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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