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Does *Phaeocystis* spp. contribute significantly to vertical export of organic carbon?

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Abstract *Phaeocystis* spp. cell and colony mass fluxes and their contribution to the vertical particulate organic carbon (POC) export from a wide range of stations were quantified by short-term sediment traps. The compilation of available data, ranging from polar to sub-arctic and boreal regions, revealed that *Phaeocystis* colonial and single cells frequently are observed in shallow sediment traps at 30–50 m depth (average of 7 ± 11% of POC export). A strong vertical export decline between 40 m and 100 m diminished the contribution of *Phaeocystis* spp. cell carbon to vertical export of POC to only 3 ± 2% at 100 m depth, with two exceptions (deeper mixed stations). Estimates of potential corresponding mucus contribution increased the average *Phaeocystis* spp. contribution to <5% of POC export. The vertical flux attenuation efficiency is higher for *Phaeocystis* spp. than for diatoms. The overall contribution of *Phaeocystis* spp. to vertical carbon export based on direct investigations of vertical organic carbon export is small.

Keywords Carbon flux · Cells and mucus · *Phaeocystis* · Transparent exopolymer particles (TEP) · Vertical export

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Introduction

Only a few phytoplankton taxa have a significant biogeochemical impact on the global scale. One of these is the colony-forming haptophyte *Phaeocystis* spp. Most phytoplankton taxa, which have a significant biogeochemical impact on the carbon cycle, such as diatoms, coccolithophorids and dinoflagellates, leave behind cell structures and distinct, relatively stable biochemical signals in sedimented matter or the sediment record. This is not the case with the key taxon *Phaeocystis* spp. Its impact on the global C flux is thus easily disregarded since evidence often derived from long-term measurements of vertical export at depth (>1,000 m) or sediment cores where signals are scant or nonexistant.

The role of *Phaeocystis* as a globally distributed key genus for biogeochemical cycling, food web structure and impact on climate is acknowledged (Schoemann et al. 2005, and refs. therein; Verity and Smetacek 1996). However, the impact of *Phaeocystis*-derived carbon on the total organic carbon export to depth is not well known. To evaluate the role of *Phaeocystis* spp. in ecosystems and biogeochemical cycling, it is of utmost importance to evaluate our knowledge on the impact of *Phaeocystis*-derived material to the total vertical carbon export to depth. The importance of vertical export for the fate of *Phaeocystis* spp. and as contribution to the vertical organic

carbon export is still a matter of controversy (e.g., Schoemann et al. 2005). Based upon visual examination and POC export, Wassmann et al. (1990) reported mass sedimentation of *P. pouchetii* from the Barents Sea. In the Antarctic region, indirect observations of vertical export through deep fluorescence signals together with elevated concentrations of DMSP and *P. antarctica* cells at >400 m in the Ross Sea (DiTullio et al. 2000), indicated that export of *P. antarctica*-derived material took place in this region. Formation of fast-sinking aggregates was suggested as a mechanism enhancing the vertical export in diatom- as well as *P. antarctica*-dominated regions of the Ross Sea (Asper and Smith 2003), although microscopic examination of the aggregate composition was not carried out. However, Gowing et al. (2001) and Pakomov et al. (2002) were unable to detect rapid and substantial export of *P. antarctica* using long- and short-term sediment traps in the Ross and Lazarev Seas, respectively. In the northern hemisphere, Smith et al. (1991) described significant blooms of *P. pouchetii* in the Norwegian and Greenland Sea, and suggested large-scale vertical export, in essence based upon the depth distribution of fluorescence signals. A *P. pouchetii* bloom in the Eastern Bering shelf, was followed by observations of cells close to the sediment surface at the shallow stations, but not in deeper regions (Sukhanova and Flint 2001). Despite significant blooms in the North Sea and observations of colonies within the benthic boundary layer (Riebesell 1993), no indications of fresh *Phaeocystis*-derived material (lipid composition) were found in surface sediments after a *P. globosa* bloom (Hamm and Rousseau 2003). Carbon budgets for a *Phaeocystis*-dominated ecosystem off Belgium, suggests sedimentation to be of minor importance (Rousseau et al. 2000).

The contradictory observations indicate that no universal rule can be applied regarding the vertical flux of *Phaeocystis* spp. and material derived from this genus. Episodic flux events that export *Phaeocystis* spp. material to deeper waters or the sediments obviously take place (based upon indirect evidence), but uncertainty exists regarding its role in biogeochemical cycles and if vertical export is important for the fate of the frequently observed, extensive *Phaeocystis* spp. biomass accumulations. What is needed is to directly measure the export of cells and colonies, evaluate the mechanisms involved and investigate the frequencies of events.

To quantify the vertical export of *Phaeocystis* spp. and its relative contribution to the particulate organic carbon (POC) export, direct measurements involving sediment traps with microscopic examination and biogeochemical analysis of the vertical flux is required. The catchment efficiency of sediment traps is at all times a matter of concern, but the assessment of Coppola et al. (2002) suggests that the majority of traps used in the current investigation measured particulate vertical export exactly. Even taxon-specific tracers such as high-performance liquid chromatography (HPLC) pigments and pigment ratios can confuse important groups such as diatoms, *Phaeocystis* spp. and dinoflagellates (Irigoien et al. 2004), highlighting the importance of time-consuming microscopic examination. Few studies are published where *Phaeocystis* spp. cells from sediment traps have been quantified through microscopic examination. As a consequence, attempts to estimate the relative contribution of *Phaeocystis* spp. to vertical carbon export are rare. Here, we bring together published and unpublished vertical export rates of *Phaeocystis* spp. for a more thorough evaluation of *Phaeocystis* export. As a final point we attempt to solve the controversy on the importance of *Phaeocystis* spp. for the contribution to the vertical organic carbon export.

Methods

Sampling sites and sediment trap measurements

Sediment trap investigations involving microscopic determination of *Phaeocystis* spp. cell fluxes have been conducted in North Norwegian fjords, the Barents Sea, the south-western part of the North Sea off the Dutch coast, and the Arctic Ocean (Amundsen Basin). Investigation sites, sampling periods, number of samplings and geographical positions are given with reference to data source in Table 1.