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Mass encystment and sinking of dinoflagellates during a spring bloom

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Abstract. The decline of a spring bloom dominated by dinoflagellates and the mass sedimentation of dinoflagellate cysts was documented in a coastal area of the northern Baltic Sea, SW Finland in 1983. The exceptionally large spring phytoplankton bloom was observed in early May. After depletion of nitrate phytoplankton biomass declined rapidly. The bloom was followed by intense sedimentation of spherical cysts and of organic matter at the end of May. These cysts were presumably hypnozygotes of *Peridinium hangoei* Schiller. Sedimentation of dinoflagellate cysts was estimated to correspond to ca. 45% of the maximum sedimentation of particulate organic carbon at this time, although most of the dinoflagellate biomass disintegrated already in the water column and was deposited as organic detritus or washed away by advection. It is concluded that the life cycle strategies of the dominant vernal phytoplankton species have a major impact on the sedimentation of the spring bloom.

Introduction

Many dinoflagellate species occurring in coastal temperate waters have been recorded to form resting cysts during impoverished environmental conditions (Dale 1977, Anderson and Wall 1978). Cysts represent a resistant, dormant stage which is formed after sexual reproduction in the life cycle of dinoflagellates (Pfiester and Anderson 1987, and references therein). Cysts deposited to sediments can remain viable in dark, anoxic conditions for long periods of time (Dale 1983). In addition to the benefits of genetic recombination, they have been proposed to promote dispersal and act as a seeding mechanism for coastal dinoflagellate populations (Dale 1977, Anderson and Morel 1979). Thus, dinoflagellate blooms are expected to terminate with the formation of cysts. Yet dinoflagellate cysts are rarely found in plankton since they are rapidly transported to the benthos after encystment (Dale 1983, Anderson et al. 1985b). Such episodic events cannot be observed through routine water-column sampling alone. However, the combination of water-column and sediment-trap studies can provides sufficient information for estimation of cyst flux to the benthos.

In the present paper, the mass encystment and sedimentation of a dinoflagellate spring bloom is described. The massive deposition of cysts is discussed within the framework of the life cycle of the dominant vernal dinoflagellate species. The morphology of the cysts is described, and the significance of the different loss processes (sedimentation, grazing, decomposition and advection) for the decline of the spring bloom is discussed. Finally, the impact of cyst deposition on the total sedimentation of organic matter during the spring period is estimated. The sedimentation of the spring bloom in 1983 was studied as part of the project concerning the pelagic carbon cycle of the northern Baltic Sea, carried out by the Finnish Institute of Marine Research.

Materials and methods

The study area was situated at the entrance to the Gulf of Finland, southeast of the Hanko Peninsula (59°47'N, 23°19'E). The sampling station was located in a small basin, with a total depth of 46 m. A typical feature of the study area is rapid displacement of water masses, mainly due to fluctuations in meterological conditions. The sampling area is influenced by surface water from the open Gulf of Finland (5 to 6‰), surface water from the inner archipelago (3 to 5‰), and Baltic deep water through upwelling (7‰) (Niemi 1975). The average duration of ice-cover is ca. 2 mo, but winters without ice cover do also occur.

Samples from the water column were taken after the break up of ice-cover from 24 March to 14 June and from 20 July to 24 September 1983. Samples were taken with a plastic 10-liter water sampler, equipped with a thermometer, from depths of 0, 2, 5, 7, 10, 15, 20, 30 and 40 m. Salinity was measured with an Autosal laboratory salinometer model 8400. Chlorophyll *a* samples were filtered on Whatman GF/C glass-fibre filters, extracted in 90% acetone, and measured fluorometrically in accordance with the recommendations of the Baltic Marine Biologists (Edler 1979). Nitrate was analyzed as described by Grasshoff (1976). Samples taken from the depths of 0, 2, 5, 7, 10 m were pooled for phytoplankton cell counts and biomass determinations, and preserved with Lugol's acid solution.

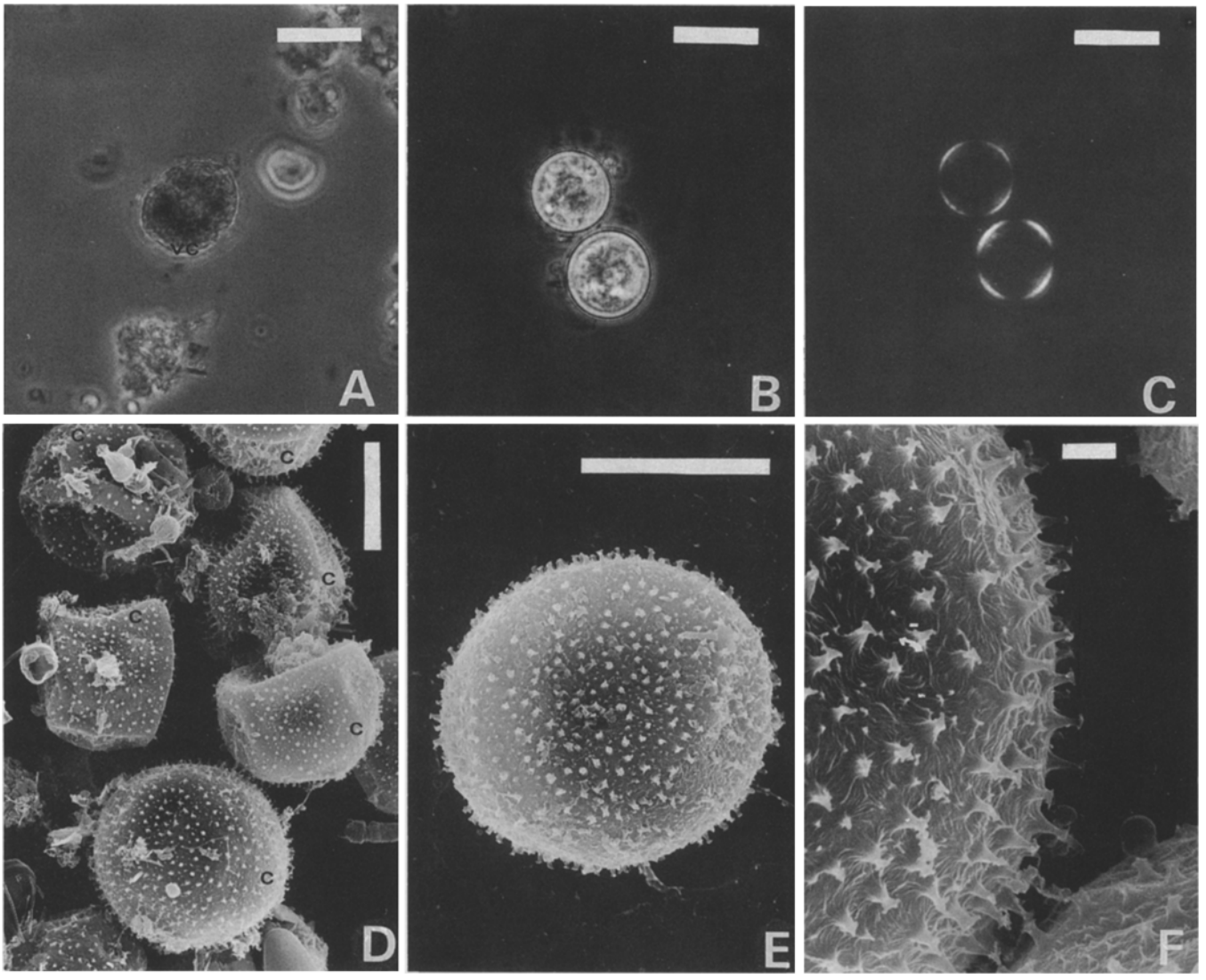

Fig. 1. *Peridinium hangoei.* (A) Vegetative cell (vc) (Lugol-AA fixed) (white bar = 20 µm), Tvärminne, Storgadden. (B) Dinoflagellate cysts (white bar = 20 µm). (C) Polarization interference figures of dinoflagellate cysts [same as in (B)] (white bar = 20 µm). (D) Scanning electron micrograph (SEM) of collapsed dinoflagellate cysts (c) (white bar = 10 µm). (E) SEM-micrograph of a single resting cyst (white bar = 10 µm). (F) SEM-micrograph of cyst surfaces showing short processes (white bar = 1 µm). [(B)–(F) from sediment trap material, Tvärminne, Storgadden]

Settling material was collected from 4 May to 9 June and from 27 July to 15 September in cylindrical sediment traps moored at 20 and 30 m depths. Sediment traps consisted of triplicate cylinders, 100 cm high and 10 cm in diameter. An additional trap was moored at 10 m depth during the summer period. Cylinders were emptied on the average once a week. No preservatives were used inside the cylinders. The contents of two cylinders were freeze-dried and weighed for dry weight determination. Following this they were combined, homogenised, and the concentration of particulate organic carbon was analyzed by high temperature combustion using an infrared gas analyzer (Uras 2T) (Salonen 1979). Settled material from the third cylinder was suspended in a precise volume of filtered seawater and preserved with buffered formaldehyde (2% final concentration) for microscopical analyses.

Phytoplankton samples were enumerated using an inverted microscope (Utermöhl 1958). At least 50 units of the most abundant species were counted when possible. Otherwise, at least a total of 500 units were counted from each sample. The phytoplankton plasma-volume and carbon biomass-values were estimated according to the recommendations of the Baltic Marine Biologists (Edler 1979) with modifications by Kononen et al. (1984). The raw counts and conversion factors used are deposited at the Finnish Institute of Marine Research, Helsinki. Dinoflagellate cysts were identified with polarized light (Fig. 1 C) according to the method described by Reid and Boalch (1987), and counted by using an inverted microscope with phase contrast. At least 400 cysts were counted from each sample, when they were sufficiently abundant. Their identification was based on shape, cyst wall thickness, surface structure, pigmentation and size (Fig. 1 B).

The carbon content of the dinoflagellate cysts was estimated by measuring their average diameter (20 µm SD 1.4 µm, $n = 50$), calculating the average volume, and multiplying this by a factor of 0.13, as was recommended for armoured dinoflagellates by the Baltic Marine Biologists (Edler 1979). Sedimentation of detrital carbon was calculated by subtracting the estimated phytoplankton and cyst carbon from the total organic carbon.

Sinking velocity of the dinoflagellate cysts was calculated according to Stoke's law for spherical forms assuming seawater viscosity of 0.015 g m^{-1} s^{-1}, seawater density of 1 g cm^{-3}, and cyst density of 1.2 g cm^{-3} (Anderson et al. 1985b). These assumptions yield a sinking velocity of 2.5 m d^{-1}.

Scanning electron microscopy was carried out on formaldehyde-fixed samples (2% final concentration). Samples were rinsed in 0.1 *M* cacodylate buffer, post-fixed for 1 h in 2% OsO_4, rerinsed in

cacodylate buffer and pipetted on Poly-L-Lysin dipped coverslips. After dehydration in ethanol (70, 90, 96 and 100%), samples were critical-point dried (Balzers Crit. Point Dryer), coated with Au/Pd in a Polaron sputter coater and examined in a Jeol 35 C Scanning Electron Microscope (Electron Microscopic Laboratory for Biological Sciences, University of Oslo, Norway). The first samples were dried in air, but since this caused the collapse of cysts, critical-point drying was performed thereafter.

Results

The spring bloom maximum was observed at the onset of May. Chlorophyll *a* (Chl *a*) values reached very high levels (208 mg m^{-3}) in a very shallow surface layer (0 to 1 m) (Fig. 2A), concurrent with elevated temperature and slightly lower salinity (Figs. 2B and 3A, B). During the bloom nitrate concentrations were depleted to undetectable levels in the surface layer (Fig. 4A). The spring bloom biomass consisted mainly of dinoflagellates (Table 1). The biomass of other groups was smaller, although members from Bacillariophyceae, Cryptophyceae, Prasinophyceae, Chlorophyceae, Euglenophyceae, and from a heterogeneous group of unidentified nanoflagellates were numerous (Table 1).

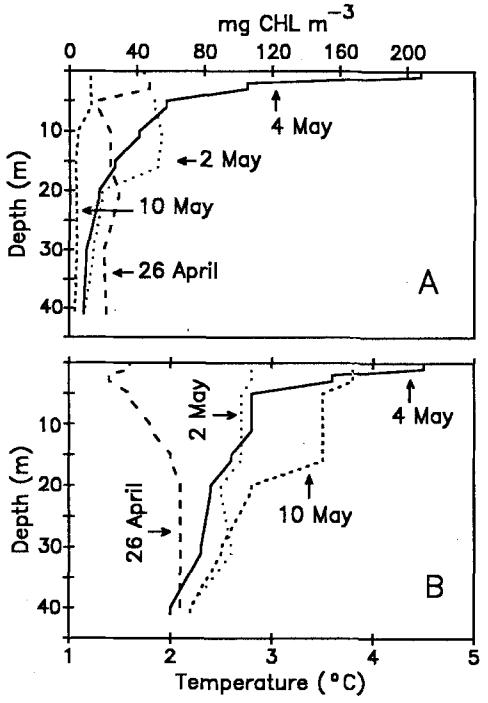

Fig. 2. (A) Vertical distribution of chlorophyll *a* (mg m^{-3}) and (B) temperature (°C) during the spring bloom peak as a function of depth (26 April to 10 May)

The large peak in phytoplankton biomass in early May, was dominated by *Peridinium hangoei* Schiller (Fig. 1A), which attained cell concentrations of 5.0×10^9 m^{-3} in the 10 m deep surface layer (Fig. 4A) and constituted more than 80% of the total phytoplankton biomass (Table 1). The chain-forming dinoflagellate *Peridiniella catenata* Levander (Balech) (syn. *Gonyaulax catenata*) was also abundant, although it contributed only ca. 8% to the total phytoplankton biomass during the bloom peak. The cell numbers of *P. hangoei* declined soon after nitrate depletion in early May (Fig. 4A).

The flux of dinoflagellate cysts was at its greatest at the end of May, when daily rates of 7.8×10^8 and 6.4×10^8 cysts m^{-2} d^{-1} were recorded at 20 and 30 m, respectively (Fig. 4C, D). The total cumulative deposition of cysts during the spring period, is compared to the maximum abundances of *Peridinium hangoei* and *Peridiniella catenata* in Table 2. In summer, the sedimentation rate of cysts was small, but increased with depth, reaching a maximum of 5.3×10^7 cysts m^{-2} d^{-1} at 30 m depth, at the end of August (Fig. 4D). In early May, the major part of the settled organic carbon consisted of phytoplankton carbon and detrital material, while at the end of May the contribution of dinoflagellate cysts had increased considerably, accounting for ca. 45% of the total organic carbon deposited (Fig. 5). Dinoflagellate cysts and phytoplankton were estimated to compose on average 19 to 26% and 28 to 32%, respectively, of the total organic carbon settled in spring. The beginning of June showed a decline in sedimentation rates of cysts and phytoplankton. During summer, phytoplankton carbon was estimated to form only a small (2 to 10%) part of the settled material, which consisted mainly of detrital material (Fig. 5). An average of 6 to 8% of settled organic carbon was estimated to consist of resting cysts during summer (Fig. 5).

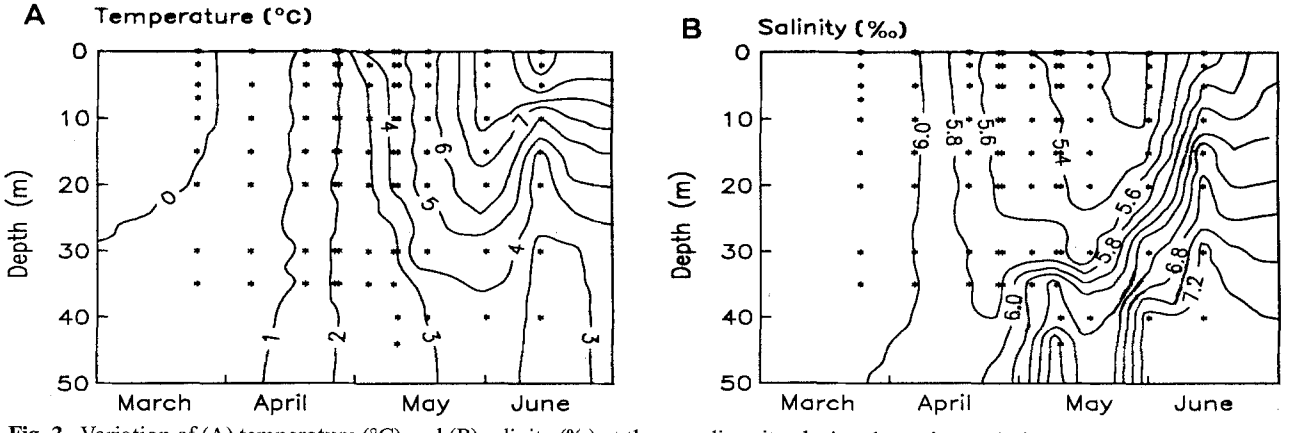

Fig. 3. Variation of (A) temperature (°C) and (B) salinity (‰) at the sampling site, during the spring period

Table 1. Cell numbers (10^5 cells l^{-1}) of the dominant dinoflagellate species and other phytoplankton groups in the surface layer (0 to 10 m) during the vernal study period. Their contribution (%) to the total phytoplankton biomass (g C m^{-3}) presented in parenthesis

Species	Date								
	7 Apr	19 Apr	22 Apr	27 Apr	4 May	11 May	18 May	1 Jun	14 Jun
Peridinium hangoei	0.9 (49)	1.7 (56)	2.5 (57)	39.2 (85)	49.6 (86)	8.2 (46)	5.6 (63)	0.1 (6)	–
Peridiniella catenata	1.3 (34)	1.3 (21)	2.7 (29)	2.2 (6)	4.1 (8)	2.5 (19)	1.9 (13)	0.1 (4)	–
Total Dinophyceae	2.2 (86)	3.1 (77)	5.3 (87)	42.3 (94)	54.7 (95)	11.4 (69)	9.1 (84)	0.3 (24)	4.4 (16)
Bacillariophyceae	4.3 (7)	6.7 (13)	3.5 (6)	10.9 (3)	7.5 (1)	20.7 (11)	38.4 (13)	16.3 (39)	6.0 (15)
Others	8.7 (7)	18.4 (11)	23.0 (7)	39.6 (3)	43.1 (4)	36.0 (21)	15.3 (4)	22.4 (37)	30.4 (68)
Total biomass (g C m^{-3})	0.3	0.5	0.8	3.5	4.5	1.1	1.3	0.1	0.1

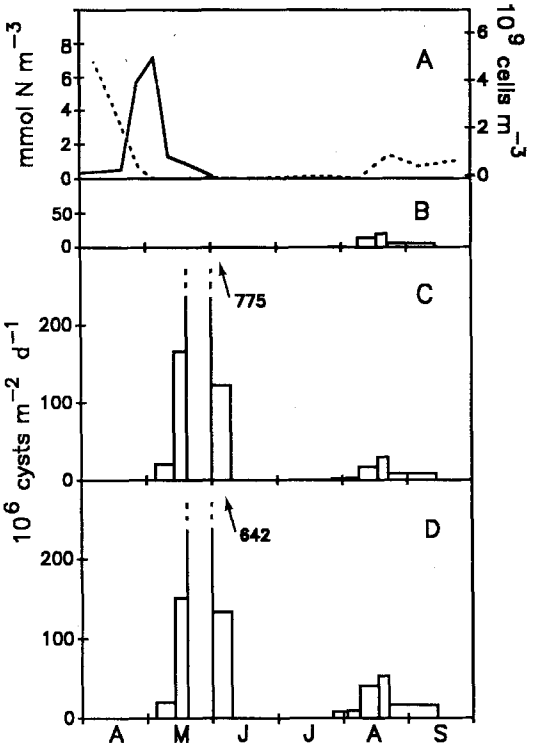

Fig. 4. (A) Cell numbers of *Peridinium hangoei* in the surface layer of 0 to 10 m (continuous line) and the mean nitrate (NO_3^-) concentration (mmol m^{-3}) in a water column of 0 to 15 m (dashed line). (B) Sedimentation rate of dinoflagellate cysts at 10 m, (C) 20 m and (D) 30 m depths, during the spring and summer periods (no traps deployed at 10 m depth during the spring period). A: April; M: May; J: June; July; A: August; S: September

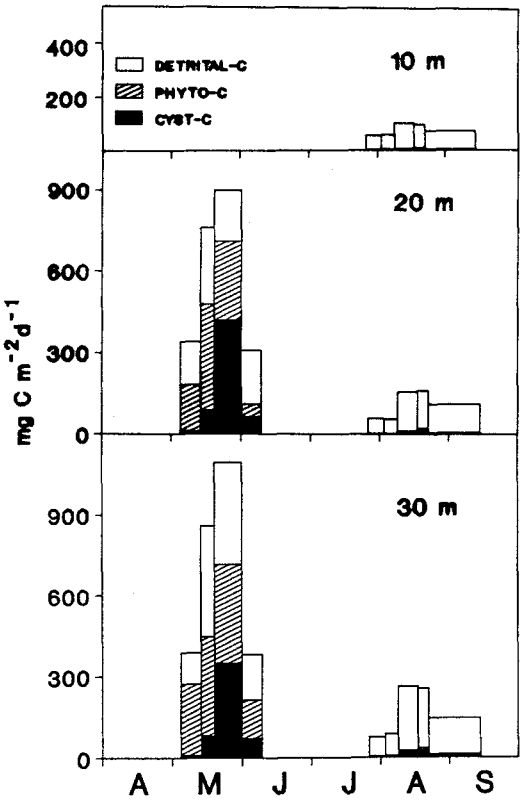

Fig. 5. Contribution of dinoflagellate cysts (CYST-C), other phytoplankton (PHYTO-C) and detrital carbon (DETRITAL-C) to total organic carbon collected by sediment traps (mg C m^{-2} d^{-1}) at 10, 20 and 30 m depths during spring and summer periods (no traps deployed at 10 m during the spring period). A: April; M: May; J: June; J: July; A: August; S: September

Discussion and conclusions

Dinoflagellates and cold water diatoms generally dominate the spring bloom in the northern Baltic Sea. The pattern is fairly regular with some differences in biomass level and the relative dominance of dinoflagellates and diatoms from year to year (Kononen and Niemi 1984). *Peridinium hangoei* and *Peridiniella catenata* are recurrent and abundant members of the phytoplankton community during the spring bloom (Niemi 1975, Niemi and Åström 1987). The phytoplankton spring bloom biomass was exceptionally large in 1983 being ca. four times

Table 2. Maximum standing crop (C; 10^9 cells m^{-2}) of the dominant dinoflagellates in the surface layer (0 to 10 m) and cumulative sinking flux of resting cysts (S; 10^9 cysts m^{-2}) at the 20 m sediment trap during the vernal study period. (Cumulative sinking flux: total sedimentation of cysts between 3 May and 9 June)

Species	C	S	S/C
Peridiniella catenata	4.1	–	2.8
Peridinium hangoei	49.6	–	0.23
Resting cysts	–	11.6	

greater than the spring-bloom maxima observed during the long-term monitoring study done from the same area (Kononen and Niemi 1984). The massive flux of spherical cysts (Figs. 1, 4) at the end of May, suggested that the spring bloom was followed by encystment of the major dinoflagellate species. The cumulative sinking flux of cysts, at 20 m depth, corresponded to 23% of the maximum standing crop of *P. hangoei* observed during the spring period, while it was almost three times higher than the maximum standing crop of *P. catenata* in the surface layer (Table 2). This indicated that the cysts were formed by *P. hangoei*. Furthermore, no other pelagic organism was sufficiently abundant in the water column to be expected to produce such a large deposition of cysts at this time.

The morphology of the cysts support the hypothesis that they were formed by *Peridinium hangoei*. The spherical cysts exhibited a symmetrical cross-shaped pattern under polarized light (Fig. 1 C), which it has been suggested is typical for some dinoflagellate cysts (Reid and Boalch 1987). However, it does not explicitly follow that the cysts originated from dinoflagellates, since bottle-shaped cysts of some ciliates, bivalve larvae, and ostracods may exhibit a similar kind of pattern, although usually non-symmetrical when examined under polarized light (Reid and Boalch 1987). Furthermore, these cysts are distinguishable from dinoflagellate cysts by their size, shape, and the form of their cross. Moreover, the cysts found during the present study were heavily pigmented, supporting the conclusion that the generative organisms were autotrophic. Further evidence has been provided by direct microscopic observations of the excystment of similar cysts, producing vegetative *P. hangoei* cells (personal communication by H. Kuosa, Finnish Institute of Marine Research, Helsinki).

Scanning electron micrographs revealed that the cysts had a relatively soft cell wall, as simple air drying before examination of the samples resulted in collapse of the cyst walls (Figs. 1 D). This indicated that the observed cysts lacked the hard and resistant three-layered wall of mature resting cysts (Bibby and Dodge 1972, Chapman et al. 1982). No accumulation bodies, typical red "eye spots" of dinoflagellate cysts, which should be visible during a later stage of encystment (Dale 1983), were observed. Closer focusing on the surface of the cysts by scanning electron microscopy revealed that they were covered with short (ca. 0.5 µm) processes with triangular-shaped ends (Fig. 1 F). No archeopyles (opening of the cyst wall for excystment) or paratabulation (tabulation resembling the vegetative cell) were observed. Since no renewed occurrence of *Peridinium hangoei* was observed during the summer, this indicates that the cysts were probably immature resting cysts (hypnozygotes), rather than temporary cysts which revert back to motile cells when favourable conditions return.

The dinoflagellate bloom culminated after nitrate attenuation, in early May, and the highest sedimentation rate of cysts was found ca. 2 wk later. Dinoflagellate hypnozygotes are produced through sexual reproduction, which has been observed to be triggered by nitrogen deficiency (Pfiester 1975, Walker and Steidinger 1979, Anderson 1980), and to begin during the maximum abundance of the vegetative stage (Wall and Dale 1968). The temporal inconsistency between the water column maximum of *Peridinium hangoei* and the major deposition of cysts indicated a probable antecedent of the hypnozygote-stage by a motile planozygote-stage. Motile planozygotes, produced after fusion of gametes, can remain viable in the water column for 3 to 20 d (Dale 1983), before losing their motility and changing into hypnozygotes (Pfiester and Anderson 1987, and references therein). Assuming that the cysts were sinking with the sinking velocity of 2.5 m d^{-1}, as calculated according to Stoke's law, it would have taken ca. 7 to 8 d for cysts to sink over 20 m and ca. 4 d more to reach the depth of 30 m. Thus, the pelagic planozygote-stage would have persisted for ca. 1 wk after the bloom peak, before changing into hypnozygotes and starting to sink. Since resting cysts were only rarely found in the water samples, and the sedimentation rates of cysts were maximal simultaneously at 20 and 30 m depths (Fig. 4), this suggested that the actual velocity could have been quite high. Also the measured sinking velocities of marine dinoflagellate cysts have been observed to be higher than the values calculated by Stoke's law (Anderson et al. 1985b). However, it was difficult to estimate the actual sinking velocity of the cysts, based on the sedimentation measurements, due to the long sampling interval (12 d) during the peak sedimentation period at the end of May.

Dinoflagellate cysts were also observed in the sediment trap samples during late summer, although in much lower numbers. Sedimentation rates of cysts were high, particularly at the lower sediment traps, suggesting a resuspension of dinoflagellate cysts from the sediment surface. Occurrence of cysts even in the 10 m trap suggested that resuspension to the surface layer may be an essential part of the seeding and life strategy of *Peridinium hangoei*. The ability of dinoflagellate cysts to sink relatively fast, and to maintain their viability in the bottom sediments over long periods of time and under adverse conditions, provides many dinoflagellate species with the means of sustaining their local population in coastal areas and enables them to act as an inoculum for vegetative growth when favourable conditions are restored (Dale 1977, Seliger et al. 1979, Dale 1983, Anderson et al. 1985a). This is analogous to the survival strategy proposed for bloom-forming diatoms, and it is probably common for many bloom-forming phytoplankton species occurring in coastal environments (Smetacek 1985).

Despite the massive flux of dinoflagellate cysts at the end of May, sinking was not the major loss process for the *Peridinium hangoei* population. Even though sedimentation of dinoflagellate cysts formed a considerable part of the settled organic carbon during spring (Fig. 5), the total deposition of cysts, estimated as organic carbon, only accounted for 17% of the decline in *P. hangoei* biomass. No vegetative cells of *P. hangoei* were observed in the settled material. Since no preservatives were used inside the sediment traps, part of the settled biomass might have been decomposed by micro-organisms during deployment. However, decomposition inside the sediment traps was calculated to account for only 7% of the total dinoflagellate biomass during spring (Heiskanen and Kononen unpublished), which was probably a reasonable estimate due to the relatively low prevailing temperatures.

Losses due to meso- and microzooplankton grazing were estimated to be small. Most of the *Peridinium hangoei* cells were larger than 20 µm in diameter (>90%), thereby being unsuitable food items for protozoan grazers (e.g. Rassoulzadegan et al. 1988). Mesozooplankton biomass did not increase considerably before the end of May (Finnish Institute of Marine Research unpublished). Therefore, mesozooplankton grazing was probably not able to control the spring-bloom phytoplankton biomass, as also observed previously in the northern Baltic Sea (Kuparinen et al. 1984).

Both the cell numbers and sedimentation rate measurements were influenced by advective transport of phytoplankton and organic matter. Although the aspect ratio [10] and size of the sediment traps were appropriate to yield reasonable trapping efficiency (Hargrave and Burns 1979, Bloesch and Burns 1980, Gardner 1980), the changing current velocities of the study site (Laakkonen et al. 1981), as well as the variable characteristics of settling particles, were likely to cause biases in the vertical flux estimates (Butman 1986). Moreover, as sediment traps integrate over the collection period of several days and because they sample settling material from the different water masses passing over the study site, the effect of advection on the sedimentation rate measurements can be considerable. The decrease of salinity and the increase of surface water temperature in early May (Figs. 2, 3) indicated advection of surface water from the inner archipelago to the study site. Although surface water exchange might have carried phytoplankton to the study site, and thus increased the phytoplankton biomass, the vertical profile of chlorophyll *a* indicated an increase of biomass partly due to the accumulation of *Peridinium hangoei* in the stratified surface layer by vertical migration (Fig. 2). The common autotrophic spring bloom dinoflagellates of the Baltic Sea have been observed to perform daily vertical migrations presumably as a response to the changing light regime (Passow 1990). In this case, the response could have been due to sharp thermal stratification combined with surface layer light levels. During the rest of May, the effect of advective transport on the water column and sediment trap measurements was probably less critical. This was indicated by the gradual warming of the surface layer, until the development of thermal stratification was interrupted by upwelling at the beginning of June (Fig. 3).

While sinking and grazing losses accounted for only a moderate part of the decline of *Peridinium hangoei* biomass, it is likely that a considerable share of the vernal dinoflagellate biomass disintegrated in the water column and settled as unrecognizable detrital material. It has been suggested that unsuccessful completion of sexual reproduction by autumnal *Ceratium* spp. is the reason for mass mortality and breakdown of cells in the water column prior to deposition as slowly settling phytodetrital material in the southern Baltic Sea (Noji et al. 1986). Although the sexual reproduction of dinoflagellates was apparently successfully accomplished during the present study, the majority of the remaining population disintegrated in the water column, before settling as organic carbon-rich phytodetritus at the end of May.

The sharp stratification of the surface layer combined with the occurrence of the exceptionally large dinoflagellate biomass in early May superficially resembled conditions during red-tide dinoflagellate blooms in more saline waters. Little turbulence and thermal stratification, coinciding with fresh water run-off and high nutrient concentrations, are typical hydrographical features, common for many coastal environments where dinoflagellate blooms occur. It has been proposed that this kind of hydrographical regime selects for species with features similar to those of many red-tide dinoflagellates, i.e., two cell forms – motile cells and resting cysts (Margalef et al. 1979). The vernal dinoflagellate species, in the northern Baltic, have not been recorded to be toxic, but an analogy with the other features in Margalefs (1978) successional sequence exists. This may indicate that the morphological and ecological adaptations to decaying turbulence and high nutrient concentrations of dinoflagellates, as described by Margalef (1978), are also valid for the spring bloom dinoflagellates in the northern Baltic Sea.

The evidence obtained from the present study shows that resting stages of the most dominant vernal dinoflagellate species form a considerable part of settled organic matter during spring, although only a relatively small part of the total dinoflagellate biomass settle as resting cysts. Sedimentation of organic matter after the spring bloom is the major annual input of organic matter to the benthic ecosystem in the northern Baltic Sea (Kuparinen et al. 1984). The life-cycle strategies of the vernal dinoflagellates – encystment and sinking of cysts – are thus crucial for the sedimentation of the spring bloom.

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