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The morphometric variation of *Actinomma boreale* (Radiolaria) in Atlantic boreal waters

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Abstract

A morphometric study on the polycystine radiolarian species *Actinomma boreale* (Cleve) from ten trigger weight core-tops from the Norwegian–Iceland Seas, three piston cores taken offshore western Norway and three surface sediment samples from Lygrepollen, Sogndalsfjord and Høyangsfjord (western Norwegian fjords) shows a variation in morphology that groups *A. boreale* into three distinct clusters, interpreted to be related to different oceanographic settings. The largest specimens of *A. boreale* are found in the western Norwegian fjords, the smallest in the Iceland Sea, giving an apparent positive correlation with temperature.

Down core studies in piston cores from the Norwegian Sea demonstrate a considerable size variation of the cortical shell of *A. boreale*. In the eastern Norwegian Sea, the climatically cold Younger Dryas had a population of *A. boreale* that was characterized by large cortical shells, while the climatically warm Holocene population was dominated by small sized cortical shells, showing a negative correlation with temperature. We suggest that the large sized cortical shell population of *A. boreale* in the Younger Dryas is not reflecting precisely the sea-surface water temperature. Another factor must play the dominant role here, probably nutrients.

1. Introduction

Radiolarians are marine planktic protozoans with a skeleton of biogenic opal. They are most common in the photic zone of the marine water column. Like other plankton groups, they are sensitive to environmental changes and therefore adapted to physical oceanographic parameters such as temperature, salinity and nutrients and may thus be used as water mass tracers, both in space and time.

Morphometric studies of radiolarians have been used in several fields including critical evaluation of the 'punctuated equilibria' hypothesis of evolution (Kellogg, 1976, 1983), and other evolutionary and taxonomic issues (Lombari and Lazarus, 1988; Granlund, 1990), as well as regional-scale distributions of different morphotypes (Granlund, 1986; Swanberg and Bjørklund, 1987).

In this study, a morphometric approach has been applied to *Actinomma boreale* (Cleve), one of the most common polycystine radiolarian species in the Northern Oceans. It was reported from the Polar Ocean by Cleve (1899), Bernstein (1934), Hülsemann (1963) and Tibbs (1967); from the Iceland and the Norwegian Seas by Bjørklund (1976a) and Molina-Cruz (1991); and from western Norwegian

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fjords by Jørgensen (1900, 1905), Bjørklund (1973) and Swanberg and Bjørklund (1986, 1987). Bjørklund (1973, table 1, p. 24) gave a detailed discussion of *A. boreale*, which we follow herein and observed that there were size differences in the diameter of the third shell between the fjord and open ocean populations of *Actinomma boreale*.

Bjørklund (1976b) demonstrated that *A. haysi* showed a size variation in the surface sediments of the North and South Atlantic Ocean. The diameter of the third shell, in both hemispheres, clearly increased with an increase in latitude or a drop in temperature. It was also demonstrated that size variation within *A. haysi* occurred down core and probably reflected surface temperature changes in the ocean. To test this hypothesis a core with a high time-resolution is needed. We have accomplished this for the present study by constructing a composite section of three well-dated piston cores.

2. Materials and methods

We have investigated a NW–SE transect, spanning 62° to 69°N and 25°W to 10°E, Fig. 1, Table 1. The surface sediment samples are from ten trigger weight (TW) core-tops from the Lamont-Doherty Earth Observatory Core Library, Columbia University, N.Y., U.S.A. collected by R/V *Vema* (core information can be obtained from the LDEO core curator). For the down-core study we used three piston cores (HM28-

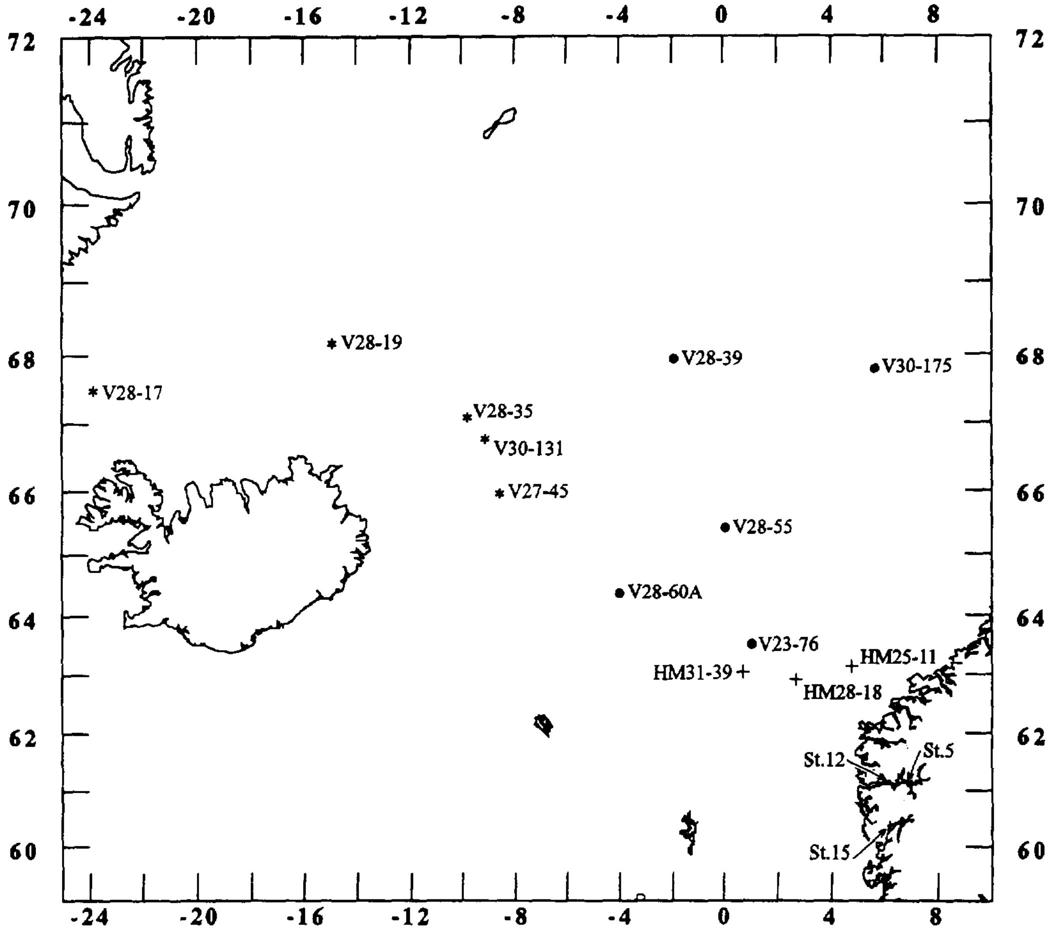

Fig. 1. Locations of the Lamont-Doherty Earth Observatory's R/V *Vema* trigger weight core-tops, separated in Iceland Sea (asterisk) and Norwegian Sea (dot), the three *Håkon Mosby*-piston cores (plus) and position of the western Norwegian fjord localities (arrows).

Table 1
Station location, water depth, number of measured specimens, average diameter of the third shell of *Actinomma boreale* (Cleve), standard deviation, summer and winter temperatures for the analyzed sediment surface samples from the Iceland–Norwegian Seas and the western Norwegian fjords. Temperatures for the Håkon Mosby cores have been extrapolated from the Levitus oceanographic data-base

Station	Latitude	Longitude	Depth (m)	No. of specim.	Ave. dia. 3rd shell	St. dev.	Temp. July	Temp. January
V27-45	66°02′54″N	08°35′30″W	1038	33	74.5	4.7	4.7	3.7
V28-17	67°30′00″N	24°14′00″W	1010	32	73.5	4.9	3.2	2.7
V28-19	68°13′00″N	15°16′00″W	1374	33	76.2	4.1	1.7	1.3
V28-35	67°07′00″N	09°34′00″W	1376	33	74.1	4.5	3.6	2.8
V30-131	66°51′00″N	09°02′00″W	1595	33	72.9	4.3	4.1	3.2
V23-76	63°39′00″N	01°22′00″E	1734	33	77.4	5.1	8.0	6.9
V28-39	67°53′00″N	01°56′00″W	3374	45	77.8	4.0	5.5	4.6
V28-55	65°31′00″N	00°12′00″E	2886	33	75.9	6.8	7.2	6.1
V28-60A	64°25′00″N	04°02′00″W	3231	33	77.4	6.2	6.9	5.6
V30-175	67°51′00″N	05°46′00″E	1383	33	77.3	5.0	7.4	6.7
HM25-11	63°09′00″N	04°31′00″E	1000	520	76.9	4.9	8.3	7.0
HM28-18	62°56′00″N	02°44′00″E	770	429	79.2	5.4	8.2	6.9
HM31-39	63°02′00″N	00°45′00″E	1309	277	84.8	4.5	8.3	7.0
St. 5	61°12′30″N	07°06′24″E	260	33	83.0	3.8	6.5	6.9
St. 12	61°11′00″N	06°02′12″E	272	33	85.1	4.0	7.2	10.3
St. 15	60°5′00″N	06°55′00″E	200	32	83.3	3.9	7.2	X

18, HM25-11 and HM31-39), collected by the R/V *Håkon Mosby*, University of Bergen (Geological Institute core repository). Foraminiferal data, stable isotope records and subdivision into stratigraphic units for these cores were presented by Jansen et al. (1983). The three surface sediment samples from the fjords were taken with a small Petterson grab (Swanberg and Bjørklund, 1986). Radiolarian slides were made following the method described in Goll and Bjørklund (1971).

A Zeiss Axiophot light microscope connected to a video camera with an external TV screen was used for all the measurements (40× objective, 2× optovar and 10× ocular as a standard setting). A micrometer scale was placed under the microscope and displayed on the TV screen, then redrawn onto plastic paper. When the parameter to be measured was displayed on the TV screen, the scale on the plastic paper was used as our micrometer scale. The accuracy of this measuring technique is about 2 μm for the 40× objective. All measurements are based on a minimum of 30 specimens from each sample.

The measured parameters were: diameter of first, second, third and fourth shell. The diameter of the first shell, the inner medullary shell, is in most cases difficult to observe as it is obscured by the second and third shells that enclose it. The second and third shells can always be measured. The fourth shell is not always fully developed, but transverse processes on the radial spines, if present, give a good indication of the position and appearance of a fourth shell (e.g. Plate I, 7).

For a detailed explanation of all the statistical techniques mentioned in the text (ANOVA, $F_{\max}$-test, Student t-test, etc.) see Sokal and Rohlf (1981).

3. Taxonomical problems

In the high northern latitudes of the Atlantic Ocean, as in the Norwegian–Iceland Seas, the polycystine radiolarian assemblage contains about 70 species (Petrushevskaya and Bjørklund, 1974). In our study we use selected species in an attempt to recognize size differences in certain radiolarian populations, map their distribution and look into their stratigraphical fluctuation and usefulness for paleoceanographic and climatic reconstructions.

Actinomma boreale (Cleve) is one of the most abundant species in these high northern waters. It was therefore natural for us to concentrate our study

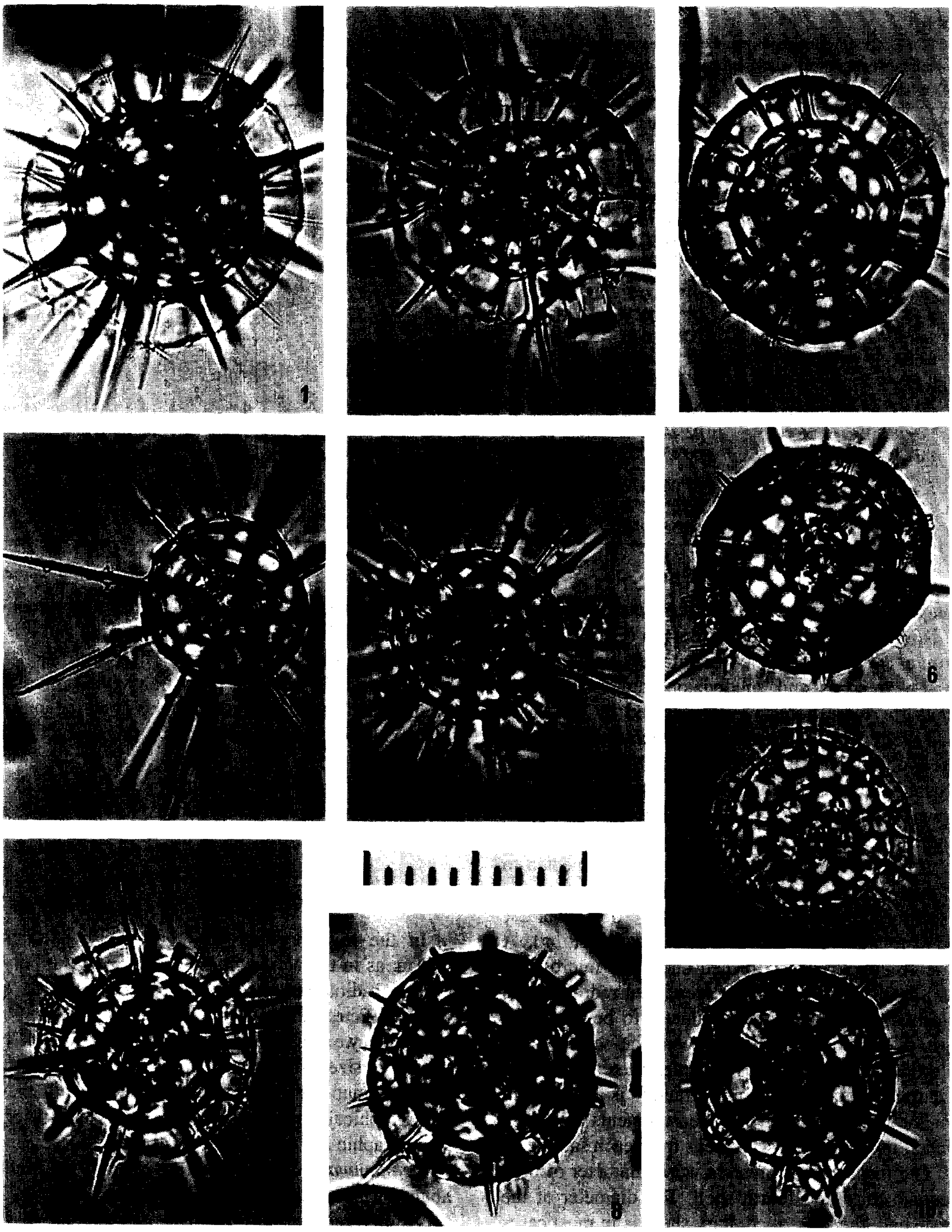

Plate I

Scale bar equals 100 μm for all figures. *Actinomma boreale*, illustrating basic morphology and variation. 1. Station 12, Høyangsfjord, core-top. 2. V28-55 core-top. 3. V28-55 core-top. 4. V28-55 core-top. 5. V28-55 core-top. 6. V28-55 core-top. 7. V28-36 core-top. 8. V28-35 core-top. 9. Station 5, Sogndalsfjord, core-top. 10. V28-36 core-top.

on this species. Typical specimens from our study are shown in Plate I.

Bjørklund (1976b) made a taxonomic emendation of the four genera *Actinomma*, *Echinomma*, *Cromyomma*, and *Cromyechinus*, where he grouped all genera into *Actinomma*, and we have adopted this suggestion here. The reader is referred to Bjørklund (1973, 1976a) for detailed taxonomical discussion and illustration of *Actinomma boreale*.

4. Results: core-top study

In total, we have measured the diameter of the third cortical shell on 1665 specimens of *Actinomma boreale* (Tables 1 and 4). A plot of these measurements with different symbols for the different areas did not show any obvious geographical grouping. We therefore calculated the average values of the diameter of the third and fourth shells from each station, and plotted them (Fig. 2). The coefficient $R^2 = 0.86$ indicates that the correlation in this plot is good and it is evident that the plot groups our stations in an Iceland Sea Group, a Norwegian Sea Group, and a Fjord Group. There is a clear trend where the fjord specimens have, on average, the largest tests, while the smallest tests are found in the Iceland Sea, with the Norwegian Sea representing an intermediate group. This plot also shows that the diameter of the third shell is a better parameter to use than the diameter of the fourth shell, in order to discriminate between the three geographical groups.

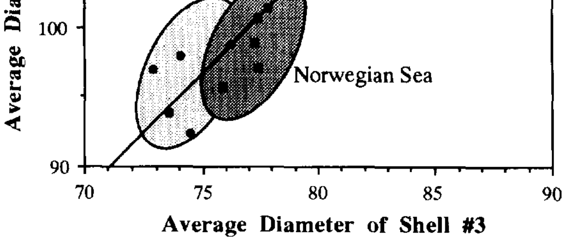

Fig. 2. *Actinomma boreale*; the average diameter of third shell plotted versus the fourth shell, surface sediment samples from all stations.

Bjørklund (1976b) demonstrated that the diameter of *A. haysi* shows a negative correlation with temperature, i.e. largest tests corresponding to lowest temperatures. This does not seem to be the case with the distribution of *A. boreale* in the Norwegian–Iceland Seas. In the Iceland Sea the average winter temperature at 50 m water depth ranges between 1.3°C and 4.7°C, in the Norwegian Sea between 4.6°C and 6.9°C, and in the fjords between 6.9°C and 10.3°C. This suggests a positive relationship between the size of the third cortical shell and the sea water temperature (Fig. 3a, Table 1).

During the summer, however, the average temperature at 50 m varies between 1.7°C and 4.7°C in the Iceland Sea, between 5.5°C and 8.0°C in the Norwegian Sea, and finally between 6.5°C and 7.2°C in the fjords (Fig. 3b, Table 1). It is important to note that there is a temperature inversion in Sognefjord at 50 m depth, see Swanberg and Bjørklund (1987, figs. 2–3). As a result, the summer temperatures are lower than the winter temperatures at that depth.

Bjørklund (1973) documented a bloom of radiolarians in Korsfjord (western Norway), during summer 1970 in the 200–100 m depth interval, with a temperature range from 5.1° to 6.1°C. *Actinomma boreale* (1528 specimens/m^3) and *A. leptodermum* (5204 specimens/m^3) made up almost 95% of the radiolarian fauna. This indicates that the *Actinomma* bloom most likely also took place below the summer 50 m inversion layer in Sognefjord.

Sediments basically reflect the biogenic production, rather than the standing stock. Therefore it is important to evaluate temperature differences at the time of maximum radiolarian production (growth). This is when a major part of the measured shells were generated. That is one of the reasons why we chose the temperature at 50 m depth, where the seasonal variation is limited to a few degrees. The same situation occurs in the Norwegian Sea. Therefore the difference in average yearly temperatures between the two areas is much larger than the seasonal temperature variation within each of the two areas.

We could also envision a scenario where juveniles were recruited from the East Greenland Current, and

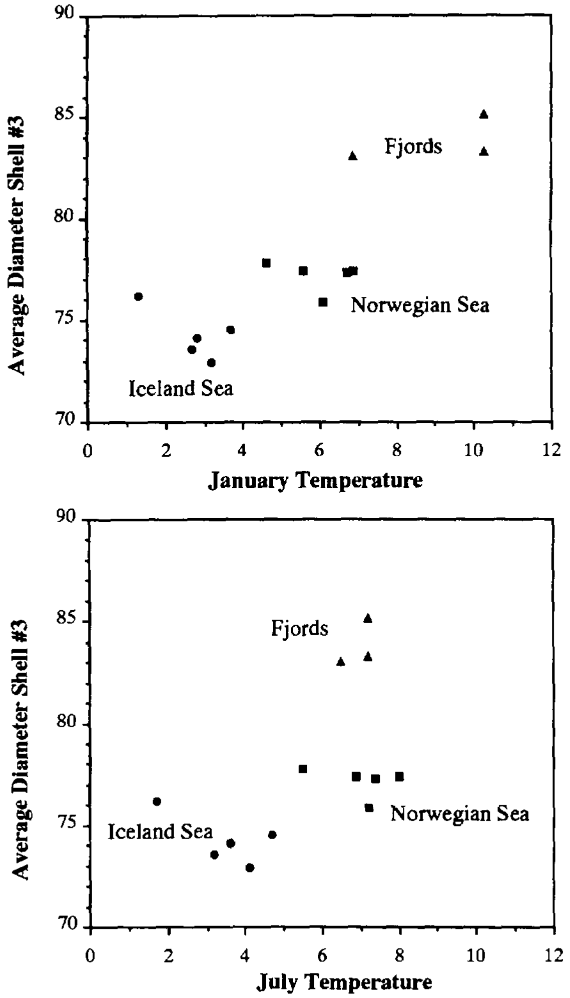

Fig. 3. *Actinomma boreale*; the winter (a) and summer (b) temperatures plotted versus the average diameter of the third shell, from all the surface sediment samples.

then transported to the Iceland Sea. Another scenario could imply the recruitment from the North Atlantic into the Norwegian Sea (Norwegian Current). Finally, a third scenario could be represented by recruitment from the Norwegian Sea into the Iceland Sea and vice versa (in the large cyclonic gyre northeast of Iceland). However, all these scenarios can be excluded by the normal size distribution (Fig. 4) displayed by our measurements on the third shell of *Actinomma boreale*. If a mixing of these populations had occurred, the size distribution would have been bimodal for each of the groups.

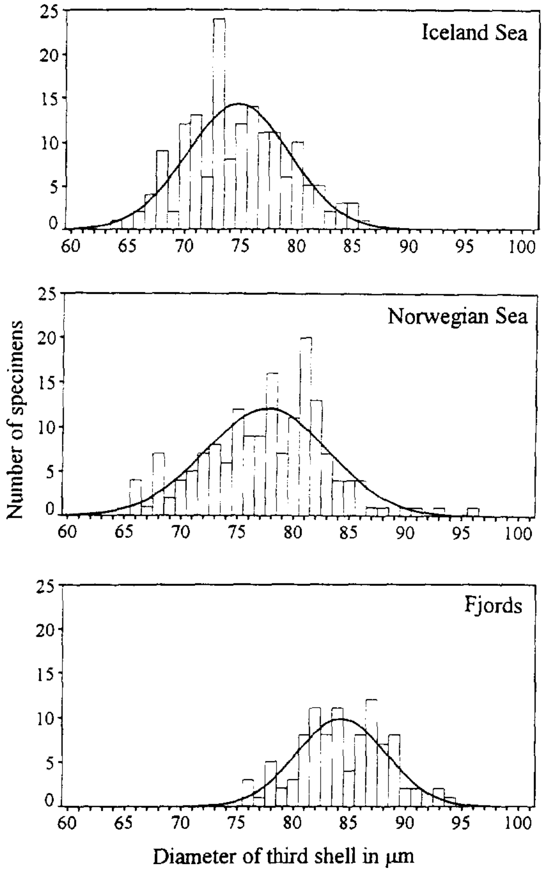

Fig. 4. The frequency distribution and the gaussian curve for the Norwegian Sea (a), Iceland Sea (b) and western Norwegian fjords (c) surface sediment populations.

It is in the fjords that the *A. boreale* populations have the largest tests, Fig. 3a, b, and it is tempting to make a direct correlation between size and temperature. However, the summer temperature does not differ significantly between the fjords and the Norwegian Sea, so size is not controlled by temperature alone. Size differences in radiolarian tests may be a result not only of growth, but also of dissolution. We are of the opinion that dissolution cannot account for the observed size differences. Dissolution only influences the skeleton thickness in spherical spumellarians, not the actual positions of their skeletal structures. The fjords must be affected by a parameter more influential than temperature which is causing the large test sizes. The fjords are great recipients of river discharge and are therefore enriched in nutrients and dissolved silica. We interpret the fjords to provide more favourable living conditions to polycystine radiolarians, in this case *A. boreale*, than the open ocean.

Primary production data for the Norwegian Sea and the fjords are necessary to substantiate the assumption that differences in food availability are responsible for the recorded differences in shell size. Unfortunately, synoptical records of primary production in the study area do not exist.

The average of the third cortical shell of all *A. boreale* specimens from each group was calculated and the size frequency analyzed. The average size of the third cortical shell for the fjords, the Norwegian Sea, and the Iceland Sea are 84 μm, 77 μm, and 74 μm, respectively (Fig. 4). It is evident that there is a large overlap in the sizes between the three groups, and we therefore wanted to use a Student *t*-test and an analysis of variance (ANOVA) to check the significance of the groupings that we had identified in our plots. As simply stated by Glantz (1987): "the t-test and ANOVA are really two different ways of doing the same thing since, when comparing the means of two groups, $F = t^2$. In other words, the t-test is simply a special case of ANOVA applied to two groups".

Running an ANOVA on three populations, or running three *t*-tests on the possible combinations of the same three populations, leads to the same conclusions.

The $F_{\max}$-test, introduced by Hartley (1950), was used to check the hypothesis of uniform variances between the three groups, which is a prerequisite to the usage of ANOVA and Student *t*-test. The test was successful at $P < 0.05$, thus allowing us to apply both the ANOVA and the Student *t*-test to the total data set within each group. The results of these tests (Table 2) show that there is a statistically significant difference between the fjord and Iceland Sea populations of *A. boreale* at <0.001 degree of confidence (as can be seen from the '$P(T \leq t)$ two tail' value). The test was successful as the t value exceeded the t_{crit} two-tail value. The situation is the same when testing the fjords against Norwegian Sea populations, and finally Iceland Sea against Norwegian Sea populations. In other words, the probability that the three sets of values are coming from the same population is close to zero, i.e. they are very different from each other.

Table 2

Summary of ANOVA (single-factor) and the Student *t*-test (two-sample assuming equal variances) on the diameter of the third shell in *Actinomma boreale* from the Iceland Sea, Norwegian Sea and the western Norwegian fjord populations

F	P-value	F_{crit}
121.1	<0.001	3.02
	Fjords	*Iceland Sea*
Mean	83.80	74.25
Variance	15.81	20.91
Observations	98	164
t	17.14	
$P(T \leq t)$ two-tail	<0.001	
t_{crit} two-tail	1.97	
	Fjords	*Norwegian Sea*
Mean	83.80	77.13
Variance	15.81	29.99
Observations	98	166
t	10.52	
$P(T \leq t)$ two-tail	<0.001	
t_{crit} two-tail	1.97	
	Iceland Sea	*Norwegian Sea*
Mean	74.25	77.13
Variance	20.91	29.99
Observations	164	166
t	−5.18	
$P(T \leq t)$ two-tail	<0.001	
t_{crit} two-tail	1.97	

The Student *t*-test was applied to evaluate the significance of the differences between all stations in the three groups. The results are shown in Table 3 where the degree of confidence is tabulated. There is good harmony in the degree of confidence values within each group and between the groups. All the proposed clusters are clearly separated as uniform groups since the degree of confidence is always <0.05 when the stations are compared with each other.

V28-19 and V28-55 are the only anomalies in our data set. We interpreted V28-55 as a transitional station since it shows faunal affinities with both the Iceland Sea group and the Norwegian Sea group. The population in V28-55 is not statistically different from any other population coming from any other station. This assumption is supported by the geographical position of the station, as it is located in an area where considerable oceanographic mixing occurs between the warm North Atlantic Drift and the cold East Greenland Current.

Station V28-19 gives results quite different from

Table 3
The degree of confidence of the Student *t*-test between all stations

	Iceland Sea					Tr	Norwegian Sea				Fjords		
Stations	V28-17	V28-19	V28-35	V30-131	V27-45	V28-55	V28-60A	V28-39	V23-76	V30-175	St. 5	St. 12	St. 15
V28-17		*0.02*	0.65	0.58	0.41	0.12	0.008	<0.001	0.003	0.003	<0.001	<0.001	<0.001
V28-19			*0.05*	*0.002*	0.13	0.82	*0.37*	*0.08*	*0.3*	*0.33*	<0.001	<0.001	<0.001
V28-35				0.29	0.69	0.21	0.017	<0.001	0.007	0.008	<0.001	<0.001	<0.001
V30-131					0.15	0.04	0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
V27-45						0.35	0.04	0.001	0.02	0.02	<0.001	<0.001	<0.001
V28-55							0.36	0.12	0.32	0.34	<0.001	<0.001	<0.001
V28-60A								0.7	0.99	0.95	<0.001	<0.001	<0.001
V28-39									0.67	0.6	<0.001	<0.001	<0.001
V23-76										0.94	<0.001	<0.001	<0.001
V30-175											<0.001	<0.001	<0.001
St. 5												0.03	0.74
St. 12													0.06
St. 15													

Tr = Transitional station. Station V28-19 (values in italics) behaves differently than expected, see discussion in text.

Table 4
The age (rounded to the closest tenth), core denomination and sample depth in cm, the number of measured specimens, and the average diameter of the third shell in *Actinomma boreale* in the composite section

Age (yr B.P.)	Core	Measured specimens	Avg. diam. 3rd shell	Age (yr B.P.)	Core	Measured specimens	Avg. diam. 3rd shell
0	HM25-11/0	33	76.2	8920	HM25-11/327	33	78.7
360	HM25-11/5.5	33	77.8	9420	HM25-11/350	33	77.1
980	HM28-18/11	33	76.9	9620	HM28-18/108	33	79.0
1830	HM28-18/20.5	33	77.2	9840	HM28-18/118	33	77.7
2270	HM25-11/35	33	77.7	9950	HM28-18/138	33	81.0
2580	HM28-18/29	33	79.5	10020	HM28-18/150	33	81.5
2820	HM25-11/57.5	33	76.6	10040	HM25-11/378.5	33	77.4
3790	HM25-11/97.5	33	77.2	10220	HM28-18/185	33	82.4
4320	HM28-18/48.5	33	76.0	10300	HM31-39/7	34	83.2
5010	HM25-11/147.5	33	77.3	10480	HM31-39/17	33	85.7
5480	HM25-11/169	33	75.0	10530	HM25-11/400	33	74.9
6010	HM28-18/67.5	33	76.4	10650	HM31-39/27	33	86.8
6150	HM25-11/200	25	77.2	10830	HM31-39/37	33	87.0
6950	HM28-18/78	33	76.6	10890	HM28-18/235	33	85.2
7240	HM25-11/250	33	76.4	11010	HM31-39/47	33	87.1
7460	HM25-11/260	33	76.4	11170	HM31-39/56	33	85.2
7610	HM25-11/267	33	77.4	11340	HM31-39/66	33	82.7
8110	HM25-11/290	33	77.5	11520	HM31-39/76	21	81.4
8730	HM28-18/98	33	79.5	11690	HM31-39/86	24	81.8

those to be expected from its geographical position. It is statistically different from any station in the Iceland Sea with which it should have resembled, and it is not statistically different from any station in the Norwegian Sea. We, so far, have no explanation for this phenomenon.

5. Results: down-core study

With the information gained from the core-top study of *A. boreale*, we proceeded to examine the size/temperature relationship over the last 13 kyr.

We chose three particularly suitable piston cores

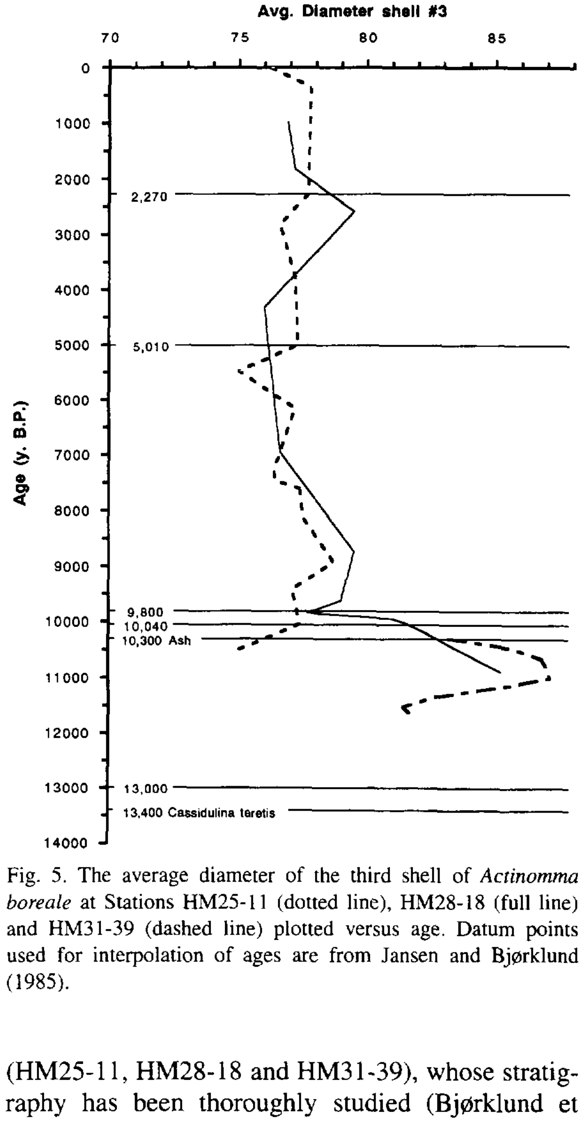

Fig. 5. The average diameter of the third shell of *Actinomma boreale* at Stations HM25-11 (dotted line), HM28-18 (full line) and HM31-39 (dashed line) plotted versus age. Datum points used for interpolation of ages are from Jansen and Bjørklund (1985).

(HM25-11, HM28-18 and HM31-39), whose stratigraphy has been thoroughly studied (Bjørklund et al., 1979; Jansen et al., 1983; Jansen and Bjørklund, 1985). These cores have a good biostratigraphy with time control based on several ^{14}C-ages and the Vedde ash layer, whose age has been recently revised to 10.3 kyr (Bard et al., 1994).

Measurements of the diameter of the third shell of *A. boreale* were carried out on 38 samples from these cores. The results are given in Table 4. The age assignments for each of our samples have been extrapolated from the existing datum-points. These datum points have been plotted in Fig. 5, together with the down-core variation of the average diameter of the third shell of *A. boreale*.

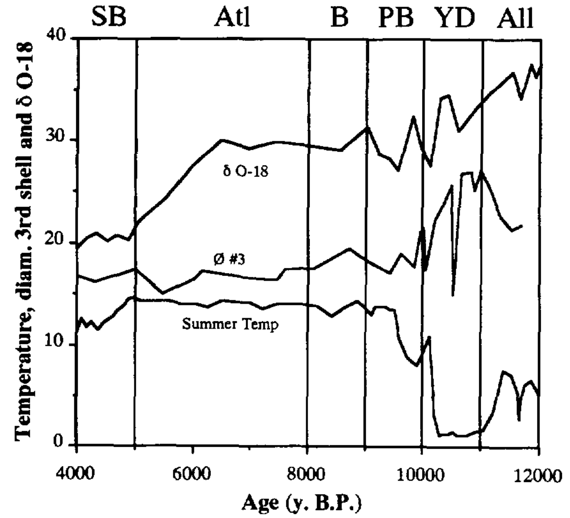

Fig. 6. Synthesis of the shell size in *Actinomma boreale* (*y*-axis add 60 to value), $\delta^{18}O$ (*y*-axis 10 times the real value), and the summer temperature (same scale as axis) at 50 m water depth, plotted versus age. *SB* = Sub Boreal; *Atl* = Atlanticum; *B* = Boreal; *PB* = Pre Boreal; *YD* = Younger Dryas; *All* = Allerød (Mangerud et al., 1974).

We then built a composite section from our three sections (Table 4), and compared this to a paleotemperature curve, calibrated with other microfossil groups, such as diatoms (Karpuz and Schrader, 1990) from the Greenland–Iceland and Norwegian Seas (Fig. 6).

At the end of Allerød, 11.8–11.0 ka (chronozones as defined by Mangerud et al., 1974), there is a drop in temperature and a corresponding increase in the size of the third shell of *A. boreale* (Fig. 6). At the termination of the Younger Dryas, 11.0–10.0 ka, and half way into the Preboreal, 10.0–9.0 ka, there is a general rise in temperature and a decrease in the size of the third shell. During the remainder of the Holocene there are no major changes in either temperature or size. There is no obvious correlation between our size curve and the $\delta^{18}O$ curve.

So in our down-core study we observe a negative correlation between temperature and the size of the third shell (Fig. 6), while our surface study revealed the opposite trend (Fig. 3).

The Younger Dryas temperatures, of Karpuz and Schrader (1990), were between 1° and 4°C, which is in the same range as the present-day Iceland Sea-surface temperatures. We would therefore expect

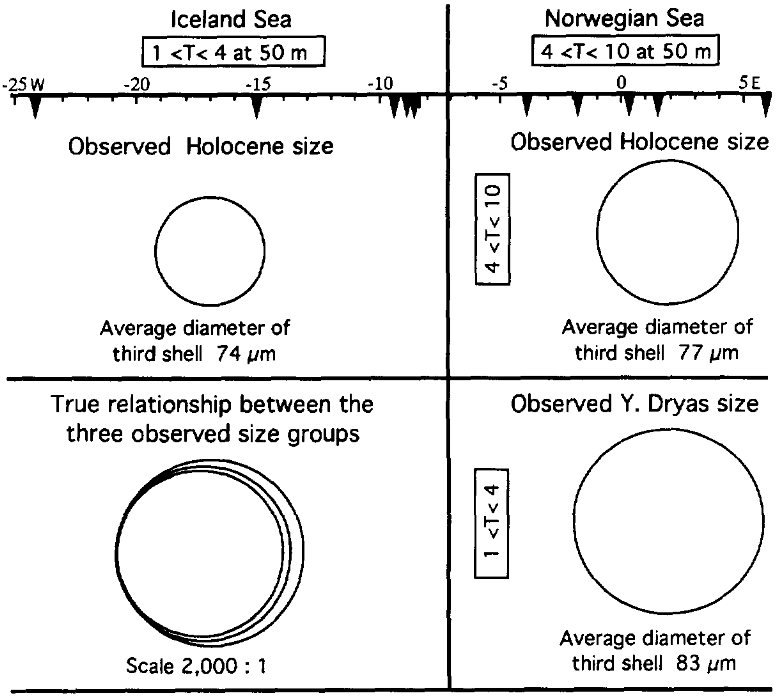

Fig. 7. The average diameter (exaggerated) of the third shell in *Actinomma boreale* from the Iceland-Norwegian Seas plotted in space and time. Black triangles on the E-W axis, indicate the station locations. Temperature ranges for the Holocene and the Younger Dryas from Karpuz and Schrader (1990).

to find a Younger Dryas population of *A. boreale* in the Norwegian Sea with an average third shell diameter roughly similar to the present-day Iceland Sea population (Fig. 7).

It was therefore a surprise when we observed an average diameter of 83 μm during the Younger Dryas, which is ca. 9 μm larger than expected. It is even larger than the average diameter of the present Norwegian Sea population.

We suggest that this large-cortical shell population of *A. boreale* in the Younger Dryas is not solely a result of the sea-surface water temperature. We believe that (as for the modern fjord population) other factors override the temperature effect. The Younger Dryas had a hydrographical situation quite different from the present.

Authors such as Broecker et al. (1985) and Sarnthein et al. interpreted as an ecological effect of the melt water lid (Morley, 1983; Morley and Hays, 1983; Ciesielski and Bjørklund, 1995). This would provide the Younger Dryas with a density gradient in the water column that does not exist in the Holocene. Such a gradient would reduce the sinking rate of marine microplankton and probably also enrich the ocean in particulate organic material around its depth interval. This will again lead to easy food access for certain animal groups.

Stabilization of the uppermost layers may enhance phytoplankton biomass build-up, as is suggested for present-day Antarctic environments after melting of the ice-sheet (Smith, 1987).

This discontinuity layer will, over time, preclude replenishment of near-surface nutrients by deep mixing, therefore feeding materials will be scarcer, giv-

Dryas may have caused the unexpected large size of the third cortical shell. The large shells in the Younger Dryas and the present-day fjord populations of *A. boreale* are not the result of temperature alone, but also a reflection of more suitable ecological conditions.

An understanding of these processes is essential for a critical approach to paleotemperature estimates based on polycystine radiolarian microfossils. As we have demonstrated, great care should be taken before assuming a direct correlation between size and temperature in these organisms.

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