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Significance of sedimentation for the termination of *Phaeocystis* blooms

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Abstract

The role of sedimentation for the termination of *Phaeocystis* blooms is exemplified through case studies from the literature as well as from anecdotal evidence. Scenarios of high and low sedimentation following *Phaeocystis* blooms exist. Mass sedimentation was found in the Barents Sea and the Ross Sea, but vertical flux below the euphotic zone was insignificant in a north Norwegian fjord and the Weddell Sea. In general, no regular and recurring pattern of sedimentation events can be expected during *Phaeocystis* blooms. Factors influencing the fate of senescent *Phaeocystis* blooms are probably water depth, turbulent energy supply, aggregate formation, release of flagellated cells from colonies, microbial degradation, zooplankton grazing as well as lysis of colonies and cells. The role sedimentation plays for the termination of *Phaeocystis* blooms seems to be determined by the physical and biological characteristics of the specific ecosystem where the bloom occurs. In general, *Phaeocystis*-dominated ecosystems tend to endorse pelagic rather than benthic mineralization.

1. Introduction

Phaeocystis blooms are reported from a wide variety of ecosystems. Situations characterized by (a) high nutrient concentrations and high mixing such as the southern North Sea, (b) weak stratification and mesotrophy such as in the southern Barents Sea and north-Norwegian fjords, (c) strong stratification and high nutrient concentrations such as in marginal ice zones, (d) significant and insignificant grazing such as the Weddell Sea and a variety of coastal environments, all support extensive blooms of *Phaeocystis* colonies. Algal blooms are situations inherently out of balance, where algal growth exceeds the ability of heterotrophic processes to control it. Given the significance of widespread *Phaeocystis* blooms in

polar, sub-polar and temperate waters for global primary production, factors determining the fate of massive accumulation of suspended biomass during these blooms are important for understanding the ecology of this genus as well as the carbon and biogeochemical element cycles of ecosystems dominated by it. Disappearance of *Phaeocystis*, as for any other phytoplankton bloom, are caused by grazing, autolysis, microbial degradation and sedimentation. The first three of these factors are evaluated by Thingstad and Billen (1994) and Weisse et al. (1994) in the present volume. Here the role of sedimentation for the termination of *Phaeocystis* blooms will be analyzed.

Several points of evidence indicate that *Phaeocystis* appears to be an exemplary organism for

the maintenance of nutrient and biomass regeneration of retention food chains controlled by flagellates and the microbial loop: (a) phase alternations between small, single, flagellated cells and large, non-flagellated, gelatinous colonies and vice versa (Rousseau et al., 1994), (b) the production of extensive amounts of mucus and dissolved organic carbon (DOC) (Lancelot, 1983; Billen and Fontigny, 1987), (c) the substantial microbial activity on decaying colonies fragments (Thingstad and Martinussen, 1991), (d) reports on positive buoyancy (Skreslett, 1988) and (e) the frequent lack of substantial amounts of *Phaeocystis*-derived material in sediment traps exposed at depth. However, recent observations in the Barents Sea revealed that events of massive sedimentation of *Phaeocystis* can take place at the end of the spring bloom with sedimentation rates $> 800 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Wassmann et al., 1990), suggesting substantial export of organic matter from the upper layers. *Phaeocystis* may thus behave in a manner comparable to the vernal vertical flux of diatoms in boreal and polar environments (Smetacek, 1985; Bodungen et al., 1986; Sancetta and Calvert, 1988; Passow, 1991; Wassmann, 1991). How can these contradictions with regard to sedimentation of *Phaeocystis* be explained? Is the ecological variability of *Phaeocystis* blooms (related to the complex life cycle of this prymnesiophyte; see Rousseau et al., 1994) sufficient to explain both high vertical loss rates as well as regeneration in the upper layers? Or do these contradictions reflect the behavior of different *Phaeocystis* species?

Evidence of *Phaeocystis* sinking or non-sinking is given through various case studies. Factors triggering sinking or retention of *Phaeocystis* blooms in surface waters and the fate of its material during sedimentation are investigated. The lack of data sets to address the role of sedimentation for the termination of *Phaeocystis* blooms adequately gives rise to lines of thought which are often closer to speculation than evidence. While this weakness is regretfully acknowledged, this contribution tries to present a careful evaluation of the present state of our knowledge and pave the way to future more in-depth investigations of the vertical flux dynamics of *Phaeocystis*.

2. Sedimentation of *Phaeocystis*: case studies

2.1. Barents Sea

Mass sedimentation of *Phaeocystis* was recorded from the Barents Sea in May/June 1987 (Wassmann et al., 1990). *Phaeocystis* is prominent in the marginal ice-edge zone as well as the open Barents Sea where it blooms following a diatom bloom in late spring or in concert with diatoms (Rey and Loeng, 1985; Skjoldal and Rey, 1989). However, at individual stations and during some years *Phaeocystis* colonies may dominate the entire spring bloom in the Barents Sea (F. Rey, pers. commun.; Wassmann et al., 1990). In 1987 station I was situated in an area dominated by Atlantic water with little stratification. Station II was in the vicinity of the Polar Front which separates Arctic from Atlantic water. Stratification in the upper layer at station II was significant due to the vicinity of meltwater from the marginal ice-zone. Mass sedimentation of the colonial forms of a dense *Phaeocystis* bloom (up to 20 g POC m^{-2} and $370 \text{ mg chlorophyll } a \text{ m}^{-2}$ in the upper 50 m) was recorded at station I, with average sedimentation rates ranging between 580 and $840 \text{ mg POC m}^{-2} \text{ d}^{-1}$ during a two weeks period (Fig. 1). *Phaeocystis* accumulated at the bottom of the cylindrical traps as a light green, slimy and up to 4–6 cm thick mass. The slimy character of the material resulted in great difficulties during filtration and, as a result of an unreported loss of mucus and DOC through GF/C filters, the calculated sedimentation rates are unquestionably underestimates of the vertical carbon flux. The situation at station II was different. Suspended biomass in the upper 50 m varied between $8\text{--}13 \text{ g POC m}^{-2}$ and $90\text{--}170 \text{ mg chlorophyll } a \text{ m}^{-2}$. Sedimentation rates below the euphotic zone were lower ($50\text{--}90 \text{ mg POC m}^{-2} \text{ d}^{-1}$; Fig. 1) and comparable to previous sedimentation rates in late spring/early summer (Wassmann, 1989). Colonies of *Phaeocystis* were also here dominating the vertical flux. While station I exemplifies a *Phaeocystis* bloom at its maximum, station II probably experienced a massive bloom earlier. The biochemical composition of the sedimented matter indicated a *Phaeocystis*

bloom in its senescence (Wassmann et al., 1990).

Sedimentation of *Phaeocystis* blooms is probably an annual event in the Barents Sea. Data from May/June 1984 indicate that, in addition to the vertical flux of diatoms, loss rates of *Phaeocystis* from the euphotic zone in the Barents Sea during post-bloom situations were significant (Table 1). Diatoms and *Phaeocystis* dominated the vernal bloom of 1984 together. On average, 59% of the sedimented phytoplankton cells consisted of *Phaeocystis*, 31% of diatoms, mainly *Chaetoceros socialis* (Table 1). Daily loss rates from the euphotic zone ranging from 4 to 33% of the suspended *Phaeocystis* colony cells were recorded (daily average 6.6%). The daily loss rates of sus-

Table 1

Sedimentation of phytoplankton and coefficient of variation (% of mean) at different stations during May and June 1984 in the Barents Sea ($\text{cells m}^{-2} \text{d}^{-1}$). Also shown are the concentration of phytoplankton cells in the water column as well as daily loss rates. Data from P. Wassmann and F. Rey (unpubl. res.)

Phyto-plankton species	Station	Water column 0–40 m (cells m^{-2})	Sedimentation at 40 m ($\text{cells m}^{-2} \text{d}^{-1}$)	Daily loss (%)
<i>Phaeocystis pouchetii</i>				
	644	$7.40 \cdot 10^8$	$2.86 \cdot 10^7 \pm 86\%$	3.86
	650	$2.13 \cdot 10^{10}$	$7.08 \cdot 10^9 \pm 41\%$	33.22
	681	$8.22 \cdot 10^9$	$4.13 \cdot 10^8$ –	5.03
	692	$3.85 \cdot 10^{10}$	$2.67 \cdot 10^9 \pm 38\%$	6.92
<i>Chaetoceros socialis</i>				
	644	$2.75 \cdot 10^{11}$	$5.16 \cdot 10^9 \pm 15\%$	1.88
	650	$6.30 \cdot 10^{10}$	$8.35 \cdot 10^8 \pm 26\%$	1.33
	681	$7.91 \cdot 10^9$	$1.42 \cdot 10^9$ –	17.96
	692	$1.40 \cdot 10^{10}$	$7.09 \cdot 10^8 \pm 46\%$	5.08
<i>C. socialis</i> (resting spores)				
	644	$5.81 \cdot 10^{10}$	$3.56 \cdot 10^9 \pm 59\%$	6.14
	650	$4.70 \cdot 10^9$	$4.91 \cdot 10^7 \pm 18\%$	1.05
	681	$8.39 \cdot 10^7$	$2.36 \cdot 10^7$ –	28.16
	692	$5.31 \cdot 10^9$	$4.22 \cdot 10^8 \pm 33\%$	7.95
Flagellates and monads				
	644	$3.01 \cdot 10^{10}$	$5.50 \cdot 10^8 \pm 15\%$	1.83
	650	$3.75 \cdot 10^{10}$	$1.39 \cdot 10^9 \pm 46\%$	3.72
	681	$1.57 \cdot 10^{11}$	$2.66 \cdot 10^8$ –	0.17
	692	$4.41 \cdot 10^{10}$	$3.96 \cdot 10^8 \pm 49\%$	0.90

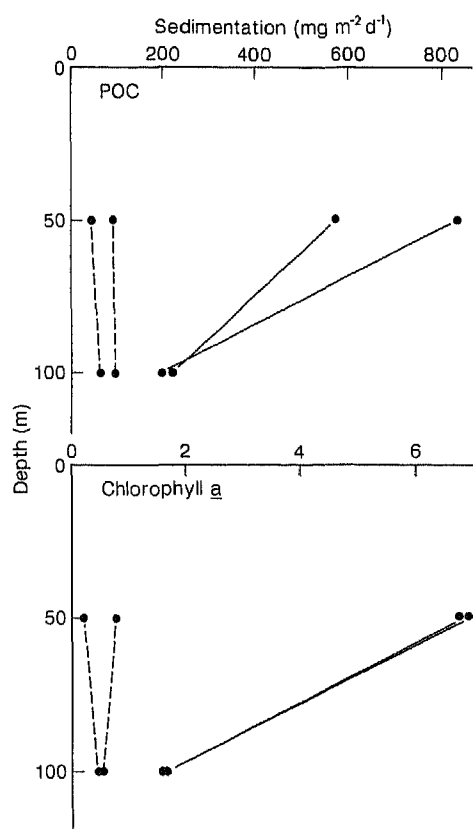


Fig. 1. Sedimentation rate of particulate organic carbon (POC) in the central Barents Sea during a *Phaeocystis* bloom (—) and a post bloom situation (---). Please observe the high sedimentation rates at 50 m and the strong decrease in sedimentation between 50 and 100 m depth during the bloom period (data from Wassmann et al., 1990).

pended *C. socialis* cells with and without resting spores ranged between 2 and 18 and 1 and 28%, respectively (daily average 6.6 and 10.8, respectively). *Phaeocystis* and diatoms can obviously exhibit similar loss and sinking rates and may execute analogous roles in the pelagic zone of some ecosystems.

Mass sedimentation in 1987 was rather a function of bloom magnitude than high sinking rates as the daily loss rates of POC from the bloom (average $3.5\% \text{d}^{-1}$) was not particularly high for vernal bloom periods in general (Wassmann, 1991) and as high as in May/June 1984. An obvious characteristic of the mass sedimentation event during May/June 1987 was the significant decrease in vertical flux between 50 and 100 m depth (Fig. 1). Given that these measurements are correct the question can be raised to what depth the vertical flux derived from a *Phaeocystis*

bloom penetrates into the aphotic zone, even during mass sedimentation episodes. Doubts might be raised whether large quantities of *Phaeocystis*-derived matter actually reaches the sediment surface of the Barents Sea.

Phaeocystis also blooms in other subarctic shelf seas, e.g. at the shelf break of the southern Bering Sea (Barnard et al., 1984), but is less dominant at this location compared to the Barents Sea.

2.2. The Greenland Sea

Blooms of *Phaeocystis* colonies are regularly observed in this area (Gradinger, 1986; Baumann, 1990; Smith et al., 1991). No data indicating sedimentation of *Phaeocystis* are as yet available from the Greenland Sea, but indirect evidence indicates that vertical flux of *Phaeocystis*-derived matter may be significant (Smith et al., 1991). During April and early May 1989 massive blooms of *Phaeocystis* were observed across the entire Greenland Sea (Smith, 1993). The new production during the 35 day long bloom period was approximately 40 g C m^{-2} and virtually no silicic acid was consumed, indicating that diatoms were during this period of time an insignificant part of the spring bloom.

The few direct measurements of vertical flux to deeper waters in the area indicate generally low rates with limited seasonal variation, but increased flux rates in May/June (Honjo, 1990; Bodungen et al., 1991; Hebbeln and Wefer, 1991). The specific prymnesiophycean pigment 19'-hexanoyloxyfucoxanthin (Buma et al., 1991) was present in sediment trap material (E. Bauerfeind, pers. commun.). This pigment probably derives from *Phaeocystis*, since other prymnesiophyte organisms, e.g. coccolithophorids, were rare. However, it is unclear if the presence of 19'-hexanoyloxyfucoxanthin originates directly from sinking colonies or indicates faecal pellets. Given the considerable quantity of new production during spring and early summer in the Greenland Sea (Smith, 1993), it is questionable if zooplankton grazing on *Phaeocystis* colonies could eventually be responsible for the termination of the bloom. Apparently other mechanisms, e.g. sedimentation

out of the euphotic zone, dissolution and residual degradation at intermediate depth play a role. The substantial pigment fluorescence recorded at depths (Cota et al., 1990; Smith, 1993), the similarity of phytoplankton dynamics in the marginal ice-zone of the Greenland Sea and Barents Sea (Wassmann et al., 1991), and the significance of mass sedimentation of *Phaeocystis* in the latter area, support the hypothesis that sedimentation of *Phaeocystis* may also be an important process for bloom termination in the Greenland Sea.

2.3. North-Norwegian fjords

Blooms of *Phaeocystis* play a dominating role for the carbon flux dynamics in the fjords and coastal environments of northern Norway. *Phaeocystis* blooms take usually place between mid April and late May and represent a prominent, recurrent phenomenon in the north-Norwegian coastal zone (Eilertsen et al., 1981). The composition of phytoplankton species dominating the vernal bloom in Balsfjord varies interannually with years dominated by diatoms, *Phaeocystis* or co-occurrence (H.C. Eilertsen, pers. commun.). Sedimentation data are available from the Balsfjord close to the city of Tromsø. During a study of the spring plankton dynamics in 1982 Lutter et al. (1989) found *Phaeocystis* in significant amounts in the upper water column and in traps at 10 m depth. However, *Phaeocystis* did not contribute considerably to the vertical flux from 50 m to the bottom of the fjord (Fig. 2). Blooms of *Phaeocystis* were also observed during extensive field studies in 1991 and 1992 in Balsfjord and the nearby Malangen fjord. *Phaeocystis* bloomed from mid April to the end of May (U. Riebesell, P. Wassmann and A. Keck, unpubl. res.). It was recognized that *Phaeocystis* was present in sediment traps at 20–40 m depth, but its contribution to the vertical flux decreased significantly between 40–60 m depth and was small from about 60 m depth and below.

Phaeocystis was never found in sediment traps deployed during spring 1983 in the Norwegian Coastal Current off the Lofoten Islands, although the algae were present in the water column in limited amounts (up to 25% of the cell numbers)

(Peinert, 1986a, b). Also in the Norwegian Sea *Phaeocystis* was never found in long-term sediment traps deployments (U. Bathmann and V. Smetacek, pers. commun.), but it is probably difficult to recognize the algae in its degraded form.

2.4. North Sea

Estimates of sedimentation based on direct measurements in the southern North Sea are not available. Annual, massive blooms of *Phaeocystis* colonies are observed mainly from mid April to mid May (Cadée and Hegeman, 1986; Lancelot, 1990; Reid et al., 1990), generally following a diatom spring bloom (e.g. Fernández et al., 1992). The lack of sedimentation measurements is

mainly due to the importance of resuspension in an environment where large areas are characterized by significant turbulent energy supply through tidal currents, making the use of sediment traps less meaningful. To be able to estimate the supply of *Phaeocystis* to the benthos, resuspension of already settled, *Phaeocystis*-derived material from the sediment surface must be quantified. This is a difficult task in general, but in particular due to the difficulty in quantifying “rebound” matter (Walsh et al., 1988; Floderus, 1991). It is, therefore, difficult to estimate the true vertical flux of *Phaeocystis*. Budget calculations (Fig. 3) indicate that about one third of the annual net primary production is provided to the sediment of the coastal zone of the southern North Sea. A substantial quantity of this supply presumably consists of *Phaeocystis* and its detritus. It could thus be speculated that *Phaeocystis* is an important part of the food supplied to the benthos and that sedimentation contributes to the termination of blooms.

Observations by divers revealed that dense layers of healthy, non-aggregated *Phaeocystis* colonies can accumulate in the turbulent, nepheloid layer in the central North Sea off Helgoland (Riebesell, 1993). Since *Phaeocystis* can compete at low light intensities (Eilertsen et al., 1981; Palmisano et al., 1986; Verity et al., 1991) and given the increased nutrient concentrations in bottom water, these favorable circumstances presumably postpone its senescence. One might presume, however, that these colonies finally enter the benthic food chain by settling to the sediment surface or by biodeposition. This is supported by observation of significant amounts of large, senescent looking colonies in sediment traps deployed in the nepheloid layer of the Oysterground, north of the Frisian front (S. Floderus, pers. commun.). That the residue of the bloom may fall to the bottom of the North Sea was already described in the 1930's when accumulations of *Phaeocystis* as well as diatoms were observed on the sediment surface off the Frisian islands (Reid, 1990). These accumulations can form surface mats on the sediment surface which reduce resuspension (Reid, 1988). Finally, these mats can get washed up onto beaches where they have been observed to pile

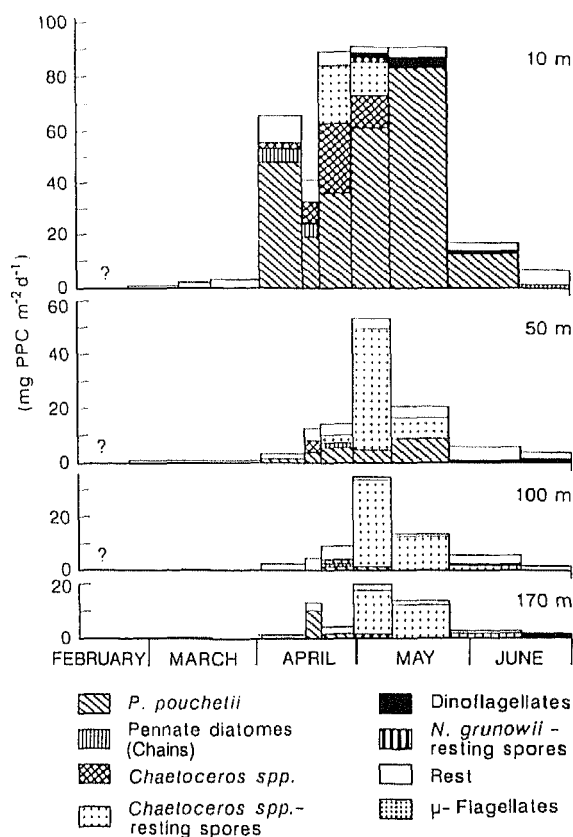


Fig. 2. Sedimentation of phytoplankton carbon (PPC) of dominating species in the subarctic Balsfjord, northern Norway (redrawn from Lutter et al., 1989).

up in large quantities in Liverpool Bay (P. Williams, pers. commun.).

The continuous resuspension of colonies due to tidal currents and annual variations in nutrients supplied by fresh-water determine the length of the bloom in the southern North Sea (Cadée, 1990). As a consequence, most of the organic matter of the rich *Phaeocystis* blooms in the southern North Sea is apparently broken down in the water column and only partly permanently removed from the water column. Biodeposition, known to govern the phytoplankton plankton dynamics of many shallow, coastal areas (Asmus and Asmus, 1991 and references therein) may play a role in this removal. Biodeposition of *Phaeocystis* colonies by *Mytilus* beds has been observed in inlets and marginal bays of the coastal zone of the southern North Sea (C. Heip, pers. commun.). Biodeposition by mussel beds may probably play a role for the dynamics of *Phaeocystis* blooms of the southern North Sea, however at selected sites only.

In conclusion, it is not clear if direct sedimentation of *Phaeocystis* colonies is of significance for the termination of blooms in the unstratified waters of the southern North Sea. The supply of

Phaeocystis-derived material to the sediment in this area (Fig. 3) could also partly be due to biodeposition. However, in the more tranquil waters off the Danish coast and along a fringe of stratified waters surrounding the central North Sea direct sedimentation may be of significance. The generally shallow character of the North Sea, the predominance of turbulent energy supply along its coastal zone and the noteworthy efficiency of *Phaeocystis* colonies to live at low light intensities creates a very different scenario for *Phaeocystis* blooms compared to deeper and less turbulent environments.

2.5. Bransfield Strait and Weddell Sea

Blooms of *Phaeocystis* colonies and their sedimentation were observed in the Bransfield Strait during ice-free conditions in November/December 1980 (Schnack et al., 1985; Bodungen et al., 1986) and the Weddell Sea during January/February 1985 (Nöthig, 1988). *Phaeocystis* co-occurred with diatoms such as *Thalassiosira antarctica*, *Coscinodiscus* spp. and *Corethron criophilum*. Both blooms developed in waters influenced by a receding ice-edge. This appears to be the general

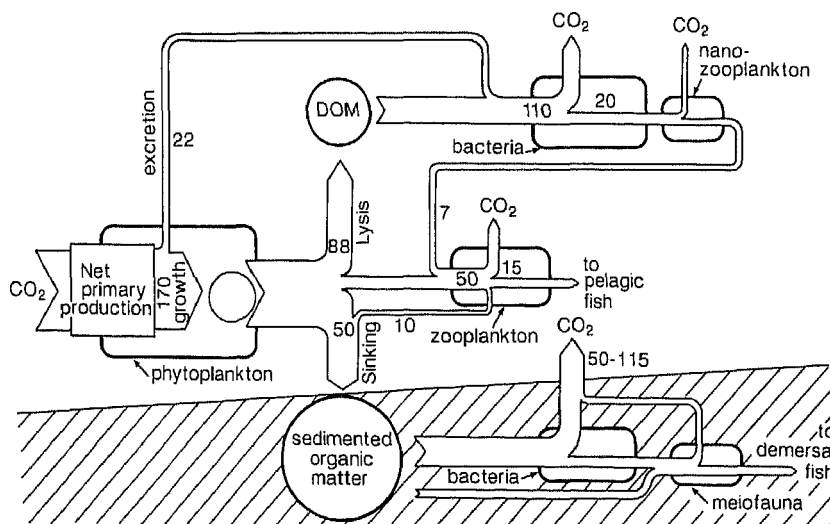


Fig. 3. Tentative budget of carbon fluxes within the continental coastal zone of the North Sea. Only 26% out of a total of $192 \text{ g C m}^{-2} \text{ yr}^{-1}$ constituting the net primary production is directly supplied to the sediment surface by sedimentation. The rest is lysed, channelled through the planktonic bacterial food web or into grazing by meso-zooplankton or (redrawn and simplified from Lancelot, 1991).

scenario for an increasing number of reports of *Phaeocystis* blooms in Antarctica (e.g. Buck and Garrison, 1983; El-Sayed et al., 1983; Sasaki and Watanabe, 1984; Garrison and Buck, 1985; Palmisano et al., 1986). In the Bransfield Strait the composition of sedimenting matter varied considerably, zooplankton faecal pellets often dominated the vertical flux, but sedimentational losses of the vigorously growing phytoplankton was generally low (Bodungen et al., 1986). Even though a part of the phytoplankton cells in the area had high sinking rates, the prevailing trend was that sedimentation of phytoplankton in general, and *Phaeocystis* in particular, was low. Sinking can apparently not explain the termination of *Phaeocystis* blooms in the current rich Bransfield Strait.

A similar conclusion can be drawn from the results of the Weddell Sea (Bodungen et al., 1988; Nöthig, 1988). *Phaeocystis* blooms were recorded close to the shore off Vestkapp in late January, but had disappeared 10 days later except for small concentrations of *Phaeocystis* cells at depth in the oceanic section of the study area. Living phytoplankton cells contributed only between 20–36% the vertical carbon flux and 0.5% of the suspended standing stock of phytoplankton sedimented daily to depths between 80–100 m. The composition of the sedimenting phytoplank-

ton reflects that algae, including *Phaeocystis*, unquestionably sedimented during the bloom, but in small amounts (Fig. 4). Despite numerous investigations of the pelagial in the Antarctic sector of the Atlantic, *Phaeocystis* has been, as a general rule, rarely found in sediment traps (U. Bathmann and V. Smetacek, pers. commun.). Sinking of *Phaeocystis* colonies contributes, therefore, hardly to the termination of blooms in the Weddell Sea and the Bransfield Strait.

2.6. Ross Sea

Dense *Phaeocystis* blooms have also been observed in the Ross Sea area (Ainly and Jacobs, 1981; El-Sayed et al., 1983; Palmisano et al., 1986; SooHoo et al., 1987), but no data on sedimentation have been published as yet. *Phaeocystis* blooms are predictable events in this area and they start before the major diatomaceous blooms (W.O. Smith, pers. commun.). It is suggested that *Phaeocystis* colonies and diatoms may form aggregates which sink in concert out of the euphotic zone (W.O. Smith, pers. commun.). Nitrogen and chlorophyll budgets as well as fluorescence profiles suggested high vertical flux rates. It is also interesting to note that sediment cores from the area revealed thick mats of *Phaeocystis* on the sediment surface at about 700 m depth, accumu-

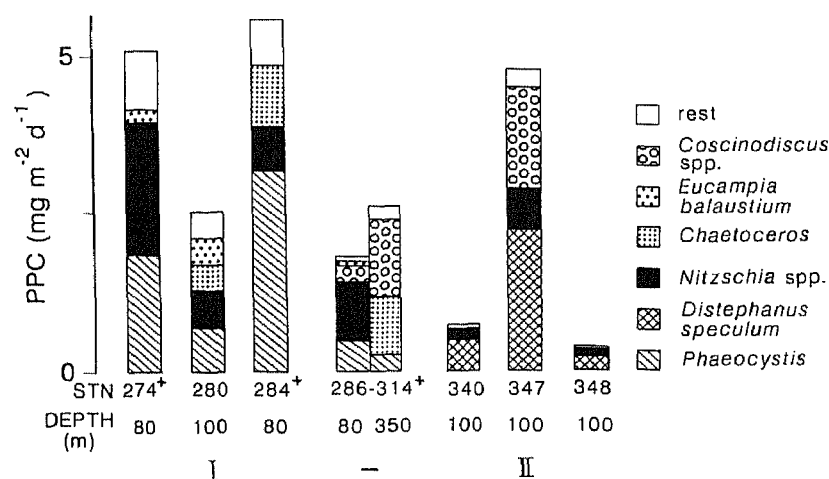


Fig. 4. Sedimentation rate of phytoplankton carbon (PPC) of dominating species at various stations (STN) and depth during Vestkapp I and II in the Weddell Sea (redrawn from Nöthig, 1988).

lating as sticky mats (W.O. Smith, pers. commun.). Based on this preliminary evidence, it appears that (a) the entire water column was traversed within a span of 2 weeks without substantial degradation, that (b) *Phaeocystis* contributed significantly to the food supply of the benthos and that (c) sedimentation indeed seems to be an important factor for the termination of *Phaeocystis* blooms in the Ross Sea.

3. Processes and controlling factors determining the sedimentation of *Phaeocystis* blooms

The case studies depicted above show that sedimentation of *Phaeocystis* can be an important process for the termination of blooms. However, this does not imply that sedimentation gives rise to an extensive supply of organic matter to deeper waters and the benthos. In contradiction to the sedimentation of diatoms sinking *Phaeocystis*-derived matter is, generally speaking, to a substantial degree disintegrated or mineralized in the upper part of the water column. Sedimentation of phytoplankton-derived matter is governed by the combination of physical and ecological mechanisms. Among the processes, one has to distinguish (a) those speeding up the transport of matter to depth [aggregate formation, sinking and indirectly by herbivory (faecal pellet production)] from (b) those transforming colonies into non-sinking material (cell and colony lysis, disruption of colonies with cell release, herbivory and the subsequent development of microbial food webs). These processes and their controlling factors are evaluated below with regard to *Phaeocystis*-derived organic matter.

3.1. Speeding up the transport of matter to depth

Aggregate formation

Mass aggregation during phytoplankton blooms, in particular for diatoms [but also for coccolithophorids (Cadée, 1986)], has been frequently documented in the field (Kranck and Milligan, 1988; Alldredge and Gotschalk, 1989). Among the interrelated causes and mechanisms for aggregation of phytoplankton cells during

blooms are supposedly enhancement of stickiness (Alldredge and Silver, 1988; Kiørboe et al., 1991; Kiørboe and Hansen, 1993) through the production of exopolymers (Lancelot, 1983; Chang, 1984; Lancelot and Mathot, 1985; Veldhuis and Admiraal, 1985) and the subsequent colonization by bacteria, protozoa and phytoplankton (Kranck and Milligan, 1980; Biddanda, 1985; Herndl and Peduzzi, 1988; Jackson, 1989; Muschenheim et al., 1989). These processes imply that aggregation is initiated (or at least significantly influenced) by biological factors. Jackson (1990) suggested that physical processes such as differential settling and shear flow could determine in addition to the extent of algal aggregation. Given a specific degree of stickiness, flocculation is dependent on the density of the particles and their collision rate, the collision rate being a function of turbulent shear and differential settling. Recently the morphology of sinking particles has been suggested to play an important role for aggregate formation. Contact due to direct interception is postulated to be more efficient than predicted by Jackson (1990) because of the irregularities of natural particles and because of entrainment of fine particles in the wake of large snow particles (Hill and Nowell, 1990). Physical coagulation processes form thus an integral dimension for the functioning of marine planktonic systems. Jackson's model, results by Hill and Nowell (1990) and data from the field and the laboratory (e.g. Alldredge and Silver, 1988; Riebesell, 1991a, b; Alldredge et al., 1993; Kiørboe and Hansen, 1993) describe aggregation processes as strongly influenced by factors such as (a) effective size and morphology of algal cells, (b) the physiological stickiness of algae and (c) the presence of large, discrete transparent particles formed by dissolved exopolymers exuded by phytoplankton and bacteria, but also by (d) specific combinations of physical condition responsible for particle behavior (e.g. differential settlement and shear). In addition, detritus and clay particles can be incorporated into marine snow particles (Avimelech et al., 1982) and aggregate formation may enhance the depletion of surface waters for particulate matter and adsorbed nutrient elements.

Aggregates originating from *Phaeocystis* colo-

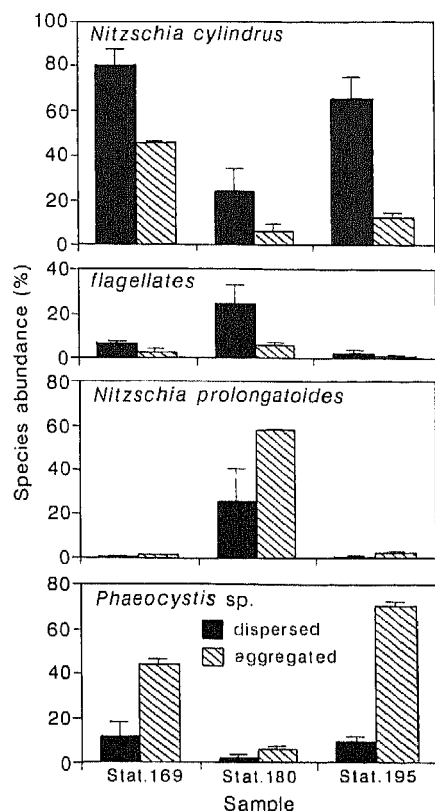


Fig. 5. Relative species abundance of ice algae in aggregates (hatched bars) and dispersed in the surrounding water (solid bars); samples of three stations collected from rotating tanks containing melted sea ice samples (redrawn from Riebesell et al., 1991).

nies have been observed in natural environments where recurrent massive *Phaeocystis* blooms are observed: the continental coastal wakes of the North Sea (Lancelot, 1990; Riebesell, 1993; Rousseau et al., 1994), the Barents Sea (Wassmann et al., 1990; Thingstad and Martinussen, 1991) and the marginal ice zone of the Weddell Sea (Riebesell et al., 1991) (Fig. 5). Using a remote observing vehicle during spring in the Bellinghousen Sea, Antarctica, a *Phaeocystis* bloom was observed which appeared to be clumping up into "cobwebs" or "nets of cells" (K. Crocker, pers. commun.). There were dense clumps of cells with several strands trailing away which came together again. These strands were

about 10 cm in length between the junctures. *Phaeocystis* colonies can form monospecific aggregates (Fig. 5) or contribute to aggregation together with other material. For example, large marine snow flocs rich in *Phaeocystis* colonies have been observed in the central North Sea (Riebesell, 1993). Aggregates presumably originate from senescent *Phaeocystis* colonies which can be covered with bacteria (Thingstad and Martinussen, 1991). Aggregate formation could thus result from increases in stickiness due to large production of exopolymers (Lancelot and Mathot, 1985; Baumann et al., 1994; Lancelot and Rousseau, 1994) and collision frequency due to the rapid increase of colony numbers and size during the bloom development (Rousseau et al., 1994).

To which extent these aggregates speed up the transfer of organic matter of *Phaeocystis* origin to depth is not exactly known. During aggregation experiments in coastal waters of northern Norway and the central North Sea no evidence was found to support the hypothesis formulated by Wassmann et al. (1990) that *Phaeocystis* blooms are terminated by the formation of *Phaeocystis* aggregates of senescent colonies (Passow and Wassmann, 1993; Riebesell, 1993). Although *Phaeocystis* was observed to form aggregates in some instances, senescent colonies did not appear to have a higher sticking efficiency than growing ones. The question to what extent aggregate formation of *Phaeocystis* colonies contributes to the termination of blooms is thus open. As compared to diatoms aggregate formation of *Phaeocystis* colonies is probably not of general significance for the termination of blooms (see however, Kjørboe and Hansen, 1993).

Sinking

To the best of my knowledge, no in situ sinking rates of *Phaeocystis* single cells, colonies or aggregates have been measured. In vitro measurements in the coastal zone of the southern North Sea using the SETCOL method revealed average colony sinking rates of about 6 m d^{-1} (van Boekel et al., 1992). Nutrient depletion did not give rise to increased sinking rates. In the Barents Sea calculations of specific sinking rates (c.f. Taguchi

and Hargrave, 1978) of *Phaeocystis* colonies and aggregates just below the euphotic zone during May/June 1984 (Table 1) revealed rates ranging from 1.5 to 13.3 m d⁻¹ (average 4.9 m d⁻¹; $n = 4$). These sinking rates are in the lower range of rates reported for diatoms which are known to sink rapidly after aggregate formation (Smetacek, 1985; Riebesell, 1989; Passow, 1991) and of the same magnitude of concomitant rates for *Chaetoceros socialis* in the Barents Sea (average 3.5 m d⁻¹; $n = 8$; Table 1). These rates imply that sinking of *Phaeocystis* colonies may add to the termination of blooms, but that sinking is not of paramount importance for bloom culmination. Unpublished results from the Ross Sea suggest high sinking rates with an average rate of about 14 m d⁻¹ (W.O. Smith, pers. commun.). Here, sinking may play a role for the termination of the blooms.

It is also necessary to emphasize that single *Phaeocystis* colonies can have positive buoyancy (Skreslett, 1988) and that marine snow aggregates and faecal pellets have been observed to stay buoyant (e.g. Krause, 1981; Alldredge et al., 1987; Stachowitsch et al., 1990). *Phaeocystis*-rich aggregates have been observed sinking, neutrally buoyant or even rising during calm weather conditions in the central North Sea (Riebesell, 1993). Strong winds coinciding with decreases of suspended aggregates in surface water revealed that removal of gas bubbles incorporated into marine snow may be an important process determining their sinking speed (Riebesell, 1993). Storms and turbulence may therefor accelerate the sinking velocity of *Phaeocystis* aggregates.

As for other phytoplankton, the sinking rate of *Phaeocystis* colonies is governed by the physical characteristics of the water column in general, but also by the size of the colonies and their density. Few of the factors controlling the relative importance of these mechanisms have presently been considered in sufficient detail with regard to *Phaeocystis*. The size of the colonies has been shown to increase with bloom development, reaching up to several mm in diameter at bloom culmination (Rousseau et al., 1994). Thus potential sinking rates increase with bloom progress. This size effect is however counteracted by the

density change of the colony proceeding at the same time. Due to the gel properties of the colonial matrix (Baumann et al., 1994; Lancelot and Rousseau, 1994) density of the colonies dramatically decreases to values close to seawater for diameters greater than 200 μm (C. Lancelot, pers. commun.). Any sudden decrease in seawater density (e.g. thermal stratification, ice-melting, fresh-water run-off) during the course of a bloom is supposed to speed up sinking. Conversely, sudden increases of density would result in rising. In addition, manganese oxyhydroxide precipitation has been shown to occur inside the mucilaginous matrix of cultured *Phaeocystis* colonies (Davidson and Marchant, 1987; Lubbers et al., 1990) as a result of increased pH caused by photosynthesis. Similar pH measurements on suspended *Phaeocystis* colonies under natural conditions suggested that the increase in pH is too low to account for manganese precipitation (H. Ploug, pers. commun.). More has to be known about the regulation of manganese oxyhydroxide precipitation/dissolution inside *Phaeocystis* colonies to assess the importance of this trace metal sequestration mechanism under natural conditions and its significance for colony density and the subsequent sinking rate of the colonies.

Do Phaeocystis species have different sinking and aggregation behavior?

Given the concern with regard to the existence of different *Phaeocystis* species and the problems to identify them (Baumann et al., 1994), any attempt to discuss the sinking and aggregation behavior of the genus must be hypothetical. However, differences in sinking and aggregation behavior could be species-specific. Sinking of single colonies is related to gel properties, size and shape of the colony while aggregation would depend on differences in stickiness, protuberances and encounter frequency. For example, differences in *Phaeocystis* colony morphology may be the result of differences in colony mucus composition (van Boekel, 1992).

All this could give rise to species-specific and radically different sedimentation rates. However, little evidence is found in the available data that differences in sedimentation could be species-

specific. Mass sedimentation of *Phaeocystis pouchetii* was for example only observed below the euphotic zone in the Barents Sea, but not in Balsfjord, off the Norwegian coast or the Norwegian Sea. Smith et al. (1991) suggested mass sedimentation of *Phaeocystis pouchetii* in the Fram Strait from the disappearance of this species from the water column and fluorescence at depth. Despite the lack of data it appears that mass sedimentation of *Phaeocystis globosa* does unlikely take place over extensive areas of the shallow southern North Sea. However, this could be the case in the central North Sea. Finally, sedimentation (Ross Sea) and retention in the water column (Weddell Sea) have been recorded from Antarctica, the region of a third species, *Phaeocystis* sp. (c.f. Baumann et al., 1994). Differences in species-specific sinking and aggregation rates are obviously unable to explain the various scenarios of high and low sedimentation.

Given the morphological and biochemical differences among various *Phaeocystis* species (Baumann et al., 1994; Rousseau et al., 1994), future investigations should in principle try to describe sinking and aggregation processes in a species-specific manner. However, having in mind the numerous perplexing challenges regarding the ecology of *Phaeocystis*, general aspects of this genus may have to be explored in greater detail before inventories with regard to species-specific differences can be approached in a constructive manner.

3.2. Transformation of colonies into non-sinking material

Cell lysis, disintegration of colonies and development of flagellated cells

Among the processes which may result in disappearance of *Phaeocystis* colonies from the water column are the frequently observed release of flagellated cells from disrupted colonies (Rousseau et al., 1994 and references therein), cell lysis during senescence (e.g. van Boekel et al., 1992), post bloom dissolution of the mucilaginous matrix in the water column (e.g. Veldhuis et al., 1986), concomitant accumulation of dissolved organic

matter in the water column (e.g. Eberlein et al., 1985) and subsequent microbial degradation (e.g. Thingstad and Billen, 1994).

Cell lysis may play a crucial role for the dynamics of *Phaeocystis* blooms. In the Dutch coastal zone cell lysis after N-depletion was of paramount significance for its decline (van Boekel et al., 1992). Neither grazing by meso-zooplankton played any outstanding role for the decline of suspended colonies at this location. However, the data suggest that the growth of bacteria and protozoa depended largely upon DOC produced by lysis of *Phaeocystis*. While the generality of these observations will have to be considered in future investigations, cell lysis is obviously a process which might counterbalance the loss of organic matter from the upper layers through vertical flux. For example, cell lysis might have contributed to the depth-related decline in sedimentation of *Phaeocystis* observed in the Barents Sea and Balsfjord (Figs. 1, 2).

Mucus released from colonies and the disruption and disintegration of entire colonies gives rise to substantial release of mucilaginous material and DOC (Bätje and Michaelis, 1986; Billen and Fontigny, 1987; Lancelot et al., 1987). The composition and properties of *Phaeocystis* colony mucus are still largely obscure. Dissolution of the matrix of senescent colonies and aggregates has been widely observed in the field (Veldhuis et al., 1986; Lutter et al., 1989; Riebesell et al., 1994) and with pure cultures in the laboratory (Riebesell, 1993). Extremely high (up to 64% of assimilated carbon) extracellular release of mostly carbohydrates during nutrient shortage furthermore leads to the high ambient concentrations of carbohydrates observed during *Phaeocystis* blooms (Guillard and Hellebust, 1971; Lancelot, 1983; Eberlein et al., 1985; Fernández et al., 1992; Thingstad and Billen, 1994). While the particulate matter is readily mineralized by microbes, the ample input of mucilaginous matter and dissolved organic matter to pelagic environments seems, although potentially biodegradable, largely resistant to microbial degradation (Thingstad and Billen, 1994).

For the time being, the fate of mucilaginous matter and DOC is a matter of dispute. At senes-

cence *Phaeocystis* colonies appeared to disintegrate at 40–60 m depth in Balsfjord (Passow and Wassmann, 1993). Laboratory studies revealed that dissolved carbohydrates derived from the colonial matrix of *Phaeocystis* formed mucous particles which attached to siliceous fibers and glued them together. Detrital mucous flocs also formed from a natural particle assemblage and dissolved carbohydrates accumulated during the *Phaeocystis* bloom when rotated. Passow and Wassmann (1993) hypothesized that cells and colonies of *Phaeocystis* may not contribute significantly to vertical flux, but that the sedimentation of mucous flocs presents a secondary pathway by which carbon assimilated during *Phaeocystis* blooms may sink to greater depth.

The commonly observed release of flagellated cells from decaying colonies is another mechanism by which *Phaeocystis* can omit sedimentational losses (Rousseau et al., 1994). This process gives rise to a separation of living cells and the colony matrix. The flagellated cells can retain in the aphotic or ascent into the euphotic zone. In both cases they will be subjected to grazing pressure by protozoa and meso-zooplankton (Weisse et al., 1994). The mucilaginous remains of the colonies, however, stay or sink into the aphotic zone where they dissolve, get mineralized or contribute to aggregation. However, not all colonies sink or get dissolved as colonies are reported to over-winter in the water column, representing a possible inoculum for next years bloom (Cadée, 1991).

3.3. Herbivory and microbial degradation

That larger zooplankton species can influence the development of spring blooms and the resulting vertical flux is well established from several oceanic environments (Frost, 1987; Peinert et al., 1989). In shallow water environments, on the contrary, the low herbivore biomass at the end of the winter period and the resulting low grazing pressure gives rise to a slow response of zooplankton to the increasing food availability (Smetacek et al., 1984; Wassmann, 1991). As a result, extensive sedimentation of ungrazed phytoplankton and phytodetritus can take place dur-

ing a senescent stage of the spring bloom. The impact of various size categories of heterotrophs on the supply of *Phaeocystis* to deeper waters and eventually the benthos has as yet not been thoroughly considered, but is of potential importance for the fate of *Phaeocystis*-derived organic matter. Grazing pressure by the zooplankton community on the spring bloom development in the Barents Sea is limited (Eilertsen et al., 1989; Båmstedt et al., 1991). Over-wintering and advection of meso-zooplankton populations are apt to considerably influence the dynamics of phytoplankton in north Norwegian fjords (Hopkins et al., 1985 and references therein). Indeed, chemical markers specific for *Phaeocystis* have been found in zooplankton, pelagic fish and sediments (Sargent et al., 1985), indicating that the *Phaeocystis*-derived biomass is channeled through the grazing food-chain and supplied to sediments. For example, krill faecal pellets were continuously present in the sediment traps of Balsfjord and Malangen, in particular during spring and early summer. In the Wedell Sea and Bransfield Strait grazing of *Phaeocystis* cells by protozoans (Nöthig and Bodungen, 1989) and *Phaeocystis* colonies by krill (Bodungen, 1986; Smetacek et al., 1990; Bathmann et al., 1991) are prevailing in the area while grazing by copepods is not likely to be of significance (Schnack et al., 1985). Fig. 3 indicates that most of the *Phaeocystis*-derived suspended biomass in the southern North Sea is channeled through the planktonic, microbial food-web (Lancelot, 1990) while meso-zooplankton grazing pressure on *Phaeocystis* is very low (Daro, 1986; van Boeckel et al., 1992). While the extra production of *Phaeocystis* following the diatom bloom is only of indirect benefit (through the microbial loop) for the overall fish yield in an shallow area like the North Sea (Lancelot, 1990) *Phaeocystis*-derived biomass is obviously channeled into the grazing food chain and fish production in deeper areas such as the Barents Sea and north-Norwegian fjords.

The considerable volume of the colonies, their assumed unpalatability and the limited size of the herbivores (as compared to the size of the colonies) have been suggested to be the cause why *Phaeocystis* colonies are rejected as food by

many species of zooplankton (see Weisse et al., 1994 and references therein). Likewise, healthy *Phaeocystis* colonies keep their surface free for bacteria (Thingstad and Martinussen, 1991) and surface material is not readily mineralized by microbes before the decline of the bloom (van Boekel et al., 1992). Grazing on healthy colonies seems, therefore, limited to large meso-zooplankton species (e.g. *Calanus* sp.) and macro-zooplankton (e.g. krill). Aggregates and senescent colonies of *Phaeocystis* origin are rapidly colonized by bacteria (Thingstad and Martinussen, 1991), protozoa (Lancelot et al., 1991) and diatoms like *Nitzschia* sp. (Estep et al., 1990; P. Wassmann, pers. observ.). It is now believed that the rejection of *Phaeocystis* colonies is temporary limited only and that grazing is a complex function of the physiological state of the colonies and microbial colonization (e.g. Estep et al., 1990), colony size and the size spectrum of the grazing community (Weisse et al., 1994). The existence of extensive *Phaeocystis* blooms implies that grazing, although influencing the bloom, cannot play an important role during its formation. To the end of the *Phaeocystis* bloom grazing gets more important in deep areas while microbes take care of the rich amounts of suspended organic matter in shallow ones (e.g. Fernández et al., 1992). However, the microbial loop based on *Phaeocystis*-derived matter seems to depend also on DOC which is mainly supplied through lysis of cells (van Boekel et al., 1992) and colonies.

Recent investigations indicate that virus are much more frequent in marine environments than previously assumed. Infestation by virus is able to negatively influence phytoplankton blooms (Bratbak et al., 1990). For example, virus can decimate blooms of *Emiliana huxleyi* in experimental enclosures (Bratbak et al., 1992). The impact of virus on blooms of *Phaeocystis* has, to the best of my knowledge, not been thoroughly investigated although some observations on free viruses coinciding with aging *Phaeocystis* colonies have been made (G. Bratbak and M. Heldal, pers. commun.). Preliminary observations indicate that infestation of *Phaeocystis* colonies by virus seems to be insignificant (M. Heldal, pers. commun.). The mucous envelop of the colonies is

most likely an unfavorable substrate for virus infestation.

Ingestion of flagellates, senescent colonies, aggregates and faecal pellets by different size categories of herbivores opens the possibility that particulate and dissolved organic matter derived from *Phaeocystis* blooms is effectively recycled at the end of the bloom and below the euphotic zone. Given a well structured food-web of planktonic microbes and larger herbivores, good timing as well as sufficient depth, it seems likely that sinking *Phaeocystis* blooms could be mineralized during settling. During such a scenario, *Phaeocystis* blooms strongly support regenerative processes of the planktonic system, resulting in a weak pelagic-benthic coupling.

4. The fate of *Phaeocystis* blooms

The question of whether *Phaeocystis* blooms are terminated primarily by sedimentation, and if so, the settling material consists of single colonies, aggregates of colonies, a mixture of colonies, aggregates and the cell-free matrix or as carbohydrate-rich detrital flakes is wide open. Several processes such as light and nutrient stress, herbivory and microbial degradation seem to play an important role. In nature these processes act more or less in concert, but their proportions vary in time and in different ecosystems. The physiological and morphological state of sinking colonies is undoubtedly an important aspect for blooms termination since it has implications for the sinking speed and processes like microbial colonization, aggregation, cell lysis, grazing and dissolution of the matrix. It is thus essential for our understanding of the vertical flux dynamics as well as for how *Phaeocystis* remains in the water column of *Phaeocystis*-dominated ecosystems that we learn more about the morphological and biological state of the sinking and non-sinking components. Since we know that *Phaeocystis* blooms can sink out of the euphotic zone, but that the penetration depth of the sedimentational puls can vary, as much emphasis has to be given to those processes which transform sinking into

non-sinking *Phaeocystis*-derived matter than sedimentation itself.

The evidence regarding the termination of *Phaeocystis* blooms depicted previously is summarized in a hypothetical scheme (Fig. 6). Some of the pathways and processes depicted in this scheme are supported by evidence, some are based on indications only. Hence this scheme is only a suggestion and will have to be reevaluated on the base of future investigations. The vertical flux of *Phaeocystis*-derived material can consist of healthy colonies, senescent colonies, aggregates and mucilaginous material. It is suggested that the fate of *Phaeocystis* blooms is different in shallow and deep waters. The most important reason for this difference is the limited impact of meso-zooplankton on the spring bloom development in shallow waters (see above). As a consequence, organic matter is channeled in different ways through pelagic food chains of shallow and deep water environments (Fig. 6). If turbulent

energy supply is high and in shallow water environments, extensive dissolution of sinking and non-sinking colonies as well as aggregates will take place in the water column. Disintegrating colonies and microbial decomposition will give rise to accumulation of mucilaginous material in the water column. Polymeric dissolved organic matter in surface waters can give rise to foam formation which can accumulate on beaches, e.g. along the southern North Sea. If turbulent energy supply is low, accumulation of healthy as well as senescent colonies and aggregates in the nutrient-rich lower part of the euphotic zone can take place. However, when light or nutrient stress gets predominant, sinking will be induced. This material either sinks to the bottom or is biodeposited. It may constitute a substantial supply of food to the benthos, may form sticky mats (e.g. in the Channel) and may get eventually washed-up onto beaches (e.g. in Liverpool Bay). In none of the shallow water environments herbivory has been

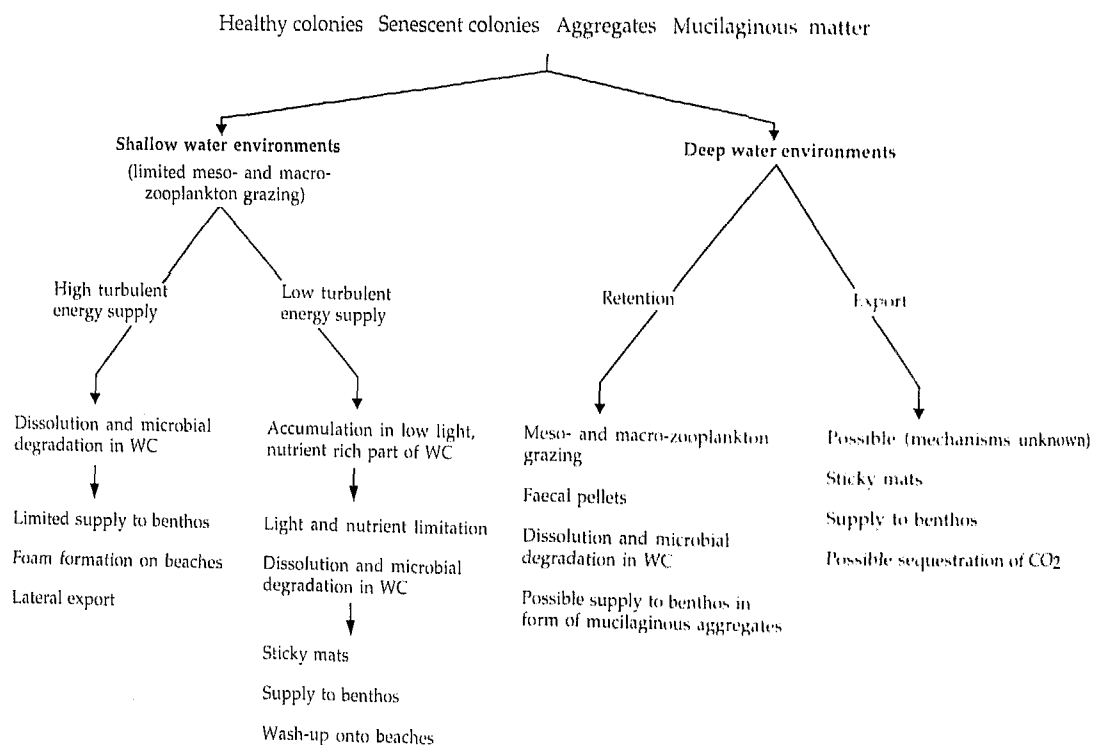


Fig. 6. Hypothetical, simplified scheme on the termination of *Phaeocystis* blooms. WC = water column. See text for explanation.

reported to have a substantial impact on the development and fate of *Phaeocystis* blooms. Lysis of cells and colonies seems to be the most significant process determining the fate of *Phaeocystis* blooms here.

In deep water environments turbulent energy supply to surface waters is variable. The main difference between shallow and deep water environments with regard to phytoplankton blooms and subsequent vertical flux is the significance of herbivory, settling time and the vertical extension over which disintegration can take place. Foam formation on beaches or on the sea surface has not been observed in deep water environments (e.g. fjords), implying that mucilaginous material does not come into extensive contact with the water surface. Grazing of meso- and macro-zooplankton usually plays an outstanding role for bloom dynamics and vertical flux of organic matter in deep water environments due to vertical migration, match, over-wintering etc. The pene-

tration depth of sinking *Phaeocystis* material is a function of sinking velocity, microbial degradation and dissolution of colonies or aggregates. If sinking velocity is high and degradation low, particulate material from a sinking bloom may reach deeper layers and the sediment, generating sticky mats (e.g. Ross Sea). However, if herbivory on *Phaeocystis* colonies and aggregates or dissolution is important, the intensity of these processes determines the extent to which *Phaeocystis* derived particulate organic matter is supplied to deeper waters and how much mucilaginous and DOC is introduced in subsurface waters. This could for example be the case in Balsfjord and the Barents Sea.

Fig. 7 is an attempt to depict some of the recorded differences with regard to the vertical flux of *Phaeocystis* blooms. Two different scenarios with sedimentation rates of *Phaeocystis* derived matter of 200 and 800 $\text{mg C m}^{-2} \text{d}^{-1}$ below the suspended biomass maximum are presented.

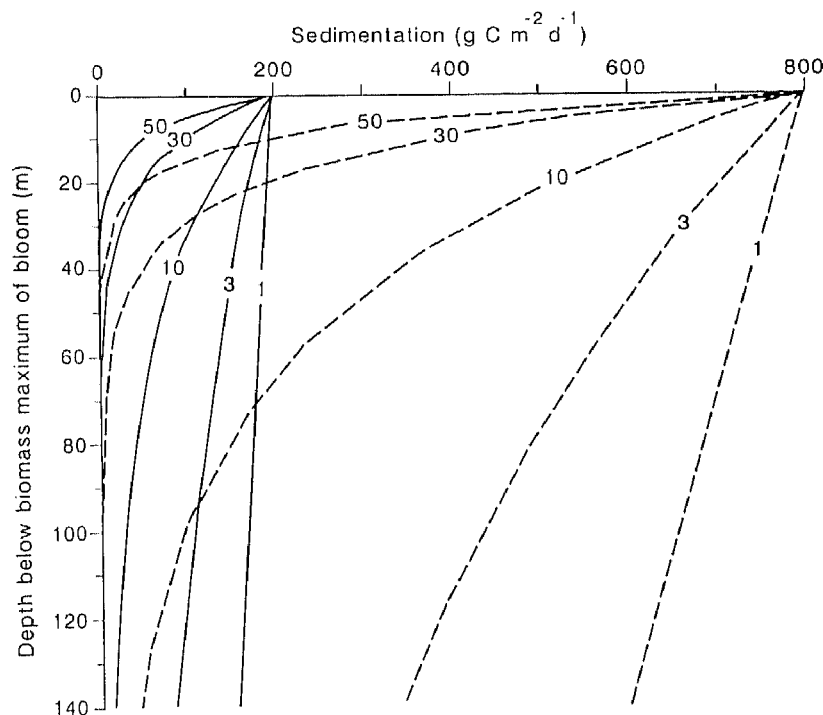


Fig. 7. The vertical flux of POC entering the aphotic zone as a function of unspecified processes counterbalancing sedimentation at rates of 3–50% d^{-1} . Two scenarios with entering fluxes of 200 and 800 $\text{mg C m}^{-2} \text{d}^{-1}$ (full and broken lines, respectively) are given. Sinking is constant (5 m d^{-1}).

Sinking rate is kept constant at 5 m d^{-1} . The vertical flux rate is subjected to unspecified processes counterbalancing sedimentation (e.g. cell lysis, grazing, dissolution) at rates of 1, 3, 10, 30 and $50\% \text{ d}^{-1}$, respectively. The two scenarios may illustrate situations encountered in Balsfjord and the Barents Sea (Figs. 1, 2). Given that the assumptions are valid, unspecified processes counterbalancing the sedimentation of *Phaeocystis* blooms in Balsfjord and the Barents Sea should be of the order of about $10\% \text{ d}^{-1}$. Under the conditions presented in Fig. 7 carbon sedimentation rates below 50 and 100 m depth come close to rates found during *Phaeocystis* blooms in the two ecosystems (Figs. 1, 2). The processes counterbalancing sedimentation of *Phaeocystis* during the vernal bloom in subpolar waters of the North Atlantic may thus be in the order of $10\% \text{ d}^{-1}$, implying that major amounts of *Phaeocystis* biomass do not reach the benthos of areas deeper than 100 m.

Except for the indication of rapidly sinking *Phaeocystis* colonies in the Ross Sea, the remaining observations so far imply that ecosystems dominated by *Phaeocystis* tend to endorse pelagic, rather than benthic mineralization. It may be that the pelagic–benthic coupling in ecosystems dominated by *Phaeocystis* is not direct through deposition of cells and colonies, but indirectly through detrital aggregates formed from exopolymeric carbohydrates derived from mucilaginous material and DOC. Despite of their significance with regard to new production rates and suspended biomass, *Phaeocystis* blooms play probably no major role for sequestration of carbon from the atmosphere in boreal and polar ecosystems. *Phaeocystis* is well adapted for the maintenance of nutrient and biomass regeneration in the upper layers. Generally speaking, retention rather than export food chains seem to be characteristic for *Phaeocystis*-dominated ecosystems.

The importance of sedimentation for the termination of *Phaeocystis* blooms is not determined by the life cycle of the genus alone. Sedimentation is an inherent feature of ecosystems giving rise to blooms. While the sedimentation of senescent diatom blooms is a recurrent pattern to be observed in boreal, coastal and shelf waters

(Smetacek, 1985; Wassmann et al., 1991), the vertical flux of *Phaeocystis* is determined by a suite of basic characteristics and inter-related processes which control the carbon cycle of a given ecosystem and can give rise to radically different scenarios of pelagic–benthic coupling: turbulence, water depth, nutrient limitation, aggregation, cell lysis, microbial colonization and mineralization, disintegration of colonies, grazing, sinking speed etc. Although some of the processes with regard to the sedimentation of *Phaeocystis* are moderately well understood, present knowledge does not imply that a general understanding is in sight. The development of *Phaeocystis* blooms is determined by the complex physical, chemical and biological relationships prevailing in an ecosystem and cannot be understood without a good grasp on the specific systems to be studied. Clear-cut relationships for the fate of phytoplankton derived biomass which are known from diatom-dominated blooms (aggregation/sinking versus grazing) are, not within reach because the complex life cycle of *Phaeocystis*. *Phaeocystis* species have a considerable impact on the over-all function of ecosystems since no other planktonic genus has been considered to dominate entire ecosystems. Despite of that, the role sedimentation plays for the termination of *Phaeocystis* blooms is probably to a much greater extent determined by characteristics of the specific ecosystem where the bloom occurs than by the physiology of the specific *Phaeocystis* species.

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