Spatial and temporal dynamics of coccolithophore communities during low production phases in the Norwegian-Greenland Sea

KARL-HEINZ BAUMANN[1], HARALD ANDRULEIT[2], ANDREA SCHRÖDER-RITZRAU[3] and CHRISTIAN SAMTLEBEN[4]

1. FB Geowissenschaften, Univ. Bremen, Postfach 330440, D-28334 Bremen, Germany

2. SFB 313, University of Kiel, Heinrich-Hecht-Platz 10, D-24118 Kiel, Germany

3. GEOMAR - Research Center for Marine Geosciences, Wischhofstr. 1-3, D-24148 Kiel, Germany

4. Geolog.-Paläontolog. Inst., University of Kiel, Olshausenstr. 40, D-24118 Kiel, Germany

ABSTRACT

The present investigation was initiated to report on species compositions and dynamics in the Norwegian-Greenland Sea during low production phases in spring and early summer. Thus, the distribution patterns of living coccolithophores during June to July, 1990, February and May, 1991, and March to April, 1995 were investigated. In general, the seasonal development of the phytoplankton started after the yearly dark period and coccolithophores increased in abundance when the water column was more stratified and both temperatures and insolation increased. Cell densities reached a maximum of 207×10^3 coccospheres/l in the southeastern part of the studied area. However, these high cell densities probably resulted from „old" populations, drifted to the Norwegian-Greenland Sea from the North Atlantic. Some of the collected samples did not contain any coccolithophores.

In total, 15 coccolithophore species were identified. The diversity was generally higher in the eastern part of the Norwegian-Greenland Sea and to the west the coccolithophore communities often were monospecific. *Emiliania huxleyi* is the dominant species, but *Calciopappus caudatus* and *Algirosphaera robusta* also considerably contribute to the communities. High cell densities of *C. caudatus* were interpreted as the result of a bloom or more probably close to bloom conditions during the general low productive period. In addition, many of the *E. huxleyi* coccoliths from the surface waters of the southeastern Norwegian-Greenland Sea were heavily corroded. These specimens may have drifted within the Atlantic water for a longer time.

INTRODUCTION

Coccolithophores are a major group of marine, unicellular phytoplankton. They form external calcified plates with a complex ornamentation, which cover the cell surface. These coccoliths form an important part of the fine fraction of deep-sea sediments and therefore are extensively used in biostratigraphic, paleoecologic, and paleoceanographic studies (e.g. McIntyre & Bé, 1967; Geitzenauer *et al.*, 1976; Roth & Coulborn, 1982; Gard, 1988; Crux & van Heck, 1989; Baumann, 1990; Baumann & Matthiessen, 1992). Many studies on recent calcareous nannoplankton in the northern Atlantic Ocean are predominantly taxonomic (e.g. Halldal & Markali, 1954, 1955; Gaarder & Markali, 1956; Gaarder & Heimdal, 1977; Heimdal & Gaarder, 1980, 1981; Kleijne, 1991; Knappertsbusch, 1993). In addition, much of the earlier plankton work from our study area in the Norwegian-Greenland Sea only included microscopic examinations of the netplankton, while the smaller nannoplankton has often been overlooked. However, a number of investigations concerning the dynamics and ecology of calcareous nannoplankton in northern North Atlantic have recently been published (e.g. Samtleben & Schröder, 1992; Knappertsbusch & Brummer, 1995; Samtleben *et al.*, 1995a). About 20 different coccolithophore species have so far been
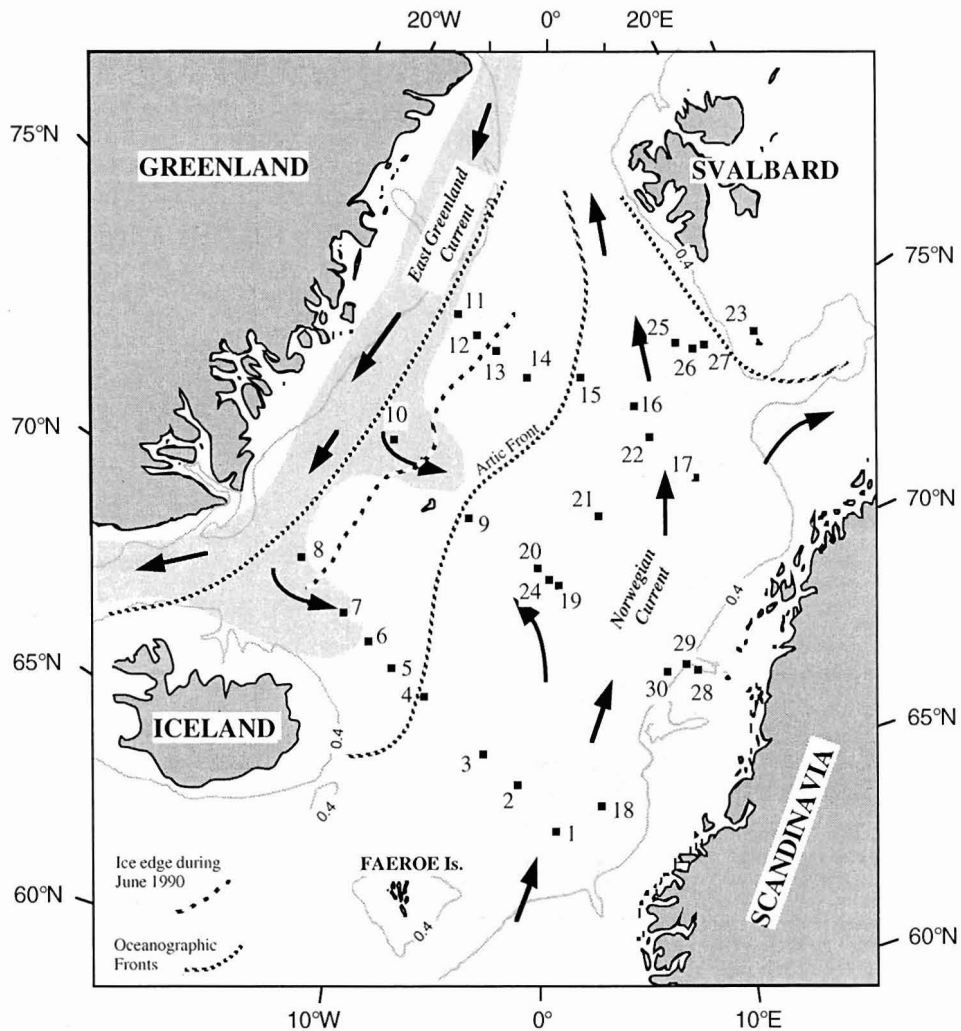
Figure 1. Map of the Norwegian-Greenland Sea including surface current pattern, oceanographic fronts, ice edge during June 1990 (from Thiede & Hempel, 1991), and locations (squares) of the plankton samples.

identified in the Norwegian-Greenland Sea (e.g. Halldal & Markali, 1955; Samtleben & Schröder, 1992; Samtleben *et al.*, 1995a). The communities with the highest diversities are found in the area of the Norwegian Current. To the north and to the west species numbers gradually decrease and only three species are found on the Greenland shelf (Samtleben & Schröder, 1992).

The Norwegian-Greenland Sea is an area of strong east to west hydrographic gradients (Fig. 1). The present surface current system on the eastern side of the Norwegian-Greenland Sea is dominated by the Norwegian Current, a relatively warm (6°-10°C), saline (>35‰) branch of the North Atlantic Drift flowing northward into the Arctic Ocean (Swift, 1986). On the western side the East-Green-

land Current carries cold (<0°C), less saline (30-34‰) polar water southward along the East Greenland coast. Between these two main currents mixed Arctic surface water is formed in two large gyres (Jan Mayen Current and East-Iceland Current) (Johannessen, 1986). The close juxtaposition of warm and cold water masses results in the formation of distinct oceanographic fronts (Fig. 1).

The Norwegian-Greenland Sea is also characterized by strong seasonal changes which are mainly controlled by cycles of insolation, water temperature, and ice cover. These seasonal changes result in distinct variations of the biological productivity (Bathmann *et al.*, 1990; Bauerfeind *et al.*, 1994; von Bodungen *et al.*, 1995). Long-term records of vertical coccolithophore flux in the Nor-

wegian-Greenland Sea demonstrated strong seasonality with peak fluxes during summer and autumn. A less distinct but still recognizable coccolith flux was observed during spring and early summer (Samtleben & Bickert, 1990; Andruleit, *in press*). However, the distribution of living coccolithophore communities during this time of the year was hitherto poorly known in the Norwegian-Greenland Sea. Thus, this study was initiated to report on species compositions and dynamics during low production phases in spring and early summer. The present investigation is part of an extensive actualistic study of the plankton community, settling assemblages, and development of late Quaternary assemblages in the Norwegian-Greenland Sea (Samtleben *et al.*, 1995b).

MATERIAL AND METHODS

The investigated plankton samples were collected

in different years since 1990 during spring and early summer in the entire Norwegian-Greenland Sea and are part of an on-going sampling project on coccolithophores in this region. A total of 76 plankton samples from 30 stations (Fig. 1) have been studied and are listed in Appendix 1 together with the geographical and hydrological data for each location.

The main portion of plankton samples was collected during PRV „Polarstern" Cruise ARK VII/1 (Thiede & Hempel, 1991) between June 12th and July 8th in 1990. Sampling took place along two transects extending from the central Norwegian Sea to the continental margin of Greenland, crossing the major surface water mass boundaries (Fig. 1). The ice edge was crossed by PRV „Polarstern" several times during ARK VII/1 (Thiede & Hempel, 1991). Thus, samples of the stations 8, 10, 11, and 12 are from below the ice cover. Ice concentra-
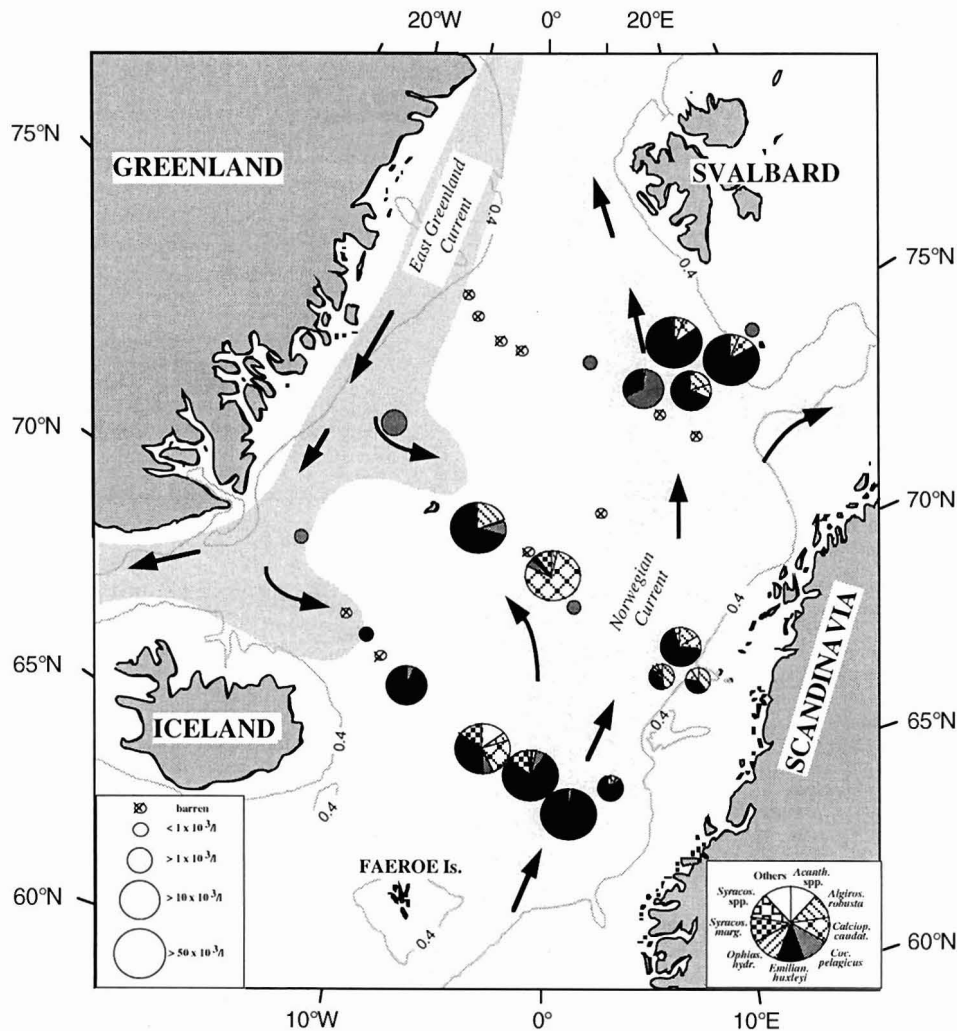

Figure 2. Cell densities and species compositions of coccolithophore communities during low production periods in spring and early summer in the Norwegian-Greenland Sea.

tions ranged from 1/10 to 9/10, but generally were about 5/10. The dominant ice type seen was 2.5m to 3.5m-thick multiyear ice, while firstyear ice was uncommon. Additional water samples were taken during a „Valdivia" Cruise in the central and northern Norwegian Sea between May 20th and 27th in 1991, and during two „Poseidon" Cruises in the eastern and northern Norwegian Sea from February 22nd to 27th 1991 and March 25th to April 6th 1995 (Appendix 1).

Generally, samples were taken in 51 Niskin bottles with a Rosette-sampler. Dependent on CTD-profiles, water was collected at the surface, above (7m-30m) and below (10m-40m) thermocline, and at around 100m water depth at each station. Additional surface water samples from 10m depth were obtained with the ship's seawater pump (Stations 1, 4, 5, 6, and 7).

The water samples were immediately filtered on board through Millipore filters (47 mm diameter, 0.45 μm pore size) by means of a vacuum pump. Without further washing, rinsing or chemical conservation the filters were dried at 40-60°C for at least four hours. The filters were then stored in plastic Petri dishes, and kept permanently dry in closed boxes with silica gel.

Coccolithophore cell densities were determined with a scanning electron microscope (SEM) at 10 KV. For that purpose, a small piece was cut from the dried filter, fixed on an SEM stub, and then coated with carbon and gold. The number of individuals and the species composition were determined by identifying and counting coccospheres on measured transects (1-2 mm^2) at a magnification of 2000x. A specimen which appeared to be a perfect or nearly perfect coccosphere was counted as one individual. Isolated coccoliths were not included in this study. For species identification the publications of Gaarder & Heimdal (1977), Okada & McIntyre (1977), Nishida (1979), Norris (1984), Samtleben & Schröder (1992), and Jordan & Kleijne (1994) were used.

RESULTS

Coccolithophore cell densities and species compositions

The standing crop varied from 207x10^3 coccospheres/l at station 2 to below 1x10^3 coccospheres/l at several stations (Appendix 1). Some of the collected samples did not contain any coccolithophores (Fig. 2). In particular, samples from the western part of the study area were characterized by very low cell densities (consistently <2.5x10^3 coccospheres/l) or were even barren. Medium (1 to 50x10^3 coccospheres/l) to high (>50x10^3 coccospheres/l) cell densities were found only in surface water samples from the eastern Norwegian Sea

which were influenced by temperate water of the Norwegian Current. This general distribution of cell densities was independent of the time of sampling; for example stations 11 to 14 from the northwestern Greenland Sea were taken during early July and were barren of coccolithophores, whereas
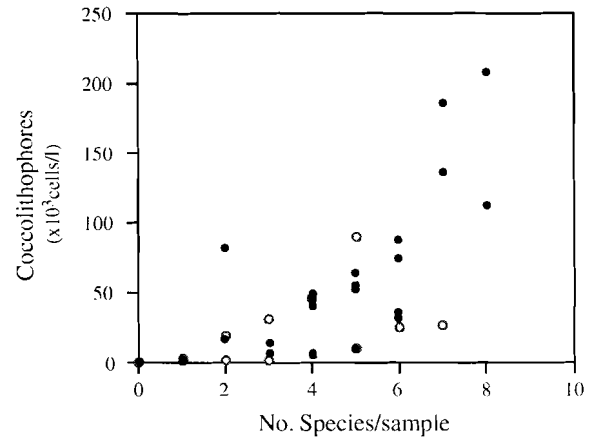

Figure 3. Numbers of species per sample plotted against cell density (black dots = 0-25m water depth, open circles = >25m water depth).
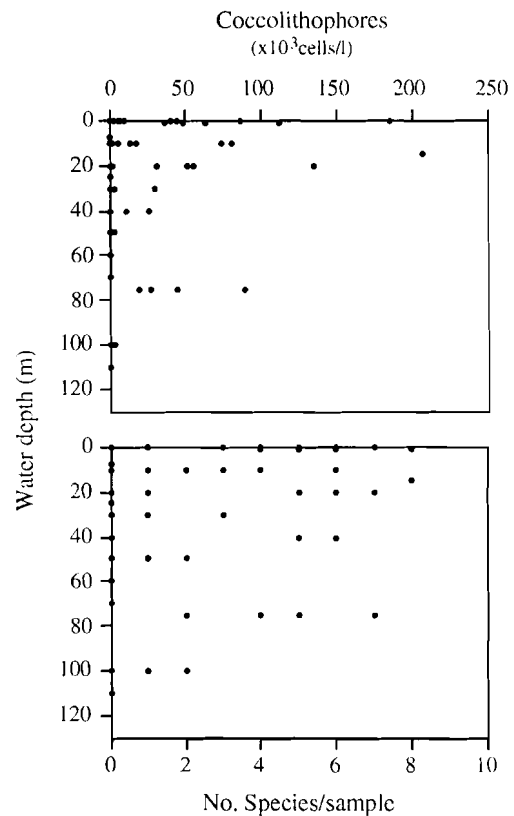

Figure 4. Cell densities and numbers of species per sample plotted against water depth.
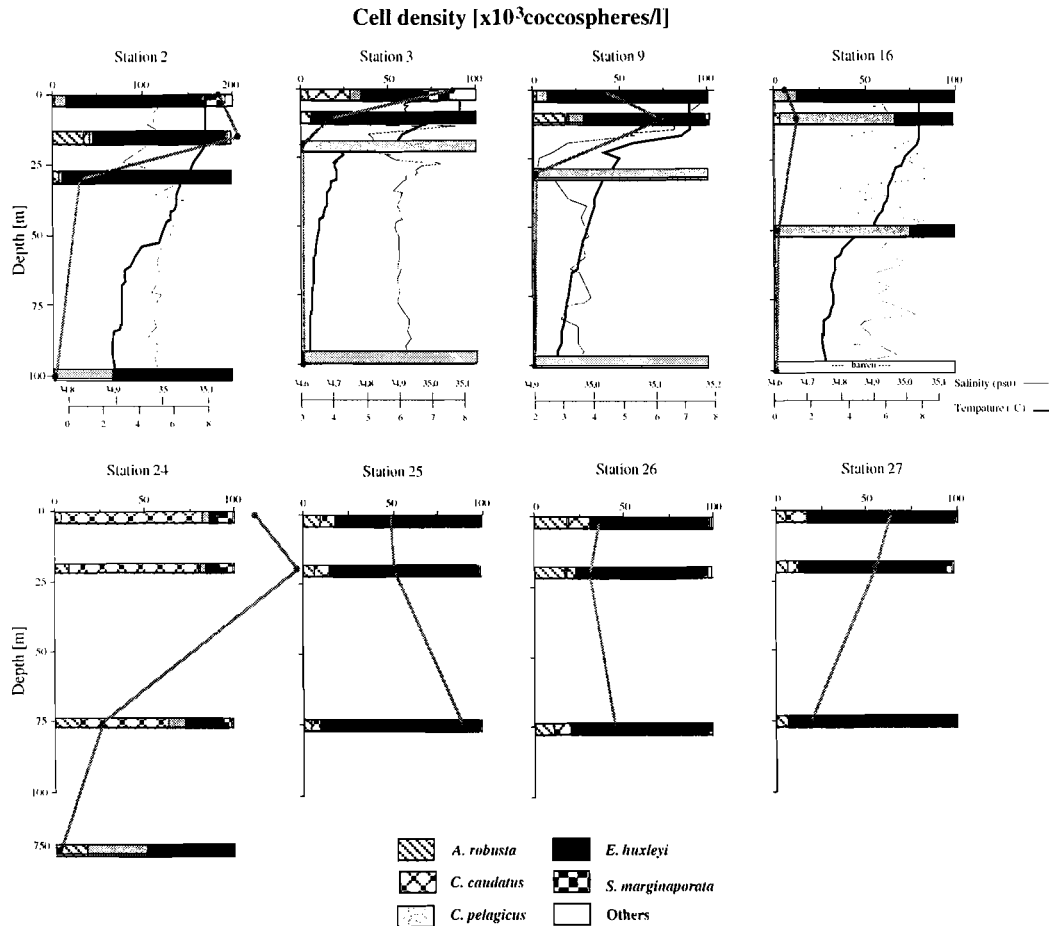
Cell density [x10³coccospheres/l]

Figure 5. Vertical distribution of coccolithophore communities from stations which have at least three samples containing coccolithophores. Salinity and temperature data for stations 2, 3, 9, and 16 are from CTD-measurements.

stations 28 to 30, taken earlier in the year during late March and early April, already exhibited medium cell densities.

Overall, a total of 15 coccolithophore species was identified during the present study (Appendix 2; Plates 1, 2). The number of species generally increased with increasing cell numbers (Fig. 3). The diversity was generally higher in the eastern part of the study area and coincides with the highest cell densities. To the west the coccolithophore communities were often monospecific.

The main component of the coccolithophore flora in surface waters was *Emiliania huxleyi*. This species almost always dominated the communities when medium to high cell densities occurred, accounting for approximately 70% of most of the sample communities. An exception was station 24 where *Calciopappus caudatus* dominated the coccolithophore community with high cell densities of about 100x10³ coccospheres/l. Other species such

as *Algirosphaera robusta*, *Acanthoica quattrospina*, *Ophiaster hydroideus*, and *Syracosphaera marginaporata*, were also well represented during the non-production phases but neither reached high cell densities nor dominated the communities. *Coccolithus pelagicus*, found in both the non-motile stage and the *Crystallolithus hyalinus* stage (motile phase), was the most frequently occurring species but was important only at station 16 with 8x10³ coccospheres/l. This species frequently was characteristic of very low diversity to monospecific communities, especially in the western part of the study area.

Sixteen of the 30 subsurface samples (> 20m water depth) yielded coccosphere communities with nine species (Appendix 1). Cell densities were highest in the uppermost 20m of the water column and decreased towards greater depth, whereas the number of species did not show equivalent changes (Fig. 4). Cell densities and species compositions

of all stations with at least three sampling depths which were not barren are depicted in Figure 5.

At all locations the communities in a mixed water layer above a thermocline were characterized by a relatively high similarity in species composition. At stations 2, 3, 9, and 16 the temperature and salinity values (Fig. 5) indicated the transition between two different water layers. Above this stratification, diverse communities with highest cell densities prevailed, often dominated by *E. huxleyi*. In contrast, in the range of the thermocline and especially below it *C. pelagicus* dominated the low diversity to monospecific communities with very low cell densities. At stations 24-27 no clear thermocline was observed and, thus, abundances and species composition were relatively similar to each other at all depths. *E. huxleyi* was the most dominant species in all of the samples at stations 25-27, whereas at station 24, *Calciopappus caudatus* dominated the coccolithophore flora. In addition, a strong decrease in cell density with increasing water depth was observed at the latter station.

Many of the June-July 1991-samples (from PRV Polarstern ARKVII/1-cruise) also contain a significant number of siliceous organisms, including diatoms and some silicoflagellates. A bloom of *Thalassiotrix longissima* was observed over the eastern Iceland Plateau; and west of Jan Mayen high concentrations of *Rhizosolenia* spp. occurred (see also Thiede & Hempel, 1991). However, most of the samples of the westernmost stations were free of siliceous organisms as well as of coccolithophores.

Corrosion of coccolithophores

The presence of highly corroded and/or dissolved coccospheres and, especially, coccoliths was a significant result of this investigation. Remarkably, corroded specimens were found only in the June-July 1991 samples within the temperate Norwegian Current. In addition, only coccoliths of *Emiliania huxleyi* were affected by this feature. Other delicate-structured forms such as *Calciopappus caudatus, Acanthoica quattrospina* did not show any signs of corrosion or dissolution. All samples also contained a relatively high number of intact *E. huxleyi* specimens. Nevertheless, more than approximately 70% of the *E. huxleyi* coccospheres in the plankton samples from surface and subsurface waters of the Norwegian Current (Stations 1, 2, 3, 4, and 16) were collapsed and many of them had an opening, possibly a pylome (Plate 2, Fig. 6).

All coccospheres seemed to have their normal shape, and only the coccoliths show a high degree of corrosion. Usually, all coccoliths on a coccosphere were affected. However, the proximal shield of the coccoliths was not or less affected by this phenomenon, and differentiation of boundaries
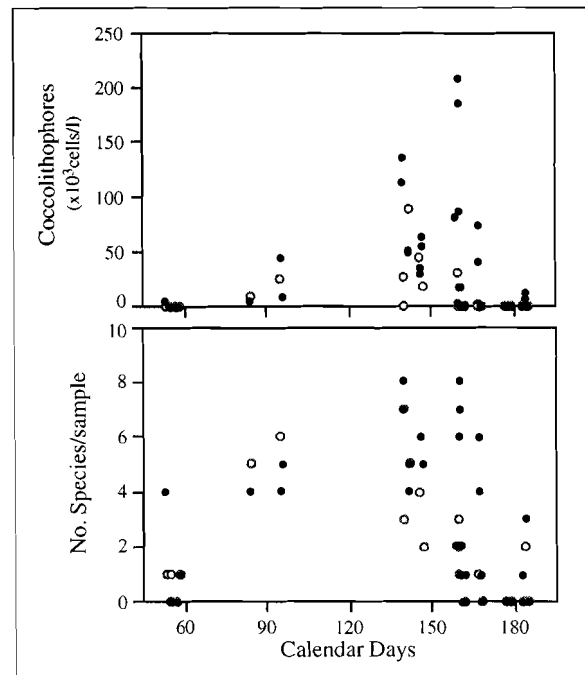
Figure 6. Cell densities and numbers of species per sample plotted against calendar days (black dots = 0-25m water depth, open circles = >25m water depth). Note that cell densities >150*10^3 cells/l probably resulted from drifted „old" *E. huxleyi* populations.

between single proximal shields was often impossible. The T-shaped elements of the distal shields were not connected to each other at the periphery and mostly their arrangement was totally disturbed. Often, single elements were heavily or totally dissolved. The elements of the central opening either were fused together without building the normal central grid or were absent (Plate 2). In addition, incomplete shields in the central area of the specimens (Plate 2, Fig. 3, 6) are probably organic and not fused calcitic elements.

DISCUSSION
Variation in coccolithophore cell densities and community dynamics

The observed coccolithophore communities are part of a recurrent seasonal cycle of communities in the Norwegian-Greenland Sea. However, the production phases and the development of coccolithophore blooms are highly variable in space and time (Samtleben & Schröder, 1992; Samtleben *et al.*, 1995a). Also, the composition and species numbers within the Norwegian Current may vary considerably from year to year. Sakshaug *et al.* (1981) found small-scale and short-term horizontal and vertical variations in standing crop of the coccolithophore flora off northern Norway in 1975 and 1976. However, generally the main production phase of coc-

colithophores in the Norwegian-Greenland Sea shifts from the southeast to the northwest during summer (Samtleben & Schröder, 1992; Samtleben et al., 1995a). While south of Iceland the first blooms occur during May/June, a high cell density is observed in the region of the Vøring Plateau during July, in the Barents Sea during August, and west of Jan Mayen not before September. In the present study, the limiting influence of low temperatures to coccolithophore thriving is clearly depicted by overall low cell densities and many barren samples during spring and early summer. This is, further supported by absence or very low cell densities of coccolithophores recorded at the western-most stations which, at least partly, were within the ice cover. The increase in coccolithophore production during spring and early summer is also indicated by a general increase in cell numbers in the investigated samples (Fig. 6). This holds true even when considering that a high portion of Emiliania huxleyi, the main component of the community, may not be part of the coccolithophore standing

crop of this region. The heavily corroded specimens most probably were the result of a plankton bloom which occurred in the North Atlantic either in fall of the previous year or in early spring and were drifted to this region by the North Atlantic Drift (see discussion below).

It is obvious that, even during low production phases in spring coccolithophore communities may exhibit a relatively high variability in both species diversity and species composition, although low cell densities prevailed during February to April (Fig. 6). Cell densities, in contrast, drastically increased in waters above about 5°C (Fig. 7). In addition, medium to high cell densities are only reached in the eastern part of the Norwegian-Greenland Sea, in an area influenced by temperate surface waters of the Norwegian Current, whereas relatively high cell concentrations in late summer were previously recorded in close proximity to the East Greenland Current (Samtleben & Schröder, 1992; Samtleben et al., 1995a). Therefore, during spring and early summer
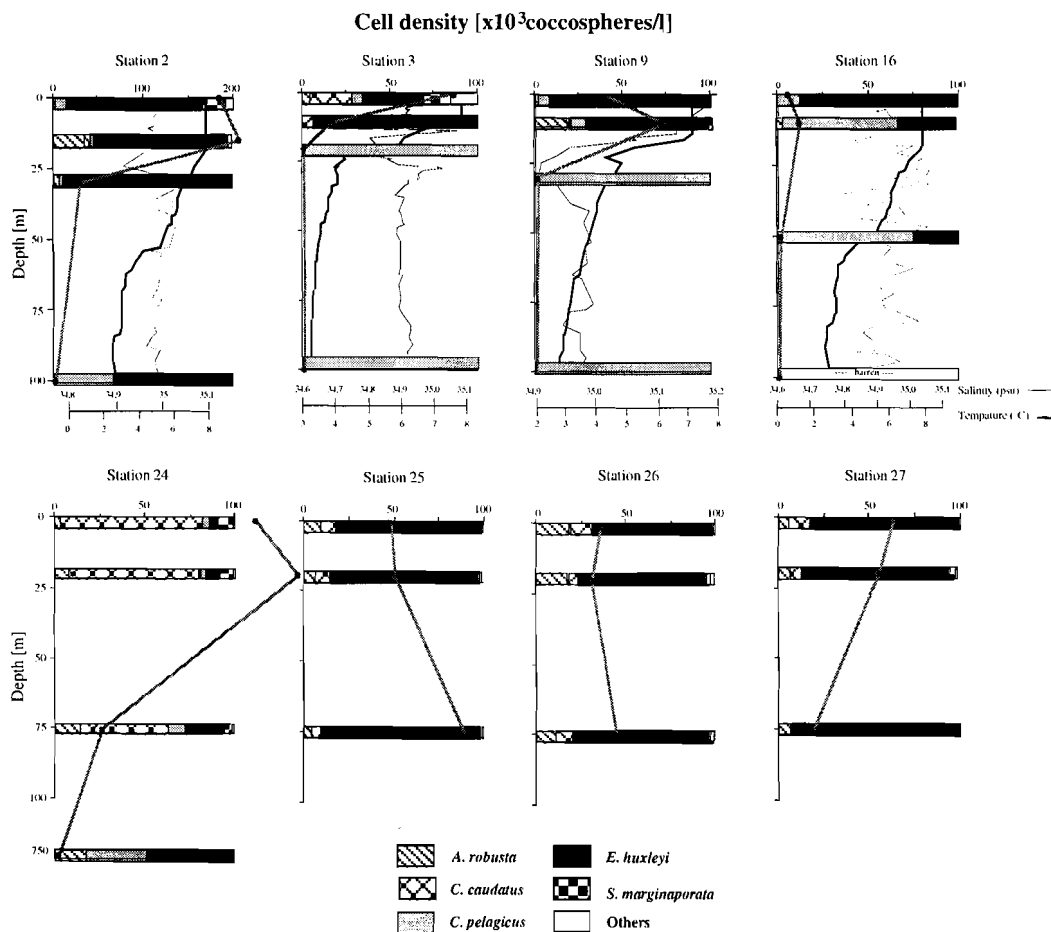

Figure 7. Cell densities and numbers of species per sample plotted against both temperature and salinity.

the oceanic fronts, such as the Arctic Front, divide the Norwegian-Greenland Sea into distinct areas of coccolithophore habitats. In the western part, which mainly coincides with the Artic water masses, only low diversity to monospecific communites were observed, whereas in the eastern part high cell densities with high diversities were already present. In contrast, in late summer during the main production phases the oceanic frontal systems probably lose their boundary function and high cell densities, especially of *E. huxleyi*, occur in the entire study area (Samtleben *et al.*, 1995b).

In general, the low standing crop as well as the increase in cell density during the period February-June corresponds well with previous findings of Halldal (1953), Braarud *et al.* (1958), Smayda (1958), Samtleben & Schröder (1992), and Samtleben *et al.* (1995a). They all reported that coccolithophores play a very subordinate role in the Norwegian-Greenland Sea before summer. Diatoms make up the bulk of the phytoplankton, but usually with small populations before May (e.g. Halldal, 1953). In the present study, this is supported by significant number of diatoms which were observed over the eastern Iceland Plateau and west of Jan Mayen during June 1990 (see Thiede & Hempel, 1991). In contrast, investigations have recorded large amounts of coccolithophores in the entire Norwegian-Greenland Sea during summer (Samtleben *et al.*, 1995a). Thereby, abundances of single species changed spatially and temporally, and strong summer blooms occurred.

Species distribution and composition
The overall species number of the investigated coccolithophore communities is only slightly lower than the total of about 25 previously described living species in the Norwegian-Greenland Sea (Halldal & Markali, 1955; Braarud *et al.*, 1958; Smayda, 1958; Ramsfjell, 1960; Sakshaug *et al.*, 1981; Samtleben & Schröder, 1992; Samtleben *et al.*, 1995a, b). This indicates that the communities of spring and early summer are already represented by typical species compositions of this area. Thus, not changes in diversity but the proportions of species seem to be the main characteristic of the high northern coccolithophore communities. This holds true especially for *Anthosphaera robusta* and *Syracosphaera marginaporata*. These two species were present in most samples which were not barren, but never reached dominant portions of the communities. However, both species are dominant members both of deep-living communities and post-bloom communities respectively in late summer and autumn (Samtleben *et al.*, 1995a).

Changes in composition and cell density of the coccolithophore community during the study period are, at least in part, dominated by changes in the abundance of *Emiliania huxleyi*. This species is by far the most abundant coccolithophore species in the investigated water samples. Moreover, it is the most important and ubiquitous species in todays world oceans. Gigantic blooms which mainly consist of *E. huxleyi* are regularly observed during early summer in the subpolar North Atlantic and the adjacent Norwegian-Greenland Sea (e.g., Holligan *et al.*, 1983, 1993; Samtleben *et al.*, 1995a). In our study, cell densities were considerably lower than previously described from this area, especially during February - April. *Emiliania huxleyi* is dominant mainly in the surface layers (<30m water depth) and, with the exception of stations 25-27, its abundance drops drastically at the thermocline. The presence of relatively high cell numbers in the subsurface samples at 75m in May 1991 (Stations 25-27, see Fig. 5) seems to indicate that this species has lived deeper in the photic zone. However, coccolith production in *E. huxleyi* is light-dependent (Westbroek *et al.*, 1989) and, thus, these high cell numbers below thermocline depth are most probably due to repopulations, introduced from the south via the Norwegian Current. In addition, the relatively high cell densities recorded in the southernmost Norwegian-Greenland Sea were probably not part of the increase in late spring/early summer *E. huxleyi* production, but rather the result of a supply from outside the Norwegian-Greenland Sea.

The large differences in the numbers of *E. huxleyi* between spring and summer are probably due to several factors. This species is dominant in water masses depleted in nutrients (Okada & Honjo, 1975; Kleijne, 1990) while diatom growth is favoured by nitrate dominated water masses (Probyn, 1993). In addition, it has been shown that *E. huxleyi* becomes abundant when the water column becomes stratified (Brand, 1994). Stable water masses further increases the growth rate of *E. huxleyi*, which is higher than those of other coccolithophore species (Brand, 1982). Therefore, this species seems to have a much higher reproduction rate than other coccolithophores.

Calciopappus caudatus was also commonly observed in our samples. This species reached medium high cell densities at station 3, and exceptionally high cell densities at station 24 which had not previously been found in the Norwegian-Greenland Sea. Samtleben & Schröder (1992) observed *C. caudatus* in abundances below 10×10^3 cells/l evenly distributed in the surface water masses of the Norwegian-Greenland Sea. Thus, we assume that the high coccolithophore cell densities, especially at station 24, were the result of a *C. caudatus* bloom or probably close to bloom conditions

during the general low productive period. Previous observations have already shown that this species can be a prominent coccolithophore in the Norwegian Sea as early as May and June (Ramsfjell, 1960; Paasche & Rom, 1962; Schei, 1975). Large populations were observed when the water temperature was only 4-6°C, although C. *caudatus* was also present at most of the localities in the warmer Atlantic water of the Norwegian-Greenland Sea. Early blooms of other species comparable to those of C. *caudatus* are not reported from this area, but have been observed in the subpolar North Atlantic south of Iceland (Knappertsbusch & Brummer, 1995). There are, however, reports of blooms of C. *caudatus* from Norwegian fjords, where large quantities were observed in both early and late summer (Schei, 1975).

Coccolithus pelagicus, which is today regarded as a cold-water adapted species (Braarud, 1979), had a high abundance in the investigated samples but did not exhibit generally higher cell densities in comparison to the summer communities (Samtleben & Schröder, 1992; Samtleben *et al.* 1995a, 1995b). C. *pelagicus* is observed with medium cell densities only in one sample (station 16), despite of being the dominant species of the poor to monospecific communities. This species seems to be a „survivor" species, i.e. it is still found at locations were other species are missing due to a too harsh environment. In the western part of the study area, where C. *pelagicus* is the most commonly found species at all depths, in many cases temperature seems to be the limiting factor. In contrast, in the eastern part C. *pelagicus* seems to dominate the communities below the thermocline. Most of the other species again were influenced by decreasing temperatures but also by reduced insolation.

There are several stations (e.g. 17 to 22) with relatively high temperatures of more than 4°C which are characterized by very low cell densities or even the absence of coccolithophores (Appendix 1, Fig. 7). These stations, located in the northeastern part of the study area, should have been permanently influenced by coccolithophore communities via the northern prolongation of the North Atlantic Drift. However, this is not the case and, therefore, temperature does not seem to be the only reason for the absence of living coccolithophores in the surface waters of the northern Norwegian-Greenland Sea. These stations were sampled in February 1991 which was the earliest time in the year of all sampling. Therefore, it becomes obvious that coccolithophores are at their limits for living probably due to low insolation intensities and not only due to low temperature. The seasonal development of the phytoplankton started after the yearly dark period and coccolitho-

phores increased in abundance when the water column was more stratified.

Corrosion of coccolithophores and coccoliths

Many of the coccolithophores (> 70%!) from the southernmost stations were highly corroded (Plate 2). However, only coccoliths of *Emiliania huxleyi* were affected and corroded specimens in the surface samples always co-occurred with intact cells. This feature may be the result of either dissolution (Schneidermann, 1977) or of malformation, which is the incomplete formation of single coccoliths (Kleijne, 1990). Malformed coccoliths were mostly described from marginal and inland seas during several seasons (Okada & Honjo, 1975; Kleijne, 1990). Young & Westbroek (1991) recently described that malformed *E. huxleyi* coccoliths commonly occurred in late stationary phase cultures, and in cultures held in artificial sea water. Thus, they concluded that a depletion in trace nutrients might be responsible for the observed malformation.

However, the recorded *E. huxleyi* specimen are not identical to the malformed coccoliths described by Okada & Honjo (1975) and Kleijne (1990). Malformation is not observed in this study, but many of the specimens from the surface waters simply were heavily dissolved. Dissolution of coccoliths in the near-surface waters has not been widely reported from the open Norwegian-Greenland Sea, but was described recently from Norwegian fjord populations (Young, 1994). Thus, it seems likely that the observed specimens drifted within the Atlantic water for a longer time and, therefore, these specimens most probably were supplied to this region from outside the Norwegian-Greenland Sea via the North Atlantic Drift. A wide range of altered morphotypes caused by different degrees of dissolution have been reported from surface sediments (Burns, 1977). It is interesting to note that a dissolution feature typical for sediment samples can be seen in the plankton samples from the Norwegian-Greenland Sea (Plate 2, Figs. 3, 4). The difference between dissolution morphotypes usually seen in surface sediments and that of plankton samples has been discussed by Young (1994). He concluded that the collapsed coccolith pattern may be the result of early dissolution, when there is still a large amount of organic matter surrounding the coccoliths.

In addition, many of the dissolved coccospheres have an opening (Plate 2), which may probably be a pylome. Young (1994, Fig. 6A) also found coccospheres of collapsed coccoliths which do have holes and described this feature as collapsed structures. This is probably the case in many, but not in all of our samples. Although a

phenomenon like a pylome in *E. huxleyi* has not been described earlier, this species is known to have several life phases (Klaveness, 1972). Besides the common coccolith-bearing cells, naked cells lacking conspicuous extracellular scales or coccoliths are commonly found in laboratory cultures (e.g. Wilbur & Watabe, 1963; Klaveness, 1972). It is also known that motile life stages alternate with non-motile stages. Possibly, these cells document a change in the life phase of an *E. huxleyi* population. However, the primary mode of reproduction in coccolithophores is asexual binary fission and each daughter cell gets about half the coccoliths of the former coccosphere (Brand, 1994). Another possibility would therefore be that this population has been grazed by small heterotrophic organisms. At least, whether this or the release of a single daughter cell accounts for the cells openings cannot be confirmed from the present material.

CONCLUSIONS
The spatial and temporal distribution of spring to early summer coccolithophore communities in the surface and subsurface waters of the Norwegian-Greenland Sea has shown considerable variability in both cell numbers and species composition. In contrast, changes in diversity do not seem to be the main characteristic features of high northern coccolithophore communities. Relatively high species numbers are already present early in spring although cell densities are still low.

Overall, a total of 15 living species is recorded from the Norwegian-Greenland Sea samples, all known from this area. Coccolithophore standing crop and species diversity are highest in the eastern part of the study area, influenced by the warm Atlantic surface water. In the western part of the Norwegian-Greenland Sea communities often were monospecific and characterized by very low cell numbers. The seasonal development of the phytoplankton started after the yearly dark period and coccolithophores increased in abundance when the water column was more stratified and both temperatures and insolation increased.

Emiliania huxleyi is the dominant species, but *Calciopappus caudatus* and *Algirosphaera robusta* also contribute significantly to the communities. High cell densities, of *C. caudatus* were interpreted as the result of bloom or more probably close to bloom conditions during the general low productive period. In addition, many of the *E. huxleyi* coccoliths from the surface waters of the southeastern Norwegian-Greenland Sea were heavily dissolved. It seems likely that they drifted within the Atlantic water for a long time and, therefore, these specimens may have been supplied to this region from outside the Norwegian-Greenland Sea via the North Atlantic Drift.

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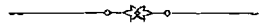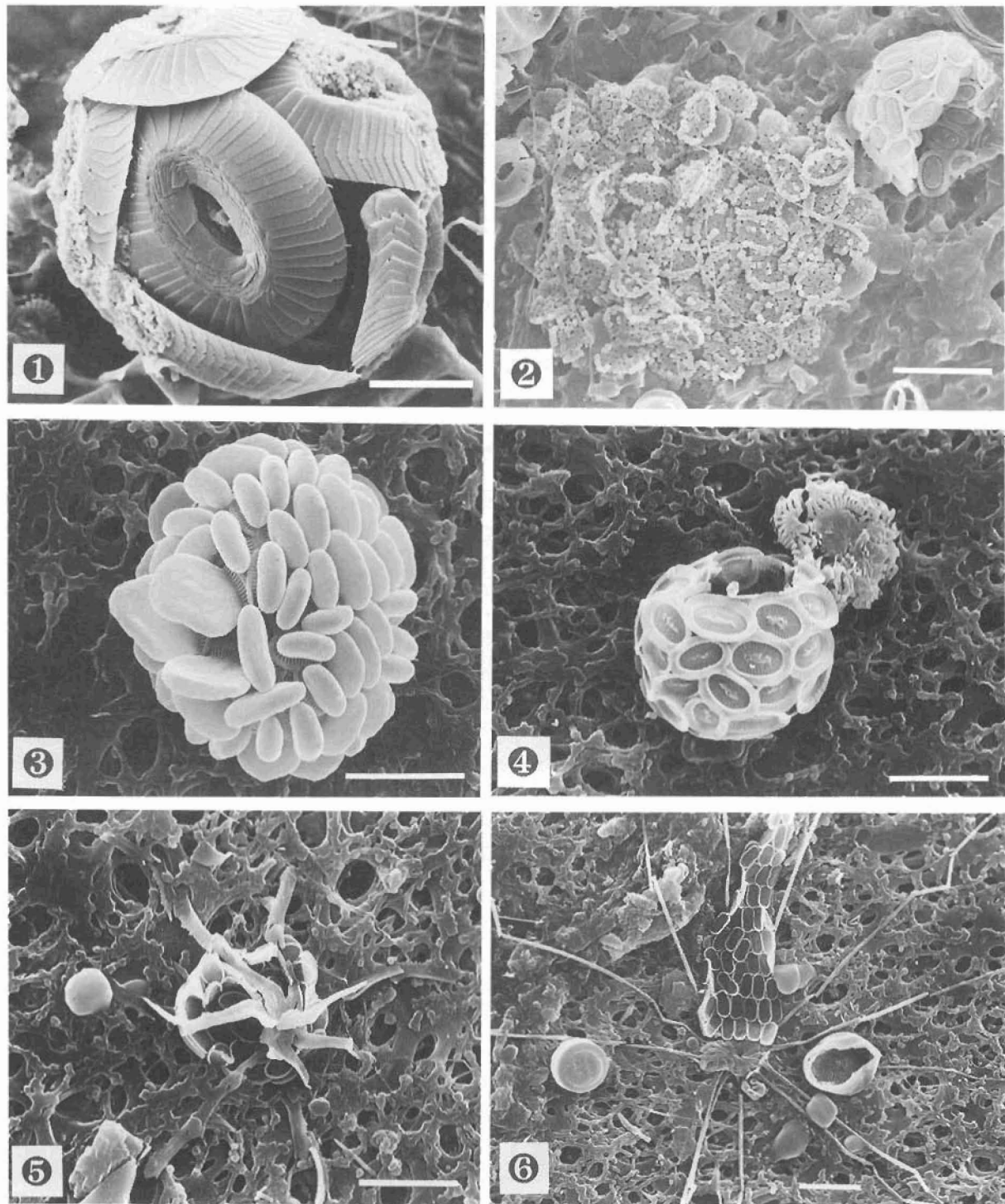
Plate 1. (Bar = 4μm). 1. *Coccolithus pelagicus* (Wallich) Schiller, Station 43, 0m; 2. *Crystallolithus hyalinus* (Gaarder & Markali and *Syracosphaera marginaporata* Knappertsbusch, Station 2, 0m ; 3. *Algirosphaera robusta* (Lohmann) Norris, Station 30, 0m; 4. *Syracosphaera borealis* Okada & McIntyre, Station 30, 40m; 5. *Ophiaster hydroideus* (Lohmann) Lohmann, Station 30, 40m; 6. *Calciopappus caudatus* Gaarder & Ramsfjell, Station 30, 40m.
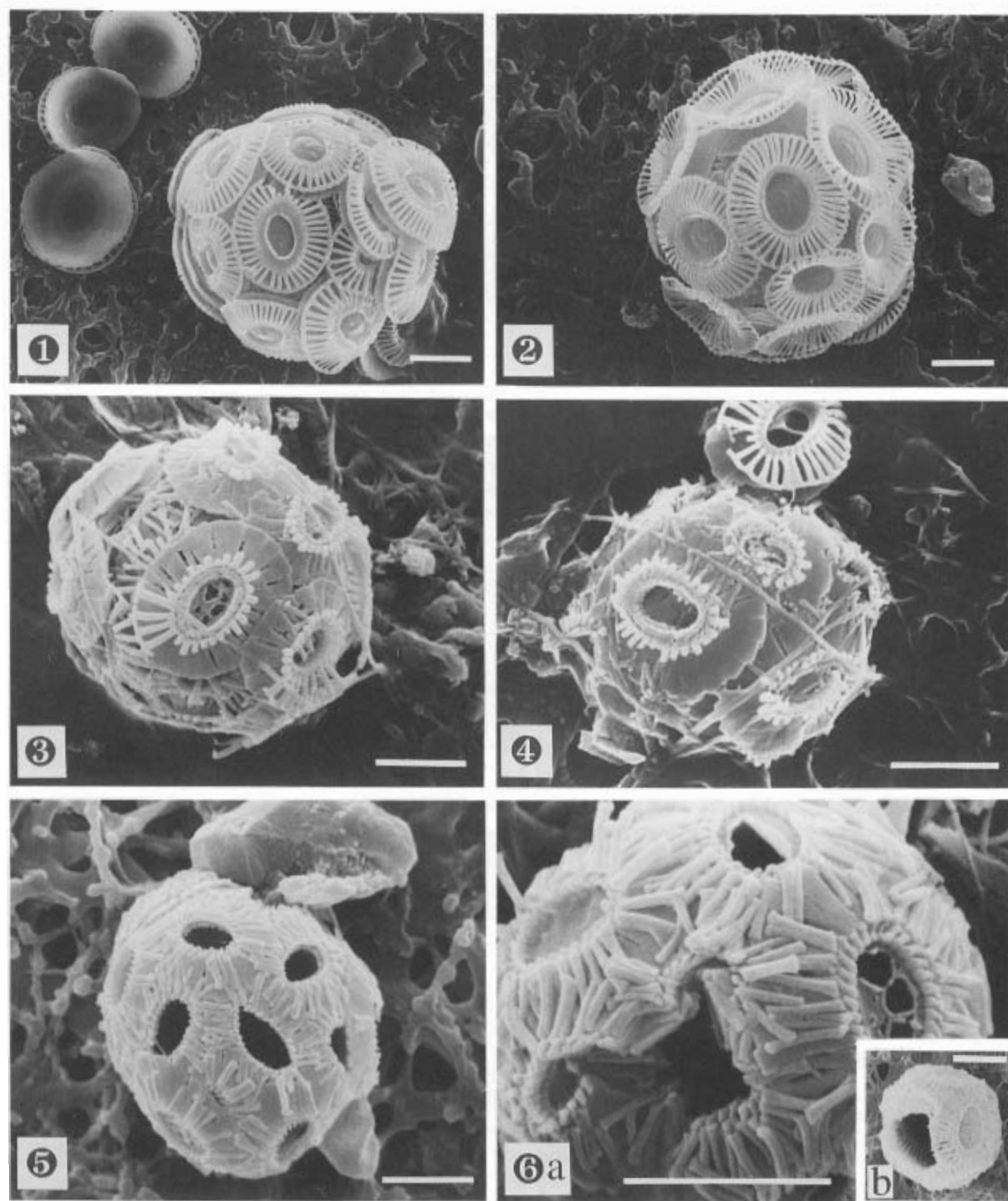
Plate 2. (Bar = 4μm). 1-6. *Emiliania huxleyi* (Lohmann) Hay & Mohler. 1. Normal coccosphere, Type A (Young & West-broek, 1991); Station 30, 0 m; 2. Normal coccosphere, Station 30, 0 m; 3. Coccosphere with corroded coccoliths, Station 2, 15 m; 4. Coccosphere with heavily corroded coccoliths and all individual elements are dissolved, Station 2, 15 m; 5. Coccosphere with severely corroded coccoliths and totally disturbed arrangement of the distal shield elements, Station 3, 10 m; 6. Coccospheres with corroded coccoliths and an opening; a) Station 2, 15 m; b) Station 3, 10 m.

Appendix 1. Station list with temperatures, salinities, and coccolitophore densities of all investigated samples (cruises: PS-Polarstern, Pos-Poseidon, V-Valdivia; x=no data)

No.	Station	Date	Geogr.	Position	Sample Depth (m)	Temp. (°C)	Sal. (ppt)	Volume (l)	Coccospheres (bulk)	Acanth. acule.	Acanth. quattro.	Algiros. robusta
1	PS-A	12.06.90	63 45.8 N	00 20.7 E	10	9.3	35.11	1.0	80640	-	-	-
2	PS-2	13.06.90	65 00.0 N	00 59.8 W	0	8.4	34.99	1,5	184760	2510	1260	2510
					15	7.5	34.98	2.0	207380	1260	1260	35190
					30	6.5	34.97	2.0	29900	-	-	1150
					100	4.4	34.95	2.0	1470	-	-	-
3	PS-3	13.06.90	65 29.9 N	03 59.9 W	0	7.9	34.99	1.5	86730	-	13200	3770
					10	7.4	34.85	1.5	16940	-	-	-
					20	5.0	34.83	2.0	420	-	-	-
					100	3.7	34.87	2.0	830	-	-	-
4	PS-C	14.06.90	66 39.9 N	8 00.2 W	10	5.3	34.74	1.5	16480	-	-	-
5	PS-D	14.06.90	67 27.1 N	9 37.7 W	10	4.6	34.67	2.0	-	-	-	-
6	PS-E	14.06.90	67 59.0 N	10 50.6 W	10	5.2	34.72	3.0	100	-	-	-
7	PS-F	14.06.90	68 41.1 N	12 35.2 W	10	5.1	34.72	2.0	-	-	-	-
8	PS-6	15.06.90	69 28.0 N	16 32.2 W	0	0.8	33.15	1.25	-	-	-	-
					10	0.4	33.70	0.55	470	-	-	-
					20	-0.8	34.25	0.6	510	-	-	-
					50	-0.5	34.76	2.0	-	-	-	-
9	PS-43	20.06.90	70 45.0 N	5 30.0 W	0	7.3	35.09	2.0	39900	-	-	950
					10	7.1	35.10	2.0	73330	-	-	13970
					30	4.4	34.95	2.0	2420	-	-	-
					100	3.0	34.95	2.0	730	-	-	-
10	PS-47	21.06.90	72 33.0 N	12 15.1 W	0	1.9	33.10	2.0	1460	-	-	-
					10	1.3	34.15	2.0	-	-	-	-
					40	-0.3	34.45	2.0	-	-	-	-
11	PS-69	30.06.90	75 50.0 N	8 11.0 W	0	-0.7	32.39	2.0	-	-	-	-
					30	-0.5	34.25	2.0	-	-	-	-
					110	2.4	34.90	2.0	-	-	-	-
12	PS-70	30.06.90	75 25.0 N	7 20.0 W	0	-0.1	32.37	2.0	-	-	-	-
					30	2.2	34.86	2.0	-	-	-	-
					70	1.7	34.92	2.0	-	-	-	-
13	PS-73	1.07.90	74 59.8 N	4 59.5 W	0	2.2	33.32	2.0	-	-	-	-
					20	-0.5	34.50	2.0	-	-	-	-
					60	-0.8	34.77	2.0	-	-	-	-
14	PS-75	2.07.90	74 32.0 N	2 19.3 W	0	2.2	34.50	1.25	-	-	-	-
					20	-0.8	34.66	2.0	-	-	-	-
					100	-1.4	34.82	2.0	-	-	-	-
15	PS-87	6.07.90	74 35.9 N	2 59.9 E	0	2.9	34.68	2.0	630	-	-	-
					7	1.9	35.09	2.0	-	-	-	-
					25	0.0	34.74	2.0	-	-	-	-
16	PS-89	7.07.90	73 58.0 N	7 40.0 E	0	7.8	34.99	2.0	6110	-	-	-
					10	7.3	35.01	2.0	12650	-	-	370
					50	5.9	34.83	2.0	1420	-	-	-
					100	1.8	34.83	2.0	-	-	-	-
17	PS-90	8.07.90	72 15.1 N	11 00.2 E	0	9.4	34.86	2.0	-	-	-	-
					10	7.6	34.97	2.0	-	-	-	-
					40	6.7	35.11	2.0	-	-	-	-
18	'os/181-20:	22.02.91	64 35N	3 30E	10	7.6	x	4.0	4800	-	-	300
					50	7.6	x	4.0	900	-	-	-
19	'os/181-20(	24.02.91	69 55.6N	0 11.1E	10	4.0	x	4.0	0	-	-	-
					50	4.0	x	4.0	300	-	-	-
20	'os/181-20:	24.02.91	70 14.5N	0 14W	10	4.6	x	4.0	0	-	-	-
					50	4.6	x	4.0	0	-	-	-
21	'os/181-21	26.02.91	71 38.3N	4 13.4E	10	4.55	x	4.0	0	-	-	-
					50	4.53	x	4.0	0	-	-	-
22	'os/181-21:	26.02.91	73 12.7N	8 21.4E	10	4.4	x	4.0	0	-	-	-
					50	3.9	x	4.0	0	-	-	-
23	'os/181-21:	27.02.91	74 52N	18 59.9E	10	x	x	4.0	300	-	-	-
					50	x	x	2.0	600	-	-	-
24	V-1	20.05.91	69 58N	0 09E	1	5.3	35.05	2.0	112000	-	510	3580
					20	5.1	35.06	2.0	135260	-	1230	10450
					75	4.8	35.07	2.0	26420	-	-	3720
					750	1.86	34.9	2.0	2030	-	-	350
25	V-3	22.05.91	75 15N	12 52E	1	x	x	2.0	48200	-	-	4610
					20	x	x	2.0	50890	-	-	3260
					75	x	x	2.0	89470	-	1110	3310
26	V-4	26.05.91	75 00N	14 42E	1	x	x	2.0	35640	-	390	6590
					20	x	x	2.0	30290	-	350	5280
					75	x	x	2.0	44720	-	-	4820
27	V-5	27.05.91	74 47N	13 52E	1	x	x	2.0	63710	-	-	3500
					20	x	x	2.0	55030	-	-	3500
					75	x	x	2.0	18430	-	-	1290
28	'os/205-18	25.03.95	67 10.9N	9 16.9E	0	6.15	34.93	2.0	5420	-	-	2090
					40	6.65	35.36	2.0	9690	-	-	3630
29	'os/205-20:	5.04.95	67 24.5N	8 41.8E	0	6.49	35.56	2.0	43590	-	-	7130
					40	6.51	35.58	2.0	24490	-	-	9430
30	'os/205-21'	6.04.95	67 07.9N	7 20.3E	0	6.76	35.39	2.0	8770	-	-	4160

Appendix 1. (cont.) Station list with temperatures, salinities, and coccolitophore densities of all investigated samples (cruises: PS-Polarstern, Pos-Poseidon, V-Valdivia; x=no data)

No.	Alisph. unic.	Calciop. caudat.	Coc. pelagic.	Cryst. hyalinus	Emilian. huxleyi	Gephyr. muell.	Ophias. hydr.	Pappos. sp.	Syracos. borealis	Syracos. marg.	Syracos. med.	Syracos. mol.	Syracos. spp.
1	-	-	1910	-	78730	-	-	-	-	-	-	-	-
2	-	-	-	12570	139510	-	-	-	3770	22620	-	-	-
	-	7540	-	3770	154600	-	-	-	2510	1260	-	-	-
	-	-	580	-	28180	-	-	-	-	-	-	-	-
	-	-	490	-	980	-	-	-	-	-	-	-	-
3	-	20470	-	5660	30170	-	-	-	-	13200	-	-	-
	-	1060	-	-	15880	-	-	-	-	-	-	-	-
	-	-	420	-	-	-	-	-	-	-	-	-	-
	-	-	830	-	-	-	-	-	-	-	-	-	-
4	-	-	1180	-	15300	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-	-	-
6	-	-	-	-	100	-	-	-	-	-	-	-	-
7	-	-	-	-	-	-	-	-	-	-	-	-	-
8	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	470	-	-	-	-	-	-	-	-	-
	-	-	-	510	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-
9	-	-	2220	320	36420	-	-	-	-	-	-	-	-
	-	700	4890	2100	50280	-	-	-	-	1400	-	-	-
	-	-	2420	-	-	-	-	-	-	-	-	-	-
	-	-	730	-	-	-	-	-	-	-	-	-	-
10	-	-	1460	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-
11	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-
12	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-
13	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-
14	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-
15	-	-	630	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-
16	-	-	380	380	5350	-	-	-	-	-	-	-	-
	-	-	8190	-	4090	-	-	-	-	-	-	-	-
	-	-	1070	-	360	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-
17	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-
18	-	-	300	-	3900	-	-	-	-	-	300	-	-
	-	-	900	-	-	-	-	-	-	-	-	-	-
19	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	300	-	-	-	-	-	-	-	-	-	-
20	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-
21	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-
22	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	-
23	-	-	300	-	-	-	-	-	-	-	-	-	-
	-	-	600	-	-	-	-	-	-	-	-	-	-
24	-	87450	1020	4600	4090	-	-	-	-	10230	-	-	510
	-	98980	1840	2460	9220	-	-	-	-	11070	-	-	-
	-	13020	1490	1120	5580	370	-	-	-	1120	-	-	-
	-	-	700	-	980	-	-	-	-	-	-	-	-
25	-	3900	-	-	39340	-	-	-	-	350	-	-	-
	-	4240	-	-	42410	-	330	-	-	650	-	-	-
	-	5160	370	-	79530	-	-	-	-	-	-	-	-
26	-	4260	90	-	23630	-	-	-	-	390	-	-	-
	350	1760	-	-	21840	-	-	-	-	704	-	-	-
	-	3950	-	-	35080	-	-	-	-	880	-	-	-
27	-	6990	-	390	52050	-	-	-	-	390	-	-	-
	-	3820	-	-	44710	-	760	-	-	1910	-	-	-
	-	-	-	-	17140	-	-	-	-	-	-	-	-
28	-	-	-	-	2090	-	830	420	-	-	-	-	-
	-	610	-	-	3630	-	1210	-	-	610	-	-	-
29	-	4750	-	-	29330	-	2380	-	-	-	-	-	-
	-	3140	-	-	8770	-	1050	-	1050	1050	-	-	-
30	-	-	-	-	3230	-	460	-	-	460	-	460	-

Appendix 2. List of observed species.

Species name	Illustration in this paper
Acanthoica aculeata Kamptner	
Acanthoica quattrospina Lohmann	
Algirosphaera robusta (Lohmann) Norris	Plate 1, Fig. 3
Alisphaera unicornis Okada & McIntyre	
Calciopappus caudatus Gaarder & Ramsfjell	Plate 1, Fig. 6
Coccolithus pelagicus (Wallich) Schiller	Plate 1, Fig. 1
*Crystallolithus hyalinus Gaarder & Markalli	Plate 1, Fig. 2
Emiliania huxleyi (Lohmann) Hay & Mohler	Plate 2, Fig. 1-6
Gephyrocapsa muellerae Bréhéret	
Ophiaster hydroideus (Lohmann) Lohmann	Plate 1, Fig. 5
Papposphaera sp.	
Syracosphaera borealis Okada & McIntyre	Plate 1, Fig. 4
Syracosphaera marginaporata Knappertsbusch	Plate 1, Fig. 2
Syracosphaera mediterranea Lohmann	
Syracosphaera molischii Schiller	
Syracosphaera spp.	

* This motile phase of *C. pelagicus* was counted separately.