Abundance, encystment and sedimentation of acantharia during autumn 1990 in the East Greenland Sea

Avan N.Antia, Eduard Bauerfeind, Bodo v.Bodungen and Ute Zeller

SFB 313 der Universität Kiel, Heinrich Hecht Platz 10, Olshausenstraße 40, 2300 Kiel, FRG

Abstract. The abundance and sedimentation of acantharia and their cysts was recorded in the water column and sediment traps in the East Greenland Sea in August–September 1990. Although acantharia constituted <1% of total suspended particulate organic carbon (POC) in the water column, up to 90% (average 55%) of the POC sedimenting in 100 m was present in the form of acantharian cysts during a 9 day drift experiment. Rapid dissolution of strontium sulphate, of which their shells and spines are constructed, was evidenced by their disappearance with depth in the water column, maximum dissolution occurring between 500 and 1000 m water depth. Mass encystment and sedimentation of this single group of sarcodine protozoa can have dramatic effects on the measurement of particulate fluxes in the open ocean, and may be a recurrent phenomenon in the eastern North Atlantic.

Introduction

Although the acantharia, a group of the sarcodine protozoa, have been recognized since the turn of the century (Haeckel, 1887; Schewiakoff, 1902), a more detailed study of their trophic behaviour has only recently received renewed attention (Michaels, 1991; Swanberg and Caron, 1991). Previously grouped among the radiolaria due to their structural similarity, they are distinguished by the celestite composition of their spicules and cyst walls. In marine environments, they are the only organisms known to precipitate strontium from the dissolved form. Since seawater is undersaturated in strontium sulphate, these hard parts dissolve rapidly upon the death of the organisms, maximal dissolution occurring between 300 and 900 m water depth (Bernstein *et al.*, 1987). For this reason, acantharia have rarely been reported in sedimenting material and are seldom preserved in plankton samples; they are absent in bottom sediments and have left no trace in the geological record. Numerically, acantharia often exceed radiolaria and foraminifera in the euphotic zone (Beers and Stewart, 1971; Bottazzi and Andreoli, 1982) and, by virtue of their algal symbionts (Michaels, 1991) and grazing activity (Swanberg and Caron, 1991), may play a dominant role in the upper water layers. Bernstein *et al.* (1987), measuring strontium in the water column and sediment traps, were able to identify a surface depletion in strontium in the North Pacific during a time of high acantharian abundance showing that, by the uptake of celestite in shallow waters and its release at depth, these organisms may play an important role in the strontium budget of the oceans.

We report here, however, on standing stocks of acantharia and their contribution to the vertical flux of organic matter. The composition of biogenic material sedimenting out of the euphotic zone to some extent reflects seasonally important processes in the productive layers, and its diminution with depth is

related to degradation and alteration patterns in mid-water layers. A high seasonal variability in the annual patterns of vertical flux is often accounted for by the foraging activity of distinct groups of 'swarmer' organisms such as krill (v.Bodungen, 1986; v.Bodungen *et al.*, 1987), salps (Bathmann, 1988) and pteropods (Bathmann *et al.*, 1991). The acantharia may form another distinct group which by virtue of their reproductive cycle and cyst formation affect the mass sedimentation of organic matter from the euphotic zone.

We report here on the abundance of vegetative acantharia and their cysts, both in the water column and sediment trap samples, during autumn 1990 in the East Greenland Sea during the cruise POSEIDON 173/2 as part of the Special Research Project (Sonderforschungsbereich) 313 of the University of Kiel, ·FRG.

Method

Investigations were conducted in the water column and using sediment traps in the East Greenland Sea at and near the position of a long-term deployment at 72°00.2′N,07°02.5′W. Sediment traps in this mooring were positioned at 500, 1000 and 2000 m water depth. A drifting (between 72°37′ and 72°19′N and 7°33′ and 7°30′W) sediment trap array with traps in 100 and 300 m was deployed from 24 August to 1 September. Between 24 August and 1 September, a mooring at 72°00.7′N,07°02.5′E was equipped with sediment traps at 100, 500, 1000 and 2000 m.

A new design of the Kiel sediment trap, as originally described by Zeitzschel *et al.* (1978), was used in all deployments with sample jars containing seawater of increased salinity and $HgCl_2$ (to a final concentration of 0.07%) as a poison. Samples were collected over 24 h intervals in both the traps of the drifting array and at 100 m in the short-term mooring; a single jar collected an integrated sample over the 9 day deployment period at 500, 1000 and 2200 m in the short-term mooring.

Prior to the treatment of sediment trap samples, swimmers were gently removed with a pipette and rinsed free of adhering material. From the drifting traps and those of the short-term mooring, a small aliquot was withdrawn from each collection cup and used for light microscopy on board. This aliquot was then stored at 4°C for later analysis by scanning electron microscopy (SEM, Cambridge 150 B). The samples were then split into aliquots of 1/16 to 1/32 on board and were stored refrigerated until further analysis. Parallel splits were filtered onto GF/F filters and stored frozen for further analysis of dry weight and particulate organic carbon (POC) in the laboratory. A detailed report on the methods and procedures of analysis ˙of our sediment trap samples has been published by v.Bodungen *et al.* (1991).

Samples from the water column were taken by means of a multiple opening and closing net (mesh size 100 μm, opening 0.25 m²). The net was towed vertically through the water column and samples were taken from 500 m to the surface at five different depth intervals. Samples were fixed with borax-buffered formaldehyde (final concentration 4%) on board. On return to the laboratory, and confirmation of the celestite structure of the cysts 6–8 weeks later,

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$SrCl_2 \cdot 6H_2O$ to a final concentration of 80 mg l^{-1} was added to both water column and sediment trap samples, in order to prevent further dissolution of acantharian skeletons and cyst walls, as recommended by Beers and Stewart (1970). Acantharia and their cysts were counted using a binocular microscope under ×25 magnification. Net samples from near-surface probes were split (one-tenth to four-tenths) prior to enumeration, whereas those from deeper layers were counted whole. Several hundred cysts were gently transferred from the deep-frozen samples onto replicate GF/F filters for subsequent determinations of dry weight and carbon content. For the determination of dry weight, each filter was rinsed three times with deionized water, counted, dried at 60°C for 12 h and then reweighed. POC was measured by high-temperature combustion with a Hereaus Rapid CHN-O analyser. This measured POC value was used in conversions of cyst number to biomass for all samples.

Observations and results

Microscopic observations

EDAX analysis (EDAX B) of several cysts revealed them all to have walls composed of $SrSO_4$ (Figure 2e), confirming that they belong to the acantharia. Scanning electron microscopy showed that the cyst wall was porous and irregular in structure, and not constructed of individual plates, as has been reported for some species of acantharia (Hollande et al., 1965; Spindler and Beyer, 1990). The shafts of spines appeared to be laterally flattened and star-shaped in cross-section with smooth edges (Figure 2b). In some cases, the cytoplast of the acantharian with remnants of spines was visible within broken cysts (Figure 2c and d), a fact that was also noticed by Spindler and Beyer (1990). Both the vegetative forms and cysts that we found appeared to belong to the same family of acantharia. Round cysts of acantharia with differing diameters and surface structures have often been reported in the literature. The form seen in this study appear similar to, although smaller than, those reported by Spindler and Beyer (1990; their plate III). A similar cyst has been observed in sediment traps from the Canadian Arctic (Hargrave et al., 1992).

Net tows in the upper 50–100 m revealed acantharia of the same species, but exhibiting differing forms with respect to the appearance of an extracapsular membrane, the degree of deposition of strontium sulphate on the cyst wall as well as the degree of resorption of the spines (Figure 1). Light microscopy of live samples in a Petri dish on board ship showed numerous vegetative individuals with compact, rotund cell bodies ~75–100 μm in diameter, containing numerous (30–50) reddish-coloured droplets. Twenty radially divergent spines ~150–250 μm in length were seen protruding from a central axis, arranged according to the Müllerian law (Figure 1a). In many individuals a transparent mucous envelope surrounded the cell body, from which the spines protruded, these spines showed some signs of dissolution (Figure 1b). Deposition of celestite on this membranous covering was seen in many specimens, with the spines protruding through the openings in the cyst wall; these appeared to be early forms of the cysts in the water column. Further deposition of celestite
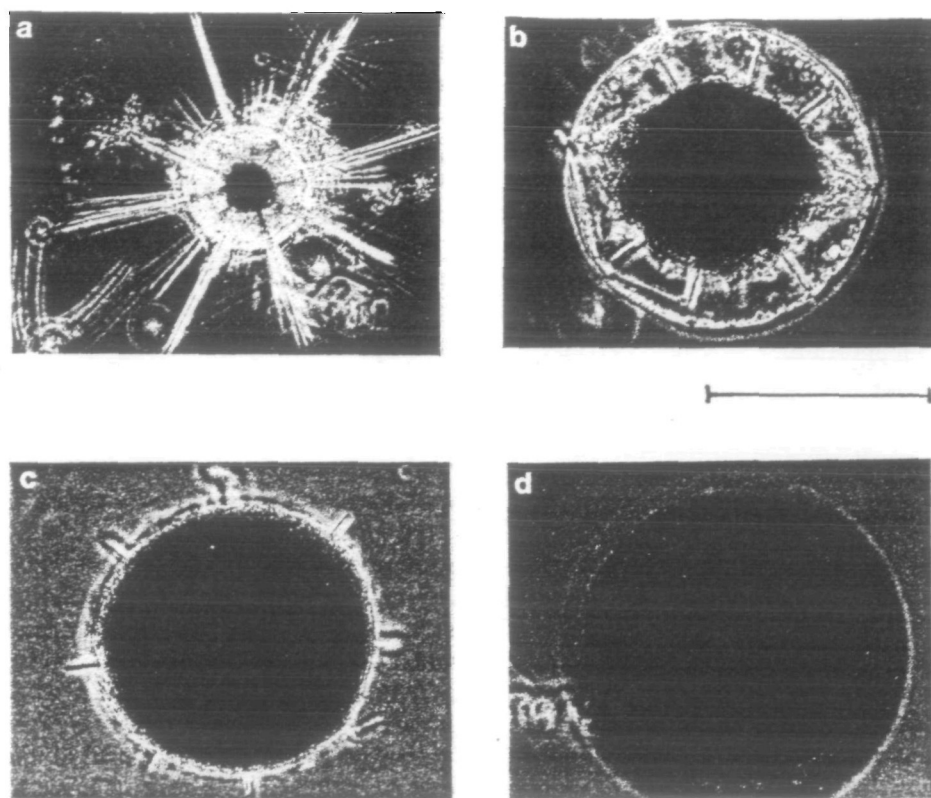
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Fig. 1. Light micrographs showing acantharia in different stages of encystment. Scale bar = 200 μm. (a) Vegetative acantharian with intact spines. (b) A mucous envelope surrounds the cytoplasm, through which the spines protrude. (c) The cyst wall is no longer opaque due to deposition of strontium on the mucous matrix. (d) Cyst with dissolved spines. The pores through which the spines protruded are still visible.

forms a cyst wall ~5–7 μm in thickness, within which the cell body is enclosed, with few remaining spines (Figure 1d); these were the primary forms of cysts found in the sediment traps. This cyst wall is thickened and slightly elevated around the openings through which the spines protruded (Figure 2a and b). As it is known that acantharians resorb the spines during cyst formation (Schewiakoff, 1926; Hollande *et al.*, 1965; Bottazzi, 1973), it is likely that cysts possessing spines represent freshly produced cysts in which the process of spine resorbtion was not completed, whereas cysts without any spines may represent a more advanced developmental stage. Acantharians are known to be susceptible to damage by net collections, which can lead to spontaneous resorbtion of spines, which severely comprises observations based on these samples. Our data, however, clearly indicate an actively encysting population in the water column, and we were able to observe numerous individuals of the various forms described above, leading us to suppose that these may be stages in the encystment process of these organisms. However, laboratory observations of

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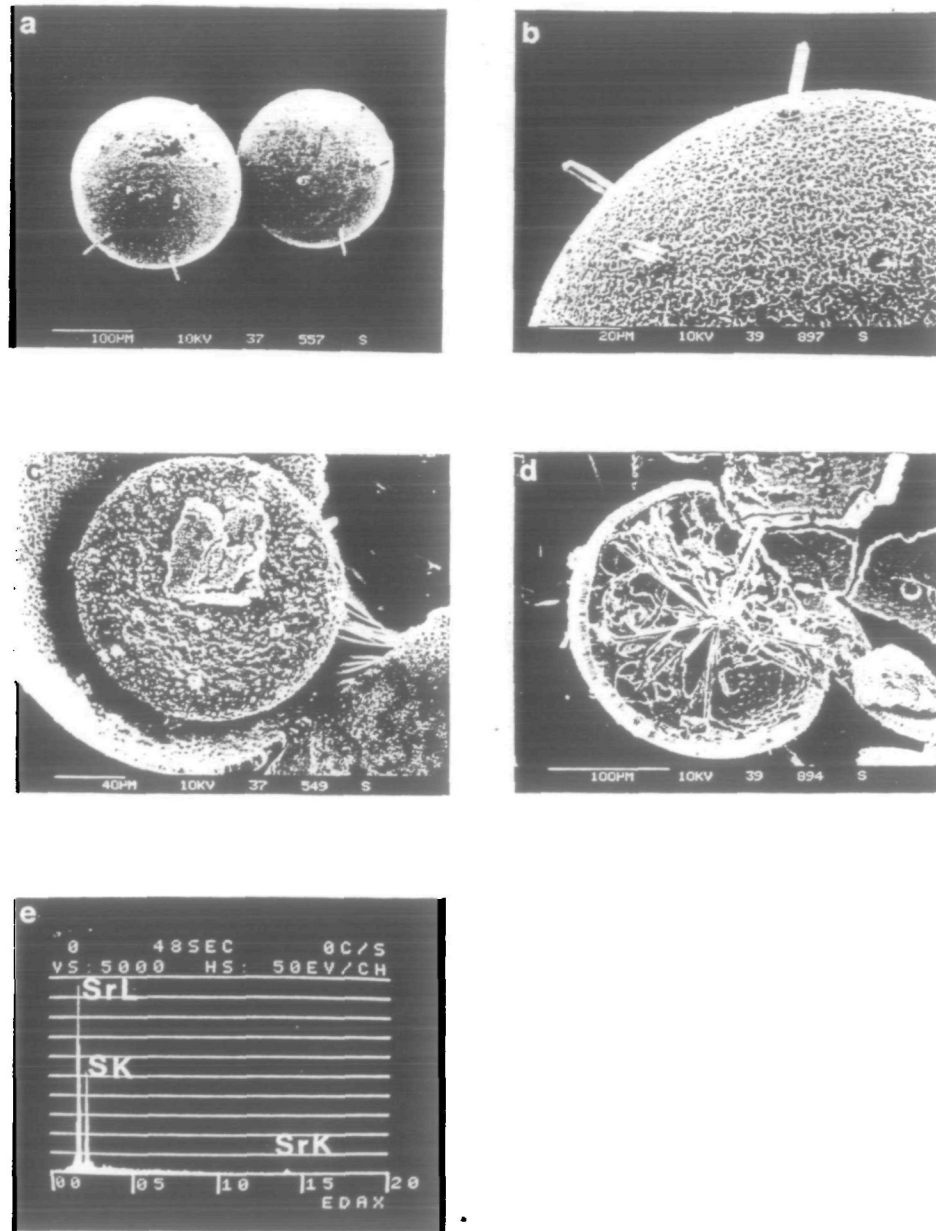
Fig. 2. Scanning electron micrographs of acantharian cysts. (a) Overview of round cysts with remnants of spines. (b) Surface of a cyst, showing irregular structure. Spines protrude from pores with elevated rims. (c) A cyst broken open, to show the cytoplast of the acantharian. Absorption of the spines is almost complete. (d) A broken cyst, with the inner part of the cytoplasm visible. Spines are arranged in a radial fashion around a central axis. (e) EDAX (EDAX B) analysis of cyst walls.

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encysting acantharia are necessary in order to achieve detailed information on the encystment process.

Cyst formation in acantharia has been incompletely studied, partly due to the difficulty in maintaining these protozoans in culture, and the rapid dissolution of $SrSO_4$ after their death. In their review of acantharian encystment, P.C.Ried and A.W.John (unpublished manuscript) recorded that encystment is seen to precede or accompany sporogenesis, forming a vital process in the reproductive cycle of acantharia (also Hollande and Cachon-Enjumet, 1957). Fission of nuclei within the cyst results in the formation of spores, which are thought to emerge during excystment from the pores left after dissolution of the spines. Hollande *et al.* (1965) described these spores as oval or elongated biflagellate cells ~10 μm in diameter, apparently indistinguishable by light microscopy from other small flagellates. We did not observe the excystment process in live material and were unable to identify acantharian spores in our plankton samples.

Distribution in the water column

Samples from net tows in the upper 500 m were counted for vegetative acantharia and cysts at three stations along the path of the drifter. Numbers of vegetative acantharia ranged from 2554 ind. m^{-3} on 25 August to 1843 ind. m^{-3} on 1 September along this transect (Figure 3) and were almost exclusively (>96% of all cells) confined to the upper 50 m of the water column, with no individuals found below 100 m. These values lie within the range of acantharia found in the North Pacific (3000–4000 ind. m^{-3}; Michaels, 1991) and Atlantic Ocean (1000–4000 ind. m^{-3}; Michaels, 1988). Bottazzi and Vannucci (1965), using extensive net tows, found somewhat lower abundances of 0–40 ind. m^{-3} in the upper 200 m in the Atlantic. Integrated abundances of vegetative forms (0–100 m) in this study ranged from 1.2 to 3.5 × 10^5 m^{-2}. Our numbers however, may represent minimum counts as net tows are thought to severely under-estimate plankton abundances (Michaels, 1988). Additionally, since $SrCl_2$ was added to the samples 6–8 weeks after collection, some dissolution may have occurred by that time.

A near-surface maximum of acantharians is a well-known feature and has been reported from different areas of the ocean (Bottazi and Vannucci, 1965; Bishop *et al.*, 1977; Michaels, 1988). Vegetative acantharia are known to have a mechanism that enables them to control their buoyancy in the water column (Schewiakoff, 1902; Cachon and Cachon, 1985). Their confinement to surface layers, often within the upper 20 m, provides the autotrophic symbionts that the acantharia are known to possess with optimal light conditions for photo-synthesis. During the period of our study, light penetration was confined to the upper 40–50 m (0.1% light level) of the water column. Integrated daily primary production rates in the euphotic zone (as measured by ^{14}C incorporation) averaged 150 mg C m^{-2} day^{-1}, a factor of three lower than those measured at an adjacent station during June–July 1989. If acantharian photosymbionts en-hanced their growth, this is likely to have been taking place at a slow rate.

Cysts were counted in two size classes, <200 and ≥200 μm, the latter being
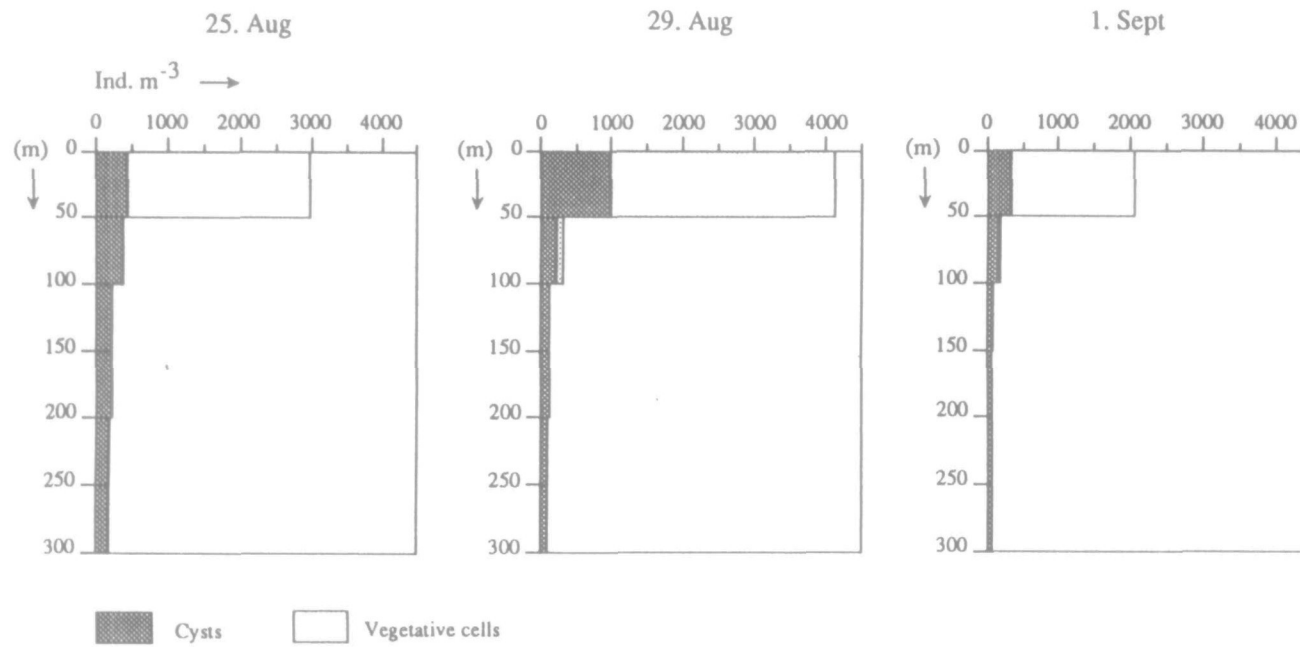
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Fig. 3. Vertical profiles of vegetative acantharia and cysts at three stations along the path of the drifting array. *X*-axis values indicate the depth intervals of net tows.

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dominant (>70% of total number) in all samples. Numbers of cysts were highest in the upper 50 m of the water column at between 434 and 986 ind. m^{-3}, decreasing to <68–171 ind. m^{-3} by 300 m. This depth distribution differs from reports in the literature where maximum cyst numbers occur between 100 and 300 m (Hollande *et al.*, 1965; Bottazzi, 1973; Spindler and Beyer, 1990). The integrated abundance of cysts in the upper 300 m of the water column varied from an initial 0.79×10^5 to 0.4×10^5 m^{-2} at the end of the study. Active encystment of vegetative cells appeared to at least partially balance their loss by dissolution and sinking, which was further borne out by our microscopic analysis, showing numerous 'freshly produced' cysts with remnants of spines still attached.

-    We were able to measure an average dry weight and organic carbon content of 5.17 ± 0.28 μg and 0.3284 ± 0.02 μg C per cyst, respectively ($n = 3$ filters containing 57, 85 and 155 cysts). We measured an average cyst diameter of 234 ± 80 μm ($n = 158$); this yielded a carbon:volume conversion of 0.048 pgC μm^{-3}. This factor is lower than that for the central capsule of acantharia of 0.08 used by Beers *et al.* (1975), which is to be expected as the internal volume of cysts was not entirely filled with cytoplasm. We used the value of Beers *et al.* (1975) and a measured capsule diameter of 100 μm (Figure 1a) to calculate a carbon content of 0.04 μg C per vegetative acantharia; and were thus able to estimate the contribution of both cysts and vegetative cells to total POC in the upper 100 m of the water column. Acantharian cysts accounted for 50–323 μg C m^{-3} and vegetative cells for 2–126 μg C m^{-3}, corresponding to a total contribution of 0.05–0.31% of water column POC. Integrated biomass values of vegetative cells in the upper 50 m of 3.38–6.3 mg C m^{-2} are comparable to, although lower than, those found by Michaels (1991) in the North Pacific (6.8–56.7 mg C m^{-2}). During an 18 month investigation, Michaels (1991) found a constant presence of acantharia in the euphotic zone, with the highest abundances in summer and autumn. We have no data on the seasonal patterns of acantharia at our station and only indirect evidence of their abundance via cysts in the annual mooring, the interpretation of which is severely compromised by dissolution problems.

Cyst sedimentation

The patterns of daily cyst sedimentation in traps at 100 and 300 m are shown in Figure 4, from which it is evident that large cysts (>200 μm) dominated in both depths. This reflects the size distribution of cysts in the water column and may be enhanced by the higher sinking velocity of larger forms. In the drifting trap array, cyst numbers at 100 m were higher during the first half of the deployment period, reaching a maximum of 112 800 ind. m^{-2} day^{-1}. The total flux within the 9 day period amounted to 575 361 cysts m^{-2}, yielding a mean sedimentation rate of 69 377 cysts m^{-2} day^{-1}. This decreased by ~50% in 300 m, due to loss by dissolution and excystment, with a mean sedimentation of 34 380 cysts m^{-2} day^{-1}. The relative contribution of acantharian POC to total POC in the sampling jars of traps in 100 m showed a decreasing trend during the time of this study. Acantharian cysts contributed between 74 and 92% of total sedimenting
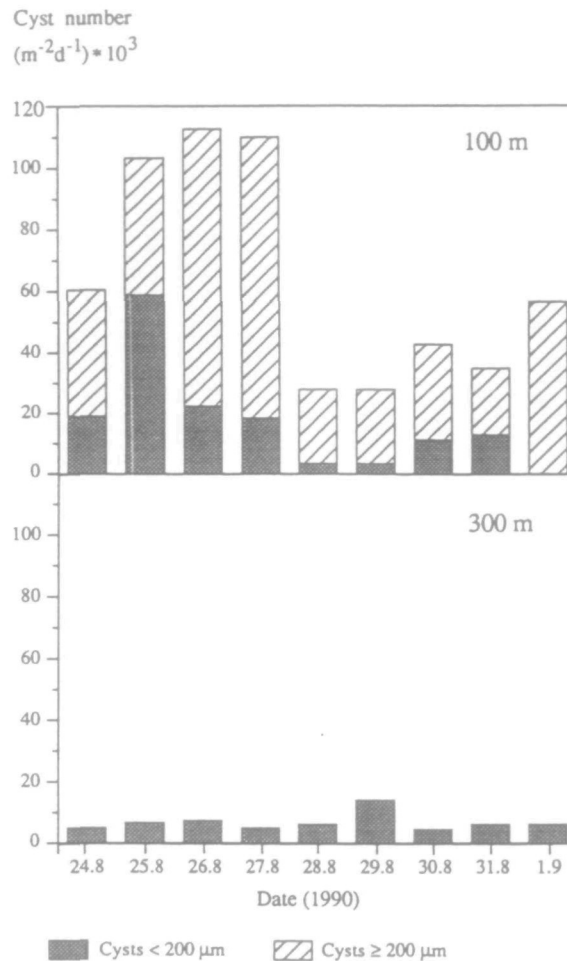
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Fig. 4. Daily sedimentation rate of acantharian cysts in drifting sediment traps at 100 and 300 m.

POC between 24 and 26 August; this decreased to ~30% of total POC during the latter half of the study. Averaged over the 9 days, 55% of total sedimenting POC in 100 m was accounted for by acantharia. In 300 m, this decreased to a mean value of 36% of the total sedimenting POC.

A short-term mooring which was anchored close to the starting position of the drifter yielded data on the sedimentation of acantharian cysts to deeper waters (Figure 5). Cyst numbers in the trap in 100 m of this mooring were somewhat lower than those encountered at 100 m in the drifter and accounted for 32% of total sedimenting POC at this depth (Table I). This value decreased almost 5-fold in 500 m, and represented 1 and <0.1% of total sedimenting POC in 1000 and 2000 m, respectively. In terms of dry weight, the contribution of acantharian cysts was similarly high, amounting to 59, 11, 3 and 0.1% of total sedimenting matter at 100, 500, 1000 and 2200 m, respectively. Rapid dissolution of cyst walls
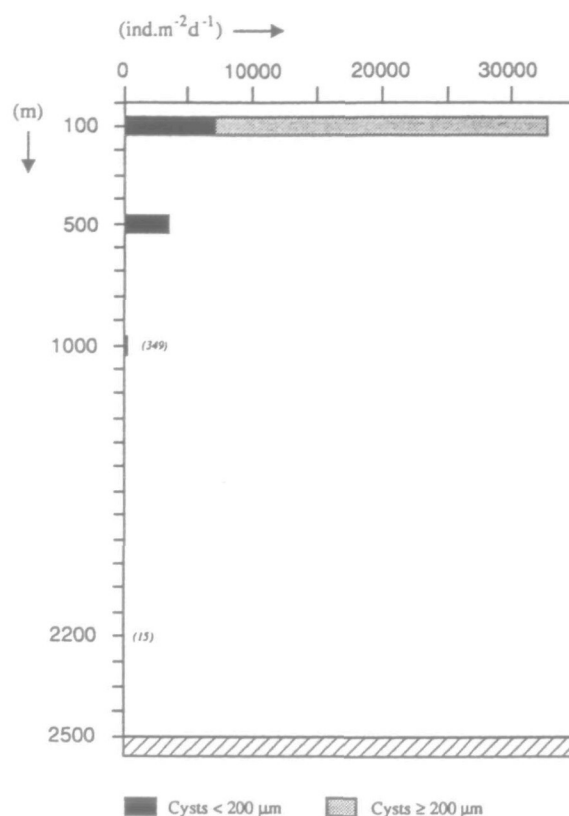
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Fig. 5. Daily sedimentation rate of acantharian cysts in the short-term mooring deployed from 24 August to 1 September 1990. The *X*-axis indicates the depth of trap deployment.

Table I. Total dry weight (DW) and particulate organic carbon (POC) fluxes in sediment traps of the short-term mooring deployed from 24 August to 1 September 1989 in the Greenland Sea. The contribution of acantharia to dry weight (Ac-DW) and POC (Ac-POC) has been calculated from cyst numbers using measured conversion factors. All values are expressed as mg m^{-2} day^{-1}

Depth (m)	Total DW	Ac-DW	(% total DW)	Total POC	Ac-POC	(as % total POC)
100	286.3	169.5	59	33.85	10.8	32
500	146.0	16.6	11	22.29	1.2	5
1000	82.94	2.17	3	14.93	0.13	0.9
2200	59.06	0.09	0.1	7.62	0.005	<0.1

has often been reported between 400 and 900 m water depth (Hollande *et al.*, 1965; Bernstein *et al.*, 1987; Spindler and Beyer, 1990) and is in accordance with our data. The contribution of acantharian cysts to sedimenting POC in our study far exceeds that by vegetative cells (9%) reported by Michaels (1991) at the base of the euphotic zone.

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Table II. Sedimentation of acantharian cysts (ind. m^{-2} day^{-1}) in sediment traps of the long-term mooring in the Greenland Sea

Sampling interval	500 m	1000 m	2200 m
15.07–01.08.89	*	16	0
02.08–15.08.89	1119	163	0
16.08–01.09.89	2158	401	0
02.09–15.09.89	268	16	0
16.09–30.09.89	0	0	0
Up to 01.08.90	0	0	0

*Sample lost.

The collection efficiency of sediment traps has been repeatedly questioned, and places limitations on the interpretation of their data. Buesseler (1991) reports a significant and random collection bias in the collection efficiency of shallow traps deployed for short periods. An additional recognized problem, especially in deployments within the upper water layers, is the influence of so-called 'swimmers'. The sediment traps we use are funnel/cone shaped with a baffle–aspect ratio of 5:1, with an opening of ~0.5 m^2. We cannot exclude a collection bias of the traps used in this study, but it is likely that large, fast-sinking particles such as the cysts reported here are adequately sampled by the traps. Large macrozooplankton swimmers are removed prior to the analysis of particulate material and are not included in POC and dry weight measurements.

From an examination of the samples of our long-term annual mooring in the East Greenland Sea, we have indications that encystment and sedimentation of acantharia may be a recurring event in this part of the North Atlantic (Table II). A small number of cysts were found in preserved samples between the middle of July 1989 and September 1989 down to 1000 m water depth. These appeared, on microscopic analysis, to be the same form of cysts as those encountered in 1990. We view these values, at best, as minimum estimates due to the problems of dissolution mentioned above, and the long time interval between sample collection and analysis. However, dissolution of cysts in the sampling jars may elevate Sr levels, slowing the process and allowing for some preservation in long-term moorings. The value of 2158 ind. m^{-2} day^{-1} at 500 m between 16 August and 1 September 1989 is nonetheless comparable to that found at 500 m in the short-term mooring deployed during this study. It is possible that cyst dissolution may have masked a much larger (and longer) acantharian sedimentation event. On subsequent cruises, we have observed acantharians and cysts in net hauls from the northern North Atlantic in the Barents and Norwegian Seas, and in shallow sediment traps during April/May 1992 at 47°N,20°W. The measurement of dissolved and particulate strontium in the sampling jars of sediment traps may be useful in order to follow the seasonal patterns of occurrence and sedimentation of acantharia.

We measured a potential sinking rate of 238 (±96) m day^{-1} (range 103–367; n = 13) of cysts in the laboratory by timing their descent in a measuring cylinder (80 cm long, 10 cm diameter, filled with filtered seawater at 6°C). This value

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closely approximates their potential sinking speed of 216 m day^{-1} as calculated from Stokes Law (using a mean diameter of 200 μm and the measured weight of 5.17 μg cyst^{-1}). It was further possible to calculate a sinking rate for cysts independent of the traps. Integrated cyst abundance in the upper 100 m amounted to 25 000–62 000 ind. m^{-2}. This agrees well with the values of 27 000–110 000 ind. m^{-2} found in the traps at 100 m. Similarly, integrated abundances between 150 and 300 m of 30 600–83 100 ind. m^{-2} correspond to cyst numbers of 18 000–51 000 ind. m^{-2} found in the trap at 300 m. This would indicate a sedimentation rate of between 100 and 150 m day^{-1}, somewhat lower than the theoretical value. The observed pattern of sedimentation cannot therefore be explained purely in terms of sinking processes. The peak in sedimentation at 100 m between 25.8 and 27.8, and its absence at 300 m, as well as the 20% decrease in numbers between these depths, indicate that other loss processes need to be accounted for. Although losses due to grazing pressure and horizontal advection cannot be ruled out, we suggest that dissolution and, perhaps, excystment, could account for the sedimentation pattern seen.

Conclusions

The trophic role of the sarcodines, and in particular the acantharia, has only recently received adequate attention. Acantharia have long been known to possess symbiotic algae and thus contribute to net photosynthesis in the euphotic zone. Michaels (1988), using symbiont production rates from the literature, estimated that vegetative acantharians in the euphotic zone may account for up to 20% of primary production. The investigation of other modes of nutrition, however, has only recently been quantified. Swanberg and Caron (1991) found that acantharia feed preferentially on ciliated protozoa, in particular tintinnids, and small metazoans in a mixed plankton assemblage. Numbers of ciliates (predominantly naked forms) in the euphotic zone were high, ranging between 5000 and 10000 ind. m^{-3} (Antia, 1991), and were found mainly in the upper 30 m of the water column. Copepod nauplii and small metazoans (<200 μm) were also present in the upper 50 m, forming a potential food source for the acantharia.

The confinement of vegetative acantharia in our study almost exclusively to the upper 50 m of the water column could thus be a response to available microzooplankton nutrition and/or an adaptation to autotrophic symbiosis. Under light microscopy, we saw numerous (30–50) reddish droplets, 5–6 μm in diameter, within individual acantharia. When stained with DAPI, a DNA-specific dye, these were seen to contain nuclear material, implying that they were either nuclei of the acantharia or their endosymbionts. However, under UV excitation we were not able to distinguish individual chloroplasts of the symbiotic algae, but observed, rather, a diffuse red autofluorescence within the cysts. We are not sure whether this was caused by refraction within the cyst walls or the digestion of the symbionts. Many protozoans are known to stop feeding and shed or digest their symbionts during reproduction and cyst formation, which may account for our observations. Moreover, we did not observe

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acantharia feeding in our live samples and their trophic role during this investigation remains unquantified.

Reports on the sedimentation of acantharians are rare, primarily due to the rapid dissolution of $SrSO_4$ in seawater after the death of the organisms (Schewiakoff, 1902). Acantharia are the only organisms known to precipitate strontium from seawater (aside from a minor contribution from coccolitho- phorid ooze and foraminifera), and are thought to play a role in the geochemical cycle of strontium in the oceans. Owing to the larger size of cysts found in this study, their contribution to strontium fluxes may be expected to exceed that reported by Bernstein *et al.* (1987) in the North Pacific. Measurements of dissolved and particulate Sr in samples from our cruise are underway and will be reported elsewhere.

From the data presented here, however, it is evident that acantharia can contribute substantially to particle sedimentation out of the upper ocean layers. During the drift experiment reported here, the contribution of acantharian cysts to total sedimenting matter collected in sediment traps below the euphotic zone exceeded by almost two orders of magnitude their relative contribution to suspended particulate matter. In order to evaluate their contribution to vertical carbon fluxes, it is of interest to know at which water depth release of carbon from their cysts occurs. Vegetative acantharia and freshly formed cysts ensure a structural integrity of spines and cyst walls, and dissolution may primarily occur subsequent to excystment and death. The partitioning of organic carbon between the cell cytoplasm and hard parts (in the form of an organic matrix upon which strontium is deposited) is uncertain and hampers our understanding of the processes leading to the release of organic material from sinking cysts.

Studies of the vertical flux of organic matter in the ocean have been numerous in the past decades (Smetacek, 1980; Honjo, 1982; v.Bodungen *et al.*, 1986) and it it recognized that the quality and quantity of sedimenting material is controlled largely by trophic interactions within the upper water column (e.g. Bathmann *et al.*, 1990). The primary vehicles of vertical transport are large particles (McCave, 1975; Bishop *et al.*, 1977) such as faecal pellets (Dunbar and Berger, 1981), hard parts of pelagic organisms (Bathmann *et al.*, 1991) and large phytodetrital aggregates (Alldredge and Silver, 1988) which can form an important periodic source of food to organisms on the sea bed (Lampitt, 1985; Graf, 1990). The role of single groups of organisms in causing short, intense pulses of organic matter sedimentation has been documented (v.Bodungen *et al.*, 1987; Bathmann, 1988; Bathmann *et al.*, 1991). We report here on one such group which undergoes complete degradation within the winter mixed layer, but can nonetheless form a major part of organic matter sedimentation in shallow traps.

A drift experiment similar to that reported here was conducted at an adjacent station during June/July 1989, during which time primary production in the euphotic zone exceeded by a factor of three that measured in this study. Daily organic carbon sedimentation at the base of the euphotic zone amounted to 0.05% overlying suspended POC in 1989, in contrast to 0.23% during August/ September 1990. Much of this material could be accounted for by the organic

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carbon contained in acantharian cysts (average 51%), illustrating the importance of this single group of organisms in the measurement of vertical particle flux. By their mass occurrence and sedimentation, and absence in deeper water layers and at the sea bottom, acantharia may play an important role in the release of dissolved organic matter in mid-water layers. During the 9 day drift experiment reported here, sedimentation rates were high in relation to primary production in the euphotic zone (Antia *et al.*, 1990), showing a temporal decoupling between production and export. The effect of acantharia in accentuating export from the upper water layers is special in terms of their dual trophic role as auto- and heterotrophs (which they share with other pelagic protozoa such as foraminifera), and unique in terms of the ephemeral nature of their skeletons and cyst walls.

Our observations pose some unanswered questions. Firstly, to what extent do acantharia contribute to productivity and/or heterotrophy in the euphotic zone? The mass occurrence of these organisms at a time when both algal productivity and algal biomass was low (Antia *et al.*, 1990) suggests an adaptability to a late summer situation. Secondly, what significance does this encystment event have in the open ocean where, unlike in shallow coastal areas, vertical mixing cannot help repopulate the pelagial when conditions are favourable? The release of spores within the winter mixed layer, where they would be mixed to the surface on an annual basis would, on the other hand, confer an advantage to the acantharia, allowing for growth when conditions become favourable. The cysts found in this study appear not to be resting spores, but rather a means of reproduction, although the significance of a growing population at a time when the diel light period was short and pelagic biomass low is uncertain. The large numbers of acantharia that we found, however, indicate their importance in the euphotic zone and further investigation of their trophic behaviour clearly merits attention.

Acknowledgements

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