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# The radiolarian fauna at the ice edge in the Greenland Sea during summer, 1988

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## ABSTRACT

Radiolaria were sampled from the plankton at 18 stations during two cruises in the Greenland Sea during summer, 1988. A total of 43 species or categories of radiolaria was found, but over 90% of the radiolarian fauna was dominated by adults or juveniles of 4 species: the spumellarian, *Actinomma leptodermum* and the nassellaria, *Amphimelissa setosa*, *Pseudodictyophimus gracilipes*, and *Peridium longispinum*. The stations sampled ranged from ice-covered areas high in nutrients to open water areas which were depleted in nutrients. These stations encompassed a gradient in the composition of the radiolarian fauna from an assemblage dominated by juveniles and adults of *A. setosa* and *P. gracilipes* at the ice edge to one dominated by *Actinomma* juveniles, *A. leptodermum*, and *P. longispinum* in open water. The total abundance of radiolaria correlated with integrated phaeopigment, but not with chlorophyll *a*. In discriminant function analysis the 'ice edge' radiolarian species listed above correlated well with chlorophyll *a* and phaeopigments, while the 'open water' species did not. Several water masses occur in the area, which complicates the interpretation considerably, but the data are consistent with the development of a radiolarian population in tempo with, and in all probability linked successionaly to the development of the phytoplankton—microplankton bloom.

## 1. Introduction

Radiolaria (Phaeodarea, Polycystinea:Nassellarida and Polycystinea:Spumellarida), are related to other marine Sarcodina such as foraminifera (Granuloreticulosea) and acantharia. They generally occur in low absolute abundance relative to other protozoan microplankton (flagellates, ciliates, etc.) in most of the world ocean, and as far as we know they usually constitute neither a major contribution to global carbon biomass nor a significant compartment mediating carbon flux. Consequently they have often been overlooked by major biological oceanographic programs which are primarily focused on the measurement of processes related to carbon flux through the upper ocean layers.

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Sarcodines are major contributors to biomineralization however (see Caron and Swanberg, 1990 for a recent review on marine planktonic sarcodine ecology), and can account for a large proportion of the flux of calcium (as calcium carbonate in foraminifera), silicon (as opal in radiolaria) and strontium (as celestite in acantharia) from the upper water column into marine sediments. They are major components of particulate standing stocks (Bishop *et al.*, 1977, 1978, 1980; Michaels, 1988) and flux (Honjo, 1978, 1980; Takahashi, 1983; Takahashi and Honjo, 1981, 1983; Michaels, 1991; Spindler and Beyer, 1990), and are thus highly relevant for questions of interest to both paleontology and biological oceanography.

The skeletons of foraminifera and radiolaria are prominent members of many marine sediment assemblages and represent the most important global zooplankton fossil signal. There are many species of acantharia, but they are far less evident in the sediment and fossil record than other sarcodines. Although the approximately 30 species of planktonic foraminifera (Bé, 1967, 1977) are more prevalent in pelagic sediments, there are about two orders of magnitude more species of radiolaria, and they are very widespread both geographically and throughout the water column (Casey, 1971a; Petrushevskaya, 1971a,b). Because of this species richness, where they occur in sediments radiolaria may hold far more information than any other group about the structure of the communities in the overlying water masses from which they are derived.

The majority of the sarcodines reproduce slowly (Bé *et al.*, 1977, 1981; Anderson, 1983; Spindler *et al.*, 1979) and, with a life cycle of one to several months (Casey *et al.*, 1970; Bé *et al.*, 1977; Anderson, 1983; Swanberg and Bjørklund, 1987), live for long periods relative to other protozoan plankton. They cannot significantly affect their own distribution (Grell, 1973; Anderson, 1983; Swanberg, 1983; Swanberg and Anderson, 1985), and are thus considered excellent indicators of water masses. Because of the scarcity of basic biological data that biologists have been able to provide, there is a tendency in the micropaleontological literature to view the occurrence of these organisms more as properties of geologic time and water-mass than as the result of a response to dynamic biological processes in the planktonic communities around them. For some purposes, such as stratigraphy, this may not matter, but for paleoecology, paleoceanography and climate reconstruction, one needs to know as much fundamental biology of the organisms as possible. If populations of radiolaria and other sarcodines respond dynamically to trophic events in plankton communities, then they should by inference be good indicators of such events. Disregarding this would represent a serious loss of information. If the various species of radiolaria comprising an assemblage could be related to trophic events in the rest of the plankton community, then the radiolarian record could tell us a great deal about the structure of both paleo- and recent (modern) marine planktonic communities.

Most radiolaria are dependent either directly on primary producers or via the

nano- and micro-plankton food web on secondary or even tertiary production (Casey *et al.*, 1979; Bé *et al.*, 1977, 1981; Anderson, 1983; Swanberg and Caron, 1991). It has been shown (Anderson, 1983; Swanberg, 1983; Swanberg and Anderson, 1985; Swanberg *et al.*, 1986a,b) that large gelatinous radiolaria which are hosts to symbiotic algae in tropical, subtropical and temperate surface waters, also feed on macrozooplankton as large as copepods, however this does not apply to all radiolaria. Aside from some of the larger Phaeodarea, the high latitude forms we present in this paper are all much smaller and qualitatively different in structure than the large tropical forms. There are few observations of the living cells of high latitude forms, but none of those we have seen have had the large extracapsular cytoplasmic masses so characteristic of the tropical Spumellarida. Casey *et al.* (1979) suggested that many of the smaller radiolarian forms, especially Nassellarida, fall into one or more of several niches: bacterivorous, herbivorous (including nano- and micro-scale), detritivorous, and symbiotic. Anderson (1983) elaborated on this to include carnivorous, microcarnivorous and omnivorous. Even though there is much speculation involved in these generalizations, it is evident that 'radiolaria' represents several very broad taxa which feed in a wide range of trophic levels. For the Nassellarida investigated in this paper we cannot dismiss bacterivory, but our best judgement is that they feed on organisms in the microplanktonic food web; most likely nanoflagellates and small ciliates. There is no particular reason to think they discriminate between auto- and heterotrophic food sources. The other major group encountered here, the actinomids, are larger and more robust, and more likely to be microcarnivores, probably feeding on larger ciliates (such as tintinnids) and micrometazoans. These hypotheses are supported by the observations of Swanberg and Bjørklund (1987) that these Nassellarida were most abundant, especially in their juvenile stages, in areas of fjord systems where standing stocks and production of microplankton are usually very high, and that the actinomids were most abundant in the open fjords, where larger organisms predominated.

Radiolaria have been reported to attain seasonally high population densities in coastal waters (Bjørklund, 1974) but we do not know whether this is in direct response to blooms of primary producers or to events further up the food web. The time scale of their response in coastal areas appears to be on the order of a few months or a season. We do not know the extent to which oceanic populations respond similarly, nor do we know what the horizontal spatial scale of such a response might be, though data on foraminifera suggest that it may be on the order of tens of km (Boltovskoy, 1971).

In this study we seek to determine whether there is a short-term change in radiolarian populations in response to major changes in the structure of the plankton food web. To do so we examine the status of radiolarian populations in gradients into the ice, which correspond to gradients in the phytoplankton bloom events at the ice edge in the Greenland Sea. We chose the Greenland Sea ice-edge bloom because it

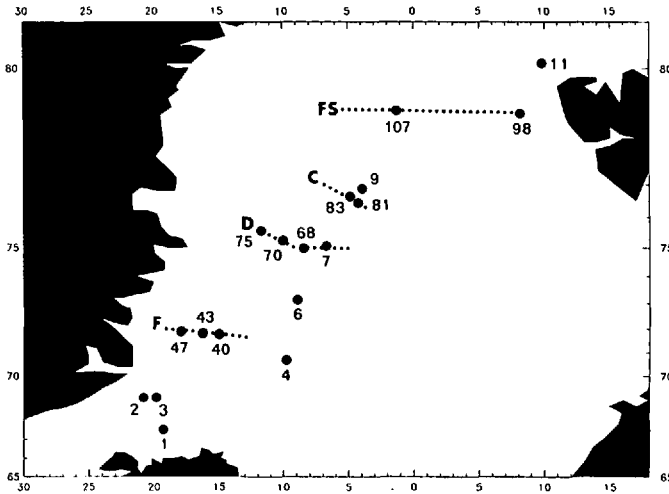


Figure 1. Map (Mercator projection) showing stations at which radiolarian samples were taken during cruises of R/V *Endeavor* (Stns 1–4, 6, 7, 9, 11) and R/V *Polarstern* (40, 43, 47, 68, 70, 75, 81, 83, 98, 107). The approximate locations of 4 hydrographic sections (F, D, C, and FS), are shown as dotted lines.

is pronounced, there is an consistent and taxonomically manageable radiolarian fauna and there are major international efforts underway to examine events during its development.

## 2. Materials and methods

Radiolaria were sampled from the plankton at 10 stations during R/V *Polarstern* Ark V/2 (5 June–5 July) and at 8 stations during R/V *Endeavor* 182 (22 July–4 Aug) in the summer of 1988 (Fig. 1). The *Polarstern* stations sampled were situated along 4 separate transects (Fig. 1; F, D, C and FS) running from the open water into the ice pack. We were unable to do this type of transect sampling on the *Endeavor*.

During the *Endeavor* cruise plankton samples were collected in vertical net hauls made with a Juday net (0.25 m<sup>2</sup>, 64 μm mesh) from 300–0 m. For reasons of hardware incompatibility we had to use different equipment on the *Polarstern* cruise, so a vertical multinet (Multi-Netz<sup>®</sup>, Hydro-Bios Apparatebau GMBH, Kiel, Germany) was used (0.26 m<sup>2</sup>, 64 μm). Non-stratified samples were taken from 400–25 m, because the high levels of phytoplankton at the surface at this time of year tended to clog the net. Although this certainly represents a source of potential error, in those samples where separate surface counts have been done, most of the radiolaria were found below 25 m. Plankton samples were preserved in 4% formaldehyde and seawater, and later wet-oxidized in the laboratory using the method of Hasle and Fryxell (1970). The remainder, which consisted mostly of diatoms and radiolarians,

was filtered and mounted on glass microscope slides in Canada Balsam as described by Swanberg and Bjørklund (1987).

Wherever possible, at least 300 radiolarian skeletons were counted and identified to species in each sample, except for 3 stations (75, 83, and 1) where there were fewer than 300 skeletons; in these cases all skeletons present (232, 198, and 285 respectively) were counted. Identifications were made to the species level using Bjørklund (1976), Schröder (1909, 1914) and Jørgensen (1905). Particular attention was paid to the distinction between juvenile and adult stages. Juvenile Nassellarida were those with a developed cephalis, but no postcephalis; juvenile Spumellarida (actinommids) were those with only their first shell. Juvenile specimens were usually only identified to genus, especially in the case of *Actinomma* and *Hexacantium*, though these are in all probability *A. leptodermum* and *H. enthacanthum*. Some unidentifiable Spumellarida were labeled 'Unknown.' We had one specimen of *Rhopalastrum* and several *Artostrobos* (all the same) which we were unable to identify to species. Aside from the juvenile forms, none of these were very abundant in our samples.

The data matrix of radiolarian species in stations was analyzed using multivariate statistics including cluster (COMPAH; Boesch, 1977) and correspondence analyses (DECORANA: Hill, 1974, 1979; CANOCO: Ter Braak, 1986, 1988).

Various categories of other data were made available to us to assist in the interpretation of these results. Data on nutrients ( $\text{NO}_3^-$ ,  $\text{NO}_2^-$ ,  $\text{NH}_4^+$ ,  $\text{PO}_4^{3-}$  and Si) were provided by Dr. G. Kattner (Kattner *et al.*, 1988) of the Alfred-Wegener-Institut für Polar- und Meeresforschung (AWI), chlorophyll *a* data were provided by Dr. H.-J. Hirche (AWI) and uncorrected raw hydrographic data were provided by E. Fahrback (AWI) and Prof. Dr. J. Meincke, Inst. für Meereskunde, Universität Hamburg.

### 3. Results

*a. Radiolarian distribution.* Radiolaria were found in all plankton hauls, even those taken far into the ice pack. A list of the species encountered and their percent abundances for both cruises is presented in Table 1. A total of 43 species or categories of radiolaria was found; an average of 14 was collected at each station. The numerically dominant species were the spumellarian *Actinomma leptodermum* (which averaged 19% of the radiolarian fauna at 18 stns), and juvenile *Actinomma* (26% at 17 stns), which were probably mostly *A. leptodermum*. The numerically dominant nassellarians were *Amphimelissa setosa* (25% at 18 stns) and its juvenile form (6% at 3 stns), *Pseudodictyophimus gracilipes* (14% at 18 stns) and its juvenile (6% at 1 stn) and *Peridium longispinum* (8% at 17 stns). Combined, adults or juveniles of these four species of radiolaria accounted for an average of 90.5% of the fauna. Aside from these, several species were common (occurred in more than half of the stations), but low in abundance where they occurred: *Phorticium clevei*, *Spongotrochus glacialis*, *Ceratocyrtis histicosus*, *Lithomelissa setosa* and *Phormacantha hystrix*.

Table 1. The species or stages of radiolaria encountered from the *Polarstern* and *Endeavor* cruises in the Greenland–Iceland–Norwegian Sea during summer, 1988. Values are percentage composition from each haul. To differentiate between the two cruises here, *Polarstern* stations are designated with a prefix PS and *Endeavor* stations are designated EN. The station numbers do not overlap, and are only designated with their numbers in the text.

	PS 40	PS 43	PS 47	PS 68	PS 70	PS 75	PS 81	PS 83	PS 98	PS 107	EN 1	EN 2	EN 3	EN 4	EN 6	EN 7	EN 9	EN 11	
Spumellariida																			
<i>Actinomma boreale</i> (Cleve)																			
<i>Actinomma leptodermum</i> (Jørgensen)	3.76	10.12	9.83	0.46	19.89	8.82	31.22	17.37	44.78	5.59	8.42	22.11	21.68	43.47	36.26	3.92	21.75	7.71	3.23
<i>Actinomma</i> sp. juvenile	32.83	51.81	24.86	0.69	47.79	21.85	28.64	39.83	18.96	42.28	7.72	29.9	29.39	10.92	35.96	7.23	13.31	9.70	9.70
<i>Actinomma</i> indet.		0.45									1.75		1.62	0.78	0.15	0.90			0.25
<i>Cladococcus viminalis</i> Haeckel																			
<i>Drymonomma elegans</i> Jørgensen	2.26																		
<i>Hexacanthium enihacanthum</i> Jørgensen						1.26				0.67	0.35								
<i>Hexacanthium</i> sp. juvenile	4.01				4.20	4.20				1.34									
<i>Laraspis minor</i> Jørgensen					0.42					0.22					0.15				
<i>Lilhelius spiralis</i> Haeckel											1.40	0.49	0.97	0.39	0.15				
<i>Photicium clevei</i> Jørgensen	0.25	0.30	1.35	1.38	1.93		0.70	0.42	1.10	1.34									0.50
<i>Rhizoplegma boreale</i> (Cleve)	0.25		0.19	0.46															
<i>Rhopalastrium</i> sp.	0.25																		
<i>Spongocochus glacialis</i> Popofsky	0.25	0.15	0.19	0.69		1.26	0.70	0.85	0.55	2.01	1.05			0.58	0.45	0.60	0.65		0.65
<i>Syrodactyla tenuispina</i> Jørgensen	0.25	0.15																	
<i>Syrodactyla validispina</i> Jørgensen	0.50																		
Nassellariida																			
<i>Acanthocorys umbellifera</i> Haeckel	23.81	11.63	17.73	28.57	5.80	14.29	4.93	8.05	4.12	8.95	68.77	25.20	46.93	21.64	7.73	53.61	42.21	49.00	49.00
<i>Amphimelissa setosa</i> (Cleve)	9.27		5.97							1.34									
<i>Amphimelissa setosa</i> juvenile			0.19																
<i>Arctocorys boreale</i> (Cleve)	0.25					1.26													0.25
<i>Arctocorys</i> sp.																			
<i>Arctocorys annulatus</i> (Bailey)		0.15			0.28		0.47	0.85	0.42	0.27	0.35		0.32				0.65		
<i>Arctocorys joergenseni</i> Petrushevskaya																			
<i>Ceratocorys galens</i> (Cleve)						1.26													
<i>Ceratocorys hystericus</i> (Jørgensen)		0.45	2.12	3.46	1.10	4.20	0.94	2.54	1.10	1.12							0.97		
<i>Ceratocorys hyperborea</i> (Jørgensen)			2.12	0.23			0.23			0.89					0.59	0.60	1.30	0.50	
<i>Cornuella profunda</i> Ehrenberg								0.42		0.22									
<i>Corocathypira craspedia</i> Jørgensen	0.50																		
<i>Cycladophora davisiana</i> (Ehrenberg)					0.28	0.84	0.23	0.42	0.55		1.05	0.49	0.32	0.39			0.97	3.23	
<i>Dicococeras acanthicum</i> Jørgensen	0.25	0.15	0.23	0.23	0.28		0.23	0.42	0.55	0.22	0.35								
<i>Lithomelissa setosa</i> Jørgensen	0.25	0.15	0.23	0.23	0.28	6.30	19.01	2.97	17.58	10.51	1.05	2.76	1.62	1.56	2.23	28.61	6.17	5.97	5.97
<i>Lithomelissa lineata</i> Ehrenberg		7.10	4.62	3.69	1.10	2.94	0.94	5.51		8.05	1.05	3.74	4.21	1.17	0.45				
<i>Pandium longiporum</i> Jørgensen										0.45									
<i>Phaenocarpa nyctea</i> Jørgensen																			
<i>Phaenocarpa nichinoides</i> Claparède																			
<i>Plectocanina oddabos</i> Jørgensen						0.42													
<i>Plectocanina microloides</i> Jørgensen																			
<i>Pseudodictyophimus gracilipes</i> (Cleve)	15.04	17.52	28.90	32.03	10.50	19.33	11.50	19.07	10.99	14.77	5.61	13.66	10.03	8.19	12.04	4.52	11.36	15.17	15.17
<i>P. gracilipes</i> juvenile	5.02					0.42	0.23												
<i>Trichocorys setata</i> (Jørgensen)						1.68													
<i>Tricerapsyrus</i> sp.																			
Phaeodarea																			
<i>Challengeron diadon</i> Haeckel						9.24													
<i>Protocystis tridens</i> (Haeckel)											0.65	0.65	0.65	0.39	3.57			3.73	0.50

Table 2. Relative abundance of the dominant radiolaria in the Greenland-Iceland-Norwegian Sea during summer, 1988. Values are normalized for haul length, and represent approximate numbers  $m^{-3}$  but are not corrected for net clogging. Station prefixes as in Table 1. Where applicable, the standard AWI CTD stations which correspond to our *Polarstern* stations are noted in parentheses.

	<i>Acti- nomma juveniles</i>	<i>Acti- nomma lepto- dermum</i>	<i>P. gracilipes</i>	<i>Amphi- melissa juveniles</i>	<i>A. setosa</i>	<i>P. longi- spinum</i>	Other	Total
<i>Polarstern</i>								
PS 40	5.09	0.58	2.33	1.44	3.69		2.37	15.50
PS 43 (F4)	13.32	2.60	4.50		2.99	1.83	0.47	25.71
PS 47 (F2)	5.01	1.98	5.83	1.20	3.57	0.93	1.63	20.16
PS 68 (D4)		4.54	5.40		4.82	0.62	1.48	16.85
PS 70 (D3)	6.72	2.80	1.48		0.82	1.51	0.74	14.06
PS 75	2.02	0.82	1.79		1.32	0.58	2.72	9.24
PS 81	4.74	5.17	1.90		0.82	3.15	0.78	16.54
PS 83	1.83	0.80	0.87		0.37	0.14	0.58	4.58
PS 98	1.34	3.17	0.78		0.29	1.24	0.25	7.07
PS 107	3.67	0.49	1.28	0.12	0.78	0.91	1.44	8.68
<i>Endeavor</i>								
EN 1	0.57	0.62	0.42		5.09	0.08	0.62	7.40
EN 2	4.78	3.53	2.18		4.03	0.44	1.01	15.97
EN 3	1.51	3.48	1.61		7.53	0.26	1.66	16.05
EN 4	2.91	11.58	2.18		5.77	0.42	3.79	26.65
EN 6	25.14	25.35	8.42		5.40	1.56	4.05	69.92
EN 7	1.25	0.68	0.78		9.25	4.94	0.36	17.25
EN 9	2.13	3.48	1.82		6.75	0.99	0.83	16.00
EN 11	2.03	1.61	3.17		10.23	1.25	2.60	20.88

The abundances of the dominant groups of radiolaria from both cruises, standardized for length of haul and expressed in approximate numbers  $m^{-3}$  are presented in Table 2. There were more radiolaria per  $m^3$  at the average station during the *Endeavor* cruise than during the *Polarstern*, and about 3 times the number of adult *Amphimelissa setosa* and *Actinomma leptodermum* at the stations in the *Endeavor* cruise when compared with the *Polarstern*. No juvenile *A. setosa* were found on *Endeavor*, with slightly fewer *A. leptodermum* juveniles than were found on the *Polarstern*.

A cluster analysis of the radiolarian data from *Polarstern* (Fig. 2a) showed three distinct station groups, with station 68 as an outlier, and two species groups (Fig. 2b), with juveniles of *Amphimelissa setosa* (Cleve) as an outlier. Correspondence analysis (Fig. 3) of the same data reliably reproduced the same grouping, and ordered the stations in a gradient from station group 3 (in order: stns 98, 81) to groups 2 (stns 70, 43, 83, 107) and 1 (stns 75, 47, 40) and stn 68 between groups 1 and 2 on the principle axis (43.7% of the variance), an outlier on higher axes. The species responsible for



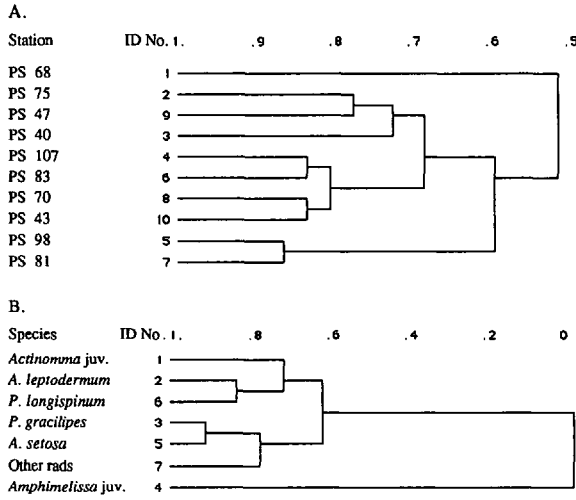


Figure 2. Cluster analysis of summarized *Polarstern* data. Cluster conditions: (A) Cluster by samples, no transformation, standardization was total on stations using percent similarity, UPGMA clustering. (B) Cluster by species: Log (N + 1) transformation, standardization was total on species using Bray-Curtis, flexible clustering with Beta = -0.25.

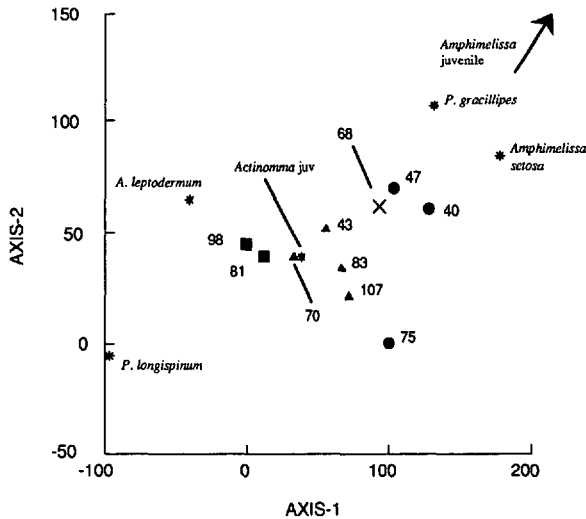


Figure 3. Detrended correspondence analysis of untransformed *Polarstern* data without downweighting. Axis-1 and Axis-2 (respectively) had eigenvalues of 0.168 and 0.036, and accounted for 43.7 and 53.0 cumulative percent of the variance. Symbols assigned according to clusters in Figure 2A: station group 0, cross; group 1, filled circles; group 2, triangles; group 3, squares. Positions of species identified by asterisks.

Table 3. Nodal analysis of averages of abundances of the principal species and age categories of radiolaria, grouped by species and stations according to the clusters in Figure 2. Data from *Polarstern*. These numbers are the average abundance of the species in a given species group over the station group to the left, divided by its average over all the station groups. Indices > 1 indicate concentrations of species above average, those < 1 indicate concentrations below average.

Station Group	Species group		
	1a.	1b.	2.
	<i>Actinomma juveniles</i> <i>A. leptodermum</i> <i>P. longispinum</i>	<i>A. setosa</i> <i>P. gracilipes</i> 'other radiolaria'	<i>A. setosa juveniles</i>
0. Stn 68	0.66	2.01	0
1. Stns 75, 47, 40	0.73	1.45	3.19
2. Stns 70, 43, 83, 107	1.18	0.70	0.11
3. Stns 81, 98	1.21	0.41	0

this grouping can best be determined from a combination of nodal analysis (Table 3) and correspondence plots where species and stations are superimposed. *A. setosa*, *Pseudodictyophimus gracilipes* (Cleve) and 'other radiolaria' were mostly responsible for the grouping of stn 68 and station group 1 (stns 75, 47, 40), with *Amphimelissa juveniles* representing a major contribution to group 1. *Actinomma juveniles*, *Actinomma leptodermum* (Jørgensen), and *Peridium longispinum* Jørgensen were primarily responsible for station groups 2 and 3 (stns 70, 43, 83, 107 and 98, 81 respectively).

When the data from *Polarstern* were compared with those from *Endeavor*, clustering divided the stations into two major groups (Fig. 4), again with stn 68 as an outlier: the separation from correspondence analysis (not shown) was analogous. The first of these groups consisted of 5 stations from the *Endeavor* cruise, the second was the *Polarstern* cruise, and the remainder of the *Endeavor* stations (stns 2, 4, 6).

*b. Chlorophyll a and nutrients.* In all sections there were general gradients in surface Si,  $\text{NO}_3^-$  and  $\text{PO}_4^{3-}$  from high values in the west to low values in the east, and an opposite trend for chlorophyll *a* concentration. There were less clear trends for  $\text{NH}_4^+$  and  $\text{NO}_2^-$ , but generally these had elevated levels to the east of each section at depth. Though the same trends were evident in all the transects, there were outstanding features and differences in the absolute levels of some nutrients, particularly  $\text{NH}_4^+$  and  $\text{NO}_2^-$  between transects.

In section F (Fig. 5) surface levels of  $\text{NH}_4^+$  were generally low, but slightly elevated ( $0.6\text{--}1.0 \mu\text{mol l}^{-1}$ ) between 20 and 60 m in stns 40–43, and also west of station 46. There were high values in surface Si,  $\text{NO}_3^-$  and  $\text{PO}_4^{3-}$  in the west (maxima in stns 46–48) and low values in the east (minima in stns 40–43), and there was an area of elevated  $\text{NO}_2^-$  ( $>0.06 \mu\text{mol l}^{-1}$ ) above 80–100 m east of stn 43.

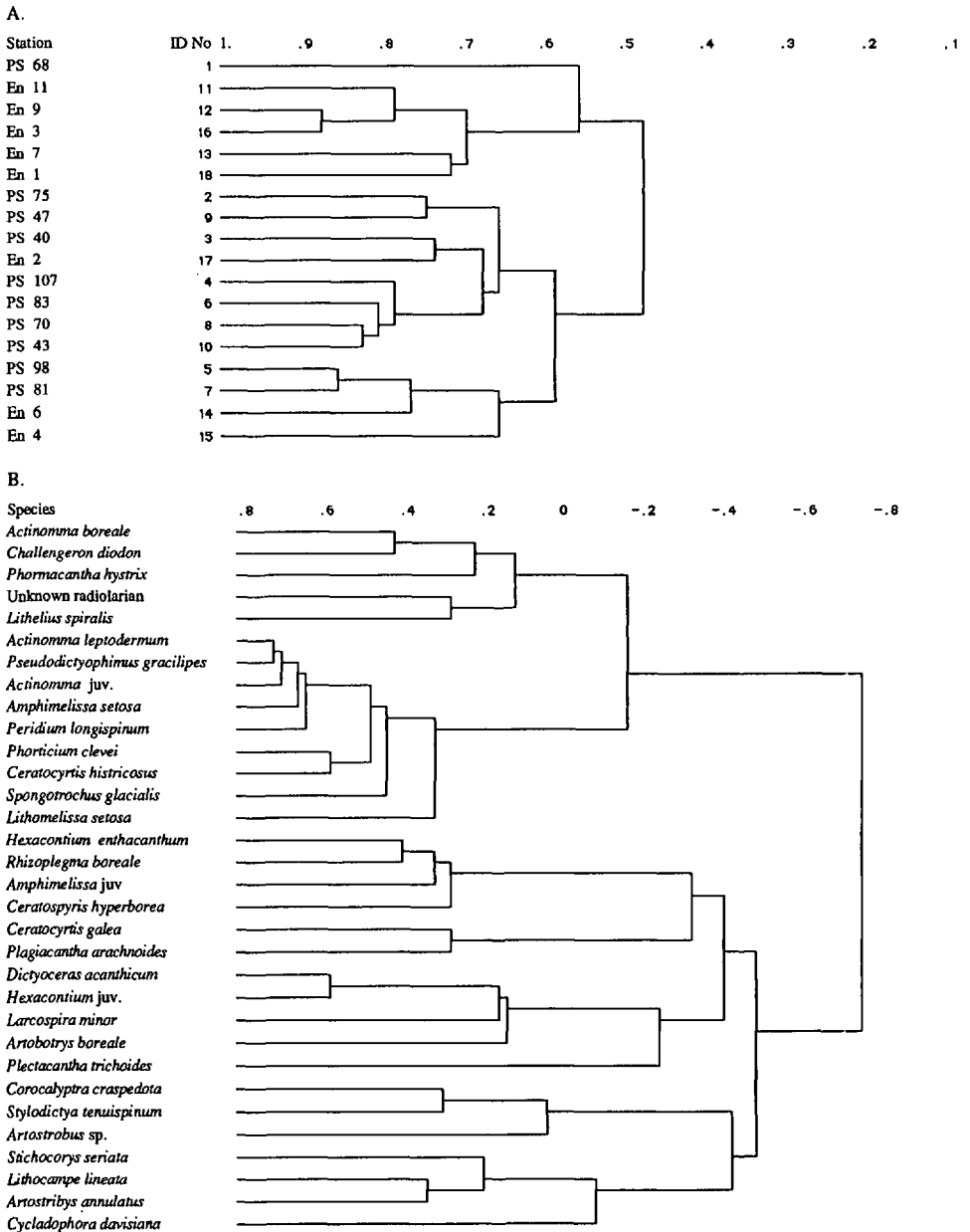


Figure 4. Cluster analysis of all species data from both R/V's *Polarstern* and *Endeavor*. Cluster conditions (A) Cluster by samples: no transformation, standardization was total on stations, percent similarity, UPGMA clustering. (B) Cluster by species: Log (N + 1) transformation, standardization was total on species, Bray-Curtis, flexible clustering with Beta = -0.25.

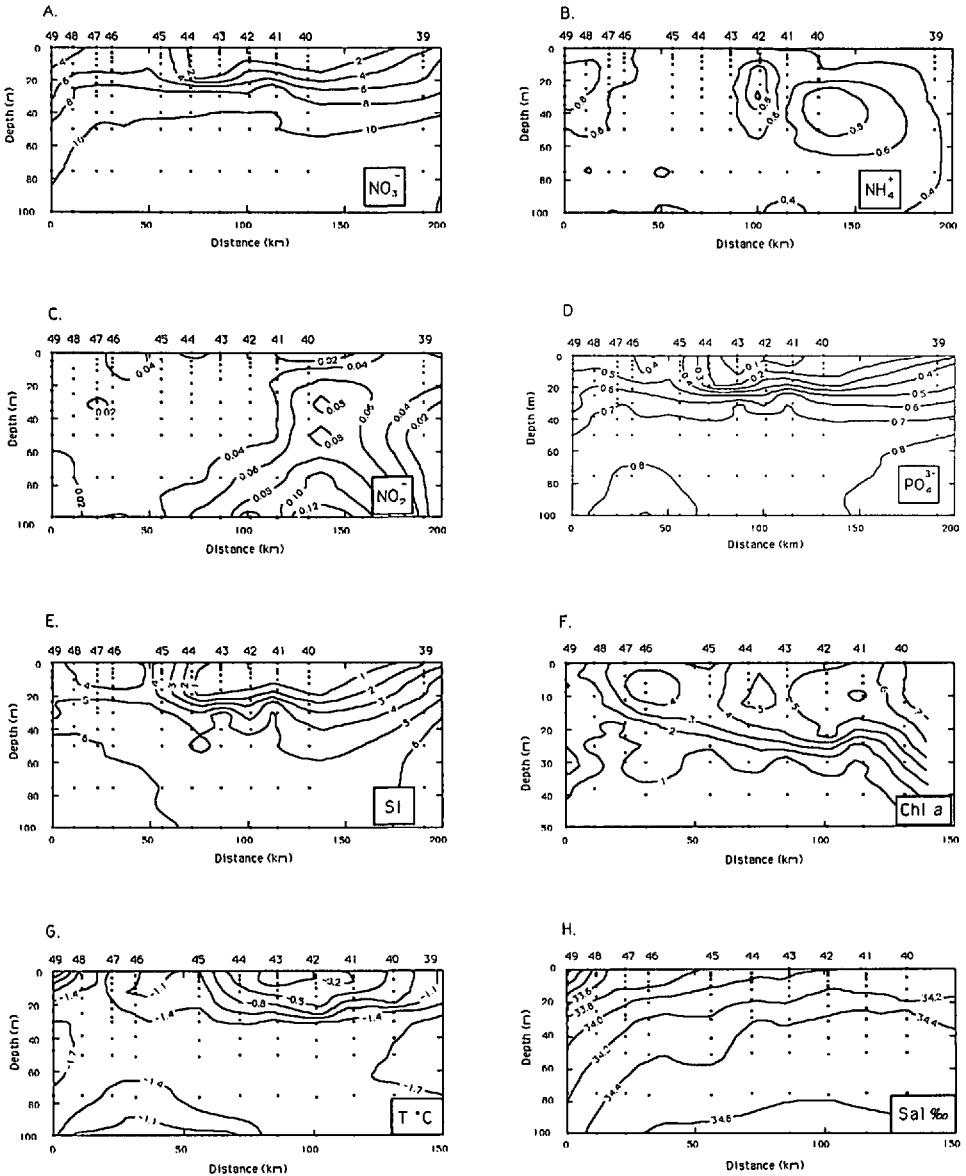


Figure 5. Nutrients and Hydrography, Section F (stns 40–49). (A)  $\text{NO}_3^-$ ,  $\mu\text{mol l}^{-1}$ ; (B)  $\text{NH}_4^+$ ,  $\mu\text{mol l}^{-1}$ ; (C)  $\text{NO}_2^-$ ,  $\mu\text{mol l}^{-1}$ ; (D)  $\text{PO}_4^{3-}$ ,  $\mu\text{mol l}^{-1}$ ; (E) Si,  $\mu\text{mol l}^{-1}$ ; (F) chlorophyll *a*,  $\mu\text{g/l}$ ; (G) Temperature,  $^\circ\text{C}$ ; (H) Salinity,  $\text{‰}$ .

Levels of Si,  $\text{PO}_4^{3-}$  and  $\text{NO}_3^-$  at stn 75 in section D (Fig. 6) were similar to those at stn 47 in section F, but levels of  $\text{PO}_4^{3-}$  and Si at stns 70 and 68 were somewhat higher than those at 43 and 40. Nitrite was not as significantly developed as in section F, but there were elevated levels ( $>0.06 \mu\text{mol l}^{-1}$ ) between stns 70 and 65 below 50 m.

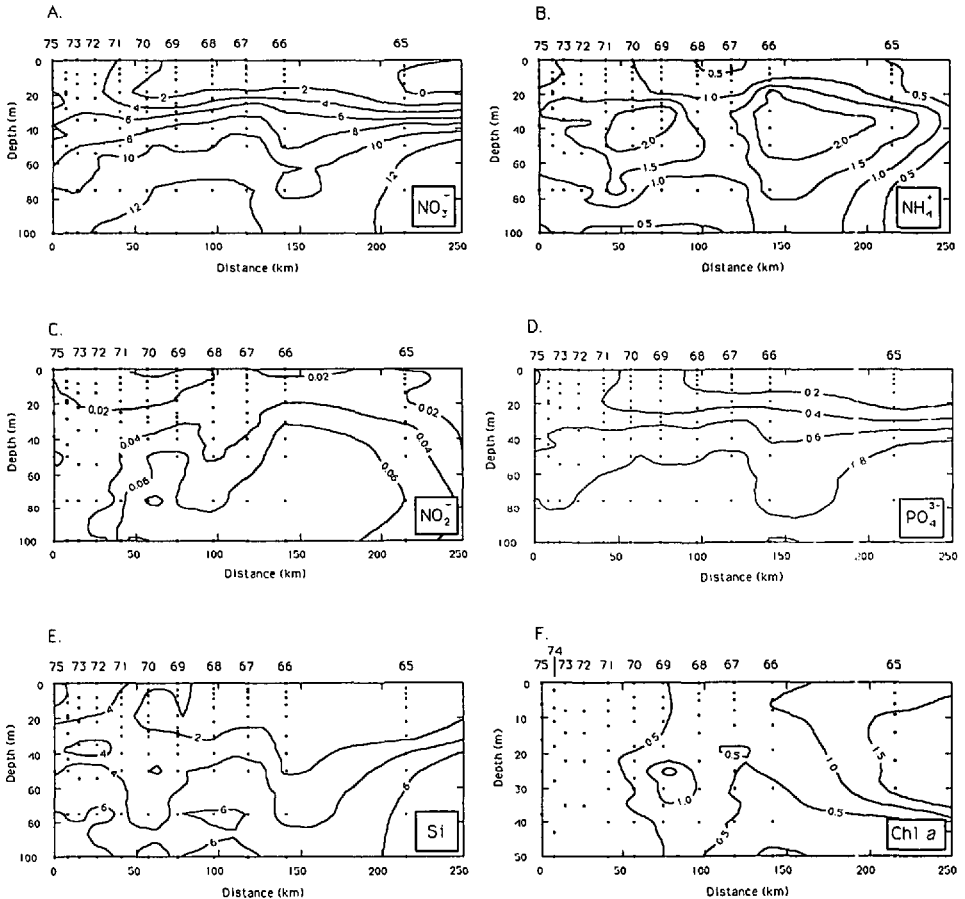


Figure 6. Nutrients and chlorophyll *a*, Section D (stns 65–75). A–F as in Figure 5. There was a significant peak of chlorophyll *a* between 20 and 40 m at stns 68 and 69.

Levels of  $\text{NH}_4^+$  were substantially higher below 20 m ( $1.5\text{--}2.0 \mu\text{mol l}^{-1}$ ) at most stations in this section than in section F.

Section C (Fig. 7) had high  $\text{NH}_4^+$  levels below 20 m ( $1.5\text{--}2.5 \mu\text{mol l}^{-1}$ ) at stns 79–82. Surface levels of Si,  $\text{NO}_3^-$  and  $\text{PO}_4^{3-}$  at stn 83 were approximately equivalent to those at stns 75 and 47 in sections D and F, respectively. Surface  $\text{NO}_2^-$  was relatively low throughout this section, though there were elevated levels ( $>0.10 \mu\text{mol l}^{-1}$ ) below 40–60 m to the east (stns 79–82).

In section FS (Fig. 8) the western part of the section (from station 103 and west) had gradients in surface Si,  $\text{NO}_3^-$  and  $\text{PO}_4^{3-}$  similar to those found in sections F, D and C, with values at stn 107 similar to those at stns 83, 75 and 47. Levels of  $\text{NO}_2^-$  were low everywhere except below 40 m between stn 98 and 103, and  $\text{NH}_4^+$  was high ( $>1.0 \mu\text{mol l}^{-1}$ ) below 30 m between stns 96 and 107.

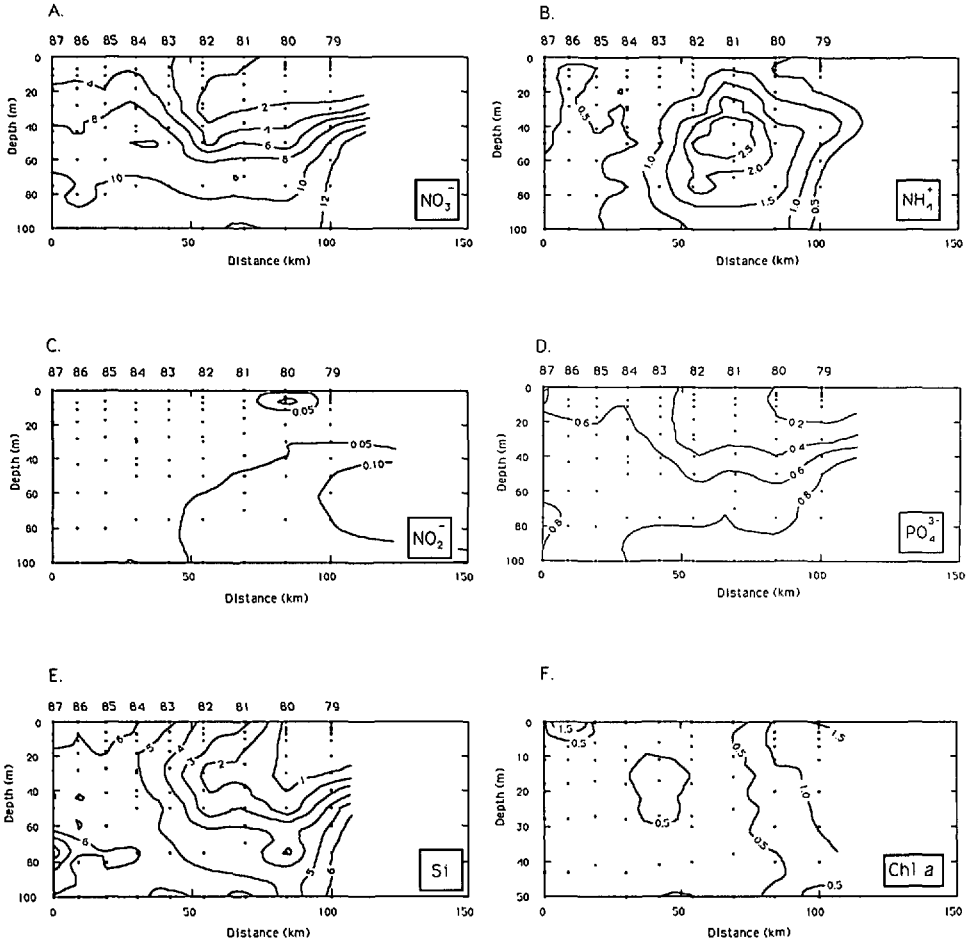


Figure 7. Nutrients and chlorophyll *a*, Section C (stns 79–87). A–F as in Figure 5.

At most hydrographic stations we had chlorophyll *a* data for the upper 50 m. When integrated over this depth, chlorophyll *a* and phaeopigment were generally low in the west and high in the east, but they were also high to the south and low in the north, so that there was a tendency for the western minimum of a southern transect to be close to the value for the eastern maximum of the transect to the north (Fig. 9). The ratios Chl *a*:Phaeopigment generally increased to the east. In Section F, the ratio Chl *a*:Phaeopigment (C:P) ranged from 2:1 in the west to 10:1 in the east. In section D, it ranged from 1.5:1 in the west to 4:1 in the east; in section C, from 1.5:1 in the west to 10:1 in the east; and in section FS, from 2.5:1 in the west to 3.5:1 in the east.

*c. Hydrography.* Section F (Fig. 5 G,H) was cold to the west, with surface temperatures below  $-1.0^{\circ}\text{C}$ . The middle area of this section (stns 41–44) was somewhat

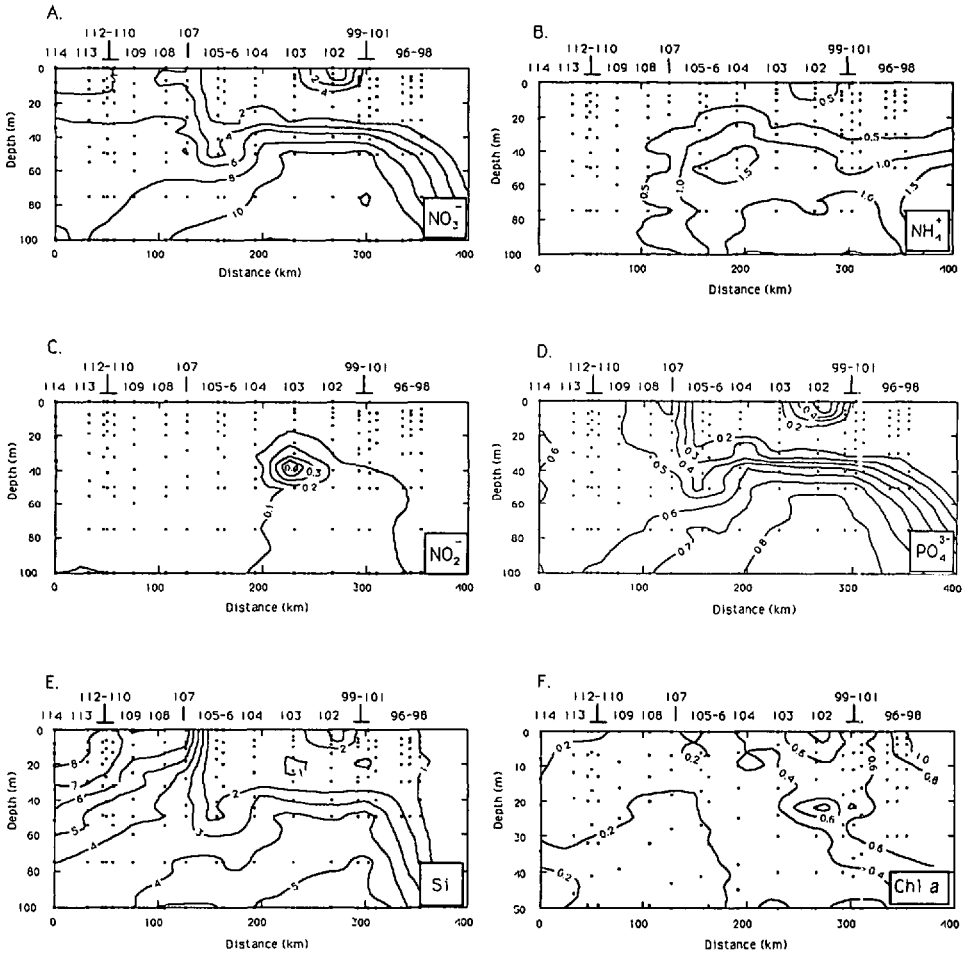


Figure 8. Nutrients and chlorophyll *a*, Section FS (Fram Strait, Stn 96–114). A–F as in Figure 5.

warmer at the surface, with temperatures above  $-0.5^{\circ}\text{C}$ . PW (Polar Water,  $T < 0^{\circ}\text{C}$ ,  $S < 34.4\text{‰}$ ) was found in the upper 100 m in the western portion of this transect, shoaling to the upper 30 m in the eastern. Underlying this and to the east was ASW (Arctic Surface Water). The western half of the transect (W of Stn 44) overlay water between 300 and 400 m which was over  $+1^{\circ}\text{C}$  and  $34.8\text{‰}$  (Fahrbach *et al.*, 1989). This AIW (Atlantic, also called Arctic, Intermediate Water) was at 150–500 m in the western part of this section.

As we did not have all the hydrographic data for the other sections we present no figures for them. These sections were essentially similar to section F and have been described hydrographically elsewhere (Fahrbach *et al.*, 1989; Auf dem Venne, 1990). The Polar Front was at the surface at station 80 in section D, with AIW below about

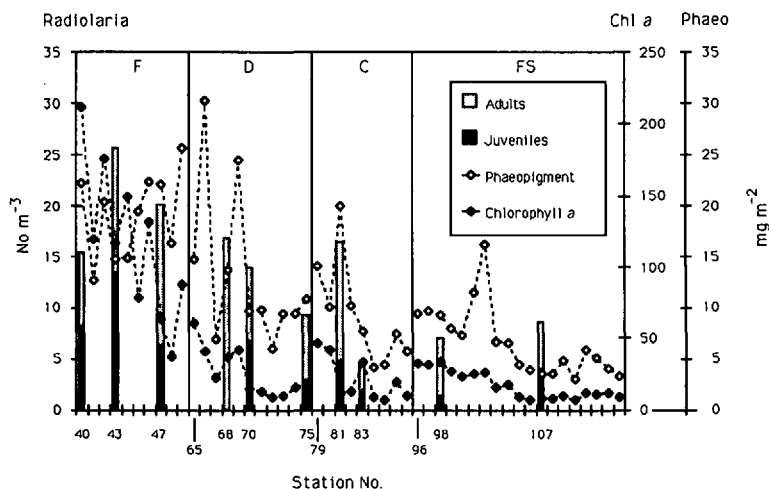


Figure 9. Distribution of chlorophyll *a*, phaeopigment and adult and juvenile radiolaria, ordered by station number. Station numbers are shown for stations where radiolaria were collected and, below the axis, where new transects start. Station numbers increment by one except at breaks between transects, and proceed from east to west (toward the ice) within a transect and south to north between transects.

80 m between stns 81 and 85 (Auf dem Venne, 1990). Most ice was west of station 86. In section C, PW was found between 70 m in the west and about 10 m in the east; under this was mixed water with AIW below 100–200 m, being shallowest at station 69. There was over 20% ice cover at all stations west of stn 68 except stn 70, which was ice-free. In general these sections crossed the Polar Front, with PW in the upper 50–100 m or so in the west, 0–20 m in the east. The Fram Strait section was somewhat different from the others, with vertical isotherms and nearly vertical isohales on the Polar Front at station 106. To the east was warmer surface water ( $> 0^{\circ}\text{C}$ ), to the west cold PW, with 20–80% ice cover.

#### 4. Discussion

The western Greenland current is a complex and dynamic area characterized by fronts between various water masses, eddies, and a strong gradient from east to west into the southbound ice pack. Mixing occurs at the interface between the southward moving PW and the AIW lying under and to the east of it. As the spring and summer approach, phytoplankton blooms are promoted by increasing light due to increasing insolation and by nutrients introduced by wind- and eddy-driven upwelling and the melting of ice (Smith *et al.*, 1985). Nitrogen generally limits these blooms (Smith *et al.*, 1985), which are followed by increases of various other organisms including microzooplankton and zooplankton (Smith, 1988).



Our primary observation is that their geographic distributions place radiolarian station-group 1 (Fig. 2A) closest to the ice, group 2 intermediate and group 3 in the most open water, with the exception that stn 40, which was in group 1, was also in open water in the eastern part of section F. Station 68 was a consistent outlier. The nutrient and chlorophyll *a* profiles from *Polarstern* data show a general trend in all of these transects from non-bloom, nutrient-rich conditions in the western side of the transects to post-bloom zooplankton-dominated communities to the east (Figs. 5F to 8F and Fig. 9). Thus stns 47 and 75 had higher levels of nutrients (Si,  $\text{NO}_3^-$ ,  $\text{PO}_4^{3-}$ ), and lower chlorophyll *a* and regenerated nitrogenous nutrients ( $\text{NH}_4^+$  and  $\text{NO}_2^-$ ) than the eastern portions of their respective sections. Stns 70, 83 and 107, and especially station 43 had depleted nutrients, but as yet undeveloped levels of regenerated nutrients, suggesting late phytoplankton bloom conditions. Stns 81, 98 and 68 had depleted levels of phytoplankton nutrients but well developed regenerated nutrients, suggesting post-bloom conditions. Station 68 had very high subsurface chlorophyll *a* levels, and its fauna, which included no juveniles was more like that of the late summer stations from *Endeavor* than any other station. Station 40 had exceptionally high nitrite levels and primary production (Gradinger *et al.*, 1989) was high at stns 40 and 47 and low at stn 43. The fauna at stn 40 included the only occurrence of large numbers of juvenile *P. gracilipes*. While for any given section these data certainly suggest high nutrients and non-bloom or early bloom conditions to the west of the sections, this is difficult to establish in any absolute sense because of the superimposed N-S gradient.

Station numbers increased from east to west and from south to north, so higher station numbers correspond approximately to earlier stages of the phytoplankton bloom (Fig. 9). There was an overall pattern of decrease in integrated chlorophyll *a*, phaeopigments and both juvenile and adult radiolaria, with increasing station numbers. The numbers of radiolaria were correlated to the chlorophyll and phaeopigment levels, but this relationship was complicated. This is to be expected if different populations of radiolaria produce juveniles of varying duration and timing in response to different biological events during the bloom. Total radiolaria (no  $\text{m}^{-3}$ ) correlated significantly (but noisily) with phaeopigments ( $R^2 = 0.44$ ,  $P = 0.037$ ,  $F = 6.26$ ,  $N = 10$ ,  $DF = 1, 9$ ), but not with chlorophyll. The total number of juvenile radiolaria appeared to co-vary with chlorophyll *a*, but this was not a significant linear relationship ( $R^2 = 0.35$ ,  $P = 0.073$ ,  $F = 4.24$ ,  $N = 10$ ,  $DF = 1, 9$ ). There was a relationship between the number of radiolaria and the total number of juveniles; this was significant with all the stations included ( $R^2 = 0.53$ ,  $P = 0.016$ ,  $F = 9.13$ ,  $N = 10$ ,  $DF = 1, 9$ ), but with the anomalous stn 68 (which had no juveniles) removed it was highly significant ( $R^2 = 0.81$ ,  $P = 0.0009$ ,  $F = 30.13$ ,  $N = 9$ ,  $DF = 1, 8$ ). When the linear relationship between juveniles and total radiolaria was extracted, there was a statistically significant positive relationship between the residuals and the ratio of chlorophyll to phaeopigment; i.e. there were more juveniles than 'expected' in areas

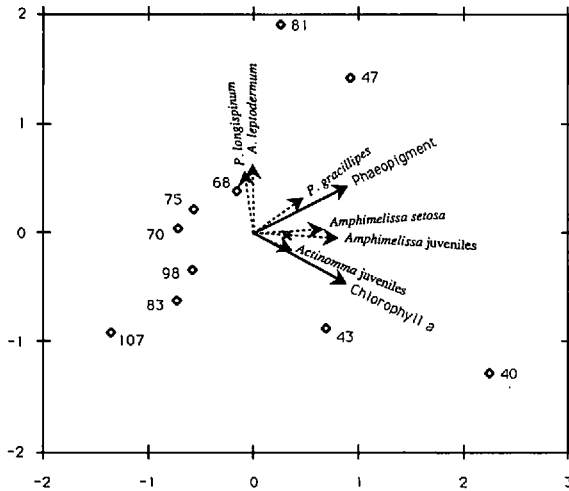


Figure 10. RDA species—environmental bi-plot showing the relationship between individual major groups of radiolaria and the distribution of integrated phaeopigment and chlorophyll *a*. Solid lines with arrows indicate environmental parameters, dotted lines with arrows indicate species. The degree to which the vector of a given species is parallel to the vector of chlorophyll *a* or phaeopigment, indicates the degree of correlation. The analysis is statistically significant (Monte-Carlo Permutation test, Axis-1,  $F = 2.58$ ,  $P = 0.03$ ). See text for details. Eigenvalues: Axis 1, 0.269; Axis 2, 0.121. Cumulative percent variance represented by each axis: (for species data) Axis-1, 26.9; Axis-2, 39.0; (for species-environment relation) Axis-1, 69.0; Axis-2, 100.

where there was higher chlorophyll:phaeopigment ( $R^2 = 0.50$ ,  $P = 0.034$ ,  $F = 6.92$ ,  $N = 9$ ,  $DF = 1, 8$ ), suggesting a relationship with chlorophyll as well. Whereas the relationship between total juveniles and chlorophyll was not significant, it appeared that various groups of juveniles responded in different ways.

These relationships were examined more closely in a species-environment bi-plot of the whole data set produced by redundancy (discriminant function) analysis (CANOCO; Ter-Braak, 1988). Here the first axis (Fig. 10), which accounted for 27% of the variance in the species data and extracted 55% of the variance in the environmental data, was correlated to phaeopigment ( $R = 0.748$ ,  $t = 1.87$ ,  $DF = 7$ ) and chlorophyll *a* ( $R = 0.736$ ,  $t = 1.75$ ,  $DF = 7$ ; these  $t$  values cannot be used to test for significance because the coefficients are canonical; here they suggest that the variables contribute about equally to the first environmental axis). The first axis was significant (Monte-Carlo permutation test,  $P = 0.03$ ). *A. leptodermum* and *P. longispinum* related poorly to phaeopigment and chlorophyll *a*. Adults and juveniles of *A. setosa* correlated equally well with chlorophyll *a* and phaeopigment, while *P. gracilipes* correlated more closely with pigments, and *Actinomma* juveniles correlated with chlorophyll *a*.

The station groups 1, 2 and 3 appear to correspond to rough station characteriza-

tions of pre-, mid- and post-phytoplankton bloom respectively, with the exception of stns 40 and 68. This is difficult to prove, as the data are not fully synoptic and do not represent a single bloom event, but rather a gradient into the ice over a fairly large distance, with a corresponding gradient in bloom conditions, subject to considerable horizontal variability. There is an unmistakable gradient in increasing chlorophyll *a* (Fig. 9) and diminishing nutrients ( $\text{NO}_3^-$ ,  $\text{PO}_4^{3-}$  and Si; Figs. 5–8) with distance from the ice edge. Auf dem Venne (1990) documented the distribution of ciliates along several of the sections of *Polarstern* Ark V/2 and nanoflagellates and bacterioplankton along section D. He found generally increasing numbers of ciliates with increasing distance from the ice edge, and very high numbers of *Mesodinium rubrum* (Lohman) Kahl at the surface at stn 68. Other ciliates also peaked at stn 68 at 40 and 100 m depth. Though one might well argue about the status of any given station, the consistent decrease in nutrients and increase in chlorophyll and microplankton activity from the ice edge to the open water in this area, indicate an overall phytoplankton - microplankton bloom gradient. The radiolarian distributions corresponded to this, suggesting a change during the course of the phytoplankton bloom from dominance of the radiolarian assemblage by juveniles and adults of *A. setosa* and *P. gracilipes* in the early bloom stations to dominance by *A. leptodermum* and *P. longispinum* in the stations with more advanced blooms.

Radiolaria are classically thought of as ideal water-mass indicators (Casey, 1971a,b). The grouping of stations we see might correspond to grouping of radiolarian populations in mixing water masses, not bloom events. The shallower regions of western stations in all of our transects are PW, there is AIW in the lower layers, and ASW, or mixed water in between. If PW were represented by group 1, AIW by group 2, and ASW by group 3, this might account for the distributions we see. The radiolarian groups were not exclusive to the station areas; with the exception of *A. setosa* juveniles, most of the abundant species were found at most of the stations. Although, during the *Polarstern* cruise a maximum of 15, and a minimum of 10 species were found at any one station, most of the commoner species were encountered within each of the three major groups. There were 8 species or stages which did not occur in group 1, but there were 9 which did not occur in group 2, and 15 in group 3, which would argue against the suggestion that what we see is simply dilution of a rich Atlantic fauna with a depauperate polar fauna. Moreover, although most of the species we encountered are common members of the Norwegian Sea water mass to the east and south, most of the commoner ones have also been reported from the Arctic Basin north of Fram Strait (Hülsemann, 1963). Both *A. setosa* and *P. gracilipes*, which were most characteristic of the early-bloom ice edge, are common members of the Norwegian Sea and the Arctic Basin.

A high proportion of juveniles were collected at all stations, especially near the ice edge. This fact certainly suggests that the radiolarian populations in and around the

ice edge were in the process of reproduction. Juveniles of *Actinomma* (*leptodermum*?) were present in all the group 1 stations, but were more abundant in group 2, and less so in group 3. They were present in all the stations in late summer on the *Endeavor*, but most abundant in the open water stations E2 and E6. Juveniles of *P. gracilipes*, *A. setosa* and *Hexacontium* were found only in the western part of the *Polarstern* sections. While it is still possible to argue that what we see in these data is water mass variation, to do so we must assume that the PW mass is characterized by juvenile radiolaria of the same species as found in the ASW to the east. Ultimately that is an untenable hypothesis. There is a gradient of abundance of juvenile radiolaria from low abundance in the PW in the ice to the west to high abundance at the ice edge and low abundance in the open water after the bloom. Mixing alone might account for a gradient in radiolarian abundance from the depauperate polar waters to the rich Atlantic waters, but we also see high numbers of juveniles which peak in the middle of this gradient, and which are much lower later in the season. It is a far simpler and more likely hypothesis that, while the radiolarian fauna may be recruited from the mixing water masses, it reproduces and grows along with the phytoplankton—microplankton bloom at the ice edge.

During their studies in Norwegian fjords, Swanberg and Bjørklund found radiolaria to be very abundant, with a gradient in total abundance corresponding inversely to exposure to the North Sea (Swanberg and Bjørklund, 1986). *Amphimelissa setosa* in particular dominated in Sognefjord, and appeared to be reproducing in the inner reaches of the fjords (Swanberg and Bjørklund, 1986, 1987). Although *A. setosa* presented a different morphotype in the fjords from that which it normally displays in the open ocean (Bjørklund and Swanberg, 1987), both morphotypes were present and distinguishable in the Norwegian Sea. It was hypothesized that one morphotype was associated with the high temperature, high-production, rapid growth conditions in the fjords and possibly in bloom conditions in the summer in the Norwegian Sea, and one was associated with the leaner conditions prevalent in winter in the open ocean. This same species was the dominant form we encountered at the ice edge in PW in the Greenland Sea. The 'rapid growth' morphotype from the fjords was not seen, but the water temperatures were mostly below 0°C, compared with fjord temperatures of over 7°C and Norwegian Sea summer temperatures of 4–5°C.

It has not been possible to isolate the rate at which radiolaria populations develop in most natural oceanic communities because one is usually presented with a mosaic of many different species in various stages of development and one rarely has such a clearly defined gradient over such a short distance. The radiolarian fauna in the Greenland Sea is dominated by relatively few species, which are low in abundance in the water under the ice, so that changes in the population are easily detectable. The data presented here suggest that the development of this community proceeds at the same tempo and probably in response to other biological events in the water column.

In discriminant function analysis adults of *A. setosa* and *P. gracilipes* and most juveniles (including those of *Actinomma*) correlated with chlorophyll *a* and phaeopigments, while adult *A. leptodermum* and *P. longispinum* did not. This is consistent with the hypothesis of juveniles developing in response to the bloom, and that the robust *Actinomma* may be slower in developing than the rather delicate *Amphimelissa*. This could mean that those groups which develop early respond more directly to events lower in the food chain, and even that they have different nutritional niches, but it is impossible from these data to determine whether any of these groups derive their nutrition directly from phytoplankton, or indirectly through the heterotrophic microplankton food web.

The differences our data show between the occurrence of *A. setosa* and *A. leptodermum* suggest that different species of radiolaria respond at different rates to events during succession in the microplankton community—not a surprising result to a biologist, but one which has not been accessible to micropaleontology. If we could sufficiently refine our understanding of the role of radiolaria in planktonic succession that we could attach trophic significance to the appearance of a given species, then the composition of the adult radiolarian community would begin to assume ecological meaning for us. This would provide a powerful tool for interpreting the ecological significance of radiolarian events in the water column and sediment traps, and allow one to attach trophic meaning to the appearance of ecologically defined subassemblages in the sedimentary record.

## 5. Conclusions

(1) There was a statistically significant correlation between the total abundance of radiolaria and phaeopigments in the upper 50 m. There were more juveniles than expected in areas where there was a high ratio of chlorophyll *a*:phaeopigment. When examined as individual species or stages in discriminant function analysis, nassellarians and juvenile actinommids correlated with chlorophyll *a* and phaeopigment, while *Actinomma leptodermum* did not.

(2) As juvenile radiolaria were increasingly important with increasing proximity to the ice-edge, there is probably a radiolarian population development in response to some component of the microplankton at the ice-edge in the Greenland Sea.

(3) There were qualitative differences between the populations of radiolaria under the ice, near the ice edge and in open water. *Amphimelissa setosa*, the more delicate of the species which dominated as juveniles close to the ice, also achieved adult populations closer to the ice edge than the more robust *Actinomma leptodermum*, which dominated in more open water and later in the year.

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