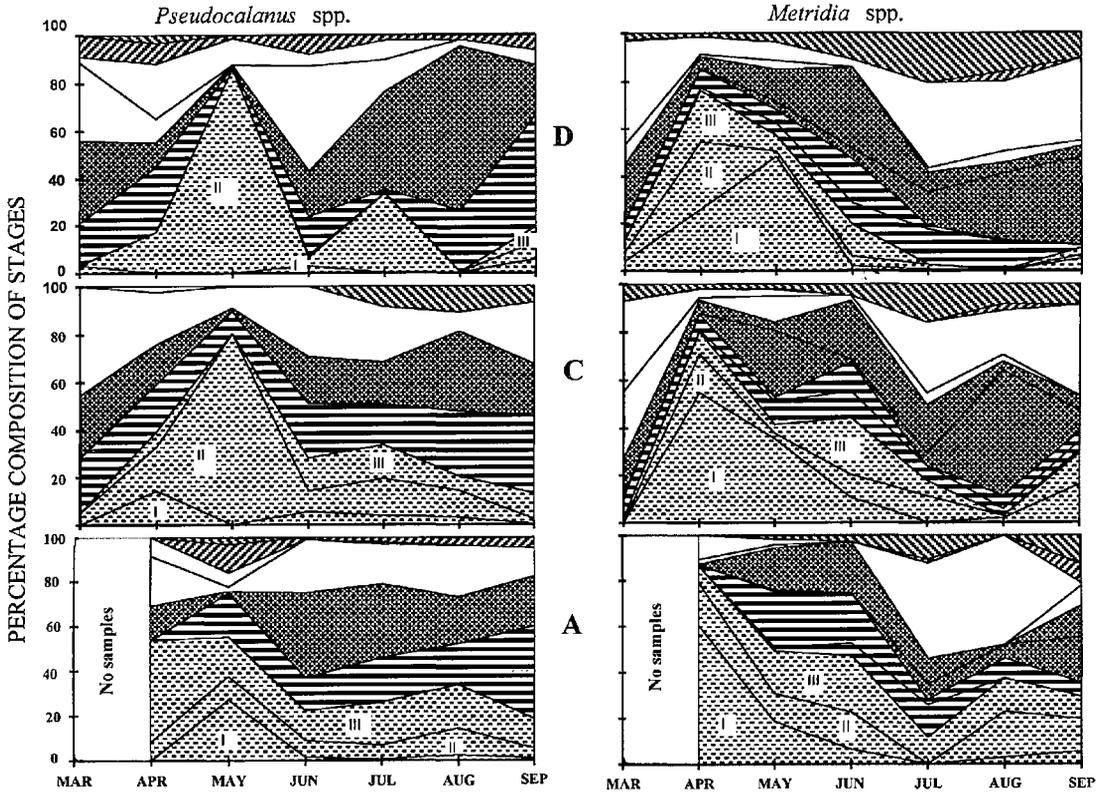


Fig. 5. Population development of *Pseudocalanus acuspes/minutus* (left panel) and *Metridia longa/lucens* (right panel) at the three stations presented as the percentage composition of stages each month. Symbols: ☞ CI-III (*Pseudocalanus* spp.), ☞ CIV (*Pseudocalanus* spp.), ☞ CV (*Pseudocalanus* spp.), □ females (*P. acuspes* and *P. minutus*), ▨ males (*P. acuspes* and *P. minutus*), ☞ CI-III (*Metridia* spp.), ☞ CIV (*M. longa* and *M. lucens*), ☞ CV (*M. longa* and *M. lucens*), □ females (*M. longa* and *M. lucens*), ▨ males (*M. longa* and *M. lucens*)

investigations in adjacent areas (see Braarud & Nygaard 1978; Rey 1981; Hegseth & al. 1995). This could be a result of bad timing with regard to the sampling period, or be due to two factors: high grazing pressure and low vertical stability. Firstly, a very low vertical stability in the water column was recorded in spring 1994 (Nordby & al. 1999), a situation which normally does not favour a phytoplankton bloom. Holligan (1981) argued that enhanced vertical mixing at the shelf break tend to postpone the onset and extend the duration of blooms at the edge of the continental shelf, compared to adjacent shelf and oceanic waters. If this is the case at the strongly flushed system at Nordvestbanken, the diatom maximum could have occurred later in May after stability had increased, coinciding with the period of high biomass of *C. finmarchicus* (K.S. Tande, unpubl. data). Thus the heavy grazing by the developing generation of this species could conceal a build up of a high diatom standing crop. Nutrient levels along the slope of

Nordvestbanken in 1994 (Wassmann & al. 1999) implies a potentially high primary production in the area, but about 90 % of the phytoplankton was comprised of small flagellates (Ratkova & al. 1999). The high copepod abundances, combined with low fluorescence values in May (Nordby & al. 1999), indicate a strong top-down regulation, where the stock of herbivorous zooplankton was able to crop the peak of the spring diatom bloom in 1994.

COMMUNITY STRUCTURE

The species composition during the period of study reflects a shift from a dominance of the predominantly herbivorous *Calanus finmarchicus* (but see Ohman & Runge 1994) in spring, towards a more diverse community in late summer. The overwintering *C. finmarchicus* spawn in early spring in close connection with the spring primary production increase (Diel & Tande 1992; Hirche 1996). When at its maximum abun-

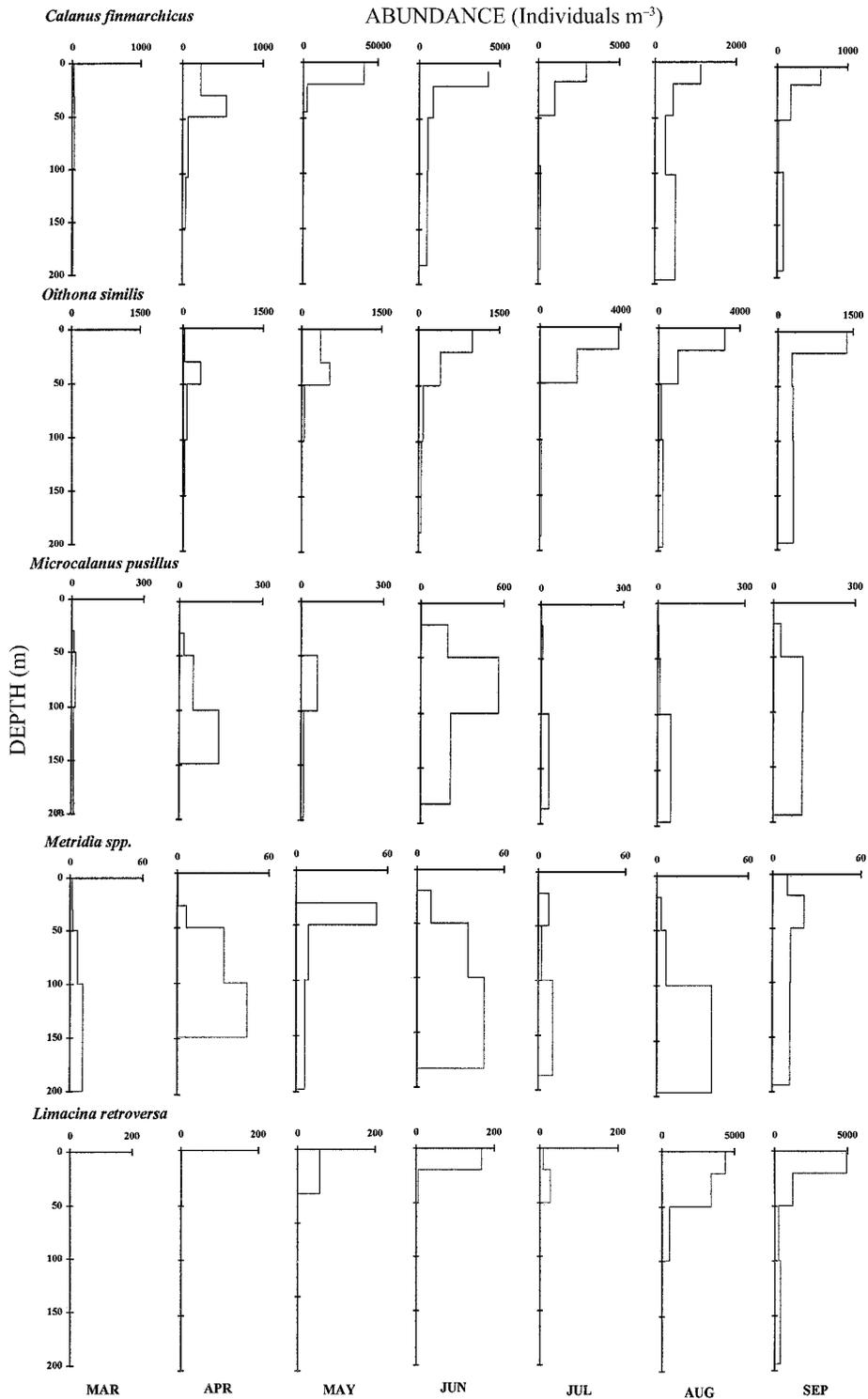


Fig. 6. Vertical distribution of five numerically important species (all stages combined) at station C for the months March-September. Note different scales on the abundance-axis.



Table 4. Summary of CCA analysis, copepod community at Nordvestbanken 1994.

Axes	1	2	3	4
Eigenvalues	0.149	0.040	0.017	0.013
Species-environment correlations	0.897	0.632	0.667	0.657
Cumulative percentage variance of species data	25.5	32.4	35.3	37.4
Cumulative percentage variance of species-environment relations	64.6	81.9	89.1	94.6

dance in May, *C. finmarchicus* totally outnumbered all other species at Nordvestbanken, both numerically and in terms of biomass (K.S. Tande, unpubl. data). Later in the summer other species increased in importance, as for instance *Oithona similis*. Although it was present during the entire study period, it peaked in abundance in July (due to the coarse mesh size, the numerical abundance of this species may be underestimated due to the loss of the smaller stages). Because cyclopoid copepods are morphologically less specialised than calanoids, they are able to survive in a wider range of habitats, and to maintain populations under more adverse conditions (Paffenhöfer 1993). For example, *O. similis* is reported to maintain an almost constant weight-specific egg production year round in the Kattegat (Sabatini & Kjørboe 1994). A small calanoid copepod, *Microcalanus pusillus*, was also quite numerous at Nordvestbanken. *M. pusillus* may be regarded as a detritivore (Krause & Radach 1989; Norrbin 1991), and like *O. similis* it is not totally dependent on the cycle of primary production.

The build-up of populations of *Pseudocalanus acuspes* and *Acartia longiremis* towards the autumn is in accordance with their neritic origin (Wiborg 1954). They were most abundant at station A, and it is probable that these species were recruited from a second generation in the fjords and near coastal waters due to offshore extension of the coastal water during summer. Wiborg (1954, 1955; see also Frost 1989) claimed that *P. minutus* is more oceanic in its distribution compared to *P. elongatus* Boeck (at Nordvestbanken *P. acuspes* could be an equivalent to the more southern *P. elongatus*) although the former according to Norrbin (1994) and Falkenhaus & al. (1997) is also present in low numbers in fjords in northern Norway. Females of *P. minutus* were found in highest numbers at station D, while station A had the highest total abundances of CIV and CV, and of *P. acuspes* females. These differences

in distribution indicate that the two species tend to have greater success in oceanic and neritic environments, respectively. The pteropod *Limacina* sp. made a substantial contribution to the zooplankton in August and September. Using a mucus net to filter very fine particles, it probably considerably reduces the settling out of particles from the upper 50 m. The species found at Nordvestbanken is most likely *Limacina retroversa*, which is regarded as a temperate-water species (Wiborg 1954) and the population originates from surface waters of the North Atlantic (Bathmann & al. 1991; Østvedt 1955; Redfield 1939). This species may be introduced to Nordvestbanken from the south by the Atlantic or Coastal Current.

The occurrence of deep water or oceanic species gives an indication of the influence of Atlantic water on the shelf. Some oceanic species never occurred at station A, which indicates that the influence of Atlantic water at Nordvestbanken is stronger at the outer shelf areas. The correlation of *Chiridius armatus*, *Pleuromamma robusta*, *Scolecitricella minor* and *Aetideus armatus* with median depth and density in the CCA-plot further supports this. In 1992, *C. armatus* and *S. minor* were frequently present at a fjord station in Malangen, just south of Nordvestbanken (Falkenhaus & al. 1997), indicating that the impact of Atlantic water may vary from year to year in the area.

POPULATION DEVELOPMENT OF *CALANUS FINMARCHICUS*

At stations D and C, CIII was the most abundant young copepodite stage in May, whereas CI was the most abundant stage at station A this month, indicating a time lag in the propagation of the stages towards the coast. The prevailing wind direction in this area gives rise to an eastward transport of surface waters (Nordby & al. 1999), advecting the nauplii and young copepodites shoreward. The abundance drop in CI-CIII in June was evident for all stations, and probably reflects the cessation of the first cohort of recruits this spring. The secondary peaks in CI-CIII in July and August are somewhat difficult to explain, since there apparently were no females present to produce them. However, the highest proportion of females at station D and C was in June, while they peaked in May at station A. The new batch of young copepodites in July may result from late spawning females originating from more oceanic wa-

Table 5. Summary of Monte Carlo tests

	Eigenvalue/ Trace	F-ratio	P-value
Test of first canonical axis	0.15	24.36	0.01
Overall test	0.23	5.81	0.01

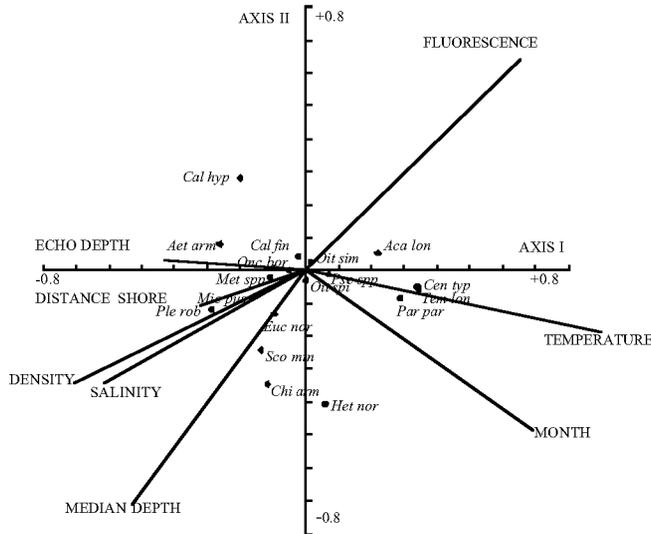


Fig. 7. CCA ordination plot of axes I and II, relating variations in the distribution of 18 copepod species to environmental variables. The joint plot of species points and environmental arrows is a biplot that approximates the weighted averages of each of the species with respect to each of the environmental variables.

ters or coastal waters further south. The results from a study in the central and eastern part of the Norwegian Sea demonstrate that there was a delay of 6-8 weeks in the seasonal propagation of stages at the westernmost station in the Norwegian Sea proper compared with the continental shelf area (B. Ellertsen personal communication, but see also Slagstad & Tande 1996). Wiborg (1954) claimed that *C. finmarchicus* has two main spawning periods in the coastal waters south of Lofoten: one in February-March, and a smaller one in June, whereas in two North Norwegian fjords, Malangen and Balsfjord, only one generation is produced each year

(Marshall & Orr 1972; Tande 1982, 1991). The second batch of early copepodites at Nordvestbanken in July might merely be an overspill from southern areas, an event that is prevented in the fjords due to their relative isolation from the Coastal Current during that time (Leth 1995). The spawning of *C. finmarchicus* is, however, influenced by the amount of food available (Hirche & Meyer 1990; Melle & Skjoldal 1994; Hirche & al. 1994), and if the frontal system at the shelf edge provides an enhanced primary production during the summer, this might be sufficient to create a spawning habitat at the shelf break.

Table 6. Weighted correlation matrix for Nordvestbanken 1994. Copepod community. Values are correlation coefficients (r). SPEC AX = species axis, ENV AX = environmental axis.

	SPEC AX1	SPEC AX2	ENVI AX1	ENVI AX2
SPEC AX2	0.0867			
ENVI AX1	0.8969	0.0000		
ENVI AX2	0.0000	0.6318		
Echo depth	-0.3877	0.0187	-0.4322	0.0297
Median depth	-0.4760	-0.4495	-0.5307	-0.7116
Temperature	0.8064	-0.1177	0.8991	-0.1864
Salinity	-0.5509	-0.2160	-0.6142	-0.3420
Density	-0.6352	-0.2167	-0.7082	-0.3430
Fluorescence	0.5823	0.4043	0.6492	0.6399
Distance shore	-0.2898	-0.0670	-0.3231	-0.1060
Month	0.6191	-0.3063	0.6903	-0.4848



THE EFFECT OF VERTICAL DISTRIBUTION ON HORIZONTAL TRANSPORT

The vertical distribution facilitates a separation between mainly shallow-water species (0-50 m) such as *Calanus finmarchicus*, *Oithona similis*, and *Limacina* sp. and species preferring deeper depth strata (50-200 m) such as *Microcalanus pusillus* and *Metridia* spp. Herbivorous species may be expected to stay within the zone of primary production, whereas detritivore feeders benefit from residing below this zone, filtering what settles out. At Nordvestbanken, the major part of *C. finmarchicus* CI-III was confined to the 0-20 m interval at all times (vertical distribution of stages not shown) facilitating horizontal propagation with strong surface currents. The females showed a less clear pattern of vertical distribution. They were distributed more or less within the 0-100 m interval, although in May they were confined to the upper 50 m. The population of females would thus be exposed to a strong vertical gradient in current velocities resulting in dispersion. From June onwards there was a downward shift in the vertical distribution of CIV and CV of this species, marking the preparation for diapause, which is carried out at greater depths. As a result of the circulation patterns on the shelf this behaviour tends to bring the animals off the shelf and to deep waters outside (Slagstad & Tande 1996). There was a marked difference in the numerical change in CIV and CV between stations D/C and A. At the outer stations, CIV and CV decreased numerically from July to September, while at station A there was a steady increase from June, resulting in a second peak in abundance of this species in September. It is possible that retention of the animals at the innermost station occur due to anticyclonic transport around the bank, as described by Sundby (1984). At the outermost stations the downward migration in autumn brings the animals off the shelf, whereas at the inner station this behaviour could lead to a temporary accumulation close to the bottom. Whether this across-shelf difference in abundance continues throughout the autumn and winter is uncertain, but overwintering stocks on the shelf could be of importance for recruitment the following spring. A combination of shelf advection and downward sea-

sonal migration has been proposed as a mechanism for aggregation of copepods in deep-shelf basins of the Nova Scotian Shelf (Herman & al. 1981).

The most abundant copepod species at Nordvestbanken constituted a group which showed little or no correlation with either of the environmental variables included in the CANOCO analysis. These species are probably present in the area throughout the season, and are breeding successfully on the shelf. A second group (*Temora longicornis*, *Acartia longiremis* and *Paracalanus parvus*) represents the more neritic, shallow water, autumn species, and their presence is probably related to the offshore extension of the coastal water during summer. A third group comprised of deep-water species such as *Heterorhabdus norvegicus*, *Chiridius armatus*, *Scolecitricella minor* and *Pleuromamma robusta* could also be distinguished, most likely introduced to the outer shelf area by events of intrusion of deeper Slope Water. This pattern resembles the inshore-offshore community gradient related to temperature, salinity and distance to shore which was found for the Scotian shelf (Tremblay & Roff 1983). In another study from the Saronikos Gulf, Greece, correspondence analysis showed that the seasonal evolution of zooplankton was correlated to environmental variables such as temperature, and hydrography, mediated via the influence of open sea and topography (Siokou-Frangou 1995). A similar setting was found here at Nordvestbanken in northern Norway, where the temporal evolution through the season in the copepod community was correlated to both a seasonal (temperature) and an inshore-offshore community gradient.

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