

# Patterns in the variations of copepod spring and summer abundance in the northeastern Norwegian Sea and the Barents Sea in cold and warm years during the 1980s and 1990s

K. S. Tande, S. Drobysheva, V. Nesterova,  
E. M. Nilssen, A. Edvardsen, and V. Tereschenko



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Abundance estimates of copepodite and adult *Calanus finmarchicus*, *Pseudocalanus* spp., *Oithona atlantica*, *O. similis*, and *Oncea borealis* have been obtained twice a year by PINRO for the northeastern Norwegian Sea and the Barents Sea for the 30-year period 1964–1994. The data cover the upper 50 m of the water column during spring or early summer (i.e. April–July) along five inshore–offshore transects at 67°30'N, 71°10'N, 72°50'N, from North Cape to Bear Island, and at Kola (33°30'E). Along the Kola transect, data are also available for three depth strata covering the entire water column. For this study, information is extracted from these data sets for eight years, three cold (1979, 1980, and 1981) and several intermediate and warm years (1983, 1984, 1989, 1991, 1992). Spatial distribution patterns and the demography of *C. finmarchicus*, the target species, are described for the study area. In the time window studied, changes in abundance of *C. finmarchicus* between years appear to be a large-scale phenomenon throughout the entire study area. Unlike the results of previous studies, no clear interannual relationship between water temperature and copepod abundance was found. A correspondence analysis including the smaller copepod forms, as well as temperature and salinity data, revealed a consistent regional difference in the demography of *Calanus*, with stages from CIV to adult more common in the southwest of the study area. Other copepod taxa dominated over the shelf in the northeast of the study area, perhaps related to differences in the physical environment and in habitat preference.

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K. S. Tande, E. M. Nilssen and A. Edvardsen: Norwegian College of Fishery Science, University of Tromsø, N-9037 Tromsø, Norway [tel: +47 77 644524; fax: +47 77 646020; e-mail: kurt@nfh.uit.no]. S. Drobysheva, V. Nesterova, and V. Tereschenko: Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO), 6 Knipovich Street, Murmansk 183763, Russia.

## Introduction

Recently, climate variability has challenged our understanding of the basic mechanisms for natural variation in the atmosphere and oceans and of the marine biota. In physical and biological oceanography, the zooplankton link has been considered a likely candidate for mediating climatologically induced signals into the marine pelagic biota. In order to understand the role of climate, time-series have been established to provide an empirical basis for substantiating how zooplankton changes with time. Such monitoring programmes have

been repetitive measurements of either zooplankton biomass or species over time, with few prior assumptions about the behaviour of the variable or the frequency spectrum of its variability (Wiebe *et al.*, 1987; McGowan *et al.*, 1996).

The need for long-term data has prompted the establishment of zooplankton monitoring programmes in several regions. The most extensive data sets have been gathered for the California Current (California Cooperative Oceanic Fisheries Investigations), and for the Gulf of Alaska, the North Atlantic, and the North Sea [Continuous Plankton Recorder (CPR)]. In addition,

several more national or regionally based data sets, such as those in Icelandic and Faroese waters, have been developed. Some of the studies have demonstrated large-scale physical and biological change throughout much of the marine habitat over the past few decades. For instance, in the Northeast Pacific Ocean, a number of studies have suggested that biological changes occurred fairly suddenly sometime around 1976/1977, concurrent with a dramatic shift in the physical regimes (see Brodeur *et al.*, 1996). Also, for the California Current a negative relationship between zooplankton biomass and temperature over time has been demonstrated for the 43-year period 1946–1988. Between 1950 and 1990, a temperature increase of 0.8°C in the upper layer of that current was associated with a dramatic large decline in zooplankton biomass (McGowan *et al.*, 1996). These studies, along with CPR studies in the North Atlantic, show that most biotic changes in space and time are of low frequency and closely associated with large-scale climatic trends in both the Pacific and the Atlantic (CPR Survey Team 1992; McGowan *et al.*, 1996).

In the Norwegian Sea and the Barents Sea, substantial research effort has been undertaken during the latter part of the 20th century, especially by Russian and Norwegian scientists. The notable variations observed in the physical environment of the Barents Sea have been proposed as having a significant effect on the general conditions to which the marine biota of the area is exposed. The variations are seen in the long time-series of temperature of the inflowing water masses (as, for instance, at the Kola meridian), where the temperature has alternated between successive warm and cold periods of about 3–5 years (Midttun, 1989). The links between climatic fluctuations in the Barents Sea have been addressed in several Norwegian studies (e.g. Skjoldal *et al.*, 1992; Loeng *et al.*, 1997), but no long-term sampling programme on zooplankton has been established (although see Skjoldal and Rey, 1989).

A Russian research programme monitoring zooplankton biomass and species composition in the northeastern Norwegian Sea and the western part of the Barents Sea has been running for 30 years (see Degtereva, 1979). The Trans-Atlantic Study of *Calanus* (TASC) project has initiated cooperation between the University of Tromsø and PINRO with the aim of reanalysing these data using modern and novel statistical approaches. The data set is valuable because of its length and the fact that the data were gathered by a sampling and processing programme that did not change throughout the >30 years. The information may, in the long term, provide a basis for new insights into the mechanisms that govern the magnitude and frequency of zooplankton variability in the region.

The objectives of the current study are to compare and contrast the variability in abundance of a suite of copepod taxa (with particular emphasis on *Calanus*

*finmarchicus*) in relation to selected variables such as temperature, salinity, latitude, longitude, depth, and time of year. For the purpose, we have selected eight individual years during the period 1979–1994 when data were obtained once or twice during the productive season of April–July. The eight years were characterized by sea temperatures that were notably high or low. Data along five transects between Lofoten in the southwest and the Kola meridian in the east were used for the purpose.

## Materials and methods

This purpose of the analysis was to reveal possible links between climate and plankton in the northeastern Norwegian Sea and the Barents Sea. The selected years had notably warmer or cooler sea temperature than the long-term mean, as recorded downstream of the study area along the Kola meridian (see Figure 1). The paper is a first effort at reanalysing the plankton data at PINRO, and owing to the workload involved, the plankton data from only those years with the largest recent temperature anomalies were selected. Those years were expected to have produced the strongest responses by the zooplankton community. The three cold years selected were 1979, 1980, and 1981; the five warm years were 1983, 1984, 1989, 1991, and 1992.

Samples were taken once or twice between the end of April and the end of July (Degtereva, 1979) along five standard sections from Lofoten in the southwest to Kola in the east (Figure 2). This sampling programme monitored the entire region every year until the late 1980s, whereafter only the two most northeastern transects were covered.

A Juday net (168- $\mu$ m mesh) with 37-cm opening diameter was used to sample the water column from 50 m to the surface at stations approximately five miles apart along each transect. Along the Kola transect, the entire water column was sampled regularly in three depth strata (0–50 m, 50–100 m, and 100 m to the bottom). Identification of zooplankton was to species level. When a sample exceeded approximately 1000 individuals, two subsamples each of 1% of the total were counted (Degtereva, 1979).

## Data extraction and analysis

Data on numerically the most important species were recorded consistently over time, so we selected five copepod taxa (*C. finmarchicus*, *Pseudocalanus* spp., *Oithona similis*, *O. atlantica*, and *Oncea glacialis*) for the current study. Staging of these five varied (see Table 1). *C. finmarchicus* were recorded as nauplii I–VI, copepodites I–V, males and females (13 categories). *Pseudocalanus* spp. were recorded as copepodites I–V, females

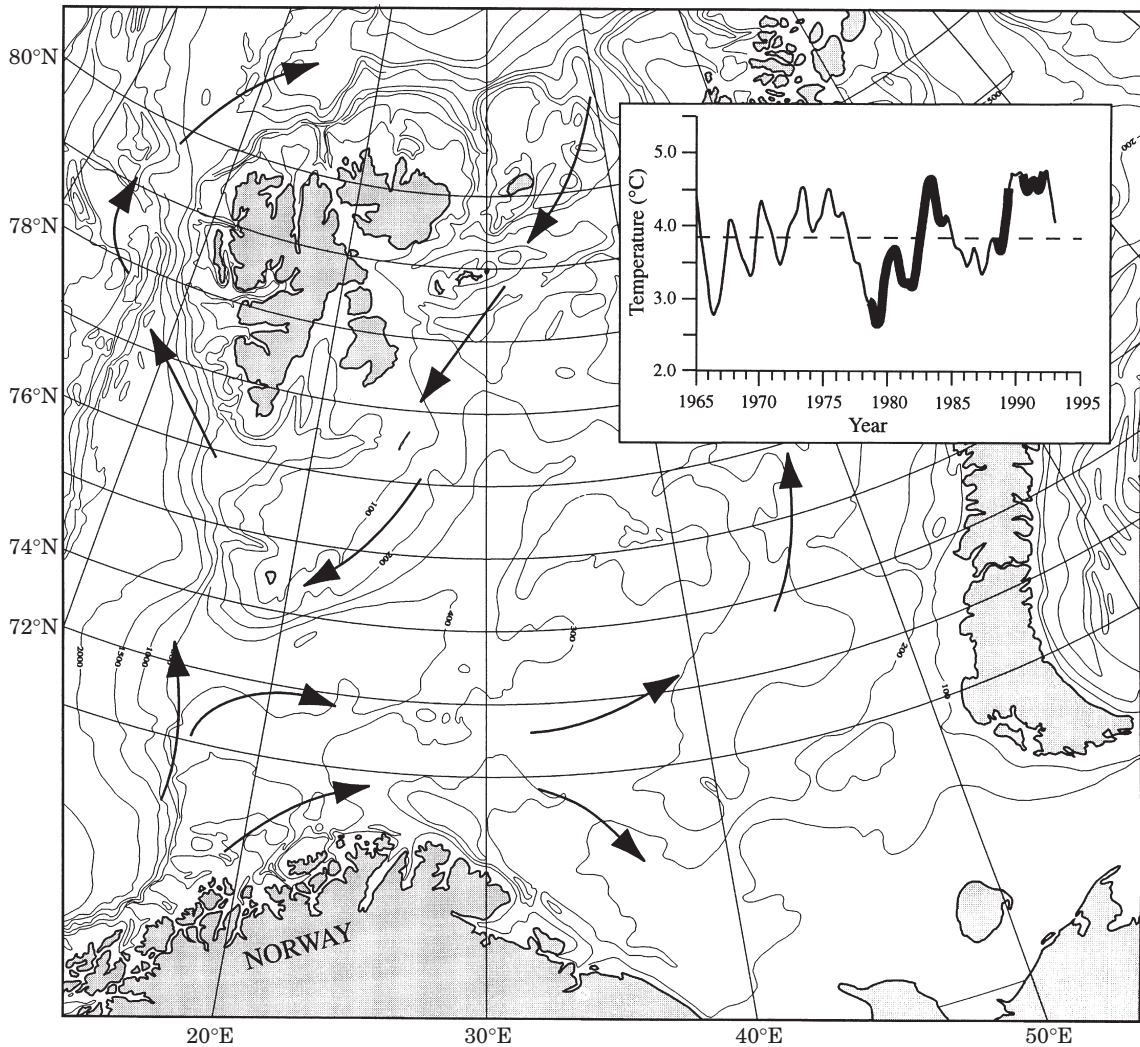


Figure 1. Map of the study area with the main bottom topography and surface current features. Sea temperature (integrated 0–200 m, Fourier treated and smoothed) at the Kola meridian transect of the Barents Sea for the period 1965–1994. The years of the current study are given in boldface. By courtesy Harald Loeng.

and males (seven categories), and the other three were grouped into three categories each, namely juvenile copepodites, females, and males. In all, there were thus 29 categories of zooplankton for the analysis.

The copepod data were available as total numbers, and we calculated the abundance per  $\text{m}^3$  based on the integrated tow for the upper 50 m by assuming 100% net efficiency over the sampled distance. Towing range was recorded, enabling us to make separate conversions for each sample on the basis of the lowest depth at each station, which varied in the range of  $\pm 5$  m around the standard depth of 50 m.

One problem in community ecology analysis is to discover how a multitude of species responds to such external factors as environmental variables. Regression

and ordination have recently been integrated into techniques of multivariate direct gradient analysis, named canonical ordination (Jongman *et al.*, 1987; ter Braak and Prentice, 1988). CANOCO (canonical community ordination), which is free from assumptions of linearity between species abundance, can detect unimodal relationships between species and environmental variables (ter Braak, 1986, 1987a, b). For a more detailed description and documentation of CANOCO, readers are encouraged to consult the literature covering, for instance, marine phytoplankton communities (Bakker *et al.*, 1990) and marine and freshwater fish communities (Copp, 1992; Wilkins and Myers, 1992).

The CA option (i.e. indirect correspondence analysis) of CANOCO was used to examine the relationship

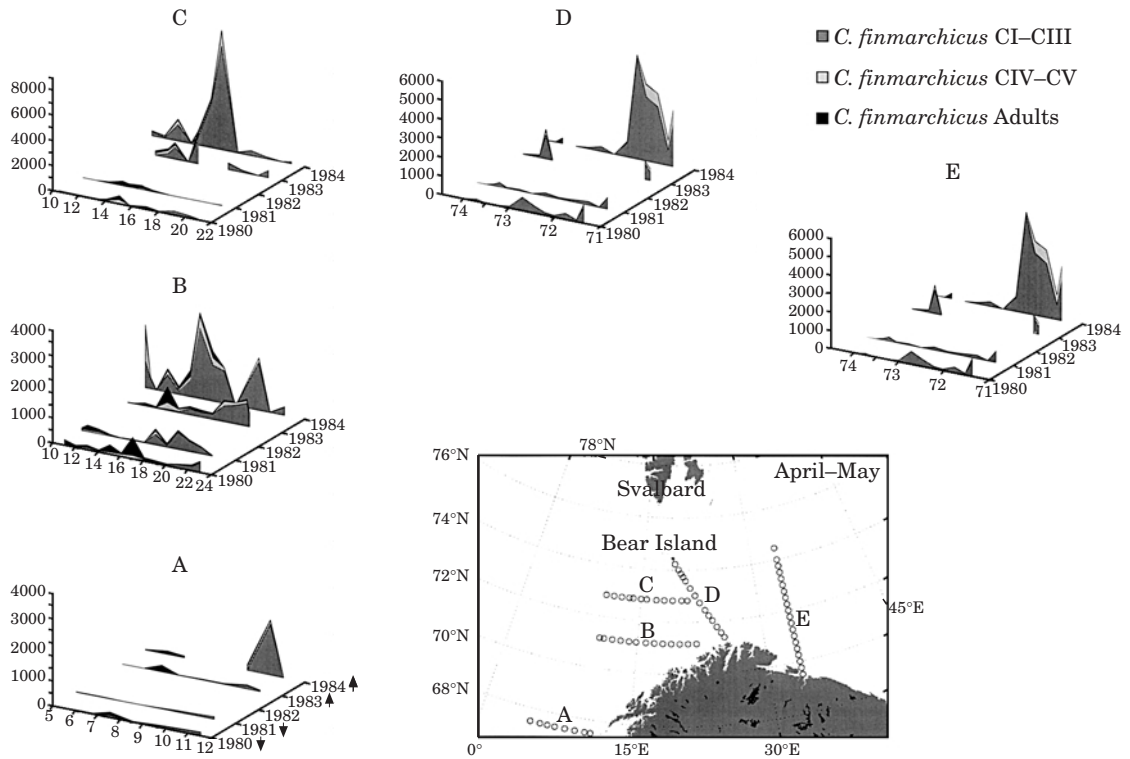


Figure 2. Abundance of *Calanus finmarchicus* in the upper 50 m of the water column during April and May (i.e. spring) for the two cold years (1980, 1981) and the two warm years (1983, 1984) along transects A–E.

Table 1. Copepod taxa and stages with symbols used in the CA analysis.

Taxon	Stage	Symbol
<i>Calanus finmarchicus</i>	Nauplii I–VI	CaN1–CaN6
	Copepodite stages I–V	CafiC1–CafiC5
	Adult male and female	CafiM and CafifF
<i>Pseudocalanus</i> spp.	Copepodite stages I–V	PsC1–PsC5
	Adult male and female	PsM and PsF
<i>Oithona similis</i>	Juvenile	OisiC1_5
	(i.e. copepodite stages I–V)	
<i>Oithona atlantica</i>	Adult male and female	OisiM and OisiF
	Juvenile	OiatC1_5
<i>Oncea glacialis</i>	(i.e. copepodite stages I–V)	
	Adult male and female	OiatM and OiatF
	Juvenile	OnglC1_5
	(i.e. copepodite stages I–V)	
	Adult male and female	OnglM and OnglF

between the abundance of copepods in the northeastern Norwegian Sea and the Barents Sea for the eight years selected. In the current analysis (square root transformation of species data), 27 copepod categories (nauplii I of *C. finmarchicus* and male *O. atlantica* were removed) and 365 samples or stations were included. Inclusion of environmental factors (depth, month, year, latitude, longitude, salinity, and temperature) demonstrates how the species and the environment are associated. It also

allows one to search for relationships; for instance, species arrayed closely together have similar distributions and affiliations to the environmental variables. The major points to be borne in mind when interpreting the CA plots are that environmental factors with long “arrows” are better correlated with the axis than those with shorter “arrows”, and accordingly are more strongly related to the species pattern in the plot (ter Braak, 1986, 1988). “Arrows” point in the direction of

Table 2. Information from the PINRO field sampling programme used in the present analysis. Sampling date for the various transects is given as the earliest one on which it was sampled, and the number of stations is given in parentheses. Note that "Summer north" D and E are identical with "Summer all" D and E. Only data in "Spring" and "Summer all" were used as the basis for the CA analysis, 345 stations with copepod information in total.

Transect	Location	Season	Date							
			1979	1980	1981	1983	1984	1989	1991	1992
A	67°30'N	Spring		26.04 (08)	26.04 (08)	24.05 (08)	24.05 (07)			
B	71°10'N		04.05 (13)	03.05 (13)	02.05 (13)	02.05 (13)				
C	72°50'N		11.05 (12)	09.05 (10)	07.05 (09)	08.05 (12)				
D	74°14'N		11.05 (12)	13.05 (14)	13.05 (09)	13.05 (13)				
E	33°30'E		24.05 (18)	21.05 (20)	21.05 (10)	24.05 (17)				
A	67°30'N	Summer all	05.06 (07)			10.06 (08)				
B	71°10'N		11.06 (13)			18.06 (13)				
C	72°50'N		14.06 (11)			25.06 (07)				
D	74°14'N		17.06 (14)			30.06 (13)				
E	33°30'E		28.06 (19)			10.07 (10)				
D	74°14'N	Summer, north	17.06 (14)			30.06 (14)		27.06 (14)	18.06 (08)	30.06 (10)
E	33°30'E		28.06 (20)			11.07 (20)		10.07 (09)	26.06 (09)	10.06 (11)

maximal change of given environmental factors in the plot, and the length of the "arrow" is proportional to the degree of change (i.e. large change is reflected by long "arrows"). Species can be projected relative to "arrows", such that the ordering of species along the axis of the "arrow" is approximately the ranked, weighted median value of the species relative to the environmental factor. The absolute length of the "arrow" is immaterial; it is the relationship between its length and its direction that is important. A Windows Version 4.0 1998 (Centre for Biometry Wageningen, The Netherlands) was used for the CANOCO analysis.

## Results

During processing of the data, especially those from the Kola transect, it became clear that there was temporal variation in the vertical descent of *C. finmarchicus* from the surface layer, and that this took place during mid-summer along the Kola transect. As the transects were sampled at different times in the selected years, we have grouped and presented the data into three time windows: (i) spring, all transects; (ii) summer, all transects; and (iii) summer, northeastern transects. Owing to the quantity of data available for all taxa, we present the data as, first, a general overview of the temporal and spatial variation of CI–CV and adult *C. finmarchicus* grouped according to the criteria given above (see also Table 2), and, second, as a CA analysis of 27 copepod categories in a search for significant links between copepod species and environment variables.

(i) *Spring, all transects* – We have four years in which the zooplankton samples were obtained during April and May, two cold (1980, 1981) and two warm (1983, 1984). The demography of *C. finmarchicus* reflects spatial

differences in the annual period of recruitment period in the study area (Figure 2), with a predominance of CI–CIII over the shelf and adults in the open ocean. This picture is only present along transects A–C, whereas the two in the northeast do not show any notable presence of adults at that time of the year. Interannual variations in abundance are strong and appear as a consistent signal throughout the entire area; in 1980, for instance, biomass was low from west of Lofoten to the central Barents Sea (i.e. at the Kola meridian). Abundance was greatest in 1984 throughout the study region; that year too *C. finmarchicus* had its highest proportion of CIV and CV in the population.

(ii) *Summer, all transects* – Copepod data covering the entire area during summer are available for 1979 and 1983 (Figure 3). Here again, the abundance of *C. finmarchicus* varies consistently over the entire area, with high values in a cold year (1979) and low values in a warm year (1983). No clear difference in demography is apparent during the two years, but there is a higher proportion of adults in the three westernmost sections in both years.

(iii) *Summer, northeastern transects* – We have data for five years for two adjacent transects in the Barents Sea (Figure 4); abundance was greatest in both a cold (1979) and a warm (1989) year. There is, however, an inverse relationship between abundance and latitude along transects D and E, with high abundance in the north of the Kola transect (the easternmost transect E) and to the west (transect D) in coastal waters to the south, where there were higher proportions of CIV and CV.

### Species–environment links (CA analysis)

The results of the CA analysis reveal the day of sampling as a significant variable, with both longitude and

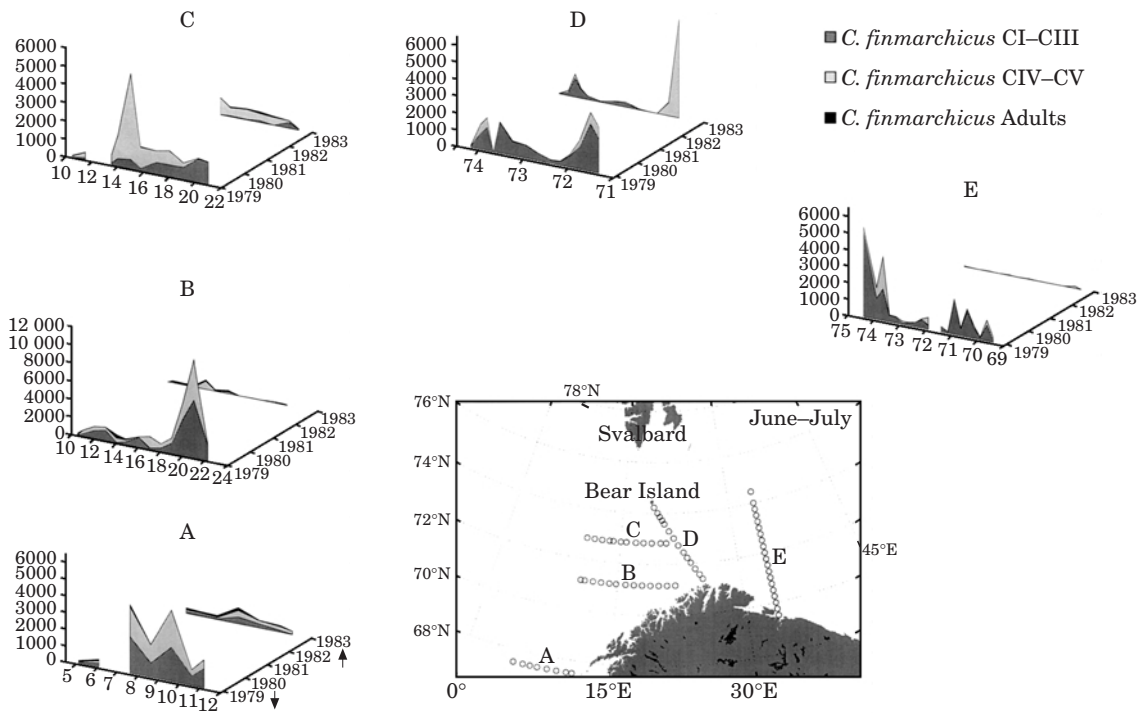


Figure 3. Abundance of *Calanus finmarchicus* in the upper 50 m of the water column during June and July (i.e. summer) for the cold (1979) and warm (1983) years along transects A–E.

latitude as two other important variables (Figure 5). These latter two were orientated opposite to total station depth and the environmental variable temperature. The species appeared to be organized into two groups (see Figure 5), one with all stages up to CII of *C. finmarchicus* plus all the other smaller copepod forms, namely *Pseudocalanus* spp., *Oithona* spp., and *Oncea glacialis* (upper left quadrant), and a second group of CIII-adult *C. finmarchicus* (lower right quadrant).

In order to emphasize possible structures in the data related to regional differences, we removed the “day of sampling” as a co-variable. The results show that the general integrity of the first analysis is intact (Figure 6), but that species orientation is rather different. The majority of species are gathered around the centre of the two axes. The copepodite stages and adults of *C. finmarchicus* are found along the longitude/latitude and depth arrow, which may indicate that the *Calanus* component has the largest variance of the species studied.

If the analysis is performed removing latitude and longitude as co-variables, there is a separation according to the geographical location of the transects (Figure 7). This means that the westernmost transects (A, B, and C) form a coherent orientation, whereas the two northeastern ones (D and E) are orientated in the opposite direction. There is high variance for CIV, CV, and adult

*C. finmarchicus* for transects A–C, whereas the other copepod entities are located more closely to the two most northern sections.

## Discussion

Variations in physical conditions in the Barents Sea are considered to be of an advective nature (Helland-Hansen and Nansen, 1909; Blindheim, 1987). Increase in water temperature changes at Lofoten and along the Kola transect with a time-lag of about one year (Midttun, 1989). This is considered to be linked to the magnitude of inflow of the Atlantic Current (as the North Cape Current) and the Norwegian Coastal Current (Loeng, 1991; Loeng et al., 1997). On the other hand, Midttun (1989) states that, although that variation in current magnitude could be forced on the Barents Sea from outside, it could just as well be a result of processes taking place in the Barents Sea itself. Clearly, therefore, the mechanisms for sea and climate change in the Barents Sea are not well understood, a statement just as valid for the links between physical forcing and zooplankton biomass.

The main scope of the paper was to analyse the copepod community during two differing climate

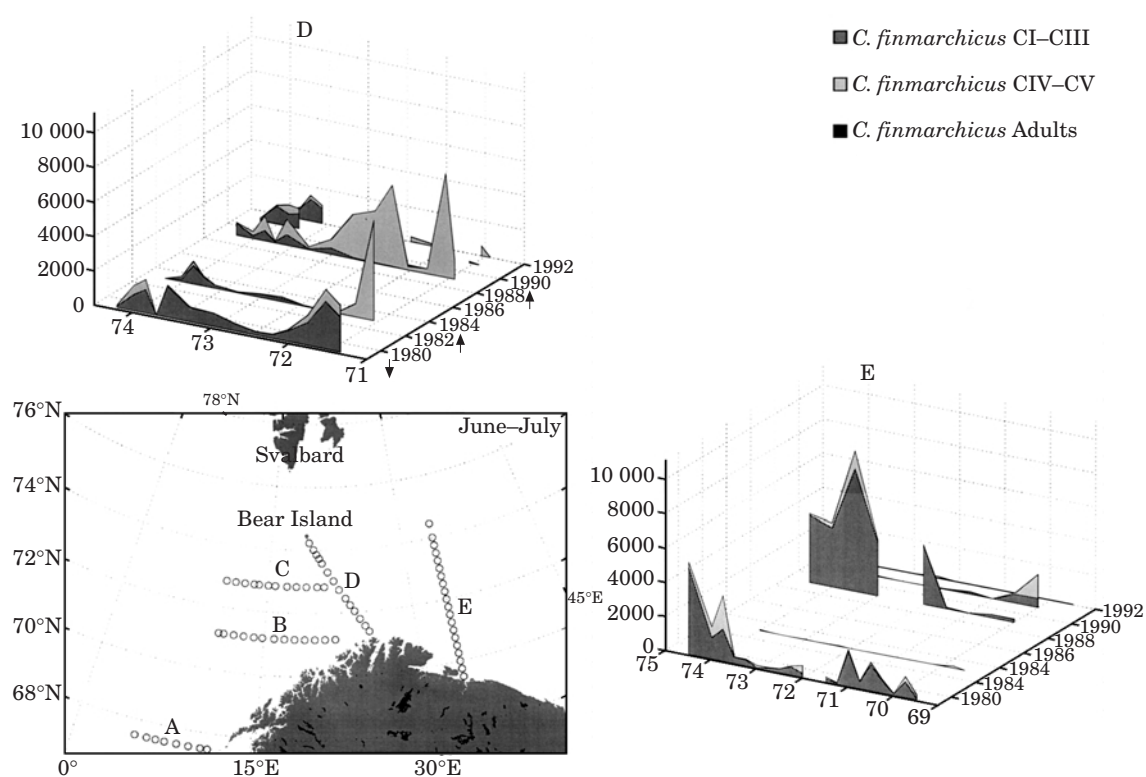


Figure 4. Abundance of *Calanus finmarchicus* in the upper 50 m of the water column for the two easternmost transects during June and July (i.e. summer) of 1979, 1982, 1989, 1991, and 1992.

periods, one with cold and one with warm water masses in the region of the Barents Sea. The analysis rests on eight selected years of abundance data for specific copepod taxa in surface waters during different time windows within the productive season. The data from the PINRO database would not in this context enable us to look for amplitudes and frequencies in the variation of plankton that may be present during the whole 30-year time period. The ontogenetic and seasonal vertical distribution of copepods is similar throughout these waters (Falkenhaug *et al.*, 1997), which means that stages aggregate in the upper 50 m during only 2–3 months (i.e. May and June). Thereafter, the stock descends to depths below the sampled strata, which may or may not be synchronized in time and space within and between years. This makes intra- and interannual comparison difficult in the present data sets, something that needs to be kept in mind when the significance of the results is being discussed.

The present analysis demonstrates that shifts in abundance of *C. finmarchicus* may be a large-scale phenomenon, i.e. that the entire study region from Lofoten to the central Barents Sea is affected in a similar manner during years of high and low abundance of the copepod (Figures 2–4). For instance, the two years with notably

high abundance (1979 and 1984) had above-average abundance along all transects, whereas in other years (1980, 1981, and 1983) abundance was consistently low. Although we have restricted the number of years in the analyses, there are a few exceptions to this pattern, mainly linked to those transects that cover the largest environmental gradient (transects A and E). In the south (transect A), there is a tendency for abundance to increase in an onshore direction. This, of course, may be linked to differences in the environment between stations in the open ocean in the west and stations over the shelf, i.e. two regimes each with its own particular timing of copepod recruitment and production (Pedersen *et al.*, 2000). Along the Kola meridian (transect E) there is a tendency for abundance to decrease towards the south (for 1979, 1980, 1981, 1989), a trend that may be rooted in differences in faunal and seasonal succession between Arctic and Atlantic water masses. Colder water masses in the north have generally greater copepod abundance and biomass and lower seasonal amplitude than Atlantic waters farther south (Tande and Slagstad, 1990; Tande, 1991).

Based on the eight years of analyses in the present paper, there is no clear relationship between water temperature and copepod abundance in the region. The

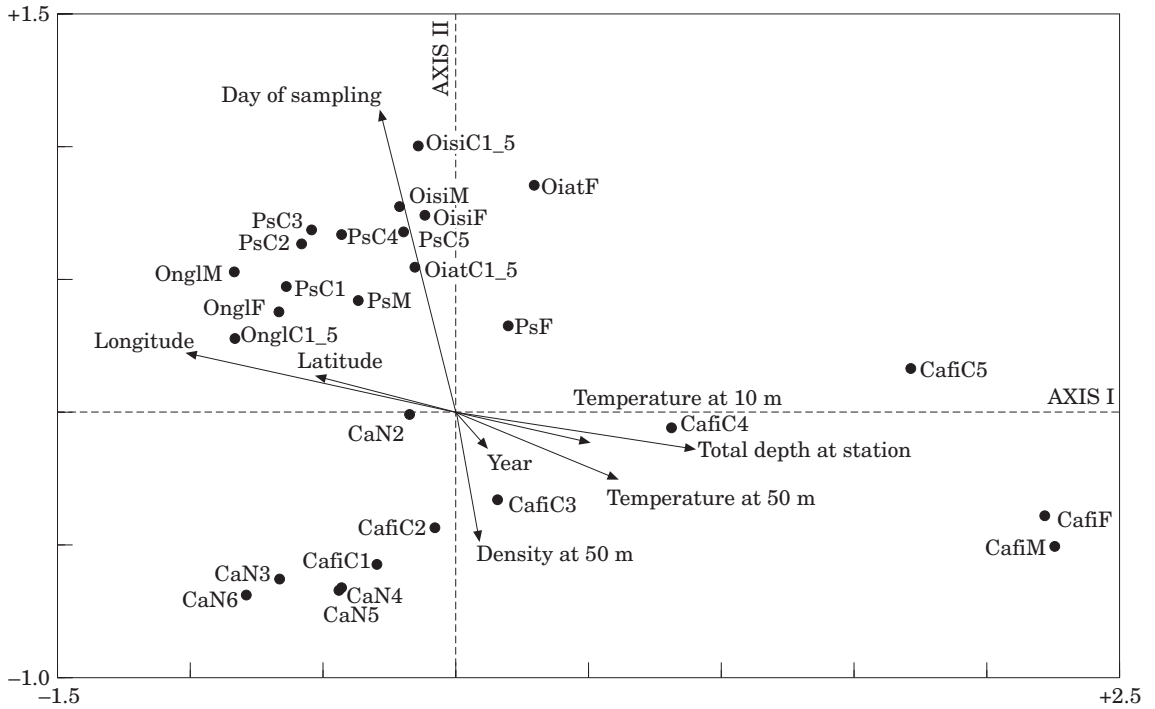


Figure 5. Correspondence analysis (axes I and II) of the variation in abundance of selected copepod taxa of the zooplankton community and their relation to temperature, salinity, and depth of sampling. See Table 1 for explanation of symbols.

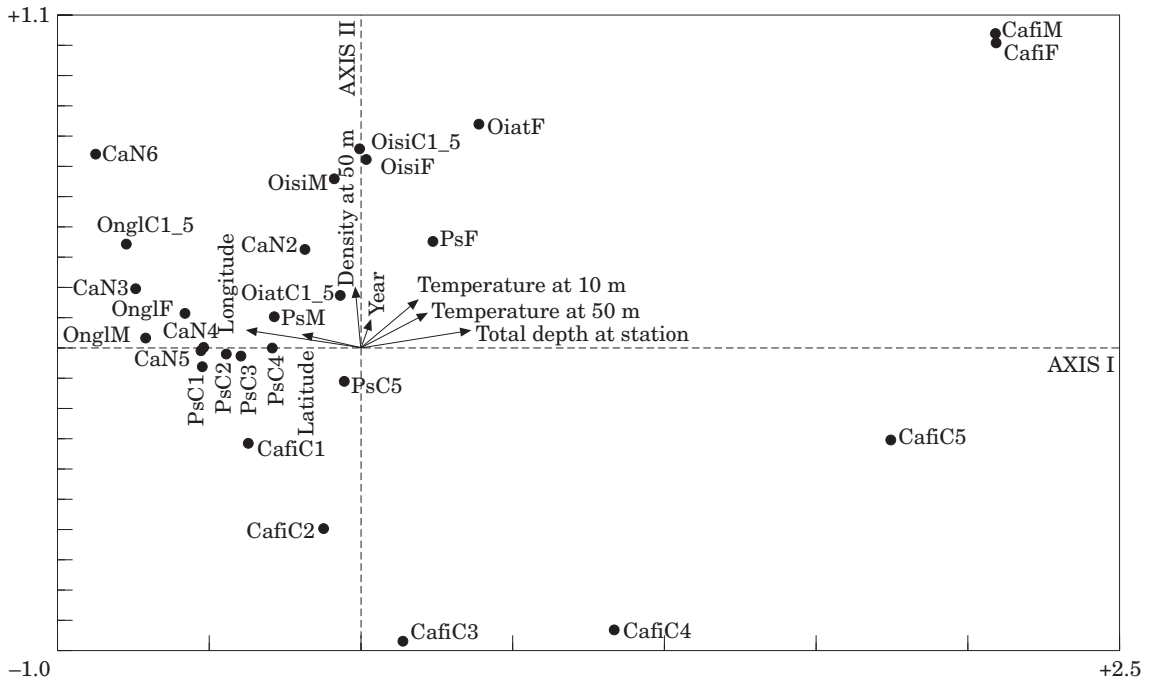


Figure 6. Correspondence analysis (axes I and II) of the variation in abundance of selected copepod taxa of the zooplankton community and their relation to environmental conditions when day of sampling was removed as a covariate. See Table 1 for explanation of symbols.



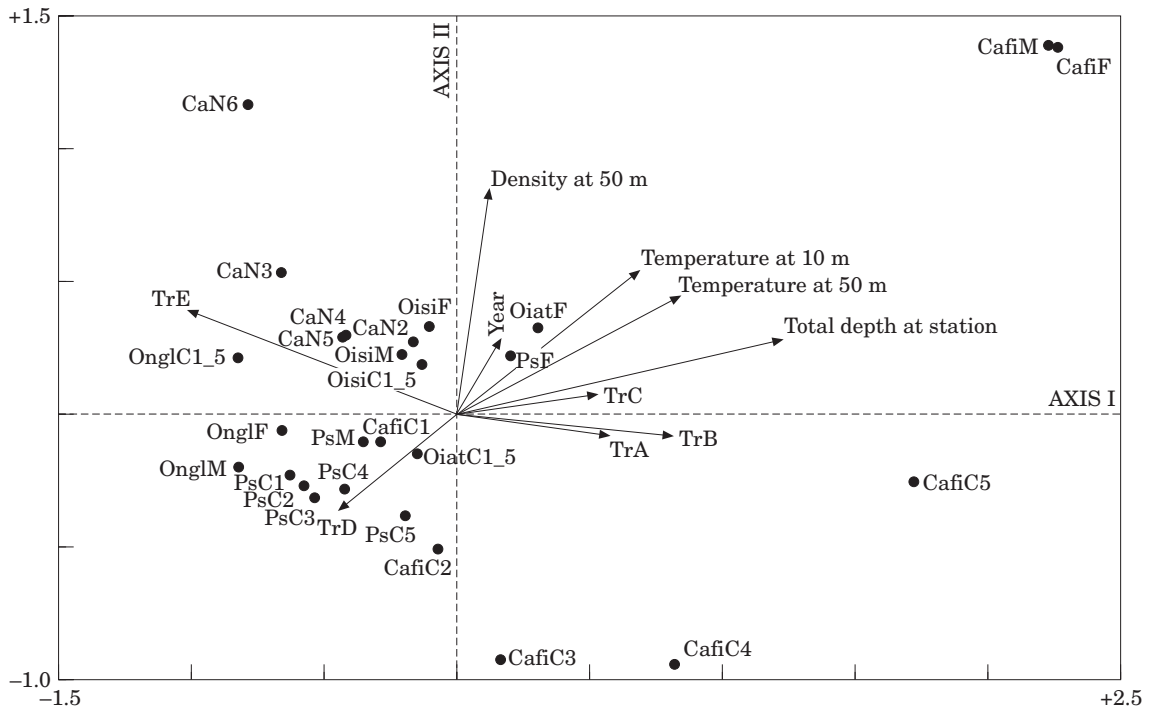


Figure 7. Correspondence analysis (axes I and II) of the variation in abundance of selected copepod taxa of the zooplankton community and their relation to environmental conditions when latitude and longitude were removed as a covariate. See Table 1 for explanation of symbols.

abundance of *C. finmarchicus* in the area of study varies extensively between years, with two examples of particularly high total population abundance (1979 and 1984). In 1979 the water temperature was cold, but it increased rapidly from a winter minimum of  $-1.5^{\circ}\text{C}$  to  $-0.2^{\circ}\text{C}$  by late summer. In 1984, the temperature was above the long-term mean. On the other hand, summer abundance appears to be low during years of high water temperature in the study region (1983, 1989, 1991, and 1992). In contrast to the present findings of no clear relationship between water temperature and copepod abundance, the mean zooplankton biomass integrated over the entire water column for the northern central region of the Barents Sea from 1979 to 1990 was inversely related to sea temperature (Skjoldal *et al.*, 1992). Biomass was at its peak during the cold periods of 1979–1982 and 1987–1988, but this is not easily explained by the hypothesized mechanisms for the advective transport of boreal plankton with the inflow of Atlantic Water to the Barents Sea advocated by Skjoldal *et al.* (1992). A significant negative correlation between macrozooplankton biomass and water temperature off California has been documented by McGowan *et al.* (1996) for the 40-year period 1950–1980. This may be linked to large-scale advection of cold-water zooplankton communities via the California Current, but the nature of the underlying causal mechanisms of the changes in advection is

complex and not yet understood. A simple and straightforward physiologically driven response of copepod population biomass to increased temperature seems not to occur in the copepod community in either the Nordic Seas or the California Current.

There is a tendency for a consistent difference in the demography of *C. finmarchicus* in the area (Figure 5). In the time periods covered, irrespective of the climate conditions, the sources of recruitment of adults appear to be particularly strong in the northwest part of the study area (Figures 2–4), where abundance of adults was high for all years. These adults may be linked to a late emergence from diapause and spawning in May–July in the Norwegian Sea proper, later than the traditional spring spawning on the shelf. This regional difference in demography is also expressed in the CA analysis, in which CIV, CV, and adult *Calanus*, probably as late-ascending  $G_0$ , are strongly associated with higher water temperatures and deep stations in the west and southwest (see Figure 5). Variation in the demography of *C. finmarchicus* appears as a patchwork generated by seasonal and regional environmental signatures, variables that are hard to separate owing to the advective nature of the study region. This is also underlined by having transects A–C and D–E orientated as two groups along axes I and II (see Figure 7). The southern three transects are characterized by CIII–CV and adult

*C. finmarchicus*. The nauplii of *C. finmarchicus* are more strongly associated with the Kola meridian (transect E), which may be linked either to an early spawning of  $G_0$  *C. finmarchicus* or to other sibling species in the north.

Of the smaller copepod taxa, *Oncea glacialis* was more strongly linked to increasing latitude and longitude than *Oithona similis* or *O. atlantica*. The latter two were, along with *Pseudocalanus* spp., more abundant during summer than spring (cf. day of sampling in Figure 5), which might indicate ecological differences among the taxa. Although these four categories have been consistently identified over time in the current material, we know that *Pseudocalanus* spp. contains two species (*P. acuspes* and *P. minutus*) and that the two *Oithona* spp. may hide a mixture of sibling species (F. Norrbin, pers. comm.). Nevertheless, the CA analysis enables us to depict two of the species according to their known ecological differences. *O. glacialis* is affiliated with colder water masses, whereas *O. atlantica* is more abundant in Atlantic waters (Brodskii, 1967).

## Conclusions

Based on the data and analysis we reach the following conclusions, which we hope can be substantiated by further analysis of the data in the PINRO database:

- (1) The abundance change of *C. finmarchicus* between years appears to be a large-scale phenomenon throughout the entire study area.
- (2) There is no clear relationship between water temperature and copepod abundance, but the analyses question the previously proposed positive relationship between water temperature (i.e. advection) and copepod abundance in the study region.
- (3) There is a consistent regional difference between the demography of *Calanus* and the abundance of the other copepod taxa studied, in particular related to longitudinal and latitudinal changes in environmental conditions.
- (4) The Kola transect, which has been monitored by PINRO with samples covering the entire water column every summer throughout the period 1969–1994, may have the potential to reveal the frequencies and links between climate and plankton in the Barents Sea.

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