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BRIEF COMMUNICATION

The colonization of two *Phaeocystis* species (*Prymnesiophyceae*) by pennate diatoms and other protists: a significant contribution to colony biomass

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Abstract The association of *Phaeocystis* spp. with small pennate diatoms during three *Phaeocystis*-dominated spring blooms were investigated in the Eastern English Channel (2003 and 2004) and in coastal waters of Western Norway during a mesocosm experiment (2005). In each of these studies, colonization of the surface of large *Phaeocystis* spp. colonies by small needle-shaped diatoms (*Pseudo-nitzschia* spp.) were observed. In the English Channel the diatom *Pseudo-nitzschia delicatissima* colonized the surface of large (>100 μm) *Phaeocystis globosa* colonies. The abundance of *Pseudo-nitzschia delicatissima* reached 130 cells per colony and formed up to 70% of the total carbon associated with *Phaeocystis* cells during late bloom stages. In Norwegian waters, the surface of large (>250 μm) *Phaeocystis pouchetii* colonies were colonized by *Pseudo-nitzschia* cf. *granii* var. *curvata* and to a lesser degree by other phytoplankton and protist species, although the abundance of these diatoms was never greater than 40 cells per colony. Based on these observations we suggest that diatoms utilize *Phaeocystis* colonies not only as habitat, but that they are able to utilize the colonial matrix as a growth substrate. Furthermore, these observations indicate that a considerable fraction of biomass (chlorophyll) associated with *Phaeocystis* colonies, especially large colonies concerned with intense and prolonged blooms, are due to co-occurring plankton species and not exclusively *Phaeocystis* cells.

Keywords Biomass estimate, colonies · Colonization · *Phaeocystis* bloom · *Pseudo-nitzschia* species

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Introduction

The coexistence of *Phaeocystis* species with pennate diatoms and other protists, although not universally observed, is a well-known and common phenomenon (Hasle 1964; Rousseau et al. 1994; Hasle and Syvertsen 1997; Peperzak et al. 1998; Wassmann et al. 1999; Throndsen et al. 2003; Hamm and Rousseau 2003). In general, the colonization of

the microphytobenthos is well known in shelf waters and in the near-shore regions of seas and oceans, pennate diatoms are also known to dominate in the community of nano- and microalgae on the surface of macrophytes and zoobenthos (e.g. Proshkina-Lavrenko 1963; Sapozhnikov 2003 and many others).

Since the genus *Phaeocystis* was first described over 100 years ago (Pouchet 1892), a large number of observations and studies have reported the conspicuous bloom-forming *Phaeocystis* spp. (see, e.g., review of Schoemann et al. 2005). However, for a long time the presence of the small needle-shaped *Nitzschia* species on and/or in *Phaeocystis* colonies was reported only by Hasle and co-workers (Hasle 1964; Hasle and Syvertsen 1997). These investigators described two diatoms species in association with the surface of *Phaeocystis pouchetii* colonies: *Pseudo-nitzschia delicatissima* and *Pseudo-nitzschia granii* var. *curvata* (Throndsen et al. 2003). Wassmann et al. (1999) reported abundant populations of *Pseudo-nitzschia* cf. *pseudodelicatissima* and the cryptophyte flagellate *Plagioselmis* sp., associated with colonies of *P. pouchetii* in the Barents Sea. In other studies microscopic examination of senescent *Phaeocystis* colonies and foam revealed the presence of large numbers of the pennate diatoms (*Nitzschia* species) on the surface of *Phaeocystis globosa* (Peperzak et al. 1998; Hamm and Rousseau 2003).

During our studies, we observed an abundance of the small needle-shaped *Pseudo-nitzschia* species on *Phaeocystis* colonies provoking interest in both qualitative and quantitative analysis of this phenomenon. If *Pseudo-nitzschia* species comprise a significant fraction of total *Phaeocystis* colony biomass, it is essential to take this fact into consideration in the studies of food webs, vertical fluxes, biogeochemical element fluxes, etc. since *Phaeocystis* is a widely distributed phytoplankter and it often develops massive blooms (Schoemann et al. 2005).

Material and methods

During a bloom of *P. globosa* in March–May 2003 and in February–April 2004 water samples were collected at several stations in the Eastern English Channel in the coastal waters off Boulogne—Wimereux, France (Fig. 1). Water samples were collected from three depth ranges including surface waters (0.5–2 m), mid-depth waters (10–12 m), and water from just above the bottom (20–22 m) using Niskin bottles during several cruises of the RVs "Sepia II" and "Côtes de la Manche". Coastal-offshore transects and 24 h drifting experiments were carried out at two sites, one located off the Wimereux-Slack estuaries and another located southward in the Bay of Somme.

Samples of *P. pouchetii* were also collected from blooms in a mesocosm experiment conducted at the marine biological field station, University of Bergen, Western Norway (60°16′ N, 05°14′ E), on 01–27 April 2005 (Fig. 2). The experiment was conducted essentially as described by Nejstgaard et al. (2006) in floating 11 m^3 polyethylene enclosures (4.5 m deep, 2 m diameter). The mesocosms were transparent with 90% penetration of photosynthetically active radiation (PAR). Mesocosms were filled on 31 March by pumping fjord water from a depth of 5 m. The water column was well mixed with an airlift-system, pumping 40 l water min^{-1}. In order to allow the introduction of new species, to avoid substantial pH changes due to primary production, and to replace the water sampled during the mesocosm experiment, 10% of the mesocosm water was renewed daily starting from April 1 by pumping fjord water from outside the mesocosm from a depth of 2.5 m. An intense bloom of *P. pouchetii* was stimulated after fertilization with NO_3 (16 μm) and PO_4 (1 μm).

Whole colonies and cells within colonies (non-motile stage) of *Phaeocystis* were identified and enumerated by light microscopy. The samples were either live or preserved with 1% glutaraldehyde-lugol solution (Rousseau et al. 1990). In addition, we used epifluorescence microscopy to enumerate and identify flagellate forms (motile stage) of *Phaeocystis* and microplankton (Sherr et al. 2000). In our modified procedure, the samples were stained with primulin, fixed with 3.6% glutaraldehyde solution with 10% glycerol added for better preservation, and gently filtered onto black-stained Nucleopore filters (0.4 μm). Identical microscopy procedures were applied for samples

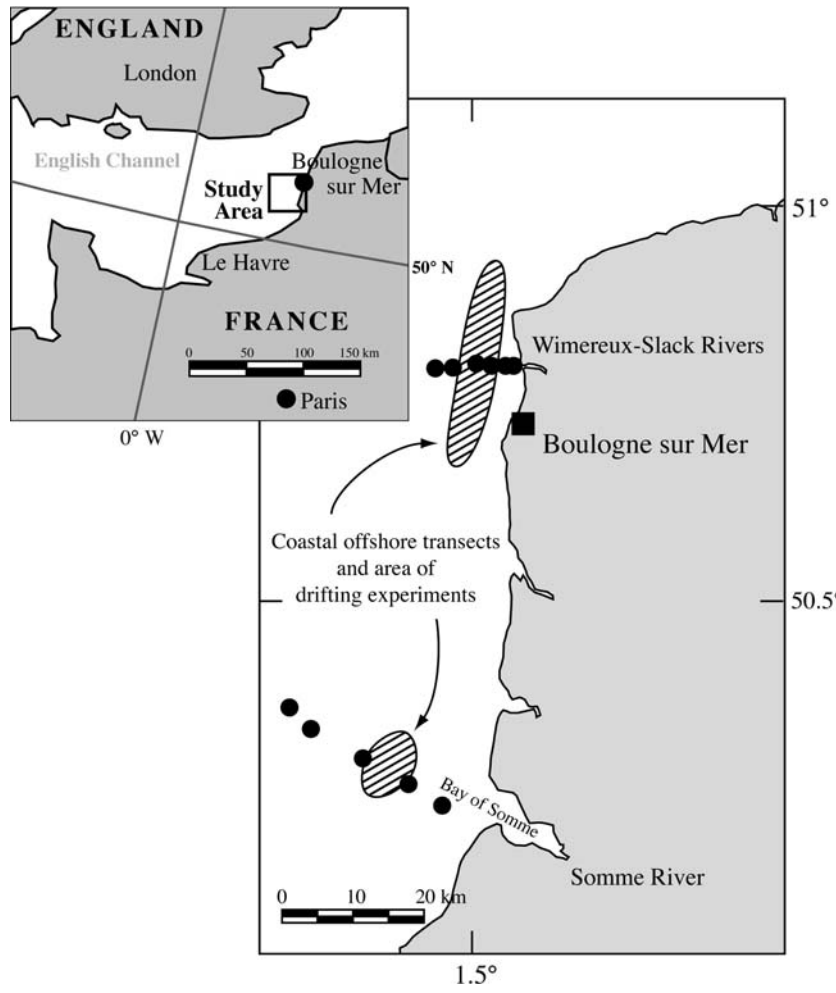

Fig. 1 Map of the sampling area in the Eastern English Channel

from the Eastern English Channel and Western Norway. Our microscopic estimation of the number of nonmotile cells of *Phaeocystis* inside colonies of different volumes corresponded to the results obtained by Rousseau et al. (1994), i.e., according to the following regression equation: $\log N_{cell} = 0.51 \log V + 3.67$ where N_{cell} is the colony cell number and V is the colonial volume expressed in mm^3. For the identification of diatom species, we used a taxonomic key based on light microscope observations (Hasle et al. 1996; Hasle and Syvertsen 1997; Throndsen et al. 2003); and electron microscope observations (Hasle et al. 1996; Priisholm et al. 2002). For *Pseudo-nitzschia delicatissima* from the English Channel, scanning electron microscopy (SEM) electron micrographs were obtained using a LEO 438 VP scanning electron microscope. Cell volume was calculated by approximation to the closest sample 3D shapes and converted into C according to Menden-Deuer and Lessard (2000). The volume of diatoms was generally less than 3000 μm^3, so we applied the following volume-to-carbon conversion formula for protist plankton: pg C $cell^{-1}$ = 0.216 × $volume^{0.939}$.

From the English Channel, 84 samples were counted. Most of the samples were preserved and colonies of *Phaeocystis* were enumerated in the total sample volume collected (100–250 ml). The samples were settled for minimum 24 h, then gently concentrated by removing surface water with a plastic syringes (ca. 10 mm diameter), passed through a 5 µm nylon mesh. All volume of concentrated subsamples (5–10 ml) was observed in 1 ml-Naumann counting chamber (Naumann 1922).

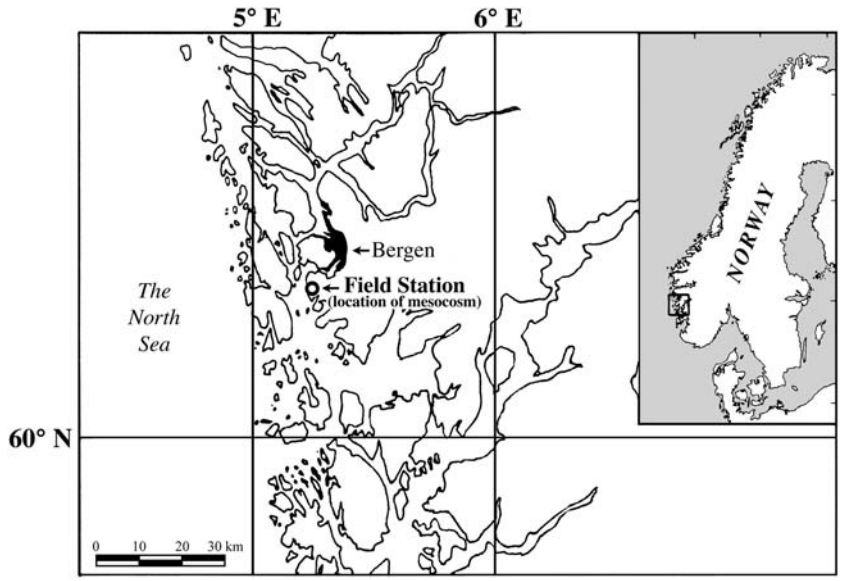

Fig. 2 Map of the location of the Norwegian mesocosm experiment

Because samples were collected from a large variety of hydrographical conditions, it was not possible to statistically analyze the samples with respect to environmental conditions (i.e., time, location, and depth). For this reason, the samples from the English Channel were divided into different groups depending on the stage of the *P. globosa* bloom. These stages were determined on the basis of various characteristics: the presence or absence of colonies, their size and shape and the number of cells within the colonies. An additional indication of one or another stage of the *P. globosa* bloom was provided by other algae, mainly diatoms which were also counted in the samples. Succession changes in phytoplankton community allowed us to make more precise grouping of the data. Three groups were distinguished. The first group included the samples collected in March and several samples collected at the end of February (start of the *P. globosa* bloom), the second group included the samples collected in April (middle of the bloom), and the third included the samples collected in May (end of the bloom). Within each group, independently of collection date, location and depth, the data were counted as one set.

In the Western Norway mesocosm experiment only live samples were analyzed. The development of the *P. pouchetii* bloom in the fertilized mesocosm was followed daily from 1 April–27 April, 2005. During this period about 30 samples were analyzed. In each sample at least 500 colonies were counted and at least 20 colonies were measured.

Results

Pseudo-nitzschia delicatissima[1] (usually as single or formed pairs) colonized the surface of the *P. globosa* colonies at all depths from the Eastern English Channel (Fig. 3a–c). Diatom growth usually started when colony size was over 100 μm (typical biomass values for *P. globosa* cells colony^{-1} are about 380 pg C) and the bloom was rather intense. At this stage, diatoms were observed on 5–14% of the *P. globosa* colonies, with about 5–7 *Pseudo-nitzschia delicatissima* cells per colony (88–124 pg C colony^{-1}) (Fig. 4). Over the course of bloom development, the frequency of colonization increased to about 30%. After one month, when colony size reached 300–600 μm (typical biomass values for *P. globosa* cells colony^{-1} about 1140–1795 pg C), the number of *Pseudo-nitzschia delicatissima* increased

[1] In a recent article (a combination of the morphological and molecular findings) *Pseudo-nitzschia delicatissima* was shown to be a complex of three different species (*Pseudo-nitzschia delicatissima*, *P. decipiens* sp. nov. and *P. dolorosa* sp. nov. (Lundholm et al. 2006).

to 25–50 cells per colony (442–883 pg C colony^{-1}). Two months after the beginning of the bloom, nearly 100% of *P. globosa* colonies were colonized by diatoms, the average colony size was above 1000 μm (biomass values for *P. globosa* cells colony^{-1} were above 3560 pg C), and the number of *Pseudo-nitzschia delicatissima* varied from a few to 120–130 cells per colony (2119–2296 pg C colony^{-1}). Similar observations were made both in 2003 and 2004. In these studies, over the duration of the bloom, the average contribution of *Pseudo-nitzschia delicatissima* to the total biomass associated with *P. globosa* colonies was 46% of total carbon (nonmotile *P. globosa* cells and diatoms). However, during late bloom stages, the biomass of *Pseudo-nitzschia delicatissima* accounted for up to 70% of the total carbon of the *Phaeocystis* cells (nonmotile stage) within the colonies. In these estimates carbon from the colony matrix was not included since noncellular material associated with the colonies contains very little carbon (Rijssel et al. 1997).

During the bloom of *P. pouchetii* in the mesocosm experiment (Norway) the first diatoms appeared when the colonies reached a size of 250 × 180 μm containing about 50 nonmotile cells (544 pg C colony^{-1}). At this stage in colony development the colonies of *P. pouchetii* were transitioning from a spherical to ellipsoid shape and we began to observe their colonization by the diatom *Pseudo-nitzschia* cf. *granii* var. *curvata* (Fig. 5a, b). During the following two weeks, the mean size of the *P. pouchetii* colonies continued to increase to about 370 × 350 μm containing about 200 cells colony^{-1} (2176 pg C of cells/colony) and the number of *Pseudo-nitzschia* cf. *granii* var. *curvata* varied from 4 to 59 cells per colony (136–2011 pg C of cells colony^{-1}), with a mean of 18 cells per colony (613 pg C of cells colony^{-1}). However, fewer than 1% (0.22–0.92%) of *Phaeocystis* colonies was colonized by diatoms (Fig. 6). In addition to *Pseudo-nitzschia* cf. *granii* var. *curvata*, *P. pouchetii* colonies were occasionally colonized by other diatom species. For example, we observed a *P. pouchetii* colony with 12 cells of *Nitzschia frigida* on the surface and other colonies with 1–3 cells of *Cylindrotheca closterium* (Fig. 7). In two samples we observed *P. pouchetii* colonies with attached suctorian ciliates (*Acineta tuberosa*) (Fig. 8). Ciliates of the genus *Acineta* have been reported to be epibionts of decapods, cladocerans, copepods, ostracods isopods and amphipods (Fernandez-Leborans and Tato-Porto 2000; Arndt et al. 2005).

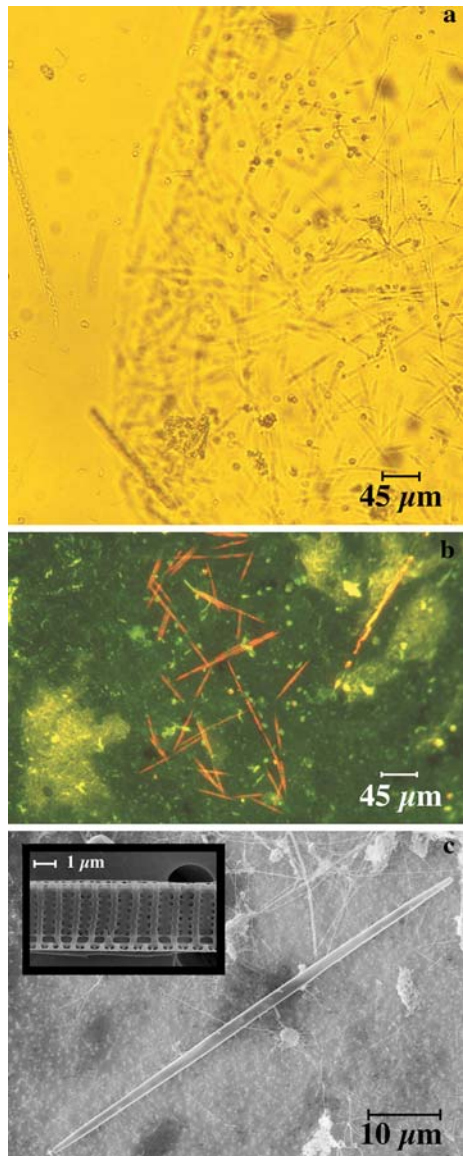

Fig. 3 (**a**–**c**) Diatom *Pseudo-nitzschia delicatissima* inhabiting the surface of the *Phaeocystis globosa* colonies from the Eastern English Channel (**a** light microscopy, **b** epifluorescence microscopy, **c** scanning electron microscopy)

Discussion

In this report we present observations of *Phaeocystis* colonies being colonized by different small

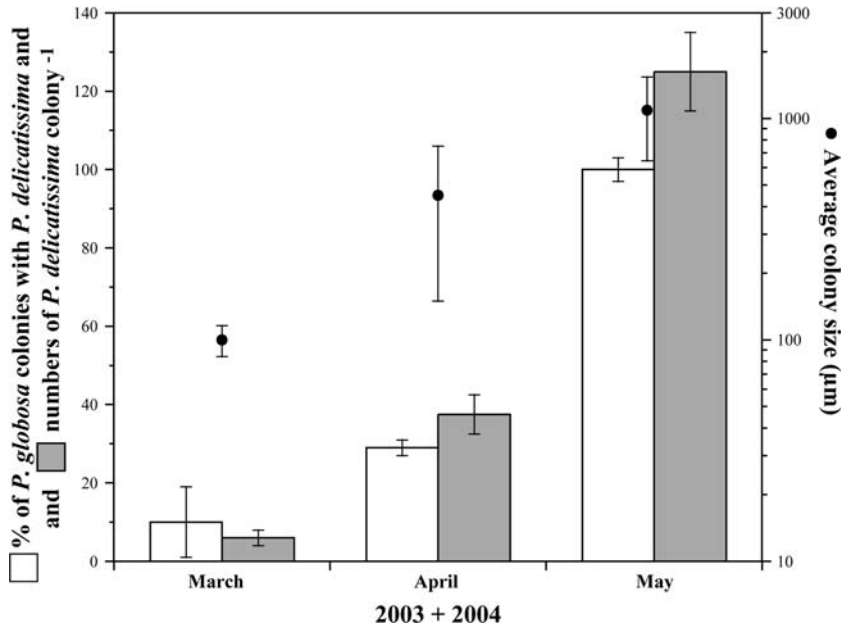

Fig. 4 Bloom and evolution of *Phaeocystis globosa* colonies and diatom *Pseudo-nitzschia delicatissima* from the Eastern English Channel in 2003 and 2004

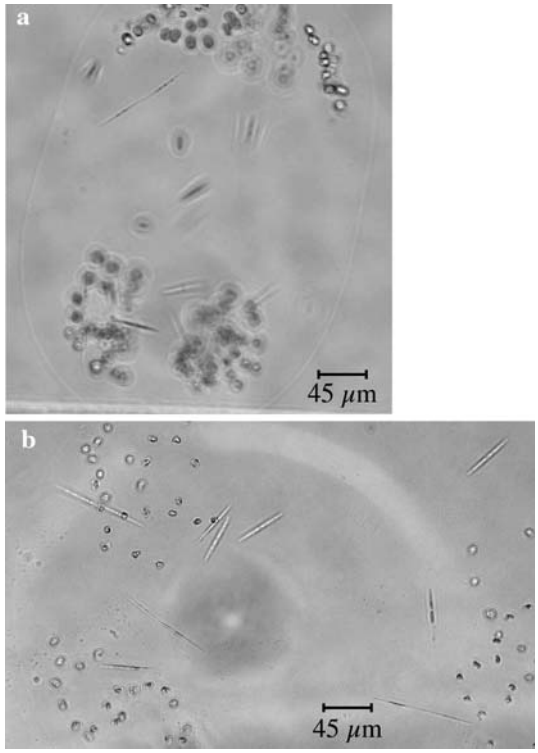

Fig. 5 (**a**, **b**) Diatom *Pseudo-nitzschia* cf. *granii* var. *curvata* inhabiting the surface of *Phaeocystis pouchetii* colonies from Western Norway (light microscopy)

needle-shaped *Pseudo-nitzschia* species to such an extent that the estimated diatom carbon at times was similar to or even exceeded the contribution of the nonmotile *Phaeocystis* cells within colonies. The colonization of *P. globosa* by *Pseudo-nitzchia delicatissima* during two successive years in the English Channel, of *P. pouchetii* by other *Pseudo-nitzschia* species in the Norwegian mesocosm experiment, and earlier reports by other authors, confirm that colonization of *Phaeocystis* colonies by diatoms and other protists appears to be widespread and common phenomenon. For example, the presence of *Calliacantha natans* (Choanoflagellida) in high abundance on senescent colonies of *P. pouchetii* was reported from the Eastern Bering Sea shelf (Sukhanova and Flint 2001), ovoid heterotrophic gymnodinoid dinoflagellates were found on senescent *Phaeocystis* colonies (Peperzak et al. 1998), and preliminary observations of *Phaeocystis antarctica* colonies collected in the Ross Sea show that small (less than 10 µm) heterotrophic protists were associated with the colonial matrix (Shields and Smith 2005). Since the colonies of *Phaeocystis* species may be intensely colonized by pigment-containing algae such as diatoms, care should be taken when estimating *Phaeocystis* colony biomass using pigment-based methods. For example, quantification by Chl *a*, or even high-performance liquid chromatography (HPLC) and chemical taxonomy (CHEMTAX) without direct inspection of the algal material (cf. Irigoien et al. 2004) may lead to significant overestimation of the *Phaeocystis* biomass. As seen in

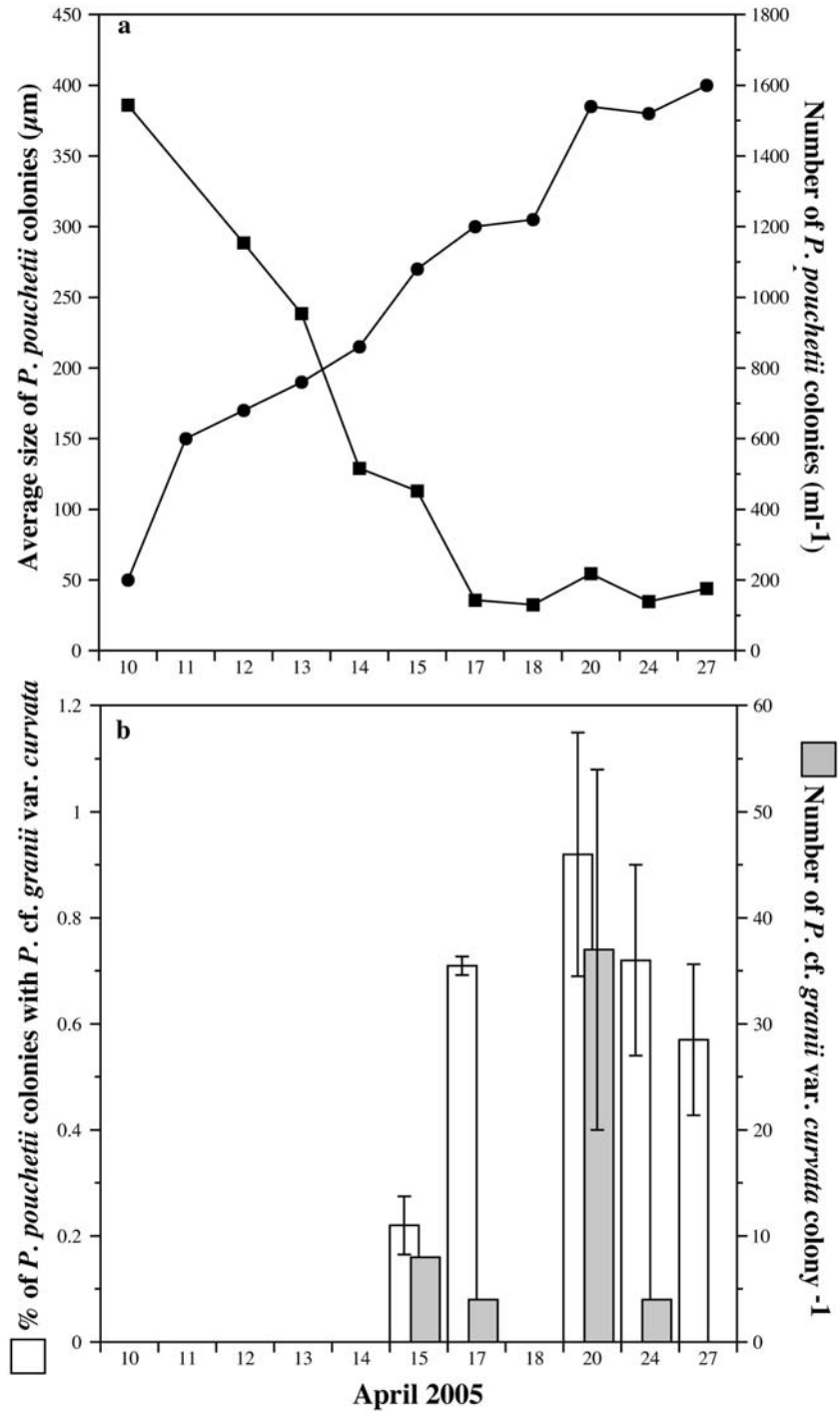

Fig. 6 Bloom and evolution of *Phaeocystis pouchetii* colonies (**a**) and diatom *Pseudo-nitzschia* cf. *granii* var. *curvata* (**b**) from Western Norway. The squares refer to the number of colonies and the circles to the average size of the colonies

Fig. 3b, the majority of total chlorophyll associated with a *Phaeocystis* colony can be derived from diatoms on the colony rather than *Phaeocystis* cells within the colony. Therefore to accurately quantify *Phaeocystis* biomass, particularly during intense and prolonged blooms, it is necessary to consider the accompanying algae on the colonies and unambiguous methods such as microscopy should be routinely utilized.

The underlying processes influencing the association between *Phaeocystis* colonies and diatoms remains incompletely understood. The relationship

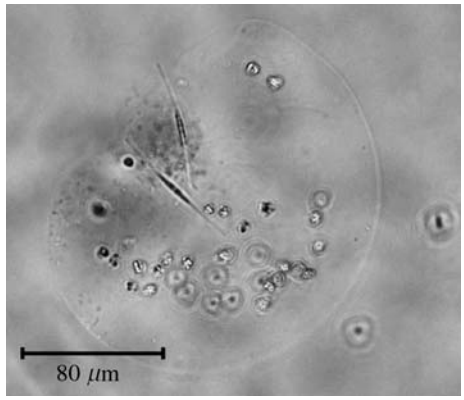

Fig. 7 Diatom *Cylindrotheca closterium* inhabiting the surface of a *Phaeocystis pouchetii* colony from Western Norway (light microscopy)

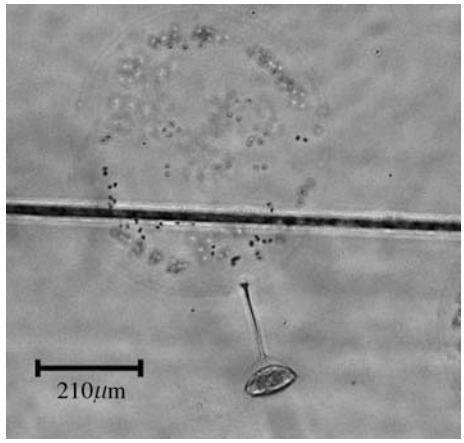

Fig. 8 *Acineta tuberosa* (Suctoria) attached to the surface of a *Phaeocystis pouchetii* colony from Western Norway (light microscopy)

between colonized *Phaeocystis* and diatoms may represent either an active or passive association. Recent studies in the Southern Ocean have demonstrated that *P. antarctica* and diatoms have similar photosynthetic capabilities and that growth of both can co-occur under similar light conditions (Hilst and Smith 2002). If this is also the case for *P. globosa*, *P. pouchetii*, and associated *Pseudo-nitzschia* species, the colonization of *Phaeocystis* colonies by diatoms might be expected to occur without advantage or disadvantage to either species under similar favorable growth conditions. Alternatively, it is well known that diatoms are able to use various organic substances, especially when photosynthesis is limited (Lewin and Hellebust 1976; Molloy and Syrett 1988; Petterson and Sahlsten 1990; Graham and Wilcox 2000). It is therefore possible that diatoms might use *Phaeocystis* spp. colonies not only as habitat, but may be able to utilize organic and inorganic substances derived from or associated with the colonial matrix. Such a commensalism could be increased as the *Phaeocystis* colony becomes older and less defended due to deterioration of the colony membrane (Hamm et al., 1999; Hamm, 2000) or becomes less allelopathic (Long et al. submitted). Still another possibility is that *Phaeocystis* might benefit from an association with *Pseudo-nitzschia* in which case their association would represent a true symbiosis. It has been reported that *Pseudo-nitzschia* species can produce specific aldehydes that reduce copepod fecundity (Miralto et al. 1999) and thus, the presence of *Pseudo-nitzschia* spp. on *Phaeocystis* colonies might provide a level of grazing protection to aging colonies. However, in our opinion the interactions of *Pseudo-nitzschia* species and *Phaeocystis* colonies are most likely to be of the facultative commensalism type, although additional studies are needed to investigate this hypothesis. Regardless, conceptual models of the life cycle of *Phaeocystis* spp. (Whipple et al. 2005) especially ecological significance of the colonial life form should now take into account *Pseudo-nitzschia*/*Phaeocystis* association.

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