Biogeochemistry (2007) 83:217–234
DOI 10.1007/s10533-007-9093-3

ORIGINAL PAPER

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

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Received: 10 April 2006 / Accepted: 10 August 2006 / Published online: 23 March 2007

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.

Table 1 Data from a wide range of localities and sampling dates relevant for *Phaeocystis* spp. blooms is included

Station	Lat.	Long.	Period	Sed. trap (m)	Depth (m)	Data source/ comment
Balsfjord	69.36	19.17	11.04.96	40, 100	190	This study
			15.04.96	40, 100		
			18.04.96	40, 100		
			22.04.96	40, 100		
			24.04.96	40, 100		
			30.04.96	40, 100		
			02.05.96	40, 100		
			07.05.96	40, 100		
			14.05.96	40, 100		
			21.05.96	40, 100		
			28.05.96	40, 100		
Balsfjord	69.37	19.12	08.04.97	40, 100	190	Reigstad et al. (2000) No SD 0–100 m
			11.04.97	40, 100		
			14.04.97	40, 100		
			18.04.97	40, 100		
			24.04.97	40, 100		
Balsfjord (n = 3)	69.37	19.12	19–25.04.01	100	190	This study
Malangen	69.50	18.35	09.04.97	40, 100	380	Reigstad et al. (2000) No SD 0–100 m
			12.04.97	40, 100		
			15.04.97	40, 100		
			17.04.97	40, 100		
			23.04.97	40, 100		
Malangen (n = 3)	69.5	18.35	18–24.04.01	100	380	This study
Ullsfjord	69.82	19.83	10.04.97	40, 100	279	Reigstad et al. (2000) No SD 0–100 m Susp. conc.
			13.04.97	40, 100		
			16.04.97	40, 100		
			22.04.97	40, 100		
			25.04.97	40, 100		
Ullsfjord (n = 3)	69.82	19.83	20–26.04.01	100	279	This study
North Sea off-shelf (n = 7)	53.93–54.11	4.35–4.71	09–29.04.02	30	45	This study, no SD
North Sea on shelf (n = 6)	52.94–53.14	4.42–4.57	07–28.04.02	15/20	25–30	This study, no SD
Barents Sea (ArW)	76.01	32.59	20.05–98	90	323	Olli et al. (2002)
Barents Sea (PF)	73.47	31.38	26.05.98	90	340	Olli et al. (2002)
Barents Sea (AW)	72.29	30.56	28.05.98	90	301	Olli et al. (2002)
Arctic Ocean (n = 6)	88–89	-9.5–3.7	02–22.08.01	90	4000	Olli et al. (2007)
Ross Sea/W Polynya (n = 5)	–76.5	–177.6–165	24.12.95–12.01.96	200		Gowing et al. (2001)
Lazarev Sea (n = 6)	–68.2–68.35	0.5–0.9	28.12.94–08.01.95	120		Pakomov et al. (2002)/this study

Each station is identified with number of samplings for averaged data (n=), and decimal positions as latitude (Lat. N) and longitude (Long. E). South and western positions are given as negative co-ordinates. Dates of sediment trap retrieval and depths of deployments (m) are given, as well as station depths (m) where available. Data sources are given with references for published data. Some stations lack suspended data (SD) from the 0–100 m depth interval

Vertical flux of particulate organic carbon (POC) and phytoplankton was measured with two parallel cylindrical sediment traps (aspect ratio 6.25), mounted in a gimballed frame equipped with a vane (KC maskiner og laboratorieudstyr, Denmark) (e.g., Reigstad et al. 2000; Olli et al. 2002). No baffles were used. The traps have been calibrated with the ^{234}Thorium technique with close to 100% trapping efficiency (Coppola et al. 2002; Lalande 2006). Sampling

depths varied for the different investigations according to Table 1, and sampling time were in general about 24 h. The mooring was drifting in a Lagrangian mode, balanced with subsurface and surface buoys or anchored to ice (Barents Sea). During the seasonal study in Balsfjord, 1996, moored traps with duplicate set of cylinders were deployed for periods of 3–14 days, one set with Lugol–glutaraldehyde mix (Rousseau et al. 1990) for phytoplankton enumeration, and the other set with formaldehyde (all other analyses). Fixatives were injected with 400 ml NaCl-enriched water (40 psu) to the bottom of the sediment trap cylinders that were pre-filled with filtered seawater (2% final fixative concentration).

Analysis and calculations

Aliquots of 50–800 ml were taken for POC analyses and filtered onto pre-burned Whatman GF/F filters, frozen until analysis on a Leeman Lab 440 CHN analyser. For further details, see Reigstad et al. (2000). Total particulate matter (TPM) were filtered onto pre-weighed and pre-burned Whatman GF/F filters (50–500 ml) and analysed according to Wassmann (1991).

Phytoplankton was counted using a combination of methods (see further details in Wassmann et al. 2005). A standard light microscope, furnished with a counting stage (Semina 1978) was used. The most abundant nanoplankton algae (2–20 μm) were counted in Fuchs-Rosenthal chambers with magnification of 400×. After the smaller phytoplankton was enumerated, the sample was slowly decanted through a glass tube covered with two layers of fine-mesh nylon gauze to a 5–10 ml concentrated sample. After gentle mixing, a subsample was transferred to a 0.05 ml. chamber. Cells were counted under magnification of 200×. In order to count rare (usually larger) forms the whole sample (100–250 ml) was reduced to 1 ml by settling in a 1.0 ml chamber. These methods allowed also counting of non-sinking cells.

Biovolumes of individual cells were calculated from linear dimensions of measured cells applied to appropriate stereometric formulae (Smayda 1978). Carbon conversion factors established by Menden-Deuer and Lessard (2000) were used to estimate carbon content for diatoms (pg C $cell^{-1} = 0{,}288 \times vol^{0.811}$), and for non-diatoms (incl. dinoflagellates, flagellates, loricate ciliates) (pg C $cell^{-1} = 0{,}216 \times vol^{0.939}$). For *Phaeocystis pouchetii*, the estimated carbon content of 2.41 pg C (cell d = 3 μm) and 16.3 pg C (cell d = 6 μm) is comparable to measured rates of cell carbon for *P. globosa* and *P. antarctica* (10.8 ± 3.47 and 3.33 pg C $cell^{-1}$, respectively) as given by Schoemann et al. (2005, and references therein).

In the seasonal Balsfjord study, subsamples for transparent exopolymer particles (TEP) analysis (n = 5) were taken from the formaldehyde preserved cylinder (5–100 ml). TEP was gently filtered onto 0.4 μm membrane filters and stained with Alcian blue (Sigma A5268) according to Passow and Alldredge (1995). The samples were stored frozen, dissolved in 80% H_2SO_4 and measured spectrophotometrically at 787 nm. The amount of TEP is expressed as gum xanthan equivalents (mg gum xanthan equiv. m^{-2} d^{-1}) based on calibration with gum xanthan (Sigma 1253).

Daily loss rates were calculated according to the following equation:

$$\text{Loss rate } (\%d^{-1}) = (A/B) * 100$$

where B is the suspended concentration over an integrated depth (0–100 m, mg m^{-2}), and A is the flux at 100 m (mg m^{-2} d^{-1}). The sinking speed is estimated as

Sinking speed (m d^{-1}) = integrated depth (m) × loss rate (% d^{-1})/100

Results and discussion

How to define vertical export of *Phaeocystis*-derived matter?

An ambiguous use of the term export has lead to an impression of considerable deep vertical export following *Phaeocystis* blooms based on high export rates out of the euphotic zone in the Barents Sea (Wassmann et al. 1990; Wassmann 1994). However, high export out of the euphotic zone does not necessarily imply that the *Phaeocystis* spp.-derived material is exported to

the sediments or deeper ocean regions as strong mesopelagic remineralisation of *Phaeocystis* spp. can take place (Wassmann 1994; Riebesell et al. 1995; Wassmann et al. 2003). Three stations from three distinct regions in the Barents Sea (e.g., the Atlantic-dominated region in southwest, the well-mixed Polar Front and Arctic water) illustrate how vertical fluxes of *Phaeocystis pouchetii* cells decline with increasing depth and in relation to the density profile (Fig. 1). The decline is not confined to any fixed depth, but strongly related to the depth of the upper mixed layer which is shallow and distinct in the strongly-stratified Arctic water, and deeper in the less-stratified Atlantic water more exposed to vertical mixing (Olli et al. 2002; Reigstad et al. 2002). The vertical flux attenuation is sharp and confined to depth between 30 m and 40 m in the Arctic waters (Fig. 1). In the less-stratified, deeper-mixed Polar Front and Atlantic water (Reigstad et al. 2002) algae are mixed deeper and the flux attenuation is weaker and continues down to 90 m depth (Fig. 1).

It is therefore important to differentiate between: (1) export of *Phaeocystis* spp. cells out of the euphotic zone as a part of a bloom termination, and (2) export of *Phaeocystis*-derived material injected into the deeper regions and benthic boundary layer (BNL) as a part of biogeochemical cycling. For the termination of a bloom it can be critical that the biomass is exported below the euphotic zone or upper-mixed layer preventing sufficient light for further growth. As a part of the larger-scale biogeochemical cycling and carbon sequestration the *Phaeocystis*-derived material must enter the deeper waters or BNL. Mass sedimentation of *Phaeocystis pouchetii* was observed at 50 m depth in the Barents Sea (Wassmann et al. 1990), but a strong decline in the vertical flux resulted in that only a fraction of this material was delivered to or below 100 m depth (Wassmann 1994). A similar pattern was encountered in a seasonal study in Balsfjord, northern Norway, in 1996, where <10% of the *P. pouchetii* cell flux at 40 m reached 100 m depth (Fig. 2). Similar observations of strong reductions in *P. pouchetii* cell flux in the 40–60 m depth interval have also been made in the Barents Sea by Andreassen and Wassmann (1998), and repeatedly in North Norwegian fjords (Lutter et al. 1989; Riebesell et al. 1995; Reigstad et al. 2000). A high vertical resolution of sediment traps in the upper 200 m of the pelagic zone is therefore indispensable. It is a precondition to

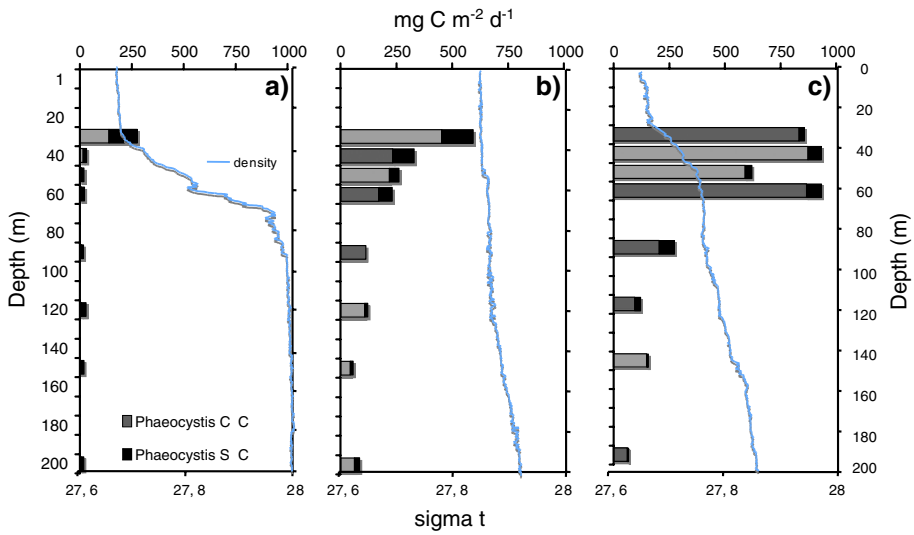

Fig. 1 Vertical pattern of *Phaeocystis pouchetii* export (mg C m^{-2} d^{-1}) in different water masses in the central Barents Sea (**a**) Arctic Water, (**b**) Polar Front and (**c**) Atlantic water measured by sediment traps at 30, 40, 50, 60, 90, 120, 150 and 200 m depth in May 1998 (modified from Olli et al. 2002). Sigma t for the water mass of the investigated stations is given. *Phaeocystis* export is differentiated into colonical cells (CS) and single cells (SC)

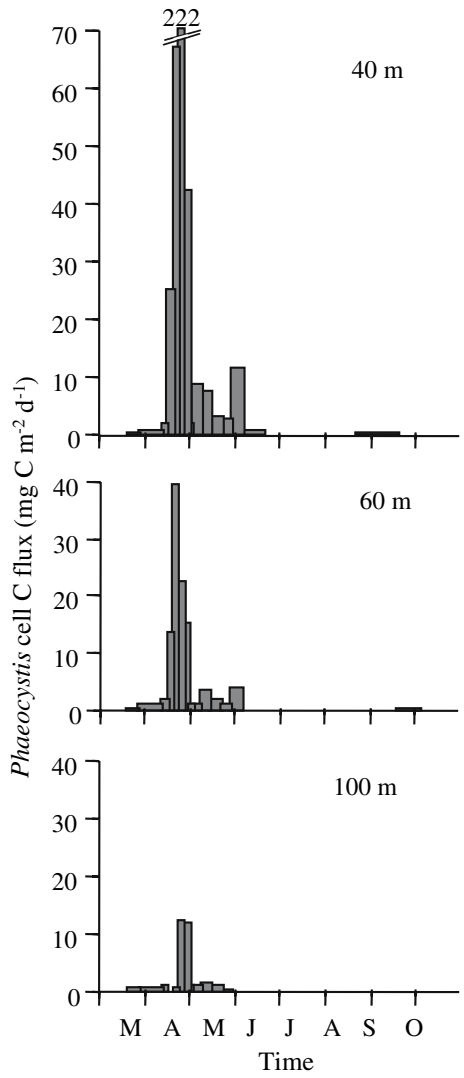

Fig. 2 Vertical flux of *Phaeocystis pouchetii* from March to October, 1996, in Balsfjord, northern Norway. Sediment traps were deployed at 40, 60 and 100 m depth, and the *P. pouchetii* cell carbon flux is given as mg C m^{-2} d^{-1}

evaluate how significantly phytoplankton and organic matter contributes to the recirculation and vertical export of bioelements.

The data compiled and presented below concern primarily *P. pouchetii* due to the abundance of sediment trap and microscopy data from the northern region, which is dominated by this species (Table 1). Limited numbers of data sets are available from regions dominated by *P. globosa* and *P. antarctica*. We will focus on the vertical export below the flux attenuation interval in the upper 50–100 m where retention, recycling, repackaging, grazing, remineralisation and aggregation shape the vertical flux profile according to ecosystem structure and environmental factors (Wassmann et al. 2003).

The morphological challenge: cells and colonies

There are several challenges in quantifying vertical flux of *Phaeocystis*-derived carbon. The quantification of exported cells and colonies and the conversion to carbon are two of the most prominent ones.

The presence of smaller and larger free-living flagellated stages (2–8 μm) as well as nonflagellated colonial cells within colonies of different size, morphology and fragility requires a dedicated microscopical approach combining several methods (Rousseau et al. 1990; Mathot et al. 2000; Gowing et al. 2001; Wassmann et al. 2005). Long-term deployments of sediment traps using formaldehyde, which does not adequately preserve flagellates, leads to an underestimation of *Phaeocystis* cells from colonies (T. Ratkova, pers. com.). Identification of single versus colonial cells can also be difficult due to loss of flagellae in formaldehyde-fixed samples. Use of short-term sediment traps without fixatives and the Lugol–glutaraldehyde cocktail recommended by Rousseau et al. (1990) improves cell and colony preservation. The fragility of *P. pouchetii* colonies combined with the handling of samples and the storage time prior to analysis does, however, result in an underestimation of size and number of colonies due to fragmentation and dissolution that is difficult to quantify exactly (Wassmann et al. 2005).

Quantification of *Phaeocystis*-derived carbon further requires appropriate carbon conversion factors for single cells and colonies in healthy as well as senescent conditions for all *Phaeocystis* species. Relationships between colony size, cell number and carbon have been established and published for *P. globosa* (Rousseau et al. 1990; Rijssel et al. 1997) and *P. antarctica* (Mathot et al. 2000) as described by Schoemann et al. (2005). Such relationships have not been established for *P. pouchetii*, and the variable colony morphology makes it problematic to apply

carbon conversion factors established for other species.

At present, we are not able to meet all the requirements for a proper quantification of the carbon content of *P. pouchetii* colonies. Neither can we assure that the vertical fluxes of *P. pouchetii* colonies are reliable, as fragmentation of colonies can overestimate the colony vertical flux in terms of number. Similarly, dissolution of colonies may lead to an underestimation of the colony number and size. Through tedious microscopical analysis we do, however, have reliable measurements of depth-dependent vertical fluxes of *Phaeocystis* spp. cells (Figs. 1, 2). To provide a preliminary determination of the potential contribution of *Phaeocystis* spp. carbon to the vertical POC export at 100 m, we select available carbon conversion rates for other *Phaeocystis* spp. species.

The relative importance of *Phaeocystis* spp. cell carbon to vertical POC export

Few studies exist where mass fluxes of *Phaeocystis* cell carbon have been quantified along with POC export. We compiled the existing data sets to evaluate the contribution of *Phaeocystis* spp. cell carbon to vertical carbon flux. *Phaeocystis pouchetii* blooms are regularly observed in North Norwegian fjords (Heimdal 1974; Eilertsen et al. 1981; Riebesell et al. 1995; Reigstad et al. 2000; Wassmann et al. 2005). Due to the close vicinity of Tromsø, many years of observations from the water column as well as from sediment trap measurements (without fixatives) are available from these localities.

Three examples with focus on the vertical flux attenuation or geographical range are provided below. First we give a specific example on loss rates and the relative contribution of *P. pouchetii* to POC export in fjords. Second, the relative ratio of *P. pouchetii* cell carbon to diatom carbon is compared suspended and in the contemporary vertical export at 40 and 100 m depth, to point to the higher vertical flux attenuation of *P. pouchetii* compared to diatoms. As a third example, available published and own data quantifying the contribution of *Phaeocystis* spp. cells to vertical carbon flux at 100 m depth is presented and compared.

Although a *Phaeocystis* spp. colony bloom may be highly recognisable in surface waters, its contribution to the vertical export at 100 m in terms of cells carbon turns out to be minor. During a three-week field period in three North Norwegian fjords in spring 2001, nine 24 h sediment trap deployments (without fixatives) were completed (Tables 1, 2). The integrated suspended biomass of *Phaeocystis pouchetii* (presented as cell carbon) displayed an average that varied by a factor of three between the fjords, but cell carbon loss rates to 100 m depth were comparable and low, ranging from 0.2% to 2.1% (Table 2). The taxonomic composition of the exported phytoplankton carbon (PPC) showed a dominance of diatoms and diatom spores (Fig. 3a), despite the abundance of *P. pouchetii* in the suspended biomass in the Ullsfjord and Malangen fjords (Table 2, Wassmann et al. 2005). Among the *P. pouchetii* cells identified in the sediment trap at 100 m, ~97% were flagellated, about 6 μm in diameter, and categorised as single cells (Fig. 3b).

This feature of stronger attenuation of *P. pouchetii* cells compared to diatoms is prominent. The disappearance of *Phaeocystis* spp. in the upper aphotic zone flux attenuation interval is illustrated by the change in the *Phaeocystis*/diatom ratio (cell C/cell C) in the integrated suspended versus sediment trap material from 40 m to 100 m depth, in North Norwegian fjords, the Barents Sea and Arctic Ocean (Table 1, Fig. 4). Ratios of >1 reflect *Phaeocystis* spp. dominance, and ratios of <1 reflect diatom dominance. At 40 m depth, the exported particulate material reflects the integrated suspended *Phaeocystis*-diatom composition. A suspended *Phaeocystis* spp. dominance at 11 out of 26 stations examined, resulted in *Phaeocystis* spp. dominated vertical export at six stations at 40 m depth (Fig. 4a). At 100 m depth, *Phaeocystis* spp. dominated the integrated suspended composition at 12 out of 19 stations, while the *Phaeocystis* signal disappeared and the exported material at 100 m were dominated by diatom C at 17 stations (Fig. 4b). Only at two stations *Phaeocystis* spp. cell C dominated the vertical export (ratios > 1)

Table 2 Daily loss rates of *Phaeocystis pouchetii* cell carbon (C) from the integrated standing stock (0–100 m) to sediment trap at 100 m depth in three North Norwegian fjords, April, 2001

Phaeocystis pouchetii	Malangen	Balsfjord	Ullsfjord
Suspended biomass (mg C m^{-2})	2,897 ± 447	1,337 ± 494	3,727 ± 1,292
Vertical C flux (mg C m^{-2} d^{-1})	29 ± 9	13 ± 7	21 ± 7
Loss rates (%)	1.0 ± 0.4	1.2 ± 0.9	0.6 ± 0.4
Sinking rate (cm h^{-1})	4.3	5.0	2.7

Average ± standard deviation of three sampling events.

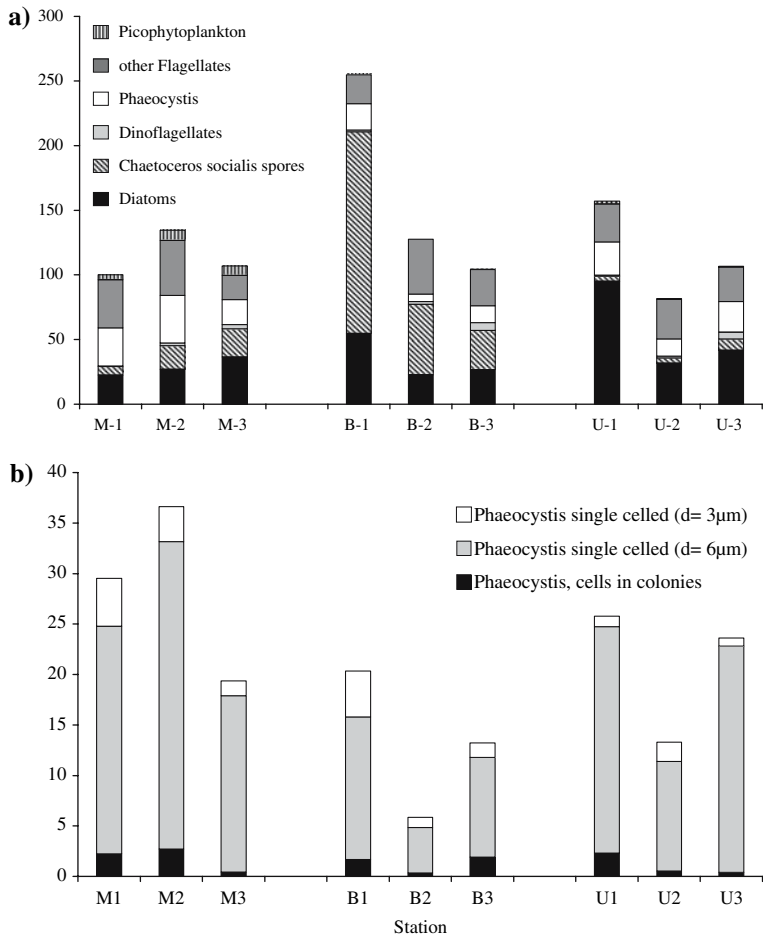

Fig. 3 (**a**) Carbon fluxes attributed to pico-, nano- and microplankton (e.g., diatoms, *Chaetoceros socialis* spores, dinoflagellates, *Phaeocystis pouchetii* cells, other flagellates and picophytoplankton) and (**b**) the carbon flux of *Phaeocystis pouchetii* cells shown as single cell (d = 3 and d = 6 µm) and colonial cells. Fluxes were measured using short-term sediment traps at 100 m depth in three North Norwegian fjords, Malangen (M), Balsfjord (B) and Ullsfjord (U), during three 24 h sampling events in each fjord in April, 2001

at 100 m depth. They were characterised by deep mixing >90 m depth in the Polar Front and the Atlantic region of the Barents Sea (Fig. 1b, c). Even if the integrated suspended biomass of *Phaeocystis* spp. was up to five times that of diatoms, the vertical export of diatoms exceeded the *Phaeocystis* export at all other stations.

A few published studies exist where *Phaeocystis* PPC as a fraction of POC has been quantified (Reigstad et al. 2000; Gowing et al. 2001; Olli et al. 2002; Pakhomov et al. 2002). Compiling these data with some previously unpublished data from investigations carried out by Wassmann and co-workers in Tromsø, Norway, provides

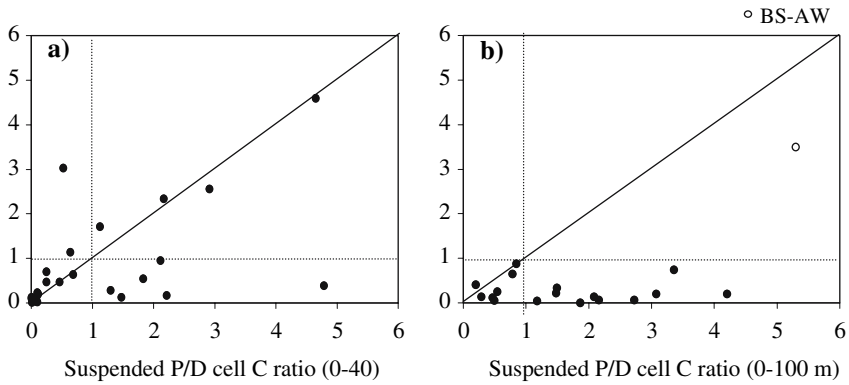

Fig. 4 *Phaeocystis pouchetii*/diatom (P/D) cell carbon ratio is compared suspended (integrated mg C m^{-2}, 0–40 and 0–100 m) and in the corresponding sediment trap material (mg C m^{-2} d^{-1}) at (**a**) 40 m and (**b**) 100 m depth during spring bloom events. The 40 m data includes measurements from North Norwegian fjords (Balsfjord in 1996 and Balsfjord, Ullsfjord and Malangen 1997, $n = 26$), and the 100 m data includes measurements from Balsfjord 1996, Ullsfjord 1997, Balsfjord, Malangen and Ullsfjord 2001, Barents Sea 1998 and Amundsen Basin, Arctic Ocean 2001 ($n = 19$) (for further details, see Table 1). A ratio >1 reflects *Phaeocystis* dominance, while a ratio <1 reflects diatom dominance. Open circles indicate stations were mixing exceeded 90 m at the Barents Sea Polar front and Atlantic water (BS-AW) region in May 1998 (for BS-AW; P/D cells C ratio = 43)

information on the contribution from *Phaeocystis* cell carbon from 15 different ecologically settings in five regions (Antarctica, coastal North Sea, North Norwegian fjords, the Barents Sea and the central Arctic Ocean; Fig. 5). Except for Balsfjord –96, all rates were obtained by short-term (24 h) sediment traps, deployed at or close to 100 m depth (± 10 m). In the shallow North Sea, sediment trap sampling was only possible at 20 m and 30 m. The vertical fluxes presented are averages of several measurements (68 observations in total) covering periods during and closely after *Phaeocystis* spp. blooms (see Table 1 and Fig. 5 legend for details).

The averaged, daily POC fluxes are highly variable between the different regions, with rates on the North Sea shelf and the central Arctic Ocean representing the extremes of 1,500 and 50 mg C m^{-2} d^{-1}, respectively. The highest and lowest PPC fluxes were also measured in these two regions (430 and 12 mg C m^{-2} d^{-1}, respectively). The polar region exhibited POC fluxes that were a factor of 10 or more below the North Sea. Within the Barents Sea, there was a distinct decrease in POC fluxes from the station in the deeper-mixed and more-productive Atlantic region, to the Polar Front, and the more-stratified station in the ice-covered Arctic region. In the North Sea, the <40 m depth obviously played an important role for the delivery of high POC fluxes 10 m above the seafloor. The flux gradient in the Barents Sea is influenced by vertical mixing in frontal zones and less-stratified waters that fertilises primary production and increase sinking speed through active vertical transport of organic carbon and phytoplankton (Olli et al. 2002; Reigstad et al. 2002). The vertical export of POC can therefore be relatively higher in shallow regions like the North Sea and vertically well-mixed regions such as the central Barents Sea, where retention time and time available for degradation is shortened.

Phaeocystis spp. was present at all stations (Fig. 5), with a *Phaeocystis*/diatom ratio (cell C/cell C) of 0.2–5.3. Despite the differences, two aspects were common for the investigated sites. First, PPC never exceeded 45% of POC flux at ~100 m depth, with an average of 26% (7–42%). This implies that a large phytoplankton-derived carbon is partly degraded before it reaches depths of 100 m. Second, the contribution from exported *Phaeocystis* spp. cell C to the POC export was small, ranging from 0.7–7%, with an average of 3% for all stations. The two deep-mixed stations made an exception with 15 and 35% *P. pouchetii* cell C of POC flux at 90 m depth, increasing the overall average to 6%. Comparatively, the diatom carbon contributed 1–27% to the 100 m measured POC flux, with an average of 11%.

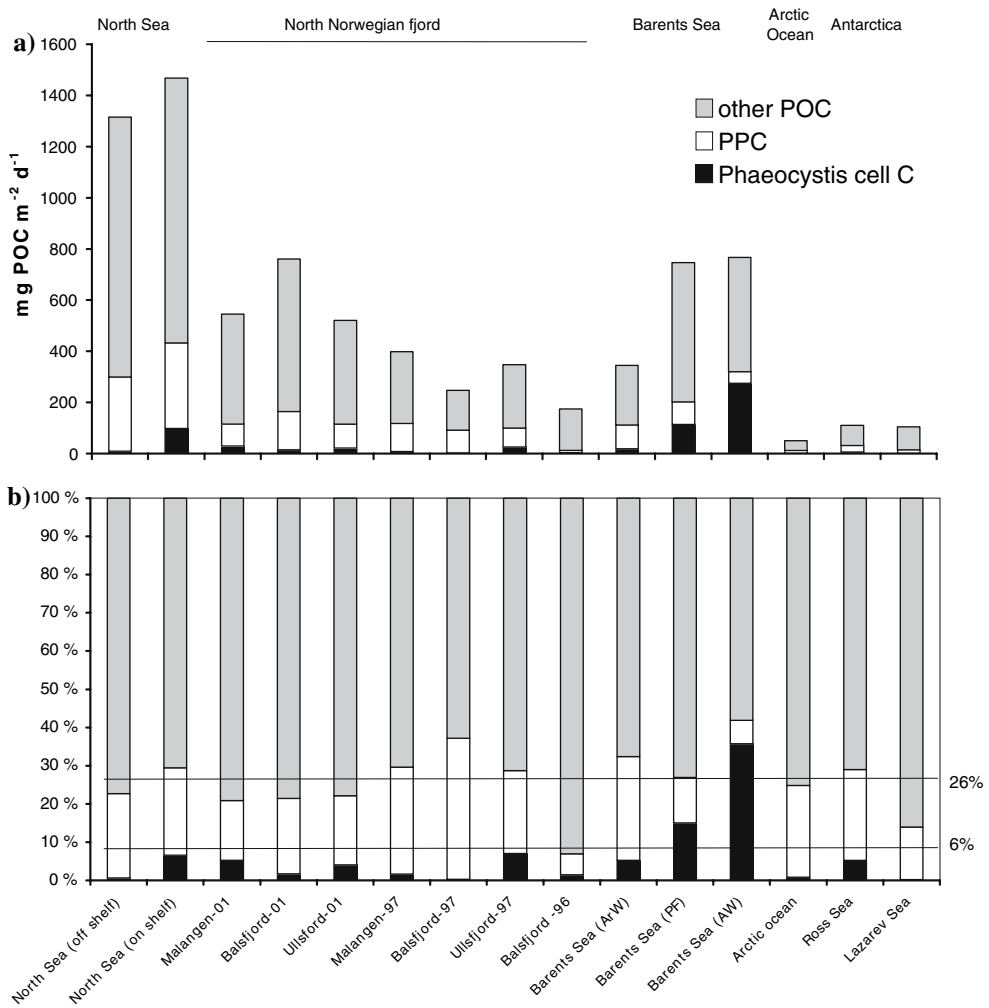

Fig. 5 (**a**) Vertical export of particulate organic carbon (POC) and (**b**) the percent contribution of phytoplankton carbon (PPC) and *Phaeocystis* spp. cell carbon at 100 m depth in different regions; on and off the shelf of the North Sea, April-98 (n = 6 and n = 7), Malangen, Balsfjord and Ullsfjord, April-01 (n = 9), Malangen, Balsfjord and Ullsfjord, April-97 (n = 15, Reigstad et al. 2000), Balsfjord 1996 (n = 11, Reigstad 2000), Atlantic water (AW), Polar Front (PF) and Arctic water (ArW) regions of the Barents Sea, May-98 (n = 1 for each region, Olli et al. 2002), Arctic Ocean, Aug-01 (n = 6, Olli et al. 2007), Ross Sea, December-95/January-96 (n = 5, Gowing et al. 2001), Lazarev Sea, December-95/January-95 (n = 6, Pakhomov et al. 2002). The number of samplings averaged in each region is given in parenthesis after each station name. For further information on geographical position and sampling dates, see Table 1. Data are obtained through microscopic examination of short-term sediment trap material, and conversion to carbon

Despite occasionally high concentrations and dominance of *Phaeocystis* spp. in the water column, calculations based on sediment-trap measurements suggest low daily loss rates, implying high retention of *Phaeocystis* cell carbon in the upper 50–100 m. Unless deep mixing accelerates vertical export, the contribution to the vertical carbon flux at 100 m is on average 3%. The conclusion is that *Phaeocystis* cell carbon does not contribute significantly to vertical carbon export.

Does mucus contribute significantly to the vertical export of *Phaeocystis* spp-derived C?

Mucus carbon estimates

The above calculations were provided without taking the contribution from *Phaeocystis* spp. colony mucus into account. Rousseau et al. (1990) established a relationship for the number

of cells per colony of *P. globosa*, and estimated a carbon content per volume of mucilaginous matter of 335 ng C mm^{-3}. The authors concluded that, when the colony size exceeded 400 μm, mucus carbon dominated the biomass, and at colony sizes of 1 mm, mucus contributed 90% of the *Phaeocystis* colony biomass. Their assumption was a colony filled with mucus structures. Rijssel et al. (1997) challenged this assumption, discovering that the total amounts of sugars and carbon were correlated with the colony surface area for *P. globosa*, indicating a hollow colony structure with a mucus layer of fixed thickness. The authors argued that the estimates by Rousseau et al. (1990) over- and underestimated the mucus carbon pool for larger and smaller colonies, respectively. Rijssel et al. (1997) measured C content including mucus of 57 pg C $cell^{-1}$ for field samples and 122 pg C $cell^{-1}$ for cultures. For *P. antarctica*, another cell-per-colony ratio and a carbon-per-unit-colony volume of 213 ng C mm^{-3} was suggested by Mathot et al. (2000) based on investigations from the Ross Sea, Antarctica.

A relationship between cells per colony or colony carbon content has so far not been established for *Phaeocystis pouchetii* (Schoemann et al. 2005). This species has lobed-formed colonies where the cells are grouped, contrasting the more spherical or elongated colonies characterising *P. globosa* and *P. antarctica*. There are also indications that *P. pouchetii* colonies are more fragile (Wassmann et al. 2005) compared to the tough structure demonstrated for *P. globosa* (Hamm et al. 1999). It is therefore likely that a difference in the cell per colony ratio as well as carbon per unit of colony exists between *P. pouchetii* and the other two species. In an attempt to suggest a possible range of contributions from mucus to vertical carbon export based on vertical export rates of *P. pouchetii* when the mucus sinks as intact colonies with cells we have chosen to apply the relationships for *P. globosa* and *P. antarctica.*

First, the range of carbon content in a colony is estimated for the smallest and largest observed colonies in the dataset from the central Barents Sea, and two different cell sizes using the available relationships (Table 3). Estimates of the relative contribution from mucus C to the total *Phaeocystis* colony carbon based on the relationships given by Rousseau et al. (1990) and Mathot et al. (2000), show that they indicate very similar mucus contributions, adding a maximum of 43–48%, for the largest colonies with small cells (d = 3 μm) (Table 3) and 10–12% for similar-sized colonies but larger cells (d = 6 μm). As colonies often contain larger cells, the addition of mucus carbon is most likely in the order of 10%, and of minor importance compared to the cell carbon for the total colony carbon content. The relationship suggested by Rijssel et al. (1997) does not allow a separation of cell and mucus carbon, but for the entire colony including cells, the estimated carbon content ranges from the upper levels suggested by the two others, to three times their highest suggested value (Table 3). The reason for this high discrepancy is likely our use of the relatively small colonies (65–115 μm) present in the preserved samples examined from the Barents Sea. Rijssel et al. (1997) based their relationship on larger colonies ranging >250–5,000 μm in diameter.

Estimated mucus contribution to carbon export

To approximate the potential impact of the estimated mucus contribution to vertical flux, maximum values of colony flux and observed colony size were applied to give an upper range (Table 4). The *P. pouchetii* fluxes are from the Arctic region of the marginal ice zone in the Barents Sea during spring, 40 m depth and above the vertical mass flux attenuation interval. The estimate of *Phaeocystis* spp. carbon export based on relationships from Mathot et al. (2000) is 25% lower compared to Rousseau et al. (1990) with 168 mg C m^{-2} d^{-1} and 225 mg C m^{-2} d^{-1}, respectively (Table 4). The mucus contribution to these estimates is however only 10% and 12%, indicating that even with very high vertical fluxes of *Phaeocystis* spp. colonies, mucus will not add more than about 10% C to estimates based on cell carbon (given the observed colony diameter of 115 μm). The total POC export measured at the Barents Sea Arctic water station was about 900 mg C m^{-2} d^{-1} (Olli et al. 2002). The *Phaeocystis* spp. carbon export estimates based on Rijssel et al. (1997) exceeded this, and were 2–3 times higher compared to the others, using

Table 3 Estimated carbon content (C) of *Phaeocystis pouchetii* colonies separated as cells and mucus carbon. Estimates are based on relationships established for living *P. globosa* (Rijssel et al. 1997; Rousseau et al. 1990) and *P. antarctica* (Mathot et al. 2000), but using colony size, cell sizes and vertical fluxes measured for *P. pouchetii*. Maximum and minimum values are examplified including smaller and larger cells and colonies (diameter = *d*). Cell carbon is calculated according to Menden-Deuer and Lessard (2000)[a,b]

	Cell size (μm)	Calculations according to		
		Rousseau et al. (1990) (*P. globosa*)	Mathot et al. (2000) (*P. antarctica*)	Rijssel et al. (1997) (*P. globosa*)
Colony size (μm)		65–115	65–115	
# cells col^{-1}		51–122	33–93	33–122
P. pouchetii cell C (pg col^{-1})	*d* = 3 [a]	122–294	79–224	
	d = 6 [b]	831–1,988	538–1,516	
P. pouchetii mucus C (pg C col^{-1})		48–267	31–170	
Total *P. pouchetii* C (cell+mucus) pg C col^{-1}	*d* = 3	170–561	110–394	
	d = 6	879–2,255	569–1,686	1,881–6,954
% mucus C col^{-1}	*d* = 3	24–48%	28–43%	
	d = 6	6–12%	5–10%	

Calculations based on Rijssel et al. (1997) assume a hollow colony structure and give C content per cell including colony mucus, where the given field data value of 57 pg C cell^{-1} is applied. Number of cells col^{-1} used is the highest and lowest from the relationships given by Rousseau et al. (1990) and Mathot et al. (2000)

Notes: [a] Cell *d* = 3 μm gives 2.41 pg C cell^{-1}

[b] Cell *d* = 6 μm gives 16.3 pg C cell^{-1}

Table 4 Estimated vertical fluxes of *Phaeocystis pouchetii* cell carbon and mucus contribution based on maximum observed colony fluxes (40 m depth in the central Barents Sea, May 1998)

Vertical flux, Barents Sea, May, 40 m	Calculations according to		
	Rousseau et al. (1990) (*P. globosa*)	Mathot et al. (2000) (*P. antarctica*)	Rijssel et al. (1997)
100,000,000 col m^{-2} d^{-1}, Max colony size *d* = 115 μm, colony cell *d* = 6 μm			(93–122 cells col^{-1})
Vertical flux *P. pouchetii* colony incl. mucus	225 mg C m^{-2} d^{-1}	168 mg C m^{-2} d^{-1}	530–695 mg C m^{-2} d^{-1}
% Mucus	12%	10%	
Assuming larger colonies (*d* = 400 μm, 170 cells col^{-1}), (average from fresh samples, Balsfjord 2004)			(170 cells col^{-1})
Total *P. pouchetii* C vertical flux	390 mg C m^{-2} d^{-1}	349 mg C m^{-2} d^{-1}	969 mg C m^{-2} d^{-1}
Underestimate of *Phaeocystis* contribution without mucus C	40%	25%	

Calculation of mucus according to relationships suggested for *P. globosa* (Rijssel et al. 1997; Rousseau et al. 1990) and *P. antarctica* (Mathot et al. 2000). The observed colonies were small, and likely fragmented larger ones. The shallow depth and probably overestimated settling colony number makes this a maximum estimate to illustrate the potential extra carbon contribution from *Phaeocystis* colony mucus. An example using colony size and cell col^{-1} measured from Balsfjord on fresh samples (T. Ratkova. unpublished) is included to illustrate the difference of larger colonies (similar vertical flux used in both examples). The carbon content of cells, including mucus, given by Rijssel et al. (1997) does not allow an estimate of the mucus fraction the total *Phaeocystis* carbon

the maximum cell colony^{-1} estimate based on Rousseau et al. (1990) and Mathot et al. (2000) of 122 and 93, respectively. Again, the small colony size is probably the reason.

Since there is a possibility of colony fragmentation (leading to colony size underestimation) caused by preservation and transportation prior to microscopic analyses, an example based on

average colony diameter of 400 μm and 170 cells col^{-1} from fresh *P. pouchetii* samples in Balsfjord, Northern Norway, is included (Table 4). Larger colonies increased the estimated contribution from colony mucus, and the assumed underestimation of *Phaeocystis* carbon export using only cell carbon is estimated to be 40% and 25% using the relationships by Rousseau et al. (1990) and Mathot et al. (2000), respectively. The comparative estimate based on Rijssel et al. (1997) is again almost tripled compared to the other estimates (Table 4), exceeding the total measured POC fluxes. We therefore assume that for smaller colonies and/or for *P. pouchetii*, this relationship overestimates the carbon values. Gowing et al. (2001) made calculations on the contribution from *P. antarctica* mucus C in the Ross Sea using the number of flagellated cells in the sediment trap, and cell per colony ratios and carbon per colony volume, according to relationships established by Mathot et al. (2000). They concluded that, while the *P. antarctica* cell carbon contributed 1–13% of the POC export, mucus contributed only 0.5–4%.

The potential underestimation of *Phaeocystis* spp. carbon by only including cell carbon is thus not likely to be >40%. Based on measurements of vertical flux around 100 m depth from Antarctica, the coastal North Sea, North Norwegian fjords, the Barents Sea and the Arctic Ocean (Fig. 5), the average carbon contribution from *Phaeocystis* spp. to the POC flux will increase from 3% to <5% by including mucus carbon. Despite the lack of appropriate species-specific carbon conversion rates for all *Phaeocystis* species, the evidence clearly indicates that *Phaeocystis* spp. mucus, sinking as intact colonies with cells, is not significantly contributing to the total POC export.

Fate of Phaeocystis colonies visualised through TEP

Aggregation is hypothesised to be important for vertical export of *Phaeocystis* spp.-derived material (Asper and Smith 2003). During experiments testing the aggregation potential of senescent *P. pouchetii* colonies, increased stickiness was not observed, but rather a lower aggregation potential was found compared to diatoms (Passow and Wassmann 1994). They hypothesised that mucus flocks derived from the dissolved colonial matrix could represent a secondary pathway for *Phaeocystis* spp.-derived carbon export. This mechanism was investigated in Balsfjord, northern Norway through a vertical flux study of transparent exopolymer particles (TEP).

TEP are formed from acid polysaccharides and stainable with Alcian blue (Alldredge et al. 1993). TEP can be formed from disintegrating senescent *Phaeocystis* spp. colonies (Passow and Wassmann 1994; Hong et al. 1997; Passow 2000; Passow 2002), and are suggested to induce mass flux events. Riebesell et al. (1995) observed continued high vertical carbon export associated with increased C/N and C/Chl *a* ratios and decreased surface-water TEP concentrations after a *P. pouchetii* bloom in Balsfjord, Northern Norway. The vertical fluxes of *P. pouchetii* cells were low, but export of *Phaeocystis*-derived carbon in the form of mucilageneous matter was suggested. Our seasonal study in Balsfjord, 1996, revealed that TEP could be closely associated with vertical export events. The maximum suspended distribution of TEP (1,415 mg xanthan equiv. m^{-3}) coincided with the termination of the *P. pouchetii* bloom. TEP were measured in sediment traps along with total particulate matter (TPM) and POC, and a sudden increase in vertical fluxes of TPM and POC (93–440 mg POC m^{-2} d^{-1}) in April, were closely associated with an increase in the flux of TEP from 95 to 400 mg xanthan equiv. m^{-2} d^{-1}, at 100 m depth (Fig. 6).

A conversion of TEP to carbon using the conversion factor established by Engel and Passow (2001; Passow 2002) reveals a TEP-C export maximum of 390 mg C m^{-2} d^{-1} at 100 m, exceeding the POC mass flux estimate of 350 mg POC m^{-2} d^{-1}. This is not impossible as TEP are retained on 0.4 μm filters, and will include a carbon size fraction that will pass through the 0.7 μm GF/F filters used for POC determination. The observations emphasize that, during transient particle flux events, a significant part of the exported carbon signal could be *Phaeocystis* spp.-derived carbon. This contribution is not detected as pigments or cells in the microscopy, and perhaps not even picked up

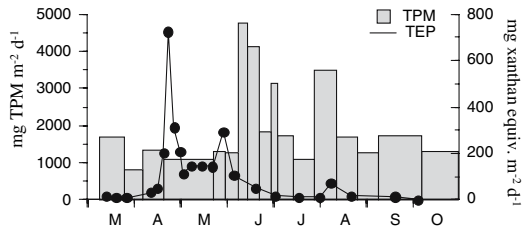

Fig. 6 Episodic vertical flux events of total particulate material (TPM) and particulate organic carbon (POC) at 100 m depth induced by *P. pouchetii*-derived material quantified as transparent polymer particles (TEP, in terms of gum xanthan equivalents) in Balsfjord, northern Norway, from March to October, 1996. Vertical flux is given as mg m^{-2} d^{-1}.

correctly by conventional POC measurements. Microscopic inspection of stained TEP from our sediment traps in Balsfjord showed that they were associated with phytoplankton cells and particles (data not shown). A second, but smaller TEP export event in late May, was not associated with any increased POC or TPM export (Fig. 6), but induced increased vertical flux of flagellates (data not shown).

Mari et al. (2005) found that nutrient limitation played a critical role for the TEP characteristics during a *P. globosa* bloom in a mesocosm experiment. While N-limitation induced a slow degradation of colonies to non-sticky mucus particles (exposed to microbial degradation and recycling), P-limitation induced rapid colony disruption resulting in heavy and sticky mucus aggregates (suggested to sink rapidly). We do not know whether the *P. pouchetii* blooms in Balsfjord were N or P limited, and we are not able to link the different fate of TEP observed in Balsfjord to the mechanisms suggested by Mari et al. (2005). Still, the fate of a *Phaeocystis* spp. bloom and the *Phaeocystis*-derived mucus carbon could strongly depend on the nutrient regime. A mass export event, like the one observed in April in Balsfjord, is thus a possible result of bloom termination induced by sticky TEP. Export of *Phaeocystis*-derived carbon and associated chemical properties like dimethylsulfide (DMS) can thus be exported in the form of TEP without being retained on the filters or visible under microscope without staining.

Mechanisms for vertical export

Having concluded that sinking colonies are not a major driver of vertical carbon export to deeper waters despite the major blooms observed, and that mucus measured as TEP only episodically induces flux events, we wish to focus also on additional mechanisms inducing vertical export of *Phaeocystis* spp.-derived carbon. Zooplankton grazing can repack cells and colonies to larger and faster-sinking faecal pellets (FP). Controversies exist regarding the impact of grazing on *Phaeocystis* spp. cells and colonies (Turner et al. 2002; Schoemann et al. 2005). With the wide size range of *Phaeocystis* morphotypes as well as potential grazers, and recent observations of cell-type-dependent grazing (Dutz and Koski 2006), grazing on *Phaeocystis* spp. becomes a complex task to investigate. In terms of vertical flux, it is mainly larger grazers that contribute through FP production, as smaller zooplankton FP are generally recycled (Turner 2002). Comparing FP production with FP fluxes suggests that 50–95% of the FP from larger copepods such as *Calanus* spp. are recycled in the upper layers rather than being exported (Urban-Rich et al. 1999; Wexels Riser et al. 2002). The resulting fraction of *Phaeocystis* spp.-derived carbon exported after mesozooplankton grazing and in the form of detritus can thus not be extensive.

Macrozooplankton producing larger and fast-sinking FP such as krill can be efficient FP exporters. Using combined fingerprint techniques (lipids and stereols), Hamm et al. (2001) argues that krill grazed *P. pouchetii* in Balsfjord, and contributed episodically to a considerably increase in the POC flux though *Phaeocystis*-containing FP export. The frequency of such episodes in northern regions is related to the distribution and patchiness of krill, which is variable and thus difficult to evaluate.

Downwelling of suspended biogenic matter that may contribute to vertical export is not a well-described process, although it may be of significant importance in certain regions and periods (Head and Horne 1993; Wassmann et al. 2000; Belviso et al. 2006). Mixing of surface water and denser coastal water at a fjord sill resulted in denser water containing fresh *P. pouchetii* cells

being advected into the fjord basin (Wassmann et al. 2000). Increased chlorophyll *a* concentrations, fresh cells and DMS at the bottom of the fjord (180 m depth) did not result from vertical export, but rather from horizontal advection combined with mixing processes in bloom-containing surface water (Wassmann et al. 2000; Belviso et al. 2006). In a similar manner, fresh biogenic material and nutrient-depleted water were present at >100 m depth in the Polar Front and Atlantic water region of the Barents Sea, resulting from extensive mixing processes of non-stratified surface waters (Reigstad et al. 2002). This process was effective in bringing *P. pouchetii* cells well below the euphotic zone in the deeper-mixed Barents Sea stations (Olli et al. 2002; Ratkova and Wassmann 2002; Reigstad et al. 2002). Locally such processes might be of importance for vertical export of *Phaeocystis* spp. especially as it has been suggested that *Phaeocystis* spp. is favoured in regions with deeper and well-mixed waters (60–80 m) (Goffart et al. 2000; Lancelot et al. 1998; Sakshaug 2004).

Concluding remarks

The main body of evidence based upon direct observations suggests that *Phaeocystis* spp. blooms are to a large extent recycled in the upper layers. Contradictory evidence derives from indirect evidence, suggesting that sediment traps may underestimate vertical export of *Phaeocystis* spp. An alternative to the deployment of sediment traps, the ^{234}Th technique, has recently been applied in concert with sediment traps in the Barents Sea during the presence of *P. pouchetii* (Lalande 2006). Sediment-trap POC fluxes were much lower than large-volume POC fluxes at almost every station in summer 2005 (Lalande 2006). This may reflect either an under-collection by the drifting sediment traps or an over-collection by the large-volume ^{234}Th sampling. The offset between the two methods may be attributed to the prominent presence of *P. pouchetii in summer 2005*, which is potentially causing the large variation observed in POC/^{234}Th ratios (Lalande 2006). Due to the large proportion of carbon released by *P. pouchetii* and because *P. pouchetii* cell C does not contribute significantly to the vertical export of biogenic matter, the utilization of large-volume sampling of ^{234}Th may yield relatively high, and possibly incorrect, POC/^{234}Th ratios and hence POC fluxes in regions where *P. pouchetii* is dominant. Large-volume ^{234}Th sampling appears to be an inadequate alternative for vertical flux estimates in *Phaeocystis* spp.-dominated ecosystems. The use of sediment traps may be more reliable for the accurately measurement of the vertical export of biogenic matter in the Barents Sea (Lalande 2006).

The fate of *Phaeocystis* spp. blooms, and the possible contribution to carbon export have been investigated and discussed for several decades (Wassmann 1994; Lancelot et al. 1998; Schoemann et al. 2005; Whipple et al. 2005). Clearly, there is extraordinary flexibility and plasticity in the ecology, life cycle and fate of this genus, related to species, morphotypes and environmental conditions (Veldhuis and Wassmann 2005). Beside the many mechanisms and processes promoting retention and recycling of *Phaeocystis* spp.-derived carbon, there are also several pathways for vertical carbon export. An attempt to summarize the different pathways is presented in a conceptual diagram (Fig. 7). The evidence presented in this publication attempts to quantify or at least examplify these export mechanisms, and illustrate their regional and episodic significance. Considering the biomass and dominance of *Phaeocystis* in pelagic systems, the vertical export of cell carbon is of minor importance. This is based on the following findings:

- A strong decline in the vertical export of *P. pouchetii* cells between 40 m and 100 m has been shown in the Barents Sea and North Norwegian fjords.
- Despite potential *Phaeocystis* spp. cell C dominance in the water column, vertical export of diatom cell C was always larger than that *Phaeocystis* spp. cell C at 100 m depth, unless deep mixing short-circuits retention.
- *Phaeocystis* spp. cell carbon contributed on average only 3% to the vertical POC flux at 100 m depth.

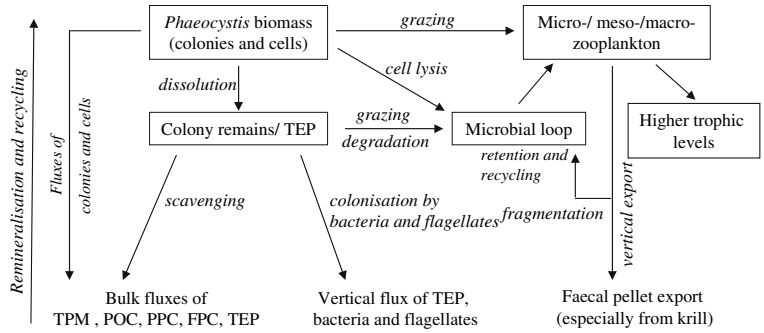

Fig. 7 Conceptual diagram indicating possible pathways for *P. pouchetii*-derived carbon

- The estimated contribution from mucus to the colony sizes observed in the north-eastern North Atlantic suggest that mucus may contribute an additional 40% (maximum) to the estimated cell C export. In concert, *Phaeocystis* spp. cell and colony C may thus contribute <5% of the vertical POC export.
- Possible grazing from krill inducing FP export, downwelling of *Phaeocystis* cell/colonies/remains through deep physical mixing processes or nutrient-related flocculation and export of senescent *Phaeocystis* spp. mucus may induce episodic *Phaeocystis* flux events.
- TEP measurements provides a method to estimate vertical export of *Phaeocystis*-derived mucus-remains that otherwise are easy to overlook based on their semiparticulate and transparent nature.

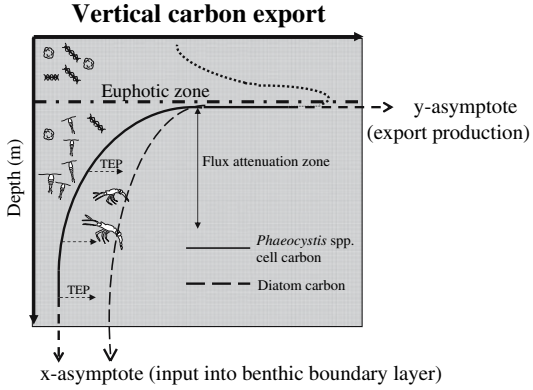

Fig. 8 Attenuation of vertical flux below the euphotic zone is stronger for *Phaeocystis* spp. cells compared to diatoms despite similar biomass in the upper mixed layer (modified from Wassmann et al. 2003). Export of transparent exopolymer particles (TEP) can reduce the attenuation of *Phaeocystis*-derived carbon

The increased vertical flux attenuation efficiency in *Phaeocystis* spp.-dominated regions has thus to be taken into account and the channelling of the *Phaeocystis* spp. biomass through the pelagic has to be carefully considered (Fig. 8). We suggest that there must be significant differences between the vertical export of *Phaeocystis* spp. and diatoms. The potential loss of TEP and mucilaginous matter on filters prior to analysis may result in an underestimation of the *Phaeocystis* spp.-associated C flux, and Fig. 8 indicates that the vertical flux attenuation efficiency during *Phaeocystis* spp. blooms may be smaller then the vertical export of cell carbon may suggest.

Acknowledgement The tedious microscopic effort by Tatjana Ratkova made this contribution possible, and is highly acknowledged. Contributions from colleagues through discussions and fieldwork over many years during the ESCAPE (EU-MAS3-CT96-0050) and BIOHAB (EU-EVK3-CT99-00015) projects, the fjord projects within North Norwegian Coastal ecology (NFR), ALV (NFR 121521/720), CABANERA (NFR 155936/700), MACESIZ (NFR 155945/700) and the Arctic Ocean Expedition-2001, are highly acknowledged as well as the economic support received through these projects. This publication is a contribution to all those projects, and to the SCOR#120 working group. We appreciate constructive comments from two anonymous referees, and thank the organisers of the symposium "*Phaeocystis, major link in the biogeochemical cycling of climate-relevant elements*" for the opportunity to publish these data.

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