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Aggregation of *Phaeocystis* during phytoplankton spring blooms in the southern North Sea

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ABSTRACT: The role of aggregation during the decline of 2 phytoplankton spring blooms dominated by the Prymnesiophycean *Phaeocystis* sp. was studied in the southern North Sea in 1989 and 1991. While marine snow aggregates were devoid of *Phaeocystis* in 1989, a large fraction of the *Phaeocystis* biomass was associated with aggregates 2 yr later. This discrepancy corresponds to a significant difference in aggregate size between the 2 years studied, which is interpreted to be a consequence of different levels of turbulent mixing. *Phaeocystis* colonies remained freely suspended during 1989 when aggregates were small, and adhered loosely to the large aggregates observed forming during 1991. Overall, the aggregation potential of *Phaeocystis* was low in comparison to diatoms. Independent of the degree of aggregation, sedimentation was the dominant loss factor of *Phaeocystis* biomass from the upper layer. The significance of a low aggregation potential for the role of *Phaeocystis* in massive foam formation along the North Sea coast is discussed.

INTRODUCTION

Massive blooms of the colony-forming Prymnesiophycean *Phaeocystis* are a recurrent phenomenon in the coastal zones of the North Sea (Lancelot et al. 1987) and have been repeatedly reported from several other locations, including the Barents Sea (Wassmann et al. 1990), the Greenland Sea (Baumann 1990, Smith et al. 1991), the Norwegian fjords (Eilertsen et al. 1981), the Weddell Sea (Buck & Garrison 1983), the Bransfield Strait (Bodungen et al. 1986) and the Ross Sea (El-Sayed et al. 1983, SooHoo et al. 1987). Despite the widespread occurrence of intense blooms of *Phaeocystis* and their potential importance for carbon cycling in the ocean, the fate of the biomass accumulated during such blooms is still unresolved (see review by Wassmann in press).

Considerable controversy exists over the role of grazing as a loss factor during the decline of *Phaeocystis* blooms. Whereas an inhibitory effect of *Phaeocystis* colonies on zooplankton predation has been suggested by several authors (e.g. Schnack et al. 1985, Verity & Smayda 1989), others have reported predation of both colonial and single-celled *Phaeocystis* by copepods and microzooplankton (e.g. Tande & Båmstedt 1987, Weisse & Scheffel-Möser 1990). While the rapid decline of *Phaeocystis* blooms was attributed to herbivorous grazing by Tande & Båmstedt (1987) and Lutter et al. (1989), Hansen & van Boekel (1991) estimated the loss due to grazing during a *Phaeocystis* bloom in the Marsdiep (The Netherlands) to be less than 1% of the phytoplankton standing stock per day.

Disintegration of *Phaeocystis* colonies and the release of small flagellated cells from the colonies during the decline of a bloom were observed by Veldhuis et al. (1986). Cell lysis after nutrient depletion was suggested to be the dominant loss factor during a *Phaeocystis* bloom in the Marsdiep (van Boekel et al. 1992). On the other hand, mass sedimentation following a *Phaeocystis* bloom in the Barents Sea was observed by Wassmann et al. (1990), who attributed the enhanced vertical flux at the end of the bloom to the formation of fast-sinking marine snow aggregates. Colonisation of senescent *Phaeocystis* colonies by phytoplankton and microheterotrophs and aggregation with detrital material was also reported by Rousseau et al. (in press). Despite this type of circumstantial evidence for aggregation of *Phaeocystis* colonies, there is as yet no direct evidence of the aggregation potential of this species. The objec-

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tive of this investigation was to characterize the aggregation behaviour of *Phaeocystis* in situ during the decline of 2 *Phaeocystis* blooms.

MATERIAL AND METHODS

Study locations and sampling procedures. Investigations were conducted in the German Bight, North Sea (Fig. 1), during 2 blooms of *Phaeocystis* cf. *globosa* in May 1989 and May 1991. In 1989, 4 stations along a W-E transect east of Helgoland Island were sampled on May 17 (Stn 1, 22 m water depth (wd); Stn 3, 14 m wd) and May 19 (Stn 2, 19 m wd; Stn 4, 11 m wd). In 1991, 3 stations in close proximity to Helgoland Island (Stn I to III, 16 m wd) were sampled on May 8 and 10.

At each station, seawater was collected in 10 l Niskin bottles at 4 depths to determine chlorophyll *a* and phytoplankton cell concentration and composition. Temperature and salinity profiles were taken with a WTW LF 191 conductivity meter. Aggregate size and abundance were determined from 36 exposures randomly taken at various depths throughout the water column with a NIKONOS-V underwater camera system (described in Riebesell 1991a). At the same depths, SCUBA divers hand-collected 10 to 20 individual aggregates, each in 1 ml polypropylene syringes (method described in Riebesell 1991b). At each depth, aggregate-free water surrounding the aggregates was sampled in 50 ml syringes.

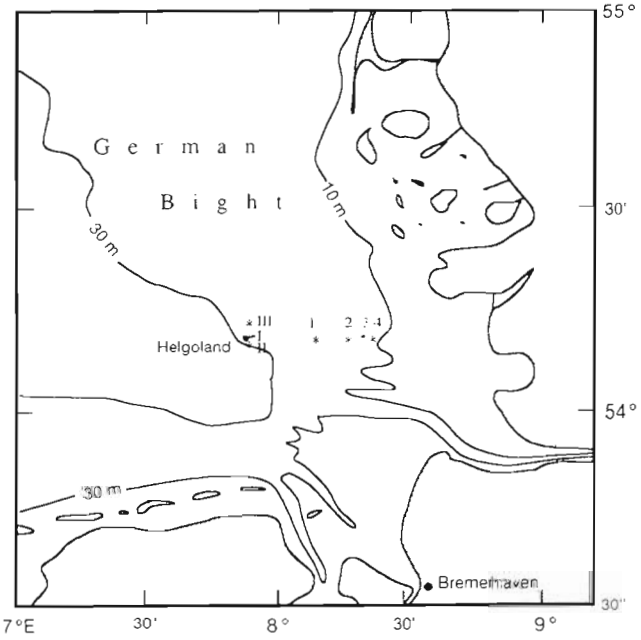

Fig. 1. Location of sites sampled in 1989 (Stns 1 to 4) and 1991 (Stns I to III)

Phytoplankton cell concentration and composition in the surface water were monitored over the course of the spring blooms at a station 2.5 nautical miles west of Helgoland Island in 1989 (data taken from Riebesell 1991b), and at the Helgoland Roads Station in 1991. The latter is monitored daily by the staff of the Biologische Anstalt Helgoland (Radach et al. 1990) and its location corresponds to Stn I of this study.

Laboratory analyses. For the determination of chlorophyll *a*, 500 ml of sample water were filtered onto 25 mm Whatman GF/C glass fiber filters. After extraction in 90% acetone (filters were homogenized with glass beads), the chlorophyll *a* concentration was measured using standard fluorometric methods (Parsons et al. 1984).

Phytoplankton cell number and composition, as well as fecal pellet abundance, were determined microscopically for individual aggregates, the aggregate-free surrounding water, and the bulk water samples collected with Niskin bottles. From each station and depth, 50 ml of bulk and surrounding water and 3 to 6 individual aggregates preserved with formalin (2% final concentration) were analysed microscopically for phytoplankton composition and concentration and fecal pellet abundance. A minimum of 200 cells of the dominant species were counted in bulk and surrounding water samples. For *Phaeocystis* colonies with more than 100 to 200 cells, known fractions of the colonies were enumerated and extrapolated to yield cell numbers of the entire colonies. In aggregates, all phytoplankton cells and fecal pellets were counted.

To account for differences in cell volume between species, phytoplankton numbers were normalized by converting to cell carbon (Strathmann 1967). Mean cell volumes used for calculating cell carbon were determined by measuring the size of 30 to 40 cells of each identified species. Rare and unidentified species were grouped in several size classes and their carbon content calculated from average cell volumes assigned to each size class. A value of 13.5 pg C cell^{-1} was used for *Phaeocystis* (Rousseau et al. 1990). Since phytoplankton cell carbon in this study serves merely as a measure for cellular biomass, extra-cellular organic compounds such as the mucus matrix of *Phaeocystis* colonies were not included.

The phytoplankton cellular carbon content associated with aggregates (C_{agg}) was calculated according to the equation

$$C_{agg} = C_{bulk} - C_{sw} \quad (1)$$

where C_{bulk} is the cellular carbon content of the bulk water samples (including aggregates); C_{sw} is the cellular carbon content of the aggregate-free surrounding water. The amount of *Phaeocystis* cell carbon associated with aggregates (C_{Phae}) was estimated from

the total amount of aggregated cell carbon (C_{agg}) according to

$$C_{Phae} = C_{agg} \times \%C_{Phae} \quad (2)$$

where $\%C_{Phae}$ is the mean contribution of *Phaeocystis* sp., determined from 3 to 6 aggregates per station and depth, to the algal cell carbon content of these aggregates. The standard deviation of $\%C_{Phae}$ ranged between 12.3 and 47.8 % of its mean.

Since large aggregates may not have been representatively collected in the 250 ml bulk water samples analysed for phytoplankton cell concentration, C_{bulk} may underestimate the total carbon content in the bulk water. Accordingly, C_{agg} and C_{Phae} may represent underestimates.

RESULTS

In 1989, *Phaeocystis* cf. *globosa* contributed significantly to the phytoplankton biomass during the spring bloom in the German Bight, while in 1991 it represented the dominant phytoplankton species (Fig. 2). At the start of the field work in both years, phytoplankton biomass had already settled out of the upper water column and accumulated in the bottom layer (see chl *a* profiles in Figs. 3A & 4A). Extremely high biomass concentrations of *Phaeocystis* were found in the bottom layer at Stn 3 in 1989 and at all stations sampled in 1991 (Figs. 3B & 4B).

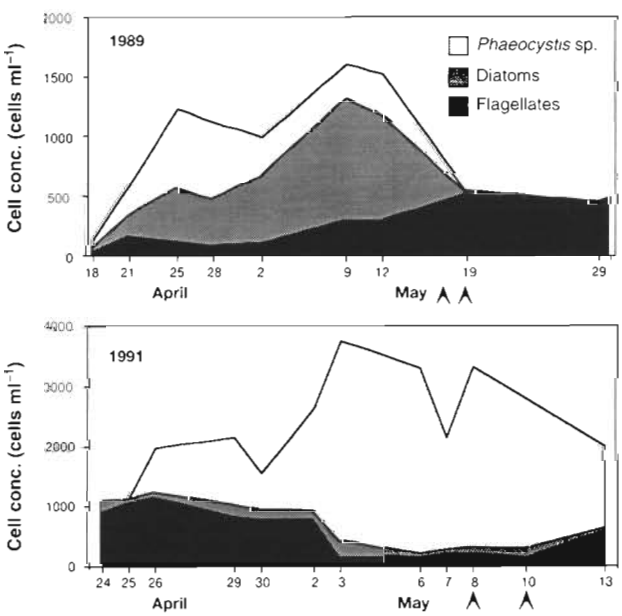

Fig. 2. Phytoplankton cell concentrations of 3 algal groups in the surface water during the spring blooms in 1989 and 1991 Arrows indicate dates of aggregate sampling

Maximum concentrations of *Phaeocystis* biomass in the surface layer measured prior to the investigation in 1991 were around 35 mg C m^{-3} (May 3 to 8). Assuming an even distribution throughout the 16 m water column results in a total *Phaeocystis* biomass of 560 mg C m^{-2}. This is in the same range as the biomass which accumulated in the bottom 2 to 3 m of the water column at the 3 stations (Fig. 4B), indicating that the loss of *Phaeocystis* biomass from the upper layers due to grazing and cell lysis was of minor importance.

At the end of both blooms, marine snow aggregates were present throughout the water column. Considerable differences between the 2 years were observed with respect to aggregate size and distribution with depth. In 1989, median aggregate sizes ranged between 0.2 and 1.0 cm in longest dimension, decreasing steadily with depth (Fig. 3C). In 1991, median sizes varied between 0.4 and 4.9 cm, with smallest sizes being recorded close to the surface and in the bottom layer (Fig. 4C).

The degree of aggregation of *Phaeocystis* biomass differed significantly between the 2 years investigated. In 1989, while being among the dominating phytoplankton throughout the water column and contributing up to 80 % to the total phytoplankton cell carbon, the relative contribution of *Phaeocystis* sp. in aggregates was < 2 % at all depths and stations (Fig. 3B). In 1991, on the other hand, *Phaeocystis* dominated both the total and aggregated phytoplankton biomass, contributing > 60 % to the cell carbon content in aggregates at all depths and stations (Fig. 4B). While in the bottom layer the relative contribution of *Phaeocystis* cell carbon was similar in the surrounding water and in aggregates, *Phaeocystis* was enriched in aggregates by a factor of 2 to 3 with respect to the surrounding water at 5 m water depth, the layer of maximum aggregate size. The enrichment tended to be positively correlated with aggregate size, i.e. the larger the aggregates, the greater the enrichment of *Phaeocystis* biomass relative to the surrounding water.

A difference in *Phaeocystis* aggregation between the 2 years is also apparent when comparing aggregated and freely-suspended biomass as calculated from Eqs. 1 & 2 (Fig. 5). Only a minor fraction of *Phaeocystis* cell carbon was incorporated in aggregates in 1989, with no significant differences being found between the surface and bottom layer. In 1991, however, over half of the *Phaeocystis* cell carbon was associated with aggregates at 5 and 10 m depth, while in the bottom layer only a small fraction of the *Phaeocystis* biomass was concentrated in aggregates. These data are also supported by visual observations made during SCUBA dives. In the upper layer, characterized by an abundance of large aggregates, colonies of *Phaeocystis* were seen attached to aggregates (Fig. 6). On the other

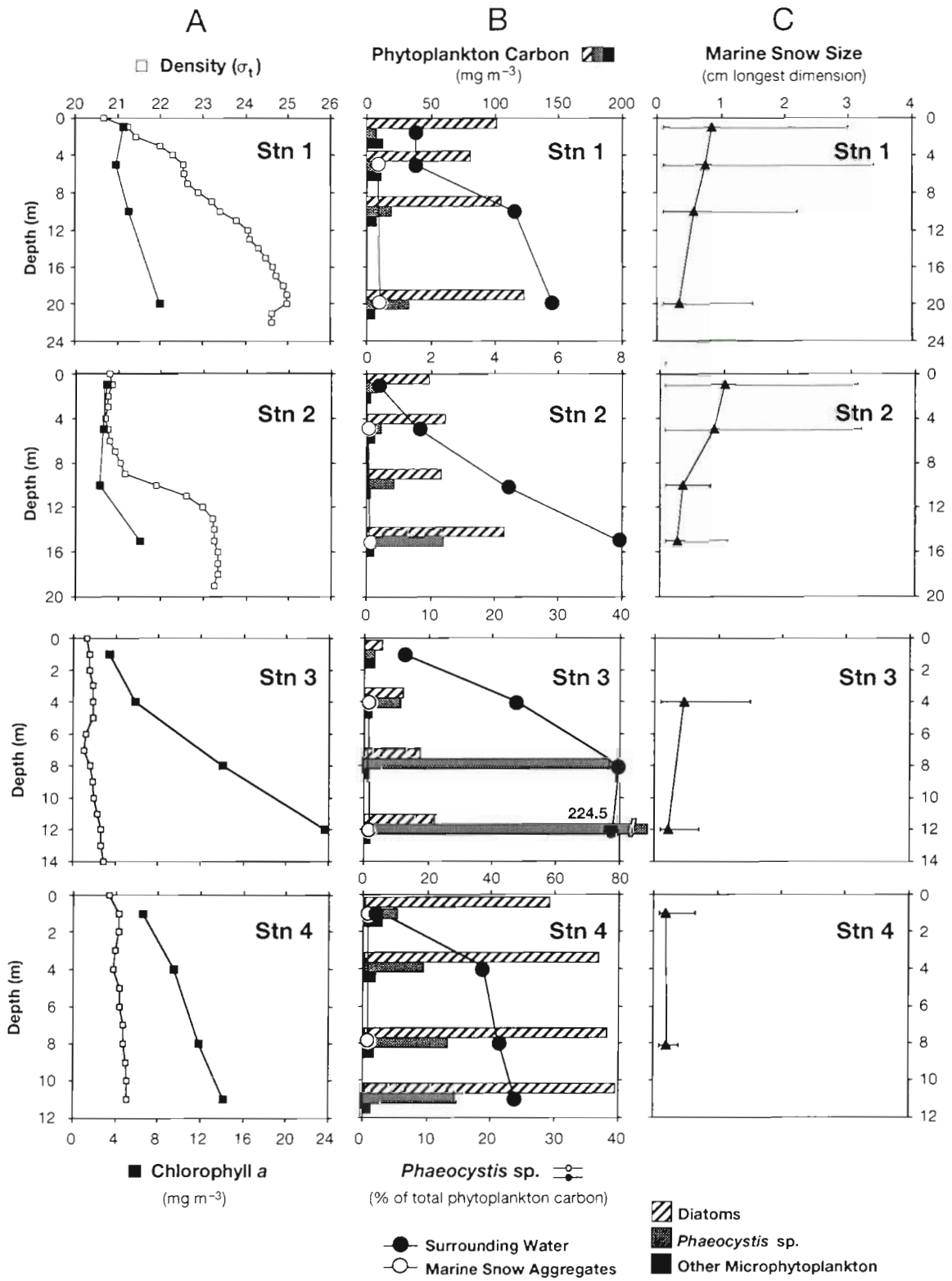

Fig. 3. Data for Stns 1 to 4 (May 17 and 19, 1989): (A) depth profiles of seawater density and chlorophyll *a*; (B) phytoplankton carbon concentrations of 3 groups (bars) and *Phaeocystis* biomass in the surrounding water (●) and in aggregates (○) as percent of total phytoplankton biomass; (C) marine snow size (▲: median values; horizontal bars: size ranges). Note differences in lower scales in (B)

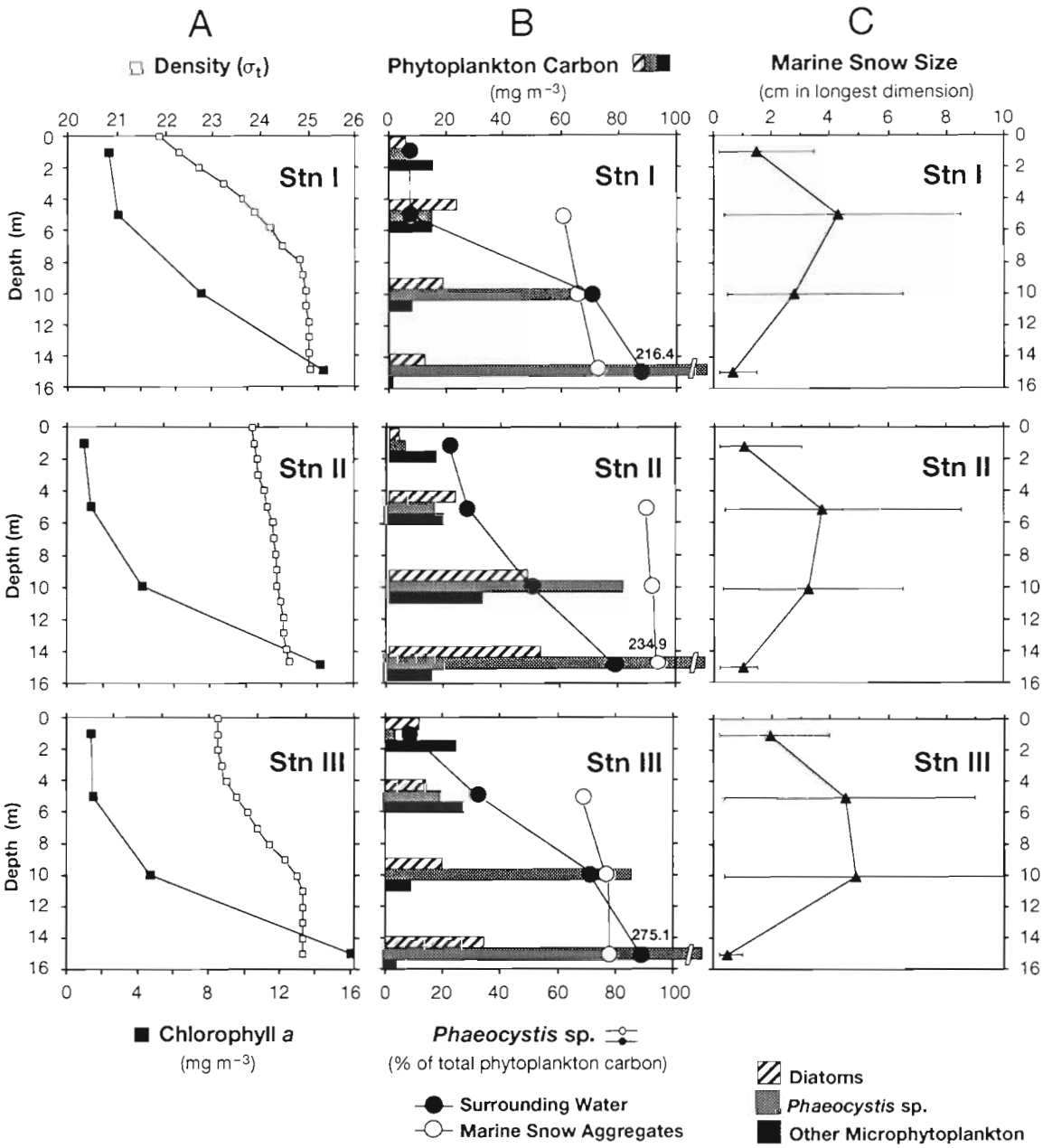

Fig. 4. Data for Stns I to III (May 8 and 10, 1991) plotted as in Fig. 3

hand, most of the *Phaeocystis* material that had settled to the bottom layer was in the form of individual, freely-suspended colonies.

In situ observation and microscopic examination revealed that colonies of *Phaeocystis* associated with aggregates were generally attached to the outside of the aggregate rather than being incorporated in the matrix. The aggregate matrix consisted mainly of densely-packed diatoms and detritus. No correlation was found between colony size and shape and the degree of aggregation. Both spherical and elongated (presumedly senescent) colonies were observed in free suspension and attached to aggregates. No detectable change with depth was found in the ratio of spherical to elongated colonies.

A comparison of the contribution of various algal groups to the phytoplankton cell carbon in aggregates with their relative contribution to the cell carbon in the surrounding water reveals differences in their aggregation potentials (Table 1). *Phaeocystis*, which largely remained unaggregated in 1989, contributed significantly to phytoplankton cell carbon in aggregates in

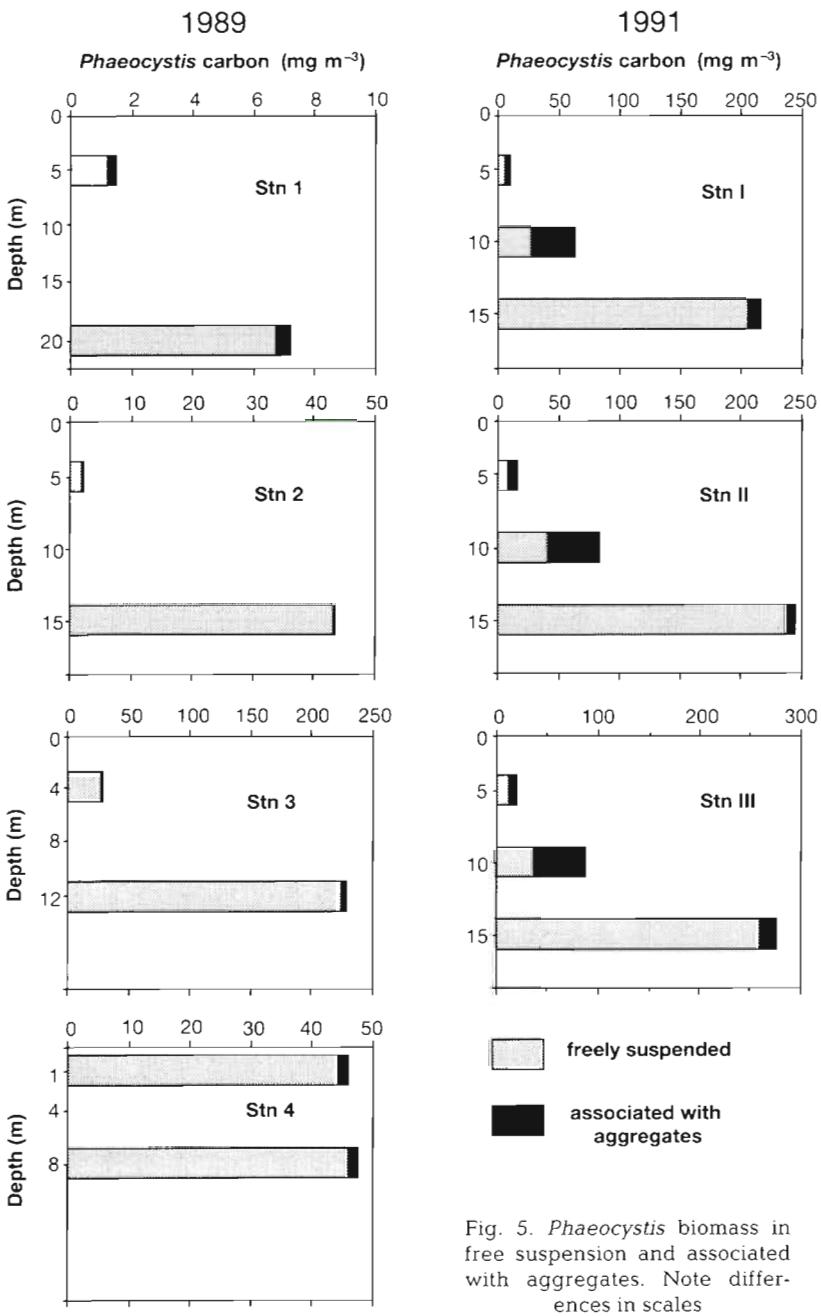

Fig. 5. *Phaeocystis* biomass in free suspension and associated with aggregates. Note differences in scales

1991. At this time *Phaeocystis* biomass was enriched in aggregates relative to the surrounding water by a factor of 1.5 to 2. In comparison, the diatoms *Chaetoceros socialis*, *Coscinodiscus* sp., *Asterionella glacialis*, and *Odontella sinensis* were highly enriched in aggregates, with enrichment factors ranging for the most part between 2 and 15, indicating a higher aggregation potential of these species relative to *Phaeocystis*. A low aggregation potential can be inferred for dinoflagellates whose relative contribution, with the exception of the heterotrophic dinoflagellate *Noctiluca miliaris*, was considerably higher in the surrounding water than in aggregates. *N. miliaris*, a species known to produce mucous nets when feeding by so-called 'mucoid-filtration' (Uhlig 1982), was found exclusively in association with aggregates. Similarly, fecal pellets were always abundant in aggregates but were not found freely suspended in the surrounding water.

DISCUSSION

The data provide seemingly contradictory evidence with regard to the aggregation behaviour of *Phaeocystis* during the decline of blooms. The scenario emerging from the 1989 investigation reveals marine snow aggregates which are nearly devoid of *Phaeocystis* cells and most of the *Phaeocystis* biomass being in the form of freely suspended colonies. In 1991, on the other hand, more than half of the *Phaeocystis* biomass in the upper water column was associated with aggregates, generally in the form of large colonies being attached to aggregates.

Considering that *Phaeocystis* colonies in aggregates were generally only loosely attached to the aggregate matrix, a possible explanation for the apparent discrepancy is suggested by the difference in aggregate size between the 2 blooms. During an 18 mo investigation in 1989/1990 in the same area, Riebesell (1992) found a correlation between aggregate size and wind-induced turbulent mixing of the water column. Based on this correlation, the observed difference in aggregate size between 1989 and 1991 can be related to a difference in the level of turbulence between the 2 years. Thus, while attachment of large particles such as *Phaeocystis* colonies to the comparatively small aggregates (generally <1 cm) forming during the decline of the 1989 bloom may have been prevented by turbulent shear, conditions during the 1991 bloom were sufficiently calm to allow formation of large (up to 10 cm) aggregates and attachment of *Phaeocystis* colonies to them.

Variability in both aggregate size and the proportion of *Phaeocystis* biomass in aggregates with depth as observed during the 1991 investigation (Figs. 4 & 5) may

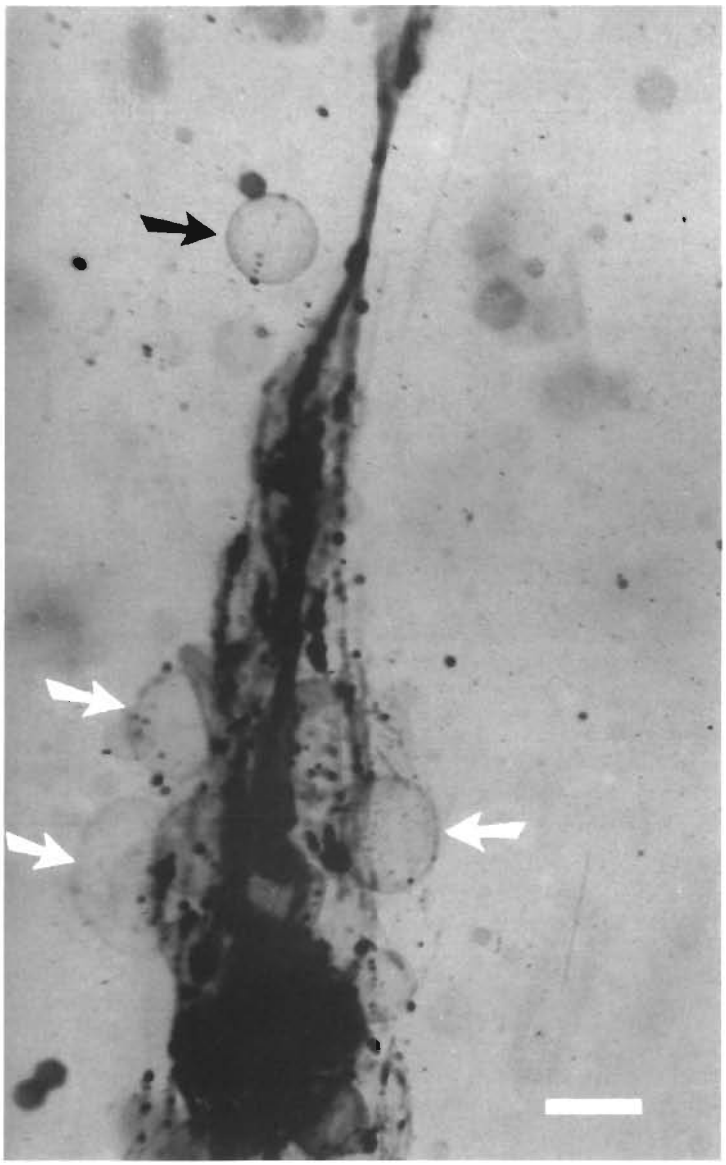

Fig. 6. In situ photograph of a marine snow aggregate with colonies of *Phaeocystis* attached to it (white arrows) and freely-suspended (black arrow); Stn III, 5 m water depth. Scale bar = 5 mm. *Phaeocystis*-rich aggregates of this kind were abundant in the upper layer during the 1991 bloom

be related to differences in the level of turbulent shear between different layers in the water column. While wind-induced mixing could account for small aggregate sizes close to the surface, tidal current-related turbulent shear decreased aggregate size and the proportion of aggregated *Phaeocystis* biomass in the bottom layer. Tidal currents may also be responsible for keeping *Phaeocystis* in suspension in the bottom layer, as observed at Stn 3 in 1989 and at all stations sampled in 1991.

Although intact colonies became attached to marine snow aggregates under low shear conditions, *Phaeocystis* appeared to be of little significance for initiating aggregate formation. This is in contrast to the diatom species present during the time of investigation, which were generally incorporated within the aggregate matrix and were significantly enriched in aggregates in comparison to the surrounding water (Table 1). While diatoms were found to be a predominant component of marine snow in many studies (see Alldredge & Silver 1988), incorporation of colonial *Phaeocystis* in marine snow aggregates was observed only for *Phaeocystis* released from Antarctic sea ice during spring melting (Riebesell et al. 1991). However, unlike pelagic microalgae which remain freely suspended by exhibiting low values of cell stickiness during favourable growth (Kiørboe et al. 1990), many ice algae produce extensive extracellular polysaccharide mucilages which permit attachment to the ice substrate (McConville 1985). Differences in stickiness between pelagic and ice-inhabiting *Phaeocystis* may be species- and/or habitat-related.

Large marine snow flocs such as the *Phaeocystis*-rich aggregates formed during the 1991 bloom have been observed to be slowly sinking, neutrally buyoant, or rising, resulting in their prolonged residence in the surface layer (Riebesell 1992). Thus, colony aggregation does not necessarily imply rapid sedimentation of *Phaeocystis* biomass. On the other hand, sinking rates of *Phaeocystis* colonies are sufficiently high (around 7 m d^{-1}; van Boekel et al. 1992) to permit sedimentation without invoking aggregation. In fact, independent of whether colonies became attached to aggregates or remained freely suspended, sedimentation was the dominant loss factor of *Phaeocystis* biomass from the surface layer during this study. Roughly the same amount of biomass which accumulated in the water column during the build-up of the *Phaeocystis* bloom was concentrated in the bottom layer after its sedimentation (see above). Hence, loss of *Phaeocystis* biomass in the upper mixed layer due to grazing or cell lysis was insignificant.

A high aggregation potential of colonial *Phaeocystis* due to increasing surface stickiness of senescent colonies during the decline of the bloom, as suggested by Wassmann et al. (1990), was not observed during this study. Aging of nutrient-limited *Phaeocystis globosa* colonies in laboratory experiments with pure cultures resulted in disintegration rather than aggregation of the colonies (Riebesell & Griebe

Table 1. Contribution of selected species/groups to the phytoplankton cell carbon in water samples free of aggregates (SW: surrounding water) and in aggregates as percent of total. Data represent mean values of samples collected throughout the water column; n = numbers of samples

Group/ Species	Stn 1		Stn 2		Stn 3		Stn 4		Stn I		Stn II		Stn III	
	SW	Aggr.	SW	Aggr.	SW	Aggr.	SW	Aggr.	SW	Aggr.	SW	Aggr.	SW	Aggr.
n	4	5	4	7	4	5	4	6	4	6	4	6	4	9
Phaeocystis sp.	13.6	10.5	1.8	0.4	45.5	1.0	2.0	0.4	32.6	64.5	39.1	79.8	47.6	75.3
Chaetoceros socialis	0	0.6	0	3.6	0	5.0	0	1.3	0.9	4.6	0.6	7.6	0.1	7.1
Coscinodiscus sp.	5.8	8.6	6.2	9.1	8.5	12.8	4.3	15.0	0	0.9	0	0.9	0	0.5
Asterionella glacialis	1.0	2.7	1.4	5.7	0.5	7.8	1.1	5.0	NP		NP		NP	
Odontella sinensis	1.5	10.7	1.3	16.8	2.5	19.0	1.8	5.6	NP		NP		NP	
Dinoflagellates	2.8	0.2	5.0	0.1	0.7	3.1	10.5	0.1	29.5	0.5	34.1	0.7	21.9	0.8
Noctiluca miliaris[a]	0	0.8	0	3.5	0	1.2	0	2.0	0	0.6	0	1.5	0	6.0
Fecal pellets[a]	0	95.5	0	102.3	0	65.8	0	315.8	0	3.0	0	7.5	0	2.5

[a]Average number per aggregate
NP: species not present

unpubl.). Colony disintegration and cell-lysis were found to be the main loss factor during the decline of a *Phaeocystis* bloom in the Marsdiep area of the North Sea with sedimentation of *Phaeocystis* being insignificant (van Boekel et al. 1992). As this is an area characterized by high current velocities, sedimenting material is subjected to continuous resuspension resulting in little net sedimentation (Jenness & Duineveld 1985). Thus, with resuspension having prevented sedimentation of *Phaeocystis* during the bloom decline, *Phaeocystis* colonies suspended in a nutrient-depleted water column may experience rapid disintegration.

As was observed during this study, disintegration can be retarded when the colonies settle into a nutrient-replete bottom layer, where on account of the shallow depth, phytoplankton experience sufficient light to continue slow growth. In deeper water, on the other hand, disintegration may become significant for colonies which have settled out of the euphotic zone. A rapid decrease in the vertical flux of *Phaeocystis* biomass below the euphotic zone was in fact observed by Lutter et al. (1989) and Wassmann et al. (1990), suggesting that colony disintegration, among other loss factors, may prevent deep flux of *Phaeocystis* biomass.

Prolonged suspension in the bottom layer of shallow coastal waters such as those of the southern North Sea would enhance the probability of *Phaeocystis* biomass becoming transported to shore, where it may cause the formation of large amounts of foam on the beaches. This has been observed along the North Sea coast after intense *Phaeocystis* blooms (Lancelot et al. 1987). Differences in aggregation between *Phaeocystis* and diatoms, as discussed above, could reinforce the role of *Phaeocystis* in foam formation. While diatoms tend to be firmly entangled in aggregates and therefore are likely to become incorporated in the sediment after settling to the bottom, loosely attached colonies of *Phaeocystis* can easily be detached from settling aggregates when subjected to tidal current-induced shear in the bottom layer. This difference in aggregation behaviour may be one of the reasons why foam formation is correlated to blooms of *Phaeocystis* rather than of diatoms.

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