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Architecture, ecology and biogeochemistry of *Phaeocystis* colonies

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Abstract

This paper discusses structure and function of the *Phaeocystis* colony skin, and relates them to the specific impact of *Phaeocystis* colonies on ecology and biogeochemistry. The potential advantage of the recently discovered tough skin around the colonies of *Phaeocystis globosa* is discussed in context with the metabolic costs of this structure, and compared to potential functions of structures around other phytoplankton. It is further proposed that mainly small, fast-growing pathogens and predators will be deterred by the colony skin. It will be shown that these theoretical predictions are consistent with available data from the literature, and can explain the dominance of the colonial form in *Phaeocystis* blooms. Finally, the peculiar biogeochemistry of *Phaeocystis* colonies, especially the sedimentation of *Phaeocystis*-derived organic matter, is argued to be a function of the susceptibility of *Phaeocystis* colonies to certain grazers, which in turn is strongly determined by the architecture and function of the colony skin. During the exponential phase of the bloom, *Phaeocystis*-derived organic matter can efficiently sink in faecal material of large zooplankton, which actively feed on the colonies. However, the integrity of the colony skin, and consequently its protection for the cells therein, seems to be closely coupled to the phase of active growth. Accordingly, the cells are massively affected by small grazers and pathogens and thus rapidly disintegrate after the culmination of the bloom, so that sedimentation of *Phaeocystis*-derived organic matter becomes probably restricted to the more refractory extracellular components of the colonies.

Keywords: *Phaeocystis* colony; colony skin; mechanical defence; top-down control; ecology; sedimentation

1. Mechanical defences of phytoplankton

Biological architecture (i.e. structure, composition, and mechanical properties) is a product of evolution and usually results from the need to unify counteracting requirements (e.g. Bertness, 1981; Tollrian, 1995). In phytoplankton, selection pressure presumably forces a trade-off between efficient protection against pathogens and predators, and fast growth rates. Globally distributed genera like *Phaeocystis*, which regularly form large blooms (Lancelot et al., 1998), appear to have optimised the product of growth and protection in many marine ecosystems. While many studies imply that grazing pressure on *Phaeocystis* colonies in the field is reduced compared to *Phaeocystis* flagellates (Weisse et al., 1994 and refs. therein), knowledge on antigrazing mechanisms of *Phaeocystis* colonies or other marine phytoplankton is still sparse. As it possesses a unicellular (6 μm) and a colonial stage (up to ca. 10 mm with several 1000 cells) with similar growth rates, *Phaeocystis* is an intriguing object to study potential defence mechanisms of phytoplankton and their impact on ecology and biogeochemistry. In this paper, I will discuss how

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the properties of *Phaeocystis* colonies might reflect the necessities for both growth and protection.

1.1. The Phaeocystis colony skin is a cheap mechanical defence strategy

As shown by Hamm et al. (1999), colonies of *Phaeocystis globosa* are surrounded by a thin yet mechanically very stable skin. In combination with a pore size of <4.4 nm, the toughness of the skin probably makes the cells within the colony inaccessible to a large number of organisms, especially viruses, bacteria and protozoa, which could otherwise readily infect or ingest organisms of the size of *Phaeocystis* flagellates. However, while efficient protection against small or filter-feeding organisms is very likely provided by the colony, its protective value seems to be insignificant in other cases, for instance against large copepods or euphausiids (Weisse et al., 1994; Hamm et al., 2000). This indicates that mechanical, and not chemical, properties are mainly responsible for the protective property of the colony envelope. Further strengthening of the skin, e.g. as a protection against large and raptorial zooplankton (e.g. *Calanus finmarchicus*, Hansen et al., 1990; Hansen, 1992, or *Thysanoessa raschii*, Hamm et al., 2000) would most likely decrease the growth rates, as more unproductive assimilates would have to be produced, and a thicker skin could restrict the diffusion of nutrients to the cells. Apparently, this disadvantage is not balanced by a potentially better protection against larger predators, which only consume a small percentage of the primary production of *Phaeocystis* blooms (Hansen and Van Boekel, 1991). Conversely, a less sophisticated architecture of the construction of a colonial envelope would probably hamper bloom formation: Comparable haptophytes such as unicellular poison-producing *Chrysochromulina* (Hanslik and Rahmel, 1995) or *Corymbellus*, which forms small colonies (Green, 1976), only sporadically dominate phytoplankton blooms. Also, the flagellate stage of *Phaeocystis*, even though at least as fast-growing as the colonies (Baumann et al., 1994), is not known to accumulate biomasses in the field comparable to those of the colonies. A possible reason is that the small *Phaeocystis* cells are difficult to recognise and are therefore easily overlooked, if they are not expected. On the other hand, blooms dominated by other small flagellates, e.g. *Chrysochromulina* (Hanslik and Rahmel, 1995) or *Pyramimonas* (Bird and Karl, 1991; Gradinger, 1996) have been perceived by marine scientists. Thus it appears unlikely that unnoticed *Phaeocystis* flagellates dominate large blooms as do the colonies, even though they may often be overlooked if other phytoplankton dominate the bloom.

Examples where only one principle (need for growth or need for protection) is necessary can be instructive: The resting stages of phytoplankters do not have to grow, and thus can reinforce their outer layers to efficiently protect their protoplasts against pathogens and predators. Consequently, many dinoflagellates (Wall and Dale, 1968) and diatoms (e.g. *Thalassiosira bulbosa*, Syvertsen and Hasle, 1994 or *Chaetoceros socialis*, Eilertsen et al., 1981) use strengthend versions of their respective typical cell walls for their resting spores. Conversely, if protection is not necessary, for instance in *Phaeocystis* cultures derived from colonies, the percentage of flagellates is often much higher than in the field, to the extent that sometimes colonies are not present at all (Janse et al., 1996). Finally, the induction of colonies from single cells of the green alga *Scenedesmus acutus* by kairomones (infochemicals) from *Daphnia* (Cladocera), *Eudiaptomus* (Copepoda) and *Brachionus* (Rotifera) (Lürling and Van Donk, 1997) shows that mechanical protection may be switched on and off, depending on whether certain predators are present or not. Though an analogous induction of colony formation is often discussed for *Phaeocystis*, conclusive evidence is still missing.

As single and colonial cells of *Phaeocystis* have similar growth rates (Guillard and Hellebust, 1971; Grimm and Weisse, 1985), the allocation of the material needed to build the colonial matrix obviously does not hamper the cell metabolism. In other words, the high stability of the colony skin is probably achieved with economical amounts of material. In fact, the colony envelope of *Phaeocystis globosa* is built with only small amounts of polysaccharides—supposedly the main components of the extracellular colonial material—which constitutes only ca. 10–34.5% of the total colony biomass (Van Rijssel et al., 1997). Since *Phaeocystis globosa* cells are able to accumulate a storage of glucan, which can constitute more than 40% of the cell carbon (Janse et al., 1996), the percentage of extracellular polysaccharides is

probably even lower. Another economical advantage for the colonial cells is that the intact skin itself appears to be very resistant to bacterial attack. This is remarkable, as much of the extracellular material is built of potentially easily degradable polysaccharides (Janse et al., 1999). Also, it suggests that the material used for colony formation is a one-time investment that does not need maintenance or reconstruction.

1.2. Analogies and differences within the genus and to other algae

The concept of the colony skin as a cheap mechanical defence is based on properties of *Phaeocystis globosa*. Since three other colony-forming species of the genus *Phaeocystis*—*P. pouchetii*, *P. antarctica* and *P. jahnii*—exist, the properties of *P. globosa* need not be representative of the genus. On the other hand, prominent features with important functions are in general functionally conservative on the genus level. Accordingly, the mechanical protection of cells, which would clearly be a fundamental function of the *P. globosa* colony skin, should principally be given by the analogous structures of *P. antarctica* or *P. pouchetii* as well. Nevertheless, functional differences between the colonies of the different species are probable. A geometric difference to the spherical *P. globosa* colony is indicated by the colony morphology of *P. pouchetii*, which typically has several lobes protruding from a central cell-free region. This and the fact that *P. pouchetii* colonies seem to be easier to disrupt than *P. globosa* colonies (Jacobsen, pers. comm., 1999) indicate that it follows a different antigrazing strategy than *P. globosa*. As an example, it is thinkable that the geometry of *P. pouchetii* colonies enables them to have the advantage of a larger diameter than the other *Phaeocystis* colonies with the same amount of cells, but makes them more susceptible to mechanical disruption. Colonies of the recently described *P. jahnii*, which appear to be largely amorphous and seem to lack a colony skin (Zingone et al., 1999), may offer an even cheaper, but also less effective mechanical defence than the highly organised colonies of *P. globosa*, *P. antarctica*, and *P. pouchetii*.

Many colonial planktonic algae of widely diverse taxonomic origin such as *C. socialis* (Bacillariophyceae), *Volvox* (Chlorococcales), or *Uroglena* (Chrysophyceae) have a geometry similar to that of the more organised *Phaeocystis* colonies. Their colonial cells are distributed at the periphery of a large cell-free space. The connecting colonial material of these colonies is often described as a gel or mucilage (Doers and Parker, 1988), sometimes (as in *Volvox*) implicitly as a cell wall (Ertl et al., 1992). Another geometric analogy exists in unicellular bloom-forming microalgae, such as the large centric diatoms *Thalassiosira* or *Coscinodiscus*. Here, the cell plasma and the chloroplasts are essentially located at the periphery of a large cell and protected by a rigid siliceous cell wall. Colonies of planktonic Cyanophyta, e.g. *Microcystis* or *Aphanizomenon*, are, like *P. jahnii*, typically less organised. Their cells are distributed throughout the colonies, and the colonies often have irregular, asymmetric forms.

Clearly, the mechanical properties of the tough but pliable colony skin (Hamm et al., 1999) differ fundamentally from those of the rigid siliceous frustules of the diatoms. Copepods feeding on *Phaeocystis* colonies and diatoms too large to be ingested as a whole need different strategies to gain access to the cell biomass. While diatom frustules may be crushed like a nutshell by copepod mandibles, this appears to be impossible for *Phaeocystis* colonies. Judging from their physical properties, which resemble those of a plastic bag or a thin metal foil (Hamm et al., 1999), they would have to be cut or torn apart by the copepods. Still, certain common features, viz. a large size and a stable shell or skin, indicate that *Phaeocystis* colonies and large diatoms may be protected against a similar spectrum of grazers or pathogens. In contrast to the *Phaeocystis* colony envelope, the mechanical barrier provided by the diatom frustule seems to have several unavoidable weak spots (i.e. the girdle region, the rimoportulae and the areolae), which are used by specialised parasitoid protists to gain access to the plasma (Schnepf and Drebes, 1977, 1986; Raghukumar, 1978; Kühn, 1997). However, it cannot be excluded that specialised, small organisms have the means to enter *Phaeocystis* colonies and feed on the cells from inside the colony. Corresponding examples exist in the rotifers *Proales parasitica* and *Cephalodella edax* (Hollowday, 1993), which are able to penetrate and feed inside *Volvox* and *Uroglena* colonies, respectively, or the parasitoid protist *Rhizopodium beauchampi*

Table 1
Sizes and growth rates of potential mortality factors and their impact on different stages of the *Phaeocystis* life cycle (+, cells are affected; o, not known; −, cells are not significantly affected. Note that though the depicted growth rates are only examples of the respective groups, the general tendency can be regarded as realistic)

Potential mortality factors	μmax (h^{-1})	Size	Single cells (ca 6 μm), μmax (h^{-1}) = 0.08[a]	Cells in intact colonies > 100 μm, μmax (h^{-1}) = 0.06[a]	Cells in disrupted/ deteriorating colonies
Viruses	0.2[b]	0.14 μm	+[b]	−[b]	+[b]
Bacteria	1	ca. 1 μm	o	−[c]	+[c]
Nanoflagellates	0.133[d]	2–20 μm	o	o	o
Dinoflagellates	0.026[d]	ca. 20–50 μm	+[e,f]	−[f]	+[f]
Ciliates	0.055[d]	ca. 70–120 μm	+[e,f,g,h]	−[e,f,g]	+[e,f,g]
Copepods	0.0066[d]	ca. 0.2–10 mm	+[i]/−[j]	+[k,l,m,n]/−[n,o,p]	+[p]
Euphausids	<0.005	ca. 15–60 mm	+[q]	+[r,s]	o
Decapod larvae	<0.005	> 0.5 mm	+[t]/−[t]	+[u]	o
Fish	<0.005	> 1 cm	o	+[v]	o

[a] Data taken from: Guillard and Hellebust, 1971.
[b] Jacobsen et al., 1996.
[c] Thingstad and Billen, 1994.
[d] Hansen et al., 1997.
[e] Weisse and Scheffel-Möser, 1990.
[f] Hansen et al., 1993.
[g] Admiraal and Venekamp, 1986.
[h] Hansen et al., 1993.
[i] Hansen, 1992.
[j] Verity and Smayda, 1989.
[k] Tande and Båmstedt, 1987.
[l] Weisse, 1983.
[m] Hansen and Van Boekel, 1991.
[n] Schnack, 1983.
[o] Daro, 1985.
[p] Estep et al., 1990.
[q] Marchant and Nash, 1986.
[r] Sieburth, 1960.
[s] Hamm et al., 2000.
[t] Hansen, 1992.
[u] Hamm and Rousseau (unpublished).
[v] Bullen, 1908.

(Chytridiomyceta), which is able to infect the cells within *Eudorina* colonies.

2. Impact of defence strategy on ecology

In the previous sections I have discussed the fact that the physical properties of the colony skin are suited to reduce grazing pressure on the cells in *Phaeocystis* colonies. But how would this translate to the role of *Phaeocystis* colonies in the ecosystem, and its impact on the ecosystem itself?

Diverse organisms, ranging from viruses to vertebrates, with sizes between ca. 140 nm (viruses) and several cm (krill, fish larvae), potentially decimate phytoplankton. It is evident that a specific defence mechanism which leaves room for competitive growth rates cannot offer complete protection against the whole range of these organisms. Thus, phytoplankton with an efficient defence against certain feeding mechanisms is likely to be susceptible to infection or attacks from organisms with different strategies. Along with its physiological characteristics, the defence strategy of a phytoplankton organism

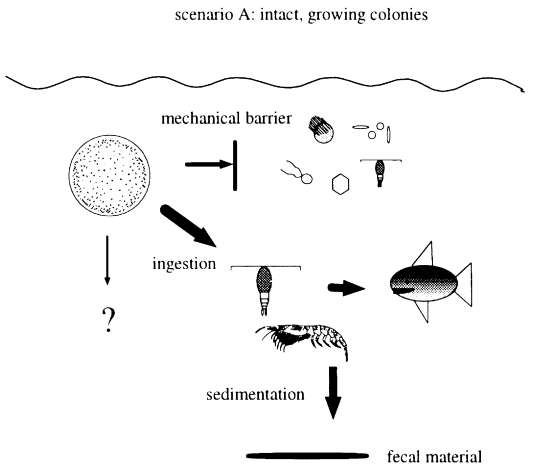

Fig. 1. Hypothetical effects of a protective colony skin on the fate of *Phaeocystis*-derived organic matter during the exponential phase of a *Phaeocystis* bloom: Viruses, bacteria, nanoflagellates, ciliates and small copepods will be deterred, but ingestion by large zooplankton such as copepods and euphausids is possible. This permits bloom formation, but also transfer of organic matter to higher trophic levels, and—in faecal material—to deeper layers. The arrows indicate the relative importance of the different pathways. Organisms not to scale.

is an adaptation to a distinct ecological niche. In the case of *Phaeocystis*, the different defence strategies of the colonies and the flagellates are reflected by the organisms which feed on them: while the flagellates are mainly affected by a broad spectrum of smaller, fast-growing organisms, large predators tend to feed more efficiently on the colonies than on the flagellates (Table 1).

Though this view is simplified and does not account for the complexities of interactions between grazers and prey, it clearly shows how biomass produced by single *Phaeocystis* cells supports a fundamentally different heterotrophic community than biomass in the *Phaeocystis* colonies. The higher growth rates of the organisms affecting *Phaeocystis* single cells, such as ciliates and dinoflagellates, compared to those of the organisms feeding on *Phaeocystis* colonies, such as euphausids (Table 1), might be decisive for dominance of the colonies in *Phaeocystis* blooms. Conversely, it might be expected that larger copepods or euphausids thrive during *Phaeocystis* blooms, while protozooplankton, being unable to feed on the colonies and being grazed by mesozooplankton, will remain at a lower biomass level.

In fact, if related to the abundant phytoplankton biomass, protozooplankton has been shown to be relatively unimportant during *Phaeocystis* blooms which consist mainly of intact colonies (Van Boekel et al., 1992; Brussaard et al., 1995; Garrison et al., 1995), but sharply increase in abundance when the colonies start to disintegrate. The effect of these blooms on the mesozooplankton community is ambiguous. While *Phaeocystis pouchetii* blooms actually coincide with the most intensive growth and production of herbivorous copepods in the Barents Sea and coastal areas of northern Norway, blooms of *Phaeocystis globosa* colonies seem to have an adverse effect on most of the indigenous copepods of the North Sea (Weisse et al. 1994). Though this may be explained by species-specific differences of the *Phaeocystis* colonies or the grazing strategies of the copepods, it remains enigmatic why such fundamentally different effects should occur within these principally similar plankton communities.

3. Impact of defence strategy on biogeochemistry

Having optimised defence and growth for many marine environments, *Phaeocystis* colonies influence the composition and limit the efficiency of the heterotrophic community, and are able to form large, almost monospecific phytoplankton blooms. But what is the impact of the defence strategy on nutrient uptake and fate of the biomass accumulated during such blooms?

3.1. Biogeochemical impact during the exponential phase of the bloom

Phaeocystis blooms deplete nutrients in different ratios than do other phytoplankters. While the C/N ratio of *Phaeocystis* colonies is only slightly higher than the Redfield ratio (Verity and Smayda, 1989), the C/P uptake ratio has been shown to be 40% higher than the Redfield ratio (Arrigo et al., 1999). These ratios are consistent with recent findings that the colony skin contains amino groups, most likely belonging to proteins (Hamm et al., 1999), and the unlikeliness that the colony skin contains phosphorous in significant amounts: in contrast to nitrogen, phosphorous is mainly confined to intracellular compounds, e.g. in membranes (as phospholipids), DNA, sugars or phosphates of nucleic acids. A high

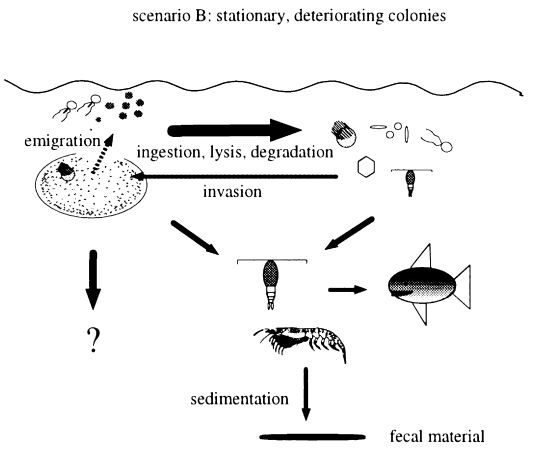

Fig. 2. Hypothetical effects of the loss of protection by the colony skin: small heterotrophic organisms efficiently decimate released cells, and accessible cells in the colony. This leads to a rapid decline of the bloom and retention and remineralisation of organic matter at the surface. Sedimentation of refractory extracellular material from the colonies is likely.

nutritional value of *Phaeocystis* colonies (including the cells), as indicated by their fatty acid composition (Hamm et al., 2000; Hamm and Rousseau, unpublished), would make them a valuable food. Since the mechanical defence mechanism described for *Phaeocystis* colonies seems to be selectively directed against smaller organisms, sedimentation of organic matter via faecal material, which is particulary efficient when caused by large zooplankton (Small et al., 1979), is more likely to occur in *Phaeocystis* colony blooms than in phytoplankton with different defence strategies, e.g. small flagellates, including those of *Phaeocystis*. Such a scenario is described by Hamm et al. (2000), where krill fed on *Phaeocystis pouchetii* when colonies were intact and actively growing, and *Phaeocystis*-derived organic matter sedimented in faecal material of krill (Fig. 1).

3.2. Fates of extracellular colony material and cells after culmination of the bloom

A mechanical defence structure such as a shell (diatom frustules, foraminiferan test, dinoflagellate armour) or a skin (such as the *Phaeocystis* skin) is likely to be difficult to degrade, and thus most likely survives the cytoplasm or cells it protects (Thingstad and Billen, 1994). In large areas of the sea floor, shells of diatoms, radiolarians and foraminiferans are the most important components in accumulating sediments. Suspended aggregates of *Phaeocystis*-derived organic matter in the North Sea were found to be virtually devoid of the essential polyunsaturated fatty acids (Hamm and Rousseau, unpublished), indicating that they contained the refractory material of the *Phaeocystis* colonies, that is, probably the colony skin (Hamm et al., 1999). Accordingly, Janse et al. (1999) have shown that storage polysaccharides from *Phaeocystis* cells are degraded much faster than the extracellular heteropolysaccharides of the colony.

A potential pathway of this nutritionally unattractive colonial material is aggregation and sedimentation. Sinking rates of aggregates depend on their size, but also on their excess density. This is consistent with the observation that *Phaeocystis* colony aggregates typically do not sink as efficiently as do the diatom aggregates (Riebesell, 1995; Hamm and Rousseau, unpublished), which contain their own skeletal material as ballast. Still, slow-sinking but refractory organic matter, which is mainly derived from the colony matrix (Thingstad and Billen, 1994; Hamm and Rousseau, unpublished), may cause efficient sedimentation of *Phaeocystis*-derived organic matter. Indeed, such a mechanism has been proposed to be responsible for the sedimentation of amorphous material after a *Phaeocystis* bloom in the Balsfjord (Riebesell et al., 1995).

The fate of the colony cells differs fundamentally from that of the colony material. Scanning Electron Microscopy (SEM) and Transmission Electron Microscopy (TEM) data suggest that the colony cells do not contain any visible, potentially protective features (Hamm, unpublished results; Van Rijssel, pers. comm., 1999, respectively). To my knowledge, this is in contrast to most other phytoplankton, even solitary cells of similar size, including *Phaeocystis* flagellates, which are covered with scales (Parke et al., 1971). Thus, once liberated and deprived of their protective skin, colony cells are probably particularly susceptible to all kinds of grazing or infection (Fig. 2). This is consistent with findings by Van Boekel et al. (1992) and Brussaard et al. (1995), who observed that unusually massive cell lysis was the main cause of the rapid decline of *Phaeocystis* blooms.

3.3. Analogies and differences to other algae

The liberation of organic matter due to massive cell lysis after the culmination of *Phaeocystis* blooms seems to be unique and is not known in this dimension from other phytoplankton. The sedimentation of *Phaeocystis*-derived organic matter in krill faecal strings observed in the Balsfjord (Hamm et al., 2000) indicated that there might be an efficient way in which nutrient-rich *Phaeocystis*-derived organic matter could be exported, like other phytoplankton, to deeper layers. However, analogous to aggregate sedimentation, the efficiency of sedimentation in faecal material not only depends on the size of the zooplankton responsible for faecal pellet production, but also on the quality of the ingested food: both specific density and degradability of organic matter within faecal material are functions of the diets on which the faecal pellets have been produced. Faecal material containing mineralised phytoplankton like coccolithophorids or diatoms has been shown to be significantly denser, and thus sink faster, than faecal material containing flagellates (Cadée et al., 1992). Additionally, faecal material containing diatoms degraded more slowly than faecal pellets produced on a nanoflagellate diet (Hansen et al., 1996). Finally, though krill faecal strings sink fast, they tend to degrade rapidly and disintegrate before reaching depths of more than 100 m (Cadée et al., 1992). The colony skin and the colony mucus presumably sink within aggregates to larger depths (Riebesell et al., 1995; Passow and Wassmann, 1994). Though this appears to be an efficient mechanism for the sedimentation of *Phaeocystis*-derived material in particular, it is not clear if it really is a unique feature of *Phaeocystis* colonies, or if refractory material from other algae, e.g. the transparent exopolymeric particles (TEP, Passow and Alldredge, 1995) derived from diatoms, have a similar fate (sensu Logan et al., 1995).

4. Perspectives for further research

The hypotheses presented here describe fundamental, qualitative mechanisms, and may be valuable for further concepts on how defence strategies of phytoplankton might affect their ecological and biogeochemical impacts. Further studies will be necessary to understand construction and functioning of the *Phaeocystis* colonies in detail, e.g. by chemically analysing isolated colony skins, and by studying their growth, e.g. with experiments similar to those used to study cell wall growth, such as extensibility of the colony skin under different conditions.

For a refined understanding of the impact of the colony skin on the general role of the genus *Phaeocystis* within the ecosystem, it would be important to study potential variabilities of the colony skin as functions of different species and strains of *Phaeocystis*, and as functions of different abiotic conditions, such as nutrient concentrations, which seem to be critical for the integrity of the colonies and thus the accessibility of the cells therein. Another important ecological question is whether the formation and strength of the colony skin is inducible by the presence of certain predators. The question of how efficient the defence strategy of a colony skin is when confronted with different feeding strategies may be best studied by directly observing how diverse zooplankters deal with *Phaeocystis* colonies.

For an improved assessment of the fate of organic matter derived from *Phaeocystis* and other algae, it is very important to further elaborate the biomarker approach used by Hamm et al., 2000. For instance, this study showed that *Phaeocystis*-specific fatty acids and sterols were useful biomarkers to study the fate of rapidly degradable organic matter derived from the colony cells. If specific biomarkers, e.g. sugars (Janse et al., 1996) or amino acids, could be identified for the colony skin, it should be possible to assess how efficient sedimentation of the more refractory colony skin material can be.

Note added in proof

A recent publication by Di Tullio et al. (2000) demonstrates that cellular material from *Phaeocystis antarctica* can sink in significant amounts to deeper layers of the Ross Sea during the exponential phase of a phytoplankton bloom. A similar scenario has also been described by Hamm et al. (2000) for *Phaeocystis pouchetii* in Balsfjorden/Northern Norway. Yet, the vehicles of particle transport seem to differ in these two regions. While the cellular *Phaeocystis*-derived material in Balsfjorden sank mainly within faecal

material to deeper layers, *Phaeocystis* aggregates, which have been shown to sink inefficiently in the North Sea (*P. globosa*; Riebesell, 1995), seem to dominate export of *Phaeocystis*-derived cellular organic matter to the Ross Sea sediments. However, while the modes of carbon export out of *Phaeocystis* blooms may be as multiform as are the manifestations of their colonies or their trophic fates, there is increasing evidence that sedimentation of *Phaeocystis*-derived organic matter must be regarded as a potentially very efficient component of the biological carbon pump.

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