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REPRODUCTION OF ZOOPLANKTON IN RELATION TO INITIATION OF SPRING PHYTOPLANKTON BLOOM IN THE BARENTS SEA

By

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ABSTRACT

The phytoplankton spring bloom development and zooplankton reproduction were investigated in April 1986 in the central and northern Barents Sea. Different stages of phytoplankton bloom development were found, reflecting differences in water column stability and illumination due to ice melting. Eggs and nauplii of Calanus, Pseudocalanus, Microcalanus and Oithona spp. occurred mostly in the upper 50 m without any pronounced maxima in their vertical distributions. The total numbers of eggs and nauplii of Calanus finmarchicus and C. glacialis tended to be higher at bloom stations than at pre-bloom stations, and also to show a general increase during the investigation period. The start of spawning was estimated to early February and was not influenced by the phytoplankton bloom development. Neither did the developmental state of the copepodite population seem to be influenced by the bloom development. The spawning activity, however, seemed to have a maximum coinciding with the early phase of the bloom development.

INTRODUCTION

Heinrich (1962) classifies copepods in three categories dependent on time of first breeding relative to the vernal spring bloom. Calanus finmarchicus and Pseudocalanus sp. is not able to bread before the bloom. C. cristatus from the Bering Sea breed independant of phytoplankton growth, and the third case is exemplified by Oithona similis breeding the year around. Østvedt (1955) writes that spawning of C. finmarchicus starts early in the spring, independant of phytoplankton bloom. From own previous investigations (Skjoldal et al, 1987) spawning of Calanus finmarchicus seems to occur in early spring (late April - early May).

In order to elucidate which relations exist between spawning and the early development of eggs and nauplii of copepods and the spring phytoplankton bloom in the Barents Sea a cruise was caried out in April 1986. The cruise was planned as a part of the national research program PRO MARE (Norwegian Research Program for Marine Arctic Ecology), where the Institute of Marine Research contributed with mapping of oceanographic data, phytoplankton, nutrients, and zooplankton studies, with stress on the early phases of development (Skjoldal 1986). The investigated area covered partly open sea, and partly ice covered areas. The present paper presents some of the results obtained during that cruise.

INSTRUMENTATION AND METHODS

The cruise was carried out with two of the Nordkapp class coastguard vessels, K.V. "Senja" (2-13 April) and K.V. "Andenes" (14-23 April). The area between the Svalbard Bank (not included here) and the Central Bank ($73^0 30'N$ - $76^0 15'N$; $20^0 E$ - $34^0 E$) was covered (Fig. 1). An extensive program was carried out at selected stations which were taken approximately once a day. The research area was partly in open sea and partly in close pack. The position of the ice border is indicated in Fig. 1.

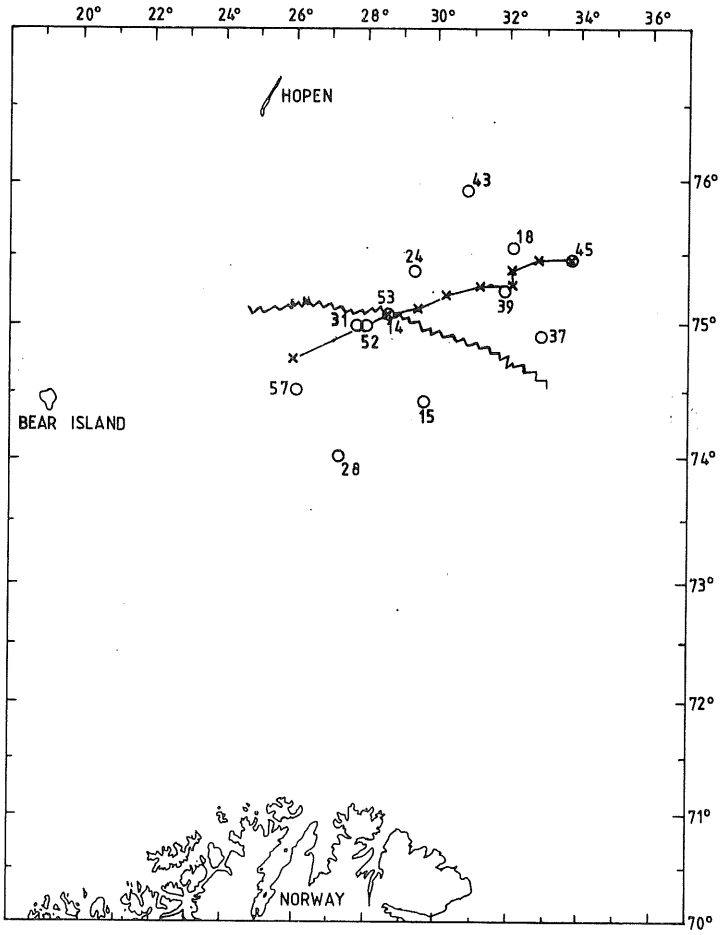

Figure 1. Map showing the major sampling stations (open circles), a transect from station 45 to 56 (x---x---x), and the ice border from medio April (zig-zag line).

Standard hydrographic sampling was carried out with a Neil Brown MK III CTD sonde coupled together with a Rossette Sampler equiped with 5 liters Niskin bottles.

Samples for nutrients analysis were kept cold at + 1^0C in the dark for a few hours until analysed with an autoanalyser using standard methods.

Samples for pigment analysis were filtered through 0.45 µm pore size membrane filters and stored frozen (-18^0C). Within a few days, the pigments were extracted with 90% acetone for at least 16 hours in the dark. After centrifugation, the fluorescence of the extract was measured both before and after acidification with 5% v/v hydrochloric acid, using a Turner Designs filter

fluorometer. Samples analysed for phytoplankton species composition were fixed to a final concentration of 2% formalin and examined with the inverted microscope method.

Microzooplankton was collected at 14 stations with 30 l Niskin water bottles at (0, 10, 20, 30 (40), 50, 75 and 100 m depths. 12-28 l of the samples were screened through 30µm mesh and preserved in 4 % formaldehyde. Copepod eggs and nauplii were sorted out with 25 times magnification under a stereo microscope, and identified with 100 times magnification. Both eggs and nauplii of copepods were separated into genera/species according to size measurements and morphological characters given in the literature (Oberg 1906, Lebour 1916, Gibbons 1933, Sømme 1934, Wiborg 1948, Ogilvie 1953, Lovegrove 1956 and Marshall and Orr 1972). Because of some discrepancies between the results from different authors the species identification was doubtful.

The vertical distribution of mesozooplankton was obtained with an in situ pump based on a Flygt 4400 mixer mounted at the end of a bent tube with 420 mm inner diameter. The construction is similar to that described in Solemdal and Ellertsen (1984). Pumping times were partly 3 minutes, and partly 6 minutes, and a flowmeter was attached to the pump in most cases. The pump was used at 11 selected stations parallell to the microzooplankton sampling, and the results from five of them are presented in this paper. The catch was divided for dry weight determinations and preservation. The dry weight portion was screened through an 850 µm and a 250 µm mesh to separate the finer fraction from the coarser one. Copepodites of Calanus usually made the bulk of the fraction > 850 µm. The copepods Oithona, Microcalanus, and partly Pseudocalanus, were typical components of the smaller fraction. The samples were placed in deepfreezer and were later dried for one day at 80^0C. Ash content was determined by burning for 12 hours at 600^0C.

The samples for species determination were preserved in 4% formaldehyde. To reduce the sample size before counting, the sample was divided with a plankton divider to 1/2 or 1/4; in some cases to 1/32. Copepods were determined to stage or stage

group. Calanus was identified to C. finmarchicus or C. glacialis depending on size of cephalothorax, and to C. hyperboreus.

A 36 cm diameter Juday net with 180 µm mesh was used to sample 100 m - 0 m, and at 100 m depth intervals below, to obtain a measure of the integrated biomass in the water column. As with the pump, net samples were used both for biomass estimates and for species determinations, and the procedures were similar. Results from 11 net sample stations are included in the report.

RESULTS

HYDROGRAPHY AND PHYTOPLANKTON DEVELOPMENT

With the exception of one station that was taken in arctic waters in the shallow Svalbard Bank, all the remaining stations were taken in the area where the northwards flowing atlantic water reaches its northernmost extension, the Hopen Depth. In order to have a wider perspective of the hydrographical and biological conditions of the area during the cruise, a section across the ice edge zone has been selected (see Fig. 1). The vertical distribution of several parameters in this section is shown in Fig. 2. In the northern part of the section near the Great Bank, the atlantic water with temperature above 0^0C and salinity above 35 o/oo meets the colder and less saline arctic water giving origin to the polar front, especially below 30-40 meters depth where no influence of the ice is observed. Although the arctic water over the Great Bank can not be considered as pure as the one found further north, nonetheless it represent the coldest water mass found during the cruise. In the upper 50 meter a fairly homogenous layer of cold melt water above the atlantic water was found across the section extending from the ice covered area until the southernmost part where it met the atlantic waters in the surface. In the ice edge zone a bloom of phytoplankton with chlorophyll a concentrations up to 9 mg m^{-3} was found which extended about 20 nautical miles into the ice towards the north and the limits

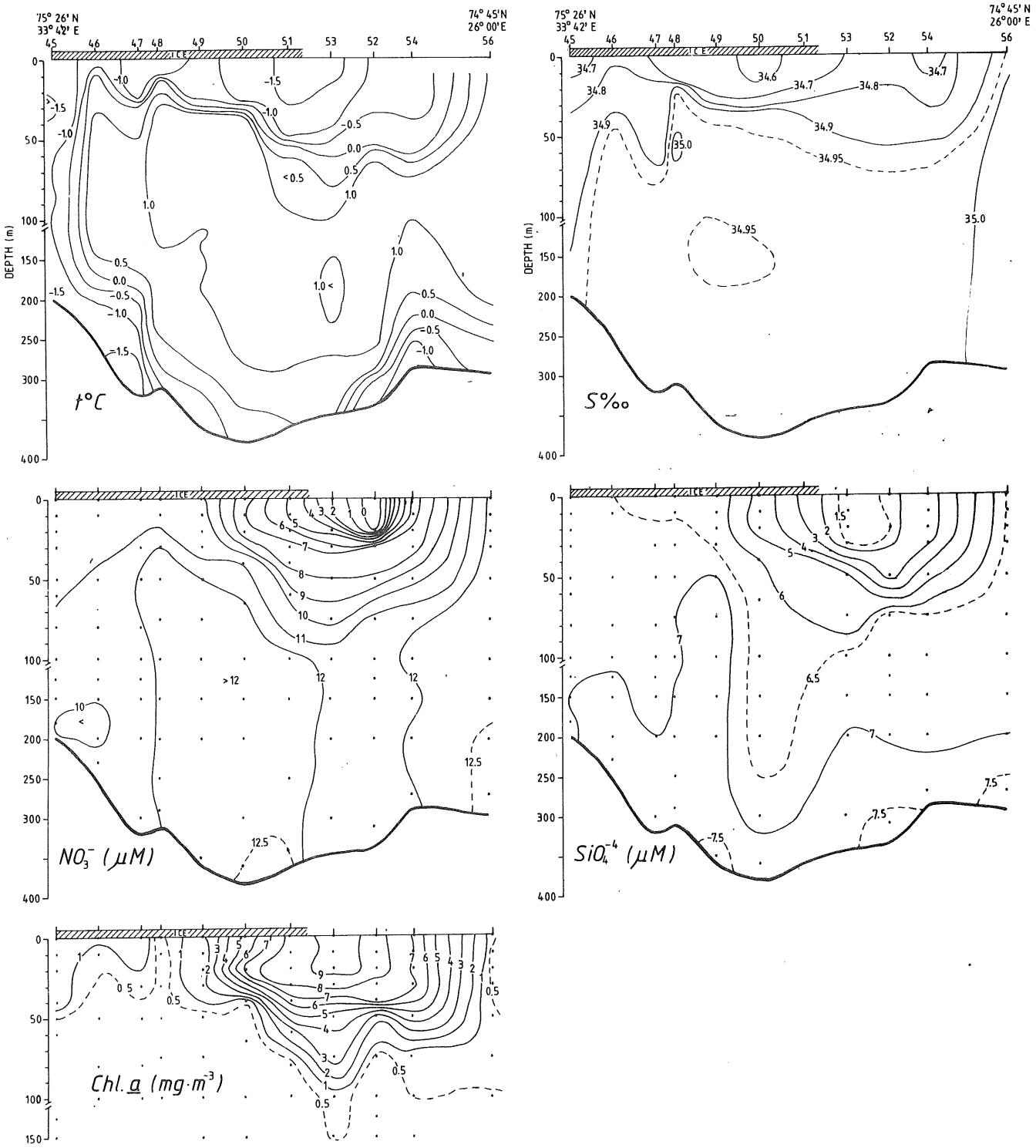

Figure 2. Temperature, salinity, nitrate, silicate, and chlorophyll a in a section across the ice border (st. 45-56).

with the atlantic water to the south. Nitrate was depleted at the core of the bloom while silicic acid concentration was strongly reduced. This bloom at the ice edge extended as deep as 80 meters depth. In the northernmost part of the section chlorophyll a concentrations were much lower but well above

the winter values usually found in this area (less than 0.1 mg m^{-3}) indicating that a certain growth of phytoplankton has taken place in this ice covered area.

The ice edge phytoplankton bloom was completely dominated by diatoms which constituted about 90-95 % of total phytoplankton carbon. Among the most important species where Thalassiosira antarctica, T. hyalina, T. nordenskioldii, Chaetoceros socialis, Nitszchia grunowii and Navicula spp. The phytoflagellate Phaeocystis pouchetii was also found together with the diatoms but only in moderate amounts accounting for no more of 2% of the total phytoplankton carbon. In the other parts of the section, where the bloom had not yet developed, diatoms where also the major constituents of the phytoplankton, although significant amounts of autotrophic small flagellates (less than 5 µm) were also found.

Since the stations where zooplankton sampling was carried out spanned over areas with different phases in the phytoplankton development, an evaluation of this at these stations is due in order to relate them to the zooplankton development. This evaluation has been made taking in consideration the above described situation and it is presented in Table 1. The stations located in atlantic water had not been covered by ice and the mixed layer was deeper than 240 meters. The very low chlorophyll concentrations and nutrients levels, typical of a winter situation, found at these stations represent a "prebloom" situation, e.g. although a certain growth of the phytoplankton could be observed, the deep mixed layer hindered the bloom to takes place. In the melt water area, two types of stations were observed according to the development of phytoplankton. At those stations where the ice was still in the form of a compact pack or had been recently broken down to an open pack stage, the chlorophyll concentrations were relatively moderate indicating that the phytoplankton bloom was in an initial phase. These stations have been identified as "early bloom" stations. At the other stations with melt water there was either an open pack ice situation or not ice at all suggesting that the ice had broken down much earlier. It was at these stations, mainly situated in the ice edge zone where

Table 1. Mixed layer average for selected physical and biological parameters at the investigated stations.

Type of water mass	Atlantic water Prebloom			Melt water Early bloom			Melt water Bloom			Arctic mixed water Early bloom	
St. No.	15	28	57	18	39	43	24	31	52	37	45
Depth mixed layer (m)	240	260	300	40	25	75	50	45	50	60	50
Temperature (^{o}C)	1.8	2.0	1.0	-0.9	-1.0	-1.8	-1.4	-1.3	-1.8	-1.8	-1.6
Salinity (o/oo)	35.0	35.0	35.0	34.7	34.6	34.6	34.7	34.7	34.8	34.9	34.8
Chlorophyll a (mg $\cdot$ m^{-3})	0.08	0.11	0.90	0.38	0.85	0.99	4.44	7.87	7.44	1.16	1.37
Phaeopigment(mg $\cdot$ m^{-3})	0.03	0.04	0.31	0.13	0.26	0.69	1.10	1.09	1.29	0.43	0.42
Nitrate (uM)	12.9	12.3	11.1	12.8	11.1	11.1	9.8	7.3	3.9	10.8	10.4
Silicic acid (uM)	7.4	6.7	6.4	7.8	6.5	6.2	6.0	2.1	2.8	6.5	6.5
Phosphate (uM)	0.89	0.83	0.55	0.86	0.58	0.77	0.68	0.49	0.20	0.60	0.56
Ice conditions*	3	3	3	2	1	1	2	2	3	1	1
Nitrate consumption (mmol $\cdot$ m^{-2})	9	15	55	18	53	107	180	288	330	75	60

* 1, Close pack; 2, Open pack; 3, None

the spring phytoplankton bloom was found. At the stations with arctic water over the Great Bank area that were covered by compact ice, a certain amount of melt water was also found in the upper 30 meters although the temperature were very low (<-1.0^{0}C) through the whole water column. The chlorophyll concentrations at these stations were just above 1 mg m^{-3} indicating also an "early bloom" situation. Also the estimation of nitrate consumption gave the same ranking of the stations in terms of phytoplankton development. This was done by substracting the integrated content of nitrate in the upper 100 m from an estimated winter content. The latter was calculated by assuming homogeneous nitrate distribution in the upper 100 m with a concentration equal to the average nitrate concentration in the layer from 100 m depth to the bottom.

BIOMASS AND ABUNDANCE OF COPEPODITES, EGGS, AND NAUPLII

The biomass of zooplankton in the whole water column at the investigated stations, is given in Fig. 3a. The stations are grouped according to the four water types described above. Fig. 3b-h gives the abundances (numbers per square meter) of the copepodite stages of the most abundant copepods.

The combined numbers of copepodite stages CIII-VI of Calanus finmarchicus were variable within the water types. Thus potential differences between the water types were obscured (Fig. 3b). Low abundances at station 31 and 57 may be explained by the deeper distributions of the biomass at these stations. As expected the abundance of C. glacialis increased from near zero in atlantic water to a maximum in the arctic influenced mixed water. C. hyperboreus was rare in samples from all water masses. The stage composition of the three Calanus species showed a typical spring situation (Gjøsæter 1983). No copepodites stage I and very few stage II were observed, indicating that the new generation had not reached the copepodite stages yet. The dominant stages in C. finmarchicus were CV and CVI, and CIII,IV and CVI in C. glacialis, which is supposed to have a biannual life cycle (Tande et al. 1986).

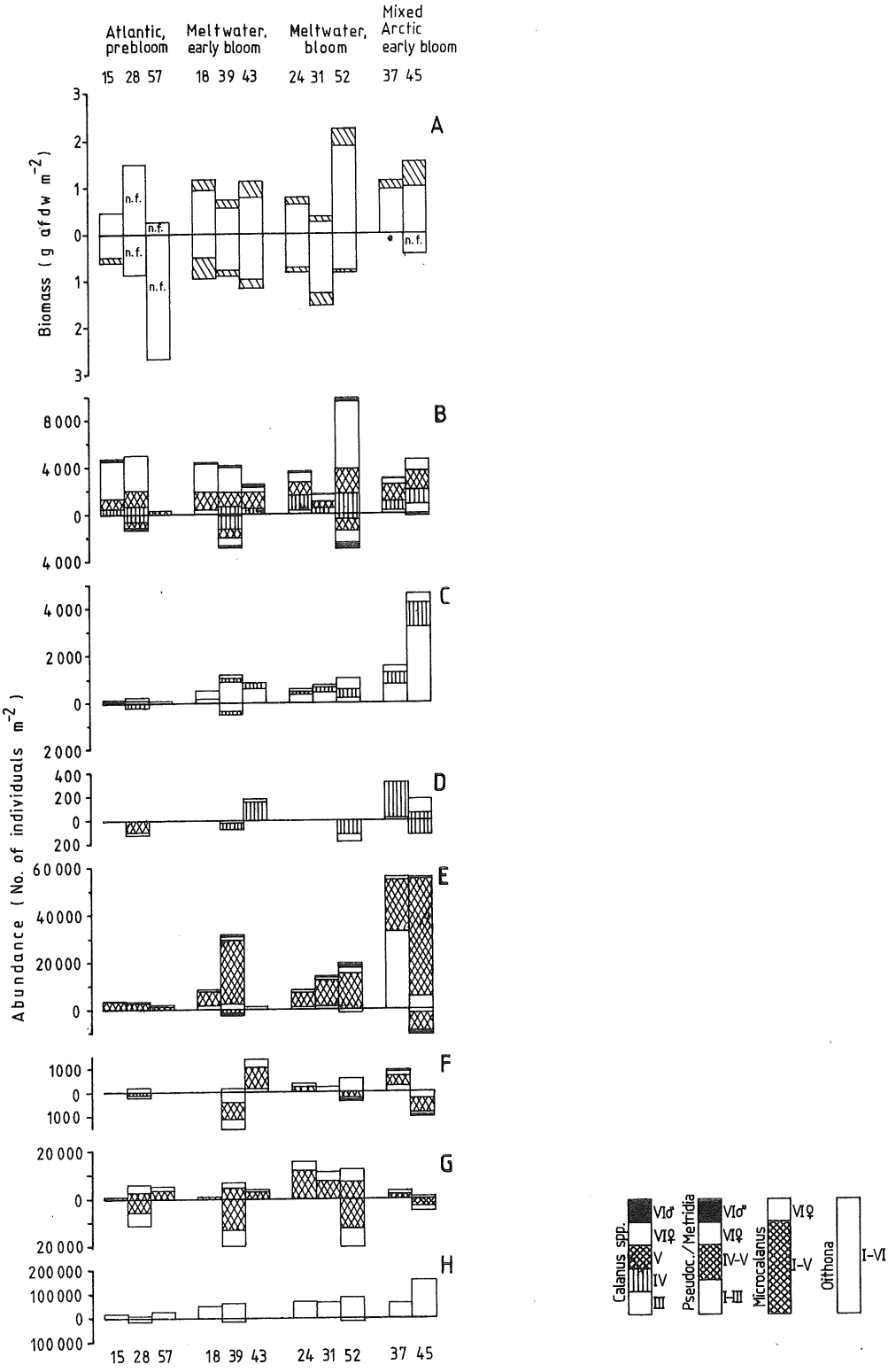

Figure 3. Zooplankton from net hauls 100-0 m (above horizontal line) and 100-200 m (or bottom) (below line). A - ash free dry weight. Open bars - >850 µm fraction, hatched bars - <850 µm fraction. n.f. - not fractioned. * - 130-0 m depth. B - Calanus finmarchicus. C - C. glacialis. D - C. hyperboreus. E - Pseudocalanus sp.. F - Metridia longa. G - Microcalanus sp.. H - Oithona similis.

Table 2. Numbers per m^2 and means with standard deviation of stage VI females, eggs and nauplii in the upper 100m. Spawning intensity as nos. of eggs per female.

		C. finmarchicus				C. glacialis			C. hyperboreus		Pseudocalanus sp.			Oithona sp.	Microcal. sp.	
Stas.	Water type	Fem.	Eggs	Naup+	Spawn. intens.	Fem.	Eggs	Spawn. intens.	Fem.	Naup.	Fem.	Eggs	Spawn. intens.	similis copepodites	Naup.	Naup.
15	Atlantic	3120	1660	4200	.5	40	0	0	0	0	280	1079	4	18240	36800	6000
28	water,	3000	31793	19980	11	140	5715	143	0	11655	520	1900	4	6320	37740	3885
57	pre-bloom	20	36947	26291	1285	0	4330	>>143	0	18680	580	10334	18	27540	79238	7580
Mean			23467	16824	6*		3348	72*		10112		4438	4*		51259	5822
SD			19060	11379	7		2981	101		9435		5123	.1		24235	1854
18	Melt-	2380	42668	21270	59	340	13530	40	0	19800	480	28434	59	53360	82985	3485
39	water,	2180	35813	22675	16	140	23198	166	0	10675	1660	8000	5	63720	66500	3900
43	early bloom	360	36440	32300	101	20	53880	2694	20	10300	660	11640	18	3860	88100	5600
Mean			38307	25415	55		30202	967		13592		16025	27		79195	4328
SD			3790	6004	48		21067	1497		5380		10900	28		11288	1121
24	Melt-	920	72390	47645	78	120	53960	449	0	26340	1180	26531	23	69980	291920	7386
31	water,	560	14572	26036	26	80	21301	266	0	5628	1140	800	.7	68720	17366	8693
52	bloom	5740	142680	68800	25	500	56080	112	0	93100	2320	6600	3	88280	114800	0
Mean			72425	47494	43		38853	275		41689		11310	9		141362	5360
SD			53027	21382	30		18723	168		45712		13496	13		139191	4687
8	Arctic	20	1535	1155	77	140	0	0	0	0	800	0	0	6260	6910	1155
37	mixed	420	182455	7900	434	260	75891	291	0	2900	1620	73384	45	66880	46300	2000
45	water, early	940	135920	28200	145	340	74240	218	120	9000	360	15520	43	158840	224500	5400
Mean	bloom		106637	12418	218		50043	169		3967		29635	29		92570	2852
SD			93948	14077	189		43347	151		4594		38675	25		115940	2247

+ nauplii of C. finmarchicus and C. glacialis.
* not including st. 57.

Abundance of Pseudocalanus sp. peaked in the arctic mixed water (Fig. 3e), the dominant copepodite stages being CIV and CV.

The horizontal distributions of abundance of identifiable eggs and nauplii, given as nos. m^{-2}, is obtained by integrating the vertical profiles given by the water bottle samples (Table 2). Very few nauplii, but some more eggs were not identified. The nauplii of Calanus finmarchicus and C. glacialis were not separated, so the naupliar numbers refers to the sum of both. The eggs of C. finmarchicus and C. glacialis were separated according to differences in diameter. As C. finmarchicus was the most numerous species at the egg stage, we believed it to dominate the naupliar stage as well.

Table 2 shows that the mean numbers of eggs of C. finmarchicus increased from the atlantic water through the melt water into the arctic mixed water. The numbers of nauplii followed the same pattern except in the arctic mixed water where the lowest abundances were found. This is well demonstrated in Fig. 4, where the relationship between egg (the sum of C. finmarchicus and C. glacialis) and nauplius numbers is described by a straigth line (r^2 = 0.94, linear regression), when station 37 and 45 in the arctic mixed water are not included.

The nauplii of all species were found in the naupliar stages NI to NVI.

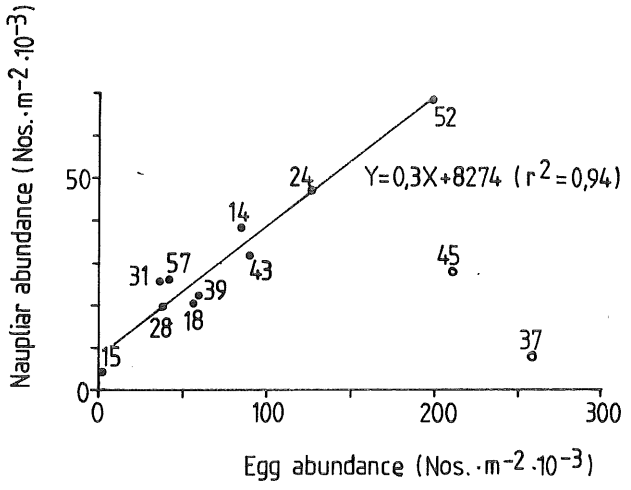

Figure 4. The combined abundances of Calanus finmarchicus and C. glacialis eggs vs. nauplii. The straight line is based on a linear regression, not including stations 37 and 45.

COPEPOD SPAWNING AND ABUNDANCES OF EGGS AND NAUPLII IN RELATION TO BLOOM DEVELOPMENT

The ratio between the sexes (adult male/adult female) and the ratio between younger copepodites and adult females, are measures of the state of development in the overwintering stocks (Table 3). The highest ratios between CV and CVI females of C. finmarchicus, indicating an early state of development, were found in the arctic mixed water.

The spawning intensity, as numbers of eggs per female (Table 2), was low in atlantic water, intermediate in the melt water and high in the arctic mixed water. Looking at single stations there also seems to be a connection between high spawning activity, high ratio of CV to CVI females and to some extent, a high sex ratio, e.g. stations 43,37 and 45. The high spawning intensity at station 57 is not reliable because of the low biomass found above 100 m. That is, most of the eggs might have been spawned by females staying below 100 m at the time of sampling, and thereby not caught in the shallow haul.

The eggs of C. glacialis were most abundant in the arctic mixed water (Table 2), while the spawning was most intense in the bloom and especially in the early bloom melt water. As no CV copepodites were found the development from the diapausing CIV (Tande et al. 1985) to CV had not started. Since CIV is a resting stage, we assumed that development from CIII to CIV was taking place. The highest ratios between CIII and CIV were found at the melt water stations, especially in the early bloom situation (Table 3).

The highest densities of Pseudocalanus sp. eggs occurred in the arctic mixed water (Table 2). Although total copepodite abundance was high here, few had developed into CVI females, giving a high ratio between CIV+CV and females (Table 3). The spawning intensity was also high at these stations. At the blooming melt water stations 31 and 52, the sex ratio was particular high (Table 3). As can be seen in Table 2 the spawning intensity was very low at the same stations. Nauplii of Pseudocalanus sp. were not found indicating that spawning

had just started at the time of our survey.

Table 3. Ratios between copepodite stage numbers in the upper 100 m.

	C. finmarchicus		C. glacialis	Pseudocalanus sp.	
St.	V/VIfem.	VImale/VIfem.	III/IV	IV-V/VIfem.	VImale/VIfem.
15	0.3	0.06	0.5	9.1	0.3
28	0.4	0.01	2.0	4.5	*
57	5.0	*	0.5	1.4	0.3
18	0.6	0.04	*	12.8	*
39	0.5	0.04	6.4	16.3	0.4
43	3.9	0.60	3.0	0.5	*
24	1.1	0.02	3.4	5.3	0.1
31	0.8	0.06	2.0	9.8	0.5
52	0.4	0.04	0.6	6.5	0.9
8	2.0	*	0.6	24.5	*
37	3.4	0.18	1.5	13.5	*
45	1.7	0.00	3.2	138.9	*

* One of the stages not found

Nauplii of Oithona sp. were most abundant in the blooming melt water and in the arctic mixed water. The eggs which were either attatched to the females or loosened during collection, were not counted. The eggs of Microcalanus sp. were identified in the samples, but not counted as they were difficult to find among the phytoplankton cells. The nauplii of Microcalanus sp. occurred in low numbers, and showed lowest abundance in the arctic mixed water. However the deep distribution of the copepodites (Fig. 3g), and the deep distribution of these nauplii found in other investigations (Krause and Trahms 1982) makes the abundances and horizontal distribution patterns based on samples above 100 m unreliable.

The developmental pattern in copepodite stages of Calanus spp. indicated that earliest stage of development was found in the early bloom phase. Given that NO_3 consumption is a measure of the phytoplankton bloom development, Figs. 5a and 5b show that

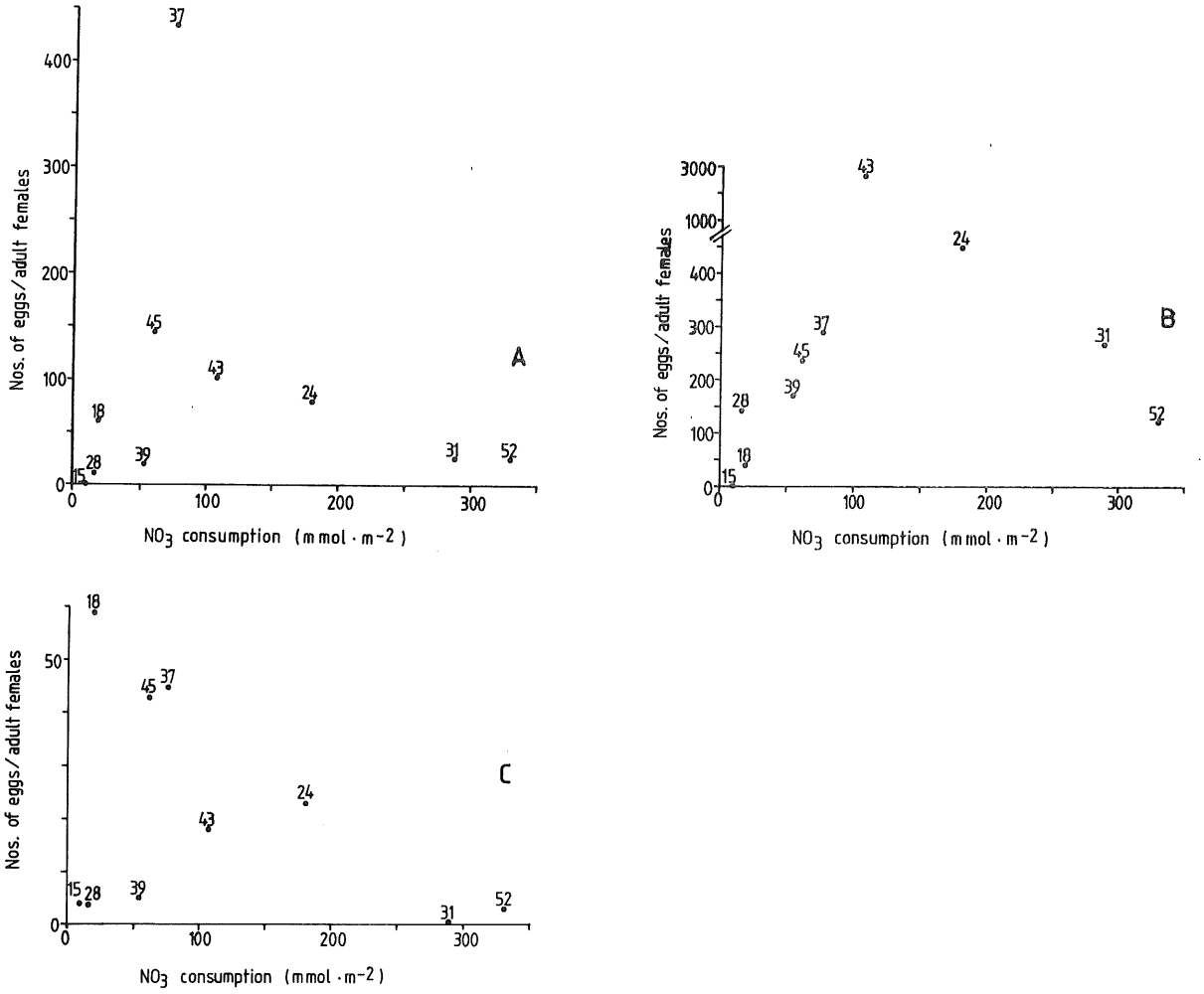

Figure 5. Spawning intensity (nos. of eggs per female) vs. nitrate consumption. A - Calanus finmarchicus. B - C. glacialis. C - Pseudocalanus sp.

spawning in both C. finmarchicus and C. glacialis was low at the start of the phytoplankton bloom. The spawning reached maximum in the early bloom phase and then decreased as bloom development continued. Also the spawning in Pseudocalanus sp. seemed to be most intense at the prebloom and early bloom stations (Fig. 5c), but gives a more confusing picture than the Calanus species.

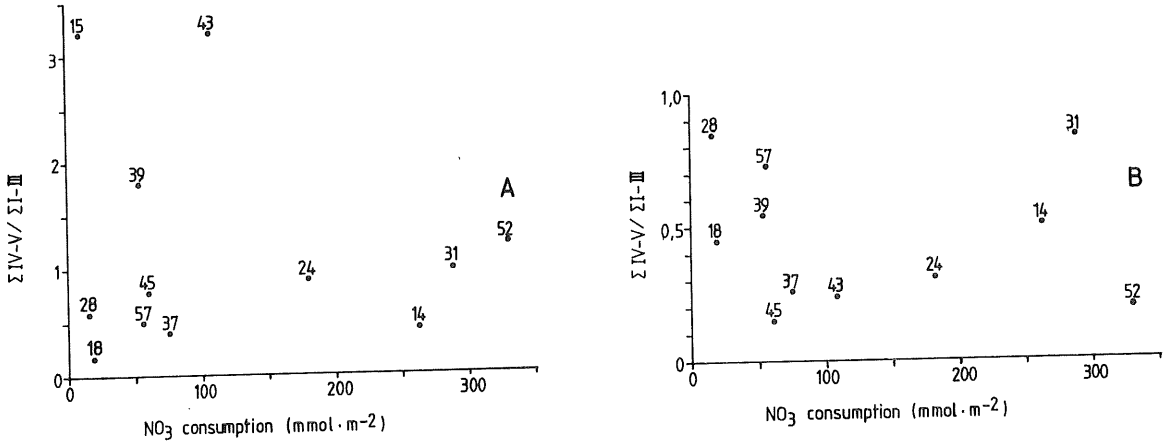

Figure 6. The ratio between the sum of nauplius stage IV-VI and the sum of nauplius stage I-III vs. nitrate consumption. A - Calanus finmarchicus/glacialis. B - C. hyperboreus.

Fig. 6a and 6b gives the relationship between the bloom development and the numerical ratio of nauplius NIV to NVI and nauplius NI to NIII. If spawning started when the phytoplankton bloom started, one could expect a positive relation between this ratio and the NO_3 consumption when plotting the different stations. This is not evident from Fig. 6a,b neither in Calanus finmarchicus/glacialis nor in C. hyperboreus. However, the abundance of C. finmarchicus/glacialis nauplii increased with increasing NO_3 consumption, showing that the accumulated production of nauplii seemed to be highest at stations with the most developed phytoplankton bloom (Fig. 7a). C. hyperboreus nauplii did not seem to be that dependent or linked to the bloom development (Fig. 7b).

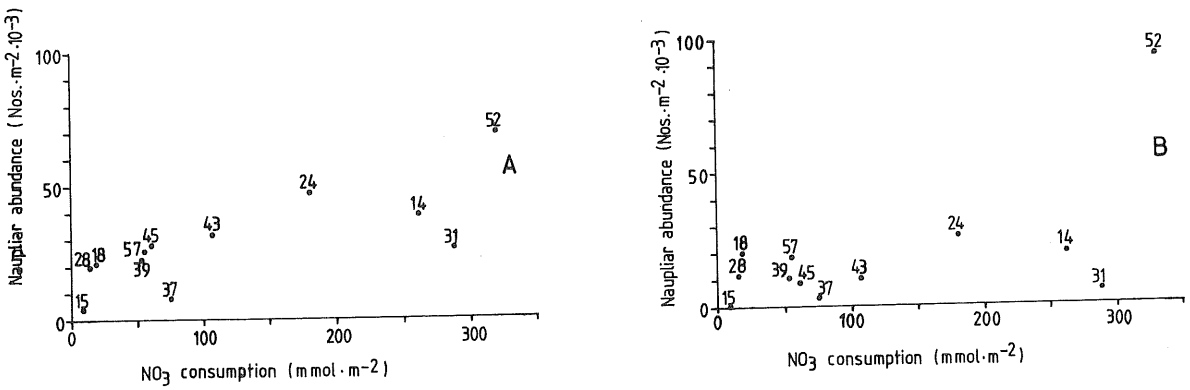

Figure 7. Naupliar abundance vs. nitrate consumption. A - Calanus finmarchicus/glacialis. B - C. hyperboreus.

VERTICAL DISTRIBUTION

Depth profiles of copepodites, eggs and nauplii of Calanus finmarchicus and C. glacialis are shown in Fig. 8. As we did not succeed in separating the naupliar stages of C. finmarchicus and C. glacialis, the vertical distributions

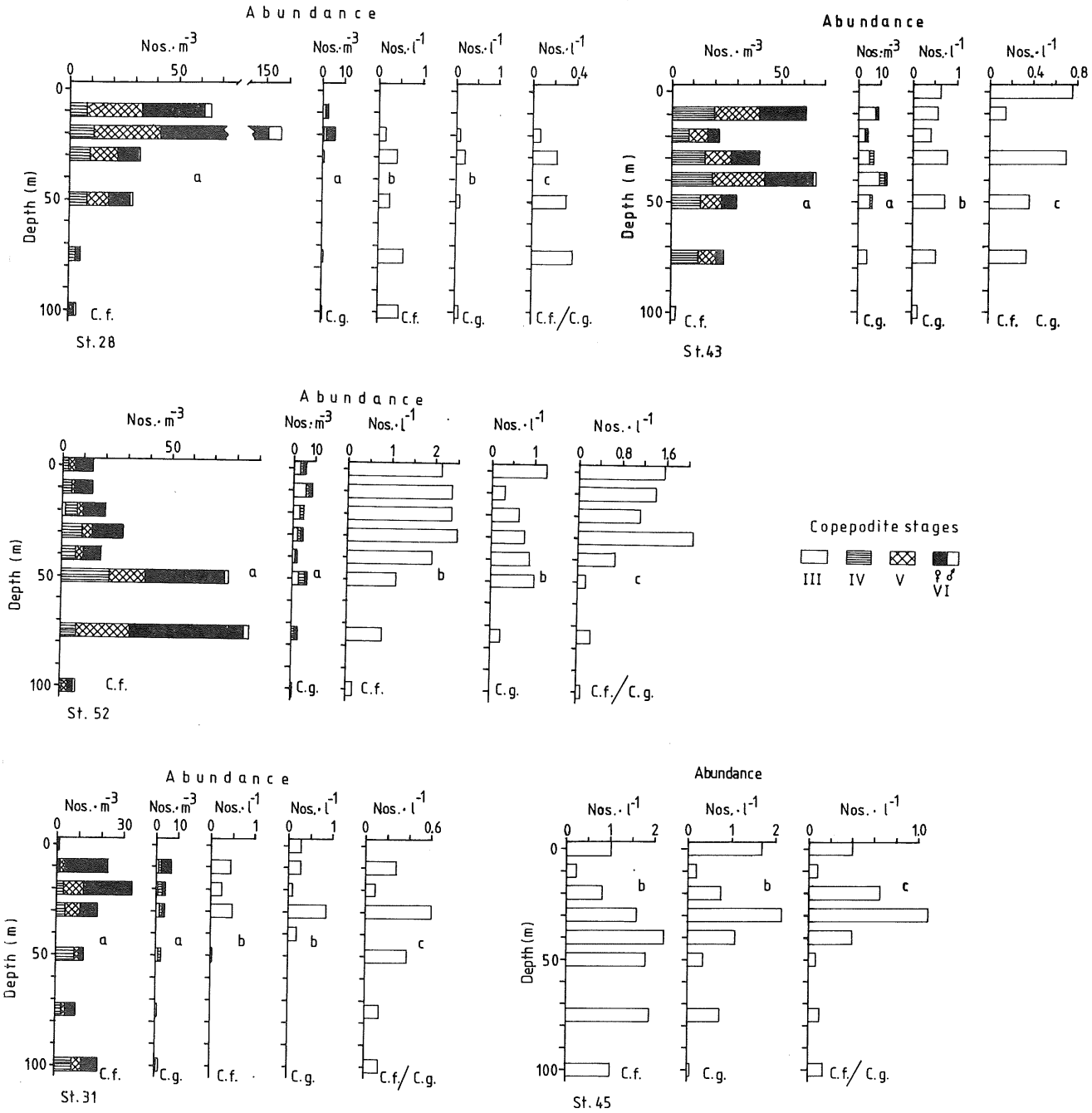

Figure 8. Vertical distributions of Calanus finmarchicus and C. glacialis obtained by the plankton pump and water bottles. A - copepodites. B - eggs. C - nauplii. C.f. - C. finmarchicus. C.g. - C. glacialis.

represent a combination of the two species. The copepodites of Calanus finmarchicus were mainly found in the upper 100 m, with varying depths of maximum abundance, but all stages were found below 100 m as well (Fig. 3b). Both eggs and the six naupliar stages were found down to 100 m depth, but were most abundant in the upper 50 m. The vertical distributions of eggs and nauplii were more shallow than the distributions of adult females. The naupliar stages I-VI did not differ in vertical distributions (results not showed here).

C. glacialis copepodites were most abundant in the upper 50 m (Fig. 8). The vertical distributions of the eggs of C. glacialis were very similar to those of the C. finmarchicus eggs.

The copepodite stages of C. hyperboreus were rare (Fig. 3d), but their vertical distributions seemed to be deeper than those of the other two Calanus species described above. The eggs of C. hyperboreus were screened out of the samples with a 250 µm net[1], so the vertical distribution is unknown. The vertical distributions of the nauplii, however, were found to resemble those of the finmarchicus/glacialis very much (Fig. 9).

Maximum densities of Pseudocalanus sp. copepodites occurred above 50 m. Just a few eggs were found that could belong to Pseudocalanus sp. according to the egg diameter measurements (100-130 µm). These had probably been lost from the egg sacs at the abdomen of the females, which in turn were held back by the 250 µm net. The distribution of eggs was even in the upper 100 m (Fig 10). No nauplii were found.

The copepodites and nauplii of Microcalanus sp. showed a deeper distribution than the other copepods, and maximum abundance was below 50 m. At station 43, however, there were high numbers above 50 m as well (Fig. 11).

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[1] This method was chosen as the samples were intended for other purposes, than those described here, as well.

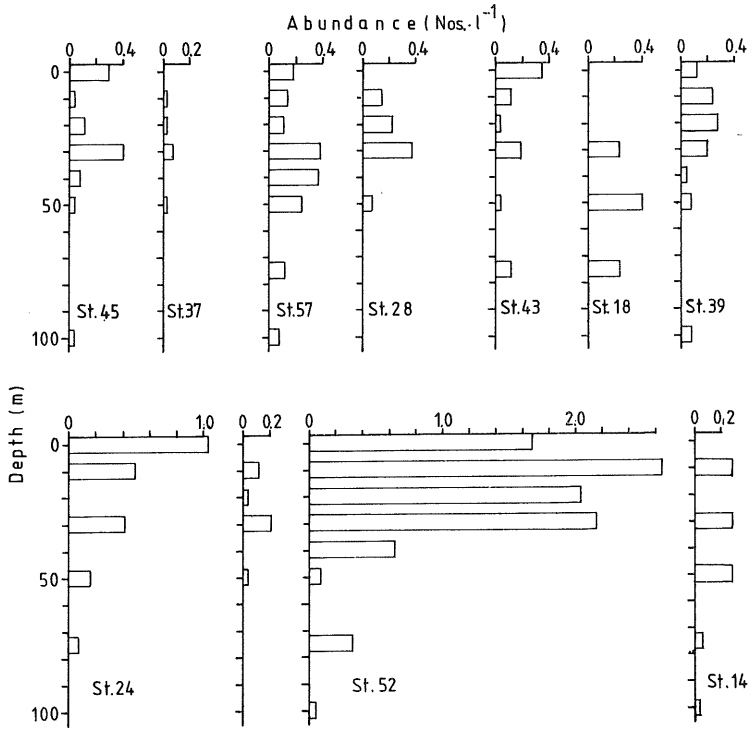

Figure 9. Vertical distributions of Calanus hyperboreus nauplii obtained by the water bottles.

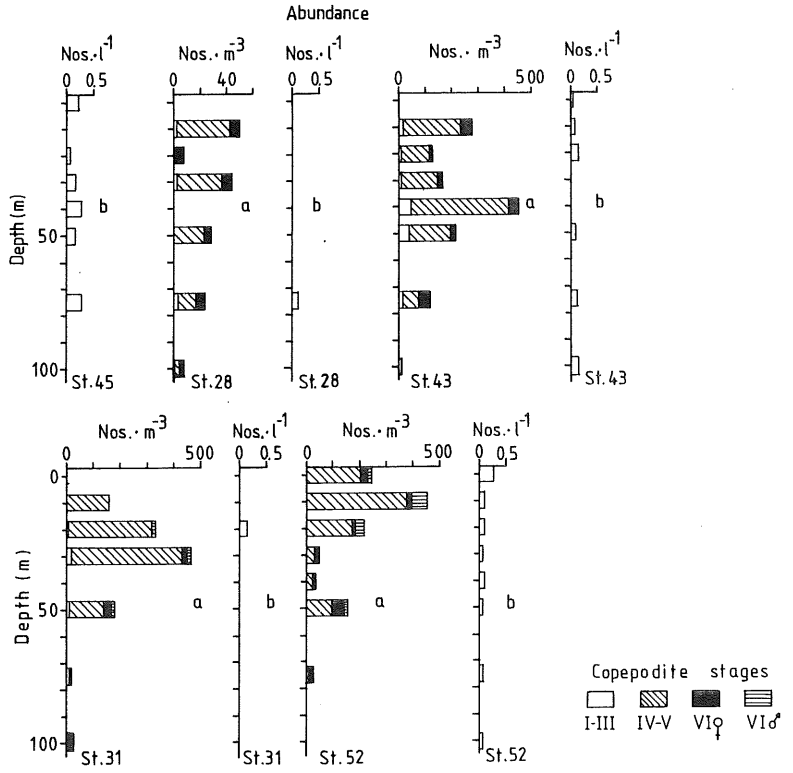

Figure 10. Vertical distributions of Pseudocalanus sp. obtained by the plankton pump and water bottles. A - copepodites. B - eggs.

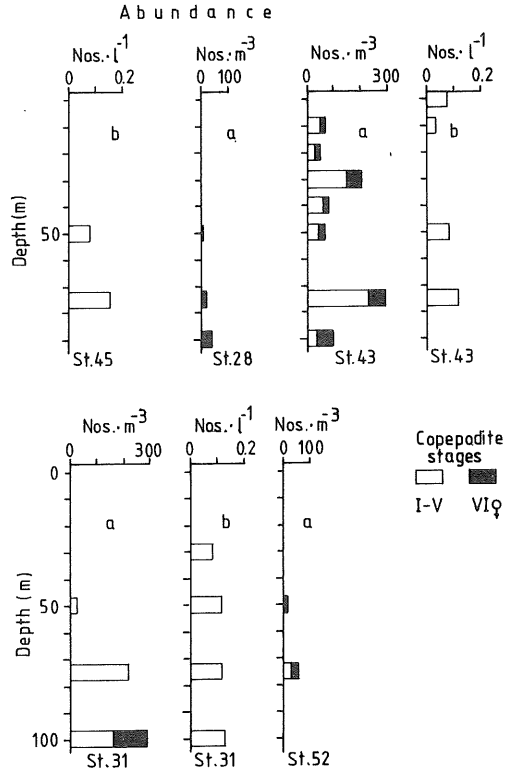

Figure 11. Vertical distributions of Microcalanus sp. obtained by pump and water bottles. A - copepodites. B - nauplii.

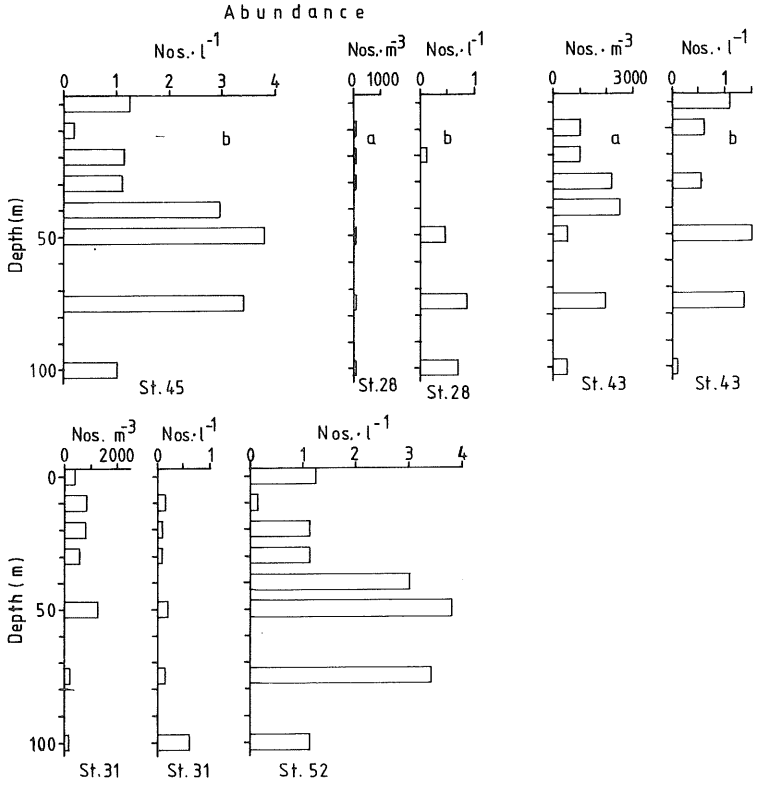

Figure 12. Vertical distributions of Oithona sp. obtained by pump and water bottles. A - copepodites. B - nauplii.

Oithona similis copepodites showed large variations in abundance between the stations. Maximum numbers seemed to be above 50 m (Fig.12). The nauplii were few and the vertical distributions were similar to the copepodites.

DISCUSSION

In the lower range of temperatures, as observed during this cruise (-1.8 - +2.0°C), little is known about the developmental rate of Calanus spp.. In the laboratory, at 14-15°C, the developmental time of Calanus finmarchicus was 12-14 days from spawning to CI (Marshall and Orr 1972). At 5°C, corresponding time was 50-60 days (Fransz and Diel 1985). Field observations of C. finmarchicus in the North Sea indicated 21 days from occurrence of maximum egg numbers to maximum copepodite numbers. In Balsfjorden (Northern Norway) the time from spawning to CI was 0.75 to 1.75 month at about 3°C (Hopkins et al. 1984). A mathematical equation describing the relationship between temperature and developmental time, based on laboratory rearings of C. finmarchicus, gives 78 days from hatching to CIII at 0°C (Runge et al. 1985). We assume that the development from spawning to CI in the Barents Sea in April takes about 2 months in C. finmarchicus/glacialis.

The absence of C. finmarchicus/glacialis copepodites stage I and the presence of nauplii stage VI of the new generation in early April, means that spawning started in early February. The same stage distribution was found in C. hyperboreus, which probably have slower developmental rate (Corkett and McLaren 1970). Thus spawning must have started prior to the spring bloom in all three species. The ratio between old and young stages of nauplii (Figs. 6a,b) do also indicate that the start of spawning was not related to the phytoplankton bloom development. C. hyperboreus has been found to start spawning before the phytoplankton bloom is developed, while breeding in C. finmarchicus is thought to be dependent of the phytoplankton bloom (see review by Heinrich 1962). On the other hand C. finmarchicus is also found to spawn before the start of the phytoplankton bloom (Østvedt 1955). A uniform start of the

breeding in Calanus spp. over wide areas (Matthews 1968), indicates that factors with less geografic variation than the spring phytoplankton bloom may induce the start of spawning. Fransz 1982 saw induction of development in calanoids as a function of abiotic factors.

In this study maximum spawning intensity of C. finmarchicus was found in the arctic mixed water (145-434 eggs/female). In Lofoten (Northern Norway) spawning intensity was close to 200 eggs/female at maximum spawning in the beginning of April (Sømme 1934). Thus, the spawning intensity observed in the Barents Sea at the early bloom stations, is likely to have been maximum spawning. The numbers of eggs/female in C. glacialis were higher than in C. finmarchicus, but the maximum intensity of spawning in C. glacialis is not known.

The spawning intensity of both C. finmarchicus and C. glacialis, was found to be linked to the phytoplankton bloom development (Figs. 5a,b), and spawning was highest in the early phase of the bloom. Thus, the females of C. finmarchicus and C. glacialis seem to be dependent of a higher phytoplankton density than what is found during the prebloom phase to increase their rate of spawning. On the other hand maximum spawning intensity was reached long before the phytoplankton bloom was fully developed.

At the stations with maximum spawning intensity, in early bloom, there were also high ratios of CV to CVI females (C. finmarchicus) and CIII to CIV (C. glacialis). These ratios were low at the bloom stations (24,31,52). Since the prebloom stations with low spawning activity did not show a high CV to CVI ratio these observations do not indicate a copepodite development from younger to older stages, along with the spring bloom development. The decrease in the relative number of females at the stations with high spawning activity can be explained by females spawning face a higher rate of mortality, giving a "shortage" in females relative to the younger stages. If the rate of development from a younger to an older stage is dependent on the density of the older stage (Miller et al. 1984), a small standing stock of females spawning at a high

rate can give rise to a high abundance of eggs, because both female recruitment and mortality is high.

The abundance of nauplii of C. finmarchicus/glacialis, but not C. hyperboreus, showed a positive relationship with the bloom development (Figs. 7a,b). The production of nauplii seemed to be low prior to the phase of high spawning during the early bloom. Nevertheless, the numbers of females at the time of spawning is unknown, making firm conclusions about the relationship between naupliar production and bloom development difficult. The lack of relationship between the abundance of C. hyperboreus nauplii and the phytoplankton bloom indicate that this species is less dependent on the phytoplankton bloom development during early life history. In Lofoten this species spawn well before C. finmarchicus (Sømme 1934).

The occurrence of eggs and lack of nauplii of Pseudocalanus sp. may indicate a later spawning than is the case with Calanus spp.. A high ratio of males to females, especially at the bloom stations, supports this conclusion. Further, the spawning intensity did not seem to be dependent on the phytoplankton bloom (Fig. 5c). The highest numbers of eggs /female observed in the Barents Sea in April is higher than laboratory observations of mean numbers of eggs/egg sac (Corkett and McLaren 1969). Thus a large proportion of the females must have been involved in the spawning at the stations with a high spawning intensity. If we observed the start of spawning in Pseudocalanus sp., then the spawning first occurred in the arctic mixed water of the polar front.

Nauplii of both Oithona sp. and Microcalanus sp. were observed in stages NI to NVI, and these species must have an earlier spawning than Pseudocalanus sp.. In the North Sea naupliar stages of both species were found to be abundant at the beginning of the spring bloom (Krause and Trahms 1982).

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