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On the trophic fate of *Phaeocystis pouchetii*. VII. Sterols and fatty acids reveal sedimentation of *P. pouchetii*-derived organic matter via krill fecal strings

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ABSTRACT: As part of a joint project on the fate of phytoplankton in Balsfjorden in Northern Norway, we investigated the trophic fate and sedimentation potential of *Phaeocystis pouchetii* by tracing the transition of biomarker patterns from a phytoplankton bloom to sediment traps and during a gut-passage experiment. The phytoplankton biomass during the spring bloom 1996 was dominated by colonial *P. pouchetii* (ca 85%) and 4 members of the diatom family Thalassiosiraceae (ca 10%). Particulate organic carbon in sediment traps largely consisted of fecal material from the Arctic krill *Thysanoessa* sp. Sterol and fatty acid biomarker patterns in the phytoplankton bloom could be reproduced by combining the individual biomarker patterns of the isolated phytoplankters *P. pouchetii* and *Thalassiosira decipiens* in a ratio of ca 75:25. In a laboratory experiment, Arctic krill (*Thysanoessa raschii*) fed with similar efficiency on *P. pouchetii* colonies and the Thalassiosiraceae. During gut passage, the abundance of Thalassiosiraceae biomarkers in fecal strings increased relative to *P. pouchetii* biomarkers, while biomarkers from krill became dominant. This transition of biomarker patterns due to gut passage in *T. raschii* closely resembled the biomarker transition from the surface bloom to material in sediment traps at 40 to 170 m depth, which was mainly composed of krill fecal strings. We conclude that krill grazed efficiently on *P. pouchetii* colonies in Balsfjorden and caused sedimentation of *P. pouchetii*-derived organic matter below the euphotic zone via fecal strings. Hence, both transfer to higher trophic levels and sedimentation of *Phaeocystis* spp.-derived organic matter can be more effective than is commonly believed.

KEY WORDS: *Phaeocystis* · Diatoms · Krill · Trophic fate · Vertical flux · Biomarkers

INTRODUCTION

The cosmopolitan colony-forming Haptophycea *Phaeocystis* spp. is one of the key phytoplankton genera in the world oceans, as it frequently forms large blooms (Verity & Smetacek 1996, Lancelot et al. 1998). Studies on the trophic fate of *Phaeocystis* spp. colonies suggest that during blooms, intact colonies are consumed by only a few larger zooplankton species, while much of the biomass produced by *Phaeocystis* spp. enters the microbial food web after disintegration of the colonies (Weisse et al. 1994 and references therein). The consequences of these specific trophic pathways for the sedimentation potential of *Phaeocystis* spp.-derived organic matter are still largely unknown (Wassmann 1994, Lancelot et al. 1998).

Microscopic evidence for export production of *Phaeocystis* spp.-derived particulate organic carbon (POC) to aphotic waters is sparse, and sedimentation

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rates of recognizable *Phaeocystis* spp. colonies and cells are low (Wassmann 1994 and references therein, Andreassen & Wassmann 1998). In contrast, the sudden disappearance of *Phaeocystis* spp. blooms from the euphotic zone, the existence of nitrate-depleted, silicate-rich water bodies with low phytoplankton concentrations in the vicinity of *Phaeocystis* spp. blooms (Wassmann et al. 1990, Smith et al. 1991), and the occurrence of pigments and dimethylsulphoniopropionate (DMSP) typical of *Phaeocystis* spp. in deeper layers and the sediment (di Tullio et al. 1996, 2000) have suggested efficient sedimentation of *Phaeocystis* spp.-derived organic matter to aphotic zones in spite of the low sedimentation potential of *Phaeocystis* spp. aggregates (Riebesell 1993, Passow & Wassmann 1994, Riebesell et al. 1995).

Arctic krill were argued to be largely responsible for the vertical flux of particulate organic carbon in Balsfjorden, where krill feces dominated sedimentation during *Phaeocystis pouchetii* blooms (Lutter et al. 1990, Riebesell et al. 1995). The resulting proposition that krill grazed efficiently on *P. pouchetii* implies that incompletely digested *P. pouchetii*-derived POC sedimented via krill fecal strings. As well as causing rapid transfer of biomass to deeper layers, grazing by krill would support the efficient transfer of *Phaeocystis* spp.-derived biomass to higher trophic levels, such as fishes (e.g. Naumenko 1987), birds (e.g. Coyle et al. 1992), and marine mammals (e.g. Nielsen et al. 1995). In contrast, recent laboratory studies did not confirm that krill feed efficiently on *P. pouchetii* colonies (Hansen et al. 1994). Since little and controversial information exists on potential effects of krill grazing on sedimentation of *Phaeocystis* spp.-derived organic matter, the goal of this study was to investigate this pathway, and to estimate the proportion of *Phaeocystis* spp. that might be ingested and hence be transferred in fecal material to sedimented material.

Our methodological approach was determined by the specific properties of the *Phaeocystis* spp. colony. Unlike other important phytoplankton species (e.g. silicified diatoms or calcified coccolithophorids) colonial *Phaeocystis* spp. lacks species-specific mineralized structures which can survive digestion by zooplankton. Thus, the tracing of *P. pouchetii*-specific chemical compounds (biomarkers) was the only possibility of assessing the contributions of *P. pouchetii* to POC in fecal material. The use of chemical compounds as markers for certain taxa has a long history (e.g. Volkman et al. 1980, Sohn 1986 and references therein, Skerratt et al. 1995), although parallel occurrences and differential oxidative or enzymatic degradation of typical markers can complicate their use for assessing the phytoplanktonic origin of degraded POC. As there is no biomarker established as being exclusively specific to *P. pouchetii*, we also investigated biomarkers in major co-occurring organisms potentially involved in POC-sedimentation. In this study, we used fatty acids and sterols to assess the phytoplanktonic origin of fecal POC which had settled into sediment traps during a *P. pouchetii* bloom. Since zooplankton are known to contribute significant amounts of their own sterols and fatty acids to fecal pellets produced from various diets (Volkman et al. 1980, Neal 1984, Prahl et al. 1984), the lipid composition of the krill responsible for the sedimentation of fecal material was also taken into account.

MATERIALS AND METHODS

All samples were taken at the station Svartnes (69° 22′ N, 19° 07′ E) in Balsfjorden (Fig. 1). The study was conducted from April 11 to 15, 1996, which was immediately after the peak of the phytoplankton bloom in Balsfjorden according to chlorophyll *a* and POC analyses (Wassmann & Reigstad unpubl. data).

The depth of the chlorophyll maximum (chl max.) was determined with a fluorometer (Backscat Model 1121) attached to a CTD (Multipar OTS 80). Water samples for POC/PON, lipid and phytoplankton analyses were taken using Niskin bottles at the depth of the chl max. Phytoplankton samples were fixed with hexamethylenetetramine-buffered formaldehyde and identified and quantified (biomass) according to Utermöhl (1958) and Edler (1979) with an inverted microscope. Zooplankton was sampled using a WP-2 net (mesh size 180 µm). Hauls were taken between 180 and 0 m. Samples were preserved using a buffered formaldehyde-propandiol solution (1:1) and the organisms were identified and quantified according to Sars (1903).

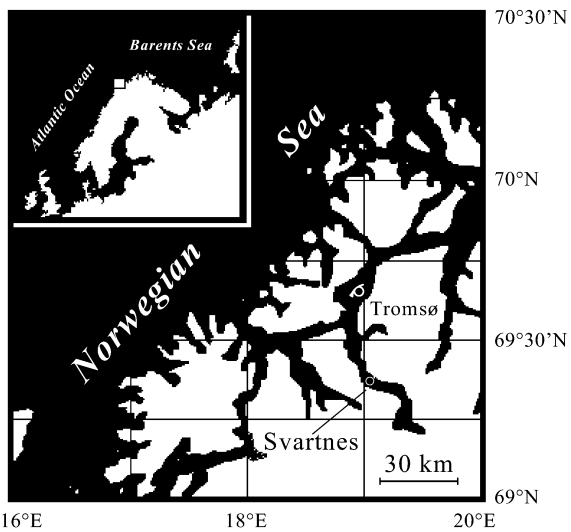

Fig. 1. Map showing sampling location Svartnes in Balsfjorden

POC samples from the water column and sediment traps were filtered onto precombusted (2 h, 550°C) GF/F-filters for chl *a*, POC/PON, fatty acid and sterol analyses. Chl *a* was extracted in 90% acetone and measured fluorometrically according to Holm-Hansen et al. (1965). POC/PON filters were exposed to a concentrated HCl-fume in a desiccator (12 h) prior to analyses to remove carbonates, and were analysed using a Leeman Lab 440 elemental analyser.

Plexiglas cylinders with an aspect ratio of 6.25 (72 mm wide, 450 mm high) were used as sediment traps. The lower part of the traps was poisoned with 2% buffered formaldehyde in filtered seawater; the density of this solution was increased by adding NaCl to a salinity of 40. The traps were deployed for 4 d. After recovery of the traps, the material therein was suspended in 2 l seawater, and 100 ml of the suspension was filtered on GF/F filters for fatty acid- and sterol analysis. Organisms suspected to have entered the sediment traps actively during deployment ('swimmers'), which were mainly the large copepods *Calanus finmarchicus* and *Metridia longa*, were removed from the filters with a forceps.

Recognizable fecal material from another subsample of the sediment traps was analyzed microscopically and grouped into different size classes and forms (cylindrical pellets: widths 20 to 60, 60 to 80, and >80 m, and 'others', which included spherical and oval pellets). A conversion factor of 69.4 µg C mm^{-3} (Riebesell et al. 1995) was applied to estimate fecal pellet carbon (FPC). A lower conversion factor (45.0 µg C mm^{-3}) has recently been measured for krill feces in this area (A. Arashkevish pers. comm.). This factor would decrease krill FPC by 35%, but krill would still be the dominant contributor to the sedimenting FPC. Cylindrical fecal material wider than 80 µm were defined as krill fecal strings, as fecal pellets produced by copepods usually do not exceed this width (Smayda 1971, Honjo & Roman 1978, Bienfang 1980, Bathmann & Liebezeit 1986, Corner et al. 1986). Cylindrical fecal pellets of intermediate size (60 to 80 µm) were presumed to include material from copepods and juvenile euphausiids; smaller cylindrical material was assumed to be exclusively produced by copepods. The origin of non-cylindrical forms was not determined.

For fatty acid and sterol analyses, and a laboratory experiment, krill from the station Svartnes was caught on April 15, 1996 using a 180 µm zooplankton net. At the same time, phytoplankton from the depth of the chl max. was sampled with a Niskin bottle. This phytoplankton was mixed (1:4, v:v) with GF/F filtered, nutrient-rich deep water from the fjord (nitrate and phosphate 5 and 0.5 µM, respectively) to ensure continuing growth. Krill (*Thysanoessa raschii*, 18 to 35 mm) were starved for 48 h in filtered seawater to ensure that they had empty guts. Individual krill were put into ten 2000 ml glass beakers which had been filled with seawater containing *Phaeocystis pouchetii*-dominated phytoplankton. These treatments were incubated under low light for 20 h. Production of fecal strings was observed in 3 beakers. From these, the krill were removed, and fecal strings were sampled by pipette and extracted for fatty acid and sterol analysis as described below. Contamination by phytoplankton lipids was negligible due to the small sample size (3 to 4 ml) and its low concentration after grazing. Phytoplankton subsamples taken prior to and after the incubation were fixed with Lugol/glutaraldehyde for microscopic enumeration (Utermöhl 1958), and measured cell sizes were transformed to phytoplankton carbon (Edler 1979). Colonial and single *Phaeocystis* spp. cells were distinguished by morphology and size.

The dominant phytoplankton genera, *Phaeocystis* and *Thalassiosira*, and the most important potential grazers of *Phaeocystis* spp. colonies, in our case *Thysanoessa raschii* and *Calanus finmarchicus*, were isolated for an assessment of their biomarker composition. Colonial *P. pouchetii* was sampled from the surface by horizontal surface tows of a zooplankton (180 µm WP-2) net which excluded smaller phytoplankton. Colonies were scraped off the net with a beaker as a highly concentrated jelly, and directly immersed in dichloromethane:methanol (2:1, v:v) for lipid extraction. Microscopic examination showed that ca 98% of this material consisted of *P. pouchetii* biomass. *Thalassiosira decipiens* was isolated from the fjord and grown in nutrient-rich, deep, fjord water at ca 100 µE and ambient temperature. Zooplankton were caught using vertical tows of the WP-2 net.

For fatty acid and sterol extraction, the POC from the water column and the sediment trap, and zooplankton and fecal material samples were filtered onto glass-fiber filters (GF/F), which were then immersed in 6 ml dichloromethane:methanol (2:1, v:v) in glass culture vials with Teflon sealed screw caps and stored at –30°C. Filters and culture vials were precombusted at 550°C for 4 h, the screw caps were rinsed with a detergent (Decon) and deionized water. Prior to use, culture vials and screw caps were rinsed with 2 ml and filled with 6 ml dichloromethane: methanol (2:1, v:v). The extraction procedure essentially followed the descriptions by Folch et al. (1957) and Bligh & Dyer (1959). Sediment trap material was sonicated, and krill were homogenized for efficient extraction. The samples were split in 3 aliquots. Water-soluble compounds were removed by mixing with 0.88% KCl and discarded after phase separation.

Aliquots of the lipid extracts in the organic phase were dried under N_2 atmosphere and used to prepare fatty acid methyl esters (FAME). Transesterification was performed for 4 h at 80°C in methanol containing 3% sulfuric acid under N_2-atmosphere. After extrac-

tion with hexane, FAME and free fatty alcohols were analysed with a Chrompack-9000 gas-liquid chromatograph on a 30 m × 0.25 mm i.d. wall-coated open tubular column (liquid phase: Durabonded Nitrophtalic acid modified polyethylene glycol [DB-FFAP]; film thickness: 0.25 µm), using temperature programming, and a flame ionization detector (FID). A standard mixture was used to identify the fatty acids and alcohols. For further details about the method see Kattner & Fricke (1986). The fatty acid 18:5 (n-3), which was not included in the standard mixture, was identified by relative retention time (Okuyama et al. 1992), and platinum-catalyzed hydration of double bonds with subsequent analysis of the quantitative increase of the 18:0 peak compared to an untreated control with expected high amounts of 18:5 (n-3). In the results, we list only fatty acids comprising >1% of the respective fatty acid patterns.

Aliquots of lipid extracts were evaporated to dryness and sterols were derivatized to trimethylsilyl-(TMS-) ethers applying N,O-bis-(trimethylsilyl)-trifluoroacetamide (BSTFA, Macherey-Nagel, Germany) at 60°C for 2 h. Analyses were performed by gas chromatography (GC) (Chrompack 9002) coupled to an FID, and by GC (HP 5890) directly coupled to a VG Autospec mass spectrometer (MS). GC parameters for sterol analysis were: 30 m × 0.25 mm fused silica capillary column; 0.25 µm HP5-MS crossbonded stationary phase (95% dimethylpolysiloxane, 5% diphenylpolysiloxane). Sterols were identified by retention times, sterol standards and mass spectra. For further details about the method see Mühlebach &Weber (1998). While the FID was routinely used as a detector, the proportions of nearly coeluting sterols, e.g. cholesta-5,24-dien-3β-ol and 24-methylcholesta-5,22*E*-dien-3β-ol, were deduced from representative samples analyzed by GC/MS (food, chl *a* max. and sediment trap at 100 m).

To ensure that no sources other than the dominant phytoplankton groups (i.e. isolated *Phaeocystis pouchetii* colonies and *Thalassiosira decipiens*) were responsible for the fatty acid pattern in the phytoplankton bloom, we sought to reproduce the *in situ* pattern (see Fig. 5C) by combining the patterns of the isolated phytoplankton taxa (see Fig. 5A,B). For this, we used the following procedure: the sum of all compounds of each pattern was set to 100%; the Euclidean distance (ED) between 2 points, A (x_A,y_A) and B (x_B, y_B), in a 2-dimensional co-ordinate system was calculated as follows (Deichsel & Trampisch 1985):

$$\mathrm{ED}(A,B) = \sqrt{(x_A - x_B)^2 + (y_A - y_B)^2}$$

This equation can be extended for co-ordinate systems with any number of dimensions (i.e. for similarity calculations concerning patterns with many compounds), and is thus widely used in cluster analysis. To reproduce the fatty acid pattern of suspended matter at the chl max., the patterns of *P. pouchetii* and *T. decipiens* were transferred to an 8-dimensional co-ordinate system, where each axis described the percentage of 1 fatty acid. For practical reasons, only fatty acids present at the chl max. were considered, and saturated (thus unspecific and refractory) fatty acids as well as fatty acids known to be only predominant in zooplankton were excluded. As only 1 sterol was found to be specific for each phytoplankton taxon, their relative abundances and their dominance at the chl max. could be used to assess the proportion and dominance of *P. pouchetii* and the Thalassiosiraceae in the phytoplankton.

For the description of the sediment-trap material, we selected 1 specific fatty acid each for *Thysanoessa decipiens*, *Phaeocystis pouchetii* and Thalassiosiraceae, and combined them in the proportions which yielded the smallest Euclidian distances to the sediment-trap material. As the selected fatty acids represented very different fractions of the total fatty acid patterns of the organisms for which they were specific, their percentages in the sediment traps were subsequently divided by these fractions. Thus, comparability with the specific sterols, which dominated the sterol patterns in the 3 key organisms, respectively, was ensured.

RESULTS

Organisms and POC

Microscopic examination showed that the phytoplankton spring bloom in the unstratified waters of Balsfjorden in April 1996 was dominated by *Phaeocystis pouchetii* colonies, which comprised >85% of the phytoplankton biomass at the chl max. at 6 m depth. The family Thalassiosiraceae, with 3 species of *Thalassiosira* (*T. decipiens*, *T. nordenskiöldii* and *T. polychorda*) and *Porosira glacialis* represented another important fraction, with approx. 10% of the biomass. Other planktonic organisms (pennate diatoms, dinoflagellates, small flagellates and ciliates) were present in minor amounts (Fig. 2). Mesozooplankton did not appear in the samples used for phytoplankton identification.

The sampling period between April 11 and 15 coincided with the highest POC concentration (>800 C mg m^{-3} at the chl max.). At the same time we observed a rapid surface depletion of phosphate and nitrate concentrations in concert with a pronounced chl *a* increase, which reached a maximum in early April with 6.5 mg chl *a* m^{-3}, and decreased subsequently to <3 mg chl *a* m^{-3} in late April. The silicate concentration slowly decreased throughout the water column during April

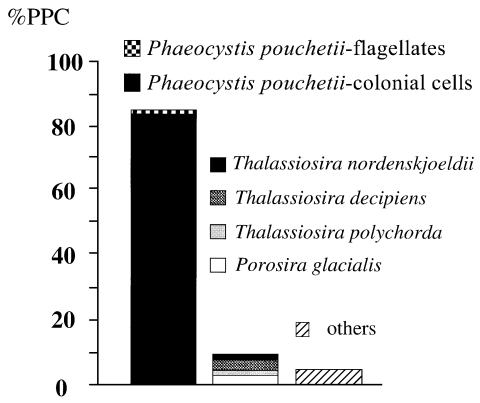

Fig. 2. Phytoplankton composition at chlorophyll maximum on April 15, 1996; 'others' includes dinoflagellates, silicoflagellates, ciliates, pennate diatoms, choanoflagellates, *Chaetoceros* spp., and some unidentified flagellates. Total phytoplankton carbon (PPC) was 120 mg m^{-3}

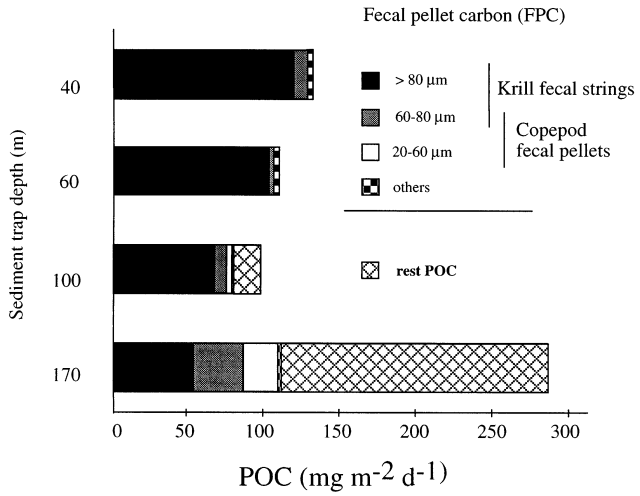

Fig. 3. Mean daily vertical POC and FPC fluxes to sediment traps between April 11 and 15

(5 to 4.5 µM), which reflected the relatively low abundance and production of diatoms.

While cyclopoid copepods such as *Oithona* sp. dominated the zooplankton composition of the water column numerically in April, calanoid copepods such as *Calanus finmarchicus*, *Metridia longa*, *Pseudocalanus* sp., and *Microcalanus* sp. dominated the mesozooplankton in terms of biovolume. Massive euphausiid abundance (mostly *Thysanoessa raschii* and *T. inermis*, and some *Meganyctiphanes norvegica*) was inferred from the dominance of krill fecal strings in the sediment traps (Fig. 3). Species composition was determined from qualitative net catches, and is typical for northern Norwegian fjords (Falk-Petersen & Hopkins 1981), however the abundance of these swarm-forming, migrating crustceans is very difficult to quantify and was not investigated here.

POC fluxes to the sediment traps between April 11 and 15 were moderate (Fig. 3). Most POC in the sediment traps occurred in fecal particles, which were mostly krill fecal strings (Fig. 3). Copepod fecal pellets, phytoplankton and amorphous detritus accounted for the rest. In the lowest trap, however, a high amount of amorphous POC was present, which is typical for sediment traps near the bottom and was attributed to resuspension (Walsh et al. 1988, Reigstad & Wassmann 1996). Because of the overwhelming dominance of krill fecal strings in the sediment traps and the knowledge that zooplankton contributes significantly to the lipids in fecal material, the apparently dominant euphausiid *Thysanoessa raschii* was analyzed for fatty acid and sterol composition.

A first assessment of the trophic relation between *Phaeocystis pouchetii* colonies and krill yielded ambiguous results. In the experiment, 3 of 10 *Thysanoessa raschii* individuals actively fed on the phytoplankton taken from the bloom, producing visible fecal material. Fig. 4 shows that the actively feeding individuals effectively and non-specifically fed on both *P. pouchetii* colonies and diatoms.

Biomarkers in key organisms, laboratory experiment and field

Purified *Phaeocystis pouchetii* colonies showed a characteristic pattern of the polyunsaturated fatty acids 18:2 (n-6), 18:3 (n-3), 18:4 (n-3), 18:5 (n-3), 20:5 (n-3), and 22:6 (n-3) (Fig. 5A). The concentrations of the saturated fatty acids 14:0 (6%), 16:0 (12%), and 18:0 (2%) (not depicted in Fig. 5A) were comparably low (see below). The fatty acids of isolated *Thalassiosira decipiens* formed a pattern which was clearly different from

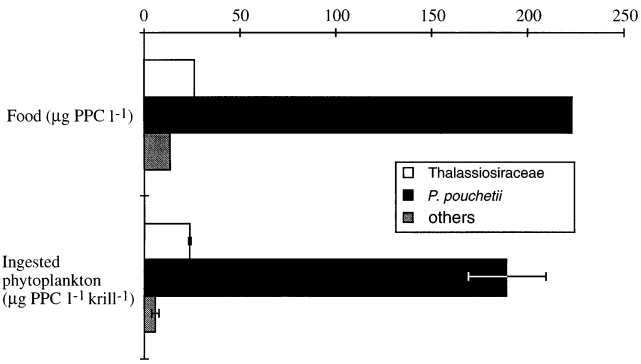

Fig. 4. *Thysanoessa raschii* (n = 3). Ingestion of phytoplankton. Note that both *Phaeocystis pouchetii* and Thalassiosiraceae biomasses were ingested with similar efficiency

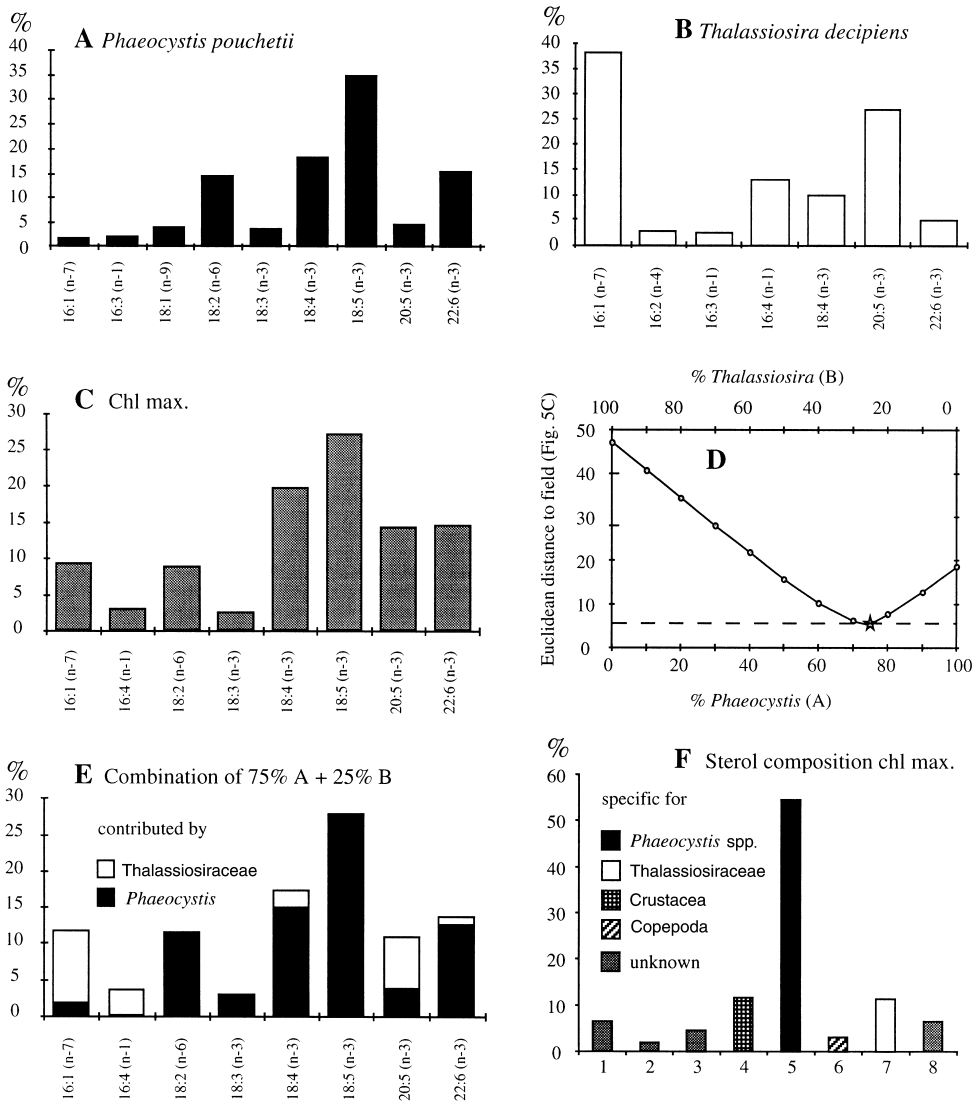

Fig. 5. Biomarker patterns. Fatty acids of (A) purified *Phaeocystis pouchetii* colonies; (B) isolated *Thalassiosira decipiens*; (C) chlorophyll *a* max. in Balsfjord; (D) Euclidean distances of diverse combinations between A and B to C; (E) combined fatty acids from *T. decipiens* (25%) and *P. pouchetii* (75%) patterns (note high similarity between [C] and [E]); (F) Sterols at chlorophyll max. (1) 24-norcholesta-5,22*E*-dien-3β-ol, (2) 27-nor-24-methylcholesta-5,22*E*-dien-3β-ol, (3) cholesta-5,22*E*-dien-3β-ol, (4) cholest-5-en-3β-ol, (5) 24-methylcholesta-5,22*E*-dien-3β-ol, (6) cholesta-5,24-dien-3β-ol, (7) 24-methylcholesta-5,24(28)-dien-3β-ol, (8) 24-ethylcholesta-5,24(28) dien-3β-ol

that of *P. pouchetii*. The dominating *T. decipiens* fatty acids were 16:1 (n-7), 16:4 (n-1), 18:4 (n-3), 20:5 (n-3), and 22:6 (n-3) (see Fig. 5B) and the saturated fatty acids 14:0 (5%) and 16:0 (31%) (not depicted in Fig. 5B).

In contrast to the purified samples of *Phaeocystis pouchetii* and *Thalassiosira decipiens*, the fatty acid patterns of particulate material from the chl max. between April 11 and 15 were dominated by the saturated fatty acids 14:0 (19.5%), 16:0 (33%), and 18:0 (10%), which implies that these were not directly associated with phytoplankton, so that they were not useful as phytoplankton markers. Likewise, the fatty acids 18:1 (n-9) and 18:1 (n-7), which can be dominant in zooplankton (Sargent & Falk-Petersen 1981), but are usually of minor importance in phytoplankton (Thompson et al. 1990, Conte et al. 1994) were excluded from phytoplankton composition analysis because their occurrence at the chl max. may have been due to the presence of few unidentified zooplankton. The remaining 8 fatty acids (Fig. 5C) formed a pattern with high concentrations of the compounds typical of *P. pouchetii* (Fig. 5A) and lower concentrations of compounds typical for the Thalassiosiraceae (Fig. 5B).

Combining the 8 selected fatty acids of the isolated *Phaeocystis pouchetii* and *Thalassiosira decipiens* in a

ratio of 75:25 yielded the smallest possible Euclidean distance, ED (if 5% steps were applied) from the fatty acid composition at the chl max. (ED = 6.01; Fig 5D). The calculated fatty acid composition from this combination is depicted in Fig. 5E, and corresponds well with the fatty acid pattern from the water column (Fig. 5C). Because of this close match despite the high number of variables, it is reasonable to assume that the observed phytoplankton community exclusively (Fig. 2) was responsible for the fatty acid composition (Fig. 5C) at the chl max., and that allochthonous fatty acids, e.g. from terrestrial sources, did not interfere significantly with our studies.

Sterols from the chl max. were dominated by 24-methylcholesta-5,22*E*-dien-3β-ol, cholest-5-en-3β-ol and 24-methylcholesta-5,24(28)-dien-3β-ol (Fig. 6B). Cholest-5-en-3β-ol was regarded as being derived from crustacean zooplankton (Goad 1978, Volkman et al. 1980), since it is found in neither *Phaeocystis* spp. nor in the Thalassiosiraceae. Minor sterols were 24-norcholesta-5,22*E*-dien-3β-ol, 27-nor-24-methylcholesta-5,22*E*-dien-3β-ol, cholesta-5,22*E*-dien-3β-ol, cholesta-5,24-dien-3β-ol, 24-ethylcholest-5-en-3β-ol and 24-ethylcholesta-5,24(28)-dien-3β-ol.

Like the fatty acids, the sterols reflected the phytoplankton composition (Fig. 2) well, as the sterol frac-

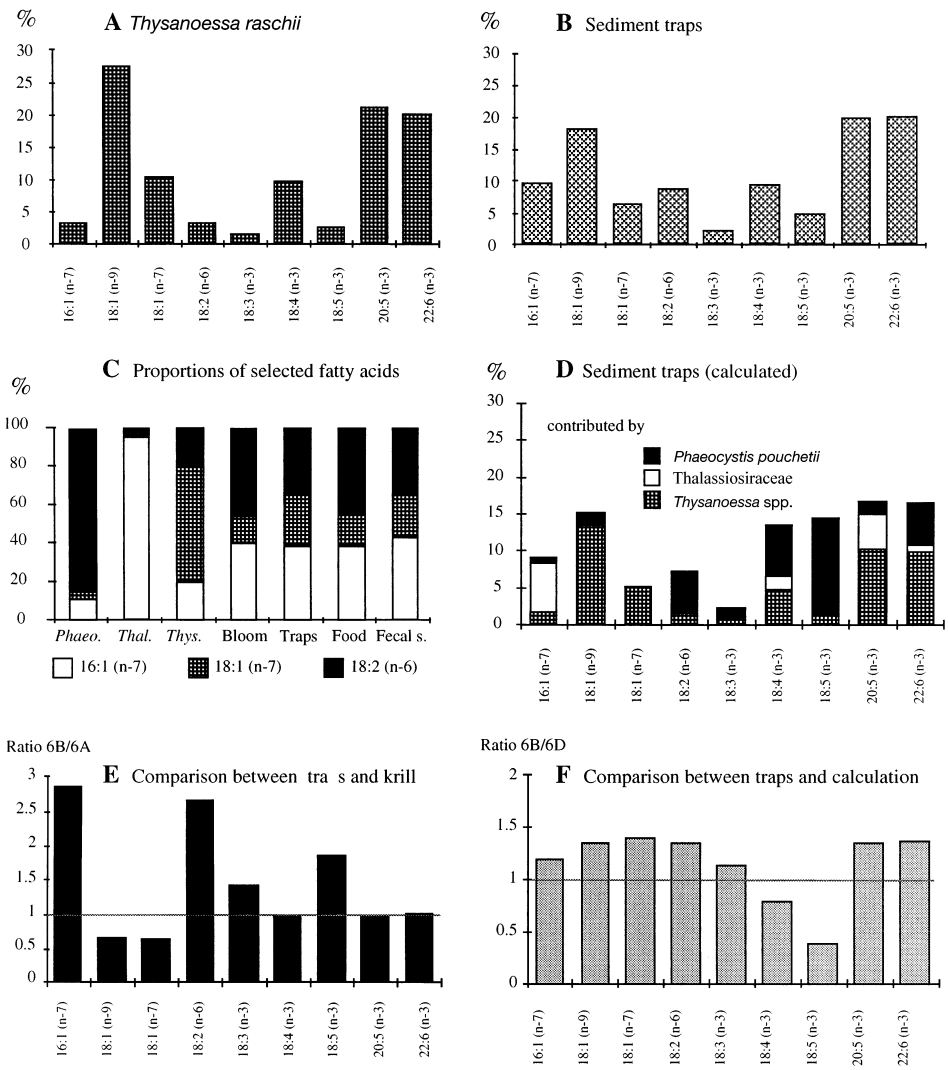

Fig. 6. Marker fatty acids in (A) *Thysanoessa raschii* (n = 5) and (B) sediment traps (average of all depths). (C) Relative proportion of selected fatty acids in *Phaeocystis pouchetii* (*Phaeo.*), *Thalassiosira decipiens* (*Thal.*), and *Thysanoessa raschii* (*Thys*), phytoplankton bloom (Bloom) and sediment traps (Traps), and food and fecal strings (Fecal s.) in laboratory experiment. (D) Pattern obtained by numerical combination of fatty acid patterns from *P. pouchetii* (36.7%: Fig. 5A), *Thalassiosira decipiens* (12.6%: Fig. 5B), and *Thysanoessa raschii* (50.7%: Fig. 6A) as described in 'Results'. (E) Ratio between sediment-trap pattern and krill pattern. (F) Ratio between sediment-trap pattern and calculated 'original' fatty acid composition

tion of *Phaeocystis* spp. is known to consist to almost 100% of 24-methylcholesta-5,22*E*-dien-3β-ol (Nichols et al. 1991). The dominating and only sterol always present in the Thalassiosiraceae is 24-methylcholesta-5,24(28)-dien-3β-ol at ca 70%, with minor amounts of diverse other sterols (Volkman & Hallegraeff 1988, Barrett et al. 1996). Since we isolated only 1 of at least 4 members of this group, we used only 24-methylcholesta-5,24(28)-dien-3β-ol as our marker for the Thalassiosiraceae.

Thysanoessa raschii sampled at the April 15 and 18, 1996 contained 16:1 (n-7), 18:1 (n-9), 18:1 (n-7), 18:2 (n-6), 18:3 (n-3), 18:4 (n-3), 18:5 (n-3), 20:5 (n-3) and 22:6 (n-3) (Fig. 6A), and the saturated fatty acids 16:0 (23%), 14:0 (3%), 18:0 (3%) (data not shown). Cholest-5-en-3β-ol comprised almost 100% of the sterols; other sterols were <1%.

The fatty acid composition of the krill was quite similar to that of krill-feces-dominated POC in the sediment traps (Fig. 6A,B). A comparison between the major sediment-trap biomarker fatty acids and the corresponding krill fatty acids, expressed by a ratio between Fig. 6A & B (Fig. 6E), revealed that the phytoplanktonic markers 16:1 (n-7), 18:2 (n-6), 18:3 (n-3) and 18:5 (n-3) (Fig. 5A,B) were considerably enriched in the sediment traps relative to their percentages in the krill. For diatoms 16:1 (n-7) is specific (Fig. 5B), 18:2 (n-6), 18:3 (n-3) and 18:5 (n-3) are major compounds of *Phaeocystis pouchetii* (Fig. 5A). In contrast, 18:1 (n-9) and 18:1 (n-7), which were only important in *Thysanoessa raschii* (Fig. 6A), were less concentrated in the sediment traps than in krill. The fatty acids 18:4 (n-3), 20:5 (n-3) and 22:6 (n-6), which were important in both phytoplankton taxa as well as in *T. raschii*, had very similar values in krill and in the sediment traps. Thus, the sediment traps probably contained material derived from *P. pouchetii*, Thalassiosiraceae and *T. raschii.*

To assess the relative contributions of the key organisms to the POC in the sediment traps, we selected specific fatty acids of similar chemical stability, which in fatty acids is inversely related to their numbers of cis-double bonds. 16:1 (n-7) was the only diatom-specific biomarker present in the sediment traps. Thus, for comparison with the other key organisms, we needed compounds specific for *Thysanoessa raschii* and *Phaeocystis pouchetii*, respectively, which were as similar in their chemical stability to 16:1 (n-7) as possible: hence the very abundant PUFA, e.g. 18:5 (n-3) for *P. pouchetii*, were not appropriate. While 18:1 (n-7) was appropriate for *T. raschii*, there was no equivalent *P. pouchetii*-specific fatty acid with 1 double bond. Therefore, we chose 18:2 (n-6) as a biomarker for *P. pouchetii*, as it was specific, and still has a stability which is comparable to those of 16:1 (n-7) and 18:1 (n-7) (sensu de Baar et al. 1983). One specific sterol was unique in each of the 3 key organisms. The following fatty acids and sterols were used to indicate the origin of sediment-trap POC: (1) 16:1 (n-7) and 24-methylcholesta-5,24(28)-dien-3β-ol for the Thalassiosiraceae; (2) 18:1 (n-7) and cholest-5-en-3β-ol for *T. raschii*, (3) 18:2 (n-6) and 24-methylcholesta-5,22*E*-dien-3β-ol for *P. pouchetii.*

The patterns of the selected fatty acids in the 3 key organisms (Fig. 6C) were combined in proportions which yielded the smallest EDs to the patterns characteristic of the phytoplankton bloom, material from the sediment traps, and the food and fecal pellets in the experiment, respectively (Fig. 6C). The combination of measured *Thysanoessa raschii*: *Phaeocystis pouchetii*: *Thalassiosira decipiens* fatty acids (Figs. 5A,B, 6A) in the composition 50.7:36.7:12.6 obtained by these ED-calculations yielded a fatty acid composition (Fig. 6D), which was indeed very similar to the composition of the sediment traps (Fig. 6B). The ratio between the actual fatty acid percentages in the sediment traps (Fig. 6B) and an 'original composition' inferred from the proportions of the selected specific fatty acids, and reconstructed using the fresh patterns of *T. raschii*, *P. pouchetii*, and *T. decipiens* (Fig. 6D) is shown in Fig. 6F. As expected, the fatty acids 18:3 (n-3), 18:4 (n-3) and 18:5 (n-3) were depleted in the sediment traps, with the degree of unsaturation, related to the 'original composition'. In contrast, the fatty acids with 1 or 2 double bonds, and, surprisingly, the highly unsaturated fatty acids which were major constituents of *T. raschii* (20:5 (n-3) and 22:6 (n-3)) showed similar percentages in the sediment traps and the original material.

Phaeocystis pouchetii-derived biomarkers dominated over diatom-derived biomarkers in the sediment traps, indicating that *P. pouchetii*-derived POC efficiently settled to deeper layers. The diatom-specific markers 16:1 (n-7) and and 24-methylcholesta-5,24(28)-dien-3β-ol increased with increasing depth relative to *P. pouchetii*-specific markers 18:2 (n-6) and 24-methylcholesta-5,22*E*-dien-3β-ol, and the compounds contributed by zooplankton 18:1 (n-7) and cholest-5-en-3β-ol became more important with depth (Fig. 7). While at the chl max., the concentration of *P. pouchetii* biomarkers was 4 to 5 times higher than the concentration of the Thalassiosiraceae-biomarkers, the ratio decreased with depth to values around 2 in the sediment traps (both substance classes, Fig. 8).

A trend similar to field studies was observed in the laboratory experiment: a 4 to 5-fold dominance of *Phaeocystis pouchetii* biomarkers over Thalassiosiraceae biomarkers in phytoplankton offered as food decreased due to gut passage to a 2-fold dominance in the fecal strings produced by *Thysanoessa raschii* (Fig. 8). Likewise, the proportion of the zooplankton-specific biomarkers increased due to gut passage (Fig. 7).

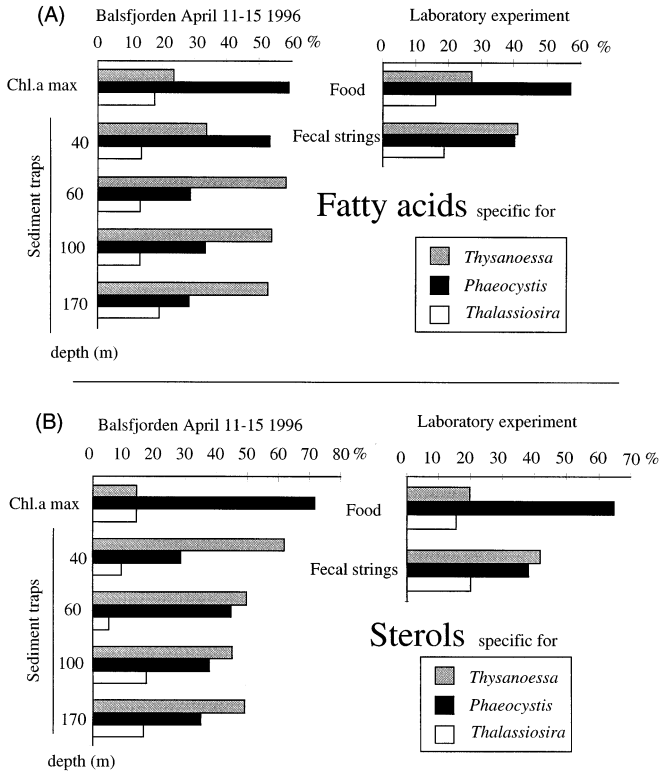

Fig. 7. Relative contributions of biomarkers representing the 3 key organisms (*Thysanoessa raschii*, *Phaeocystis pouchetii* *Thalassiosira decipiens*). (A) Fatty acids; (B) sterols. Note similarity between biomarker transitions from chlorophyll *a* max. to sediment traps in fjord, and from food to fecal strings in laboratory experiment

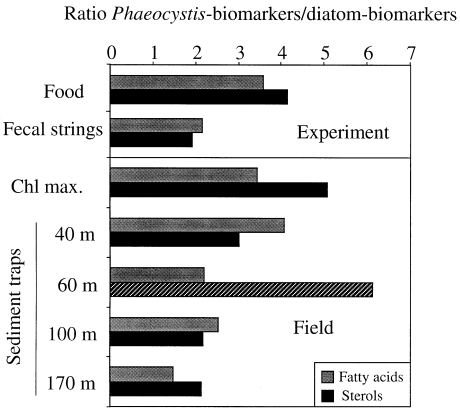

Fig. 8. Decrease of *Phaeocystis pouchetii*-specific biomarkers relative to Thalassiosiraceae-specific biomarkers with depth in Balfjord, and as a function of gut-passage in krill during laboratory experiment. Except for strong dominance of *P. pouchetii*-specific sterols at 60 m (hatched column), dominance of *P. pouchetii*-specific biomarkers tended to decrease with increasing depth of sediment trap

DISCUSSION

Ecological and biogeochemical implications

Sedimentation of *Phaeocystis pouchetii*-derived POC via krill fecal strings, as proposed by Lutter et al. (1990) and Riebesell et al. (1995) for *Phaeocystis* spp. bloom situations in Balsfjorden, was the most important process in the vertical flux of phytoplankton POC during our study. Krill fecal strings have been shown to dominate vertical flux in other regions, and to much deeper sediment traps than in our study (Wefer et al. 1988, Cadée et al. 1992). Thus, the concept of *Phaeocystis* spp. as organisms mainly fueling the microbial food web and leading to retention of organic matter at the surface (van Boeckel et al. 1992, Brussaard et al. 1995) has to be modified to include a mechanism which causes energy transfer to higher trophic levels and additionally allows efficient vertical flux of *Phaeocystis* spp.-derived POC.

Assuming that this process can be generalized, the co-occurrence of *Phaeocystis* spp. blooms and krill swarms should lead to a transfer of *Phaeocystis* spp.-derived POC to deeper layers over extensive areas in many regions, since both krill and *Phaeocystis* spp. are widely distributed and very common (Verity & Smetacek 1996). For example, the described interactions between krill and *Phaeocystis* spp. could be important in the distribution areas of *Thysanoessa raschii*, *T. inermis* (e.g. Mauchline & Fisher 1969, Richard & Haedrich 1991, Hunt et al. 1996) and *P. pouchetii* (Baumann et al. 1994b), which co-occur in parts of the Arctic Ocean and the adjacent seas, but also in large areas of the Antarctic Ocean, where blooms of *P. antarctica* (e.g. di Tullio & Smith 1993, Smith et al. 1995) could be a food reservoir for extensive swarms of *Euphausia superba* (Siegel & Loeb 1995) or *E. crystallorophias* (Makarov et al. 1991).

In addition to the direct evidence from the incubation experiment (Fig. 4), *in situ* ingestion of *Phaeocystis pouchetii* colonies by krill was indicated by 3 findings: (1) the sediment trap material, which was dominated by fecal strings, contained a high proportion of *P. pouchetii* biomarkers (Fig. 8); (2) the transition of fatty acid- and sterol biomarker compositions between bloom and sediment-trap material was similar to that from food to fecal strings in the feeding experiments (Fig. 8), which implies that the krill diet consisted mainly of *P. pouchetii* biomass in the field; (3) typical *Phaeocystis* spp. biomarkers such as the fatty acids 18:3 (n-3) and 18:5 (n-3), which are not abundant in diatoms and which are not regular compounds in *Thysanoessa* spp. (Sargent & Falk-Petersen 1981), were present in *T. raschii* caught on April 15 (Fig. 7A), which implies that *P. pouchetii* was ingested by krill (sensu Graeve et al. 1994).

These results contradict those of previous laboratory studies (Hansen et al. 1994), which showed that *Thysanoessa raschii* did not readily ingest *Phaeocystis pouchetii* colonies. This difference might result from differing sizes/physiological conditions of the *P. pouchetii* colonies used (sensu Estep et al. 1990): intact, actively growing colonies (such as the colonies we used) were shown to be less susceptible to grazing by copepods than deteriorating colonies. In our experiment, however, only 3 of 10 individual *T. raschii* actually fed on phytoplankton which was taken from the same culture. Apparently, the feeding behaviour of krill individuals is highly variable under laboratory conditions and should be interpreted with caution. In contrast, the biomarker compositions of the fecal strings in the sediment-trap material and in individual krill should have reflected the feeding activity of the krill in Balsfjorden and can thus be regarded as realistic indicators for the trophic relationship between *P. pouchetii* and krill *in situ*. Also, active feeding of large zooplankton on the *P. pouchetii* colonies is consistent with the observation that *Phaeocystis* spp. colonies are mechanically protected by a tough skin, whose protective value may be inversely related to grazer size and therefore inefficient against large zooplankton such as krill (Hamm et al. 1999, Hamm 2000).

The relative increase of the diatom markers 24-methylcholesta-5,24(28)-dien-3β-ol and 16:1 (n-7) compared to *Phaeocystis pouchetii* markers 24-methylcholesta-5,22*E*-dien-3β-ol and 18:2 (n-6) (Figs. 7 & 8), which occurred during (experimental) gut-passage in *Thysanoessa raschii* and during the transport from POC at the chl max. to the sediment traps, suggests differences in digestibility. Pond et al. (1995) found that in Antarctic krill (*Euphausia superba*), the mean gut-residence time for *Thalassiosira decipiens* was about 5 times longer than that for the haptophyte *Isochrysis galbana*. Nevertheless, the krill had similar uptake rates and assimilation efficiencies for both algae, which suggests that it is able to adjust its gut-passage time according to the digestibility of the food ingested.

Thysanoessa species possess well-developed gastric mills (Suh 1996), so we assume that the haptophytes *Isochrysis* spp. and *Phaeocystis* spp. should be of similar digestibility even when the *Phaeocystis* colonies are surrounded by a tough skin. Thus, by analogy with the results of Pond et al. (1995), we propose that in our case the large, silicified Thalassiosiraceae were harder to digest than the small *P. pouchetii* cells, and therefore would have required a longer gut-residence time to be digested to a similar extent. Since krill were ingesting a mixture of phytoplankton dominated by material which was easily digested (i.e. 85% *P. pouchetii*), they probably maintained a fast gut passage time, and digested *P. pouchetii* more efficiently than the diatoms, which in turn led to the relative enrichment of diatom biomarkers in fecal strings and sediment traps.

Assuming assimilation efficiencies of 75% for zooplankton feeding on *Phaeocystis pouchetii* (sensu Pond et al. 1995), we can infer an assimilation efficiency of ca 50% for the Thalassiosiraceae, which would be required to increase the diatom-derived biomarkers by a factor of 2, as shown in Fig. 8. Assuming a fecal matter production rate of ca 125 mg POC m^{-2} d^{-1} (Fig. 3), (mainly) krill would have been ingesting approx. 500 mg POC m^{-2} d^{-1}, which represents ca 2.5% of the integrated standing stock of POC or about 25% of the integrated standing stock of phytoplankton carbon (PPC) (Wassmann pers. comm.). Other grazers which are known to feed on *Phaeocystis* spp. colonies, e.g. *Calanus finmarchicus*, were present and might have caused additional loss.

However, the phytoplankton bloom did not decline rapidly, and the importance of *Phaeocystis pouchetii* decreased only slowly. In contrast to observations in the open ocean, where a rapid disappearance of *Phaeocystis* spp. blooms by sedimentation have been described (Smith et al. 1991), and in the North Sea, where cell lysis can cause a rapid decline of *Phaeocystis* spp. blooms (van Boeckel et al. 1992, Brussaard et al. 1995), *P. pouchetii* seems to be abundant in the ecosystem of Balsfjorden throughout the growth period, and is apparently not subject to sudden mass mortality (Eilertsen et al. 1981, Lutter et al. 1990, Riebesell et al. 1995). Prolonged sedimentation of moderate amounts of *P. pouchetii*-derived organic matter in fast-sinking fecal material, as described in this study, however, might well supply large amounts of POC from this alga to deeper layers or the sea floor on a yearly basis.

Advantages and constraints of biomarker approach

Further estimates on the proportions of *Phaeocystis* spp.- and diatom-derived biomass in amorphous organic matter of sediment traps could be based on ratios between biogenous silica (Si) and carbon (C), chl c_{1+2} and chl c_3 (sensu Jeffrey 1989), glucose and O-methylated sugars (sensu Janse et al. 1996), or between fucoxanthin and 19′-acyloxyfucoxanthins (sensu Wright & Jeffrey 1988). However, for our purpose these components would be less specific and less compatible biomarkers than the fatty acids and sterols we used: in our opinion, the key to such an assessment is a selection of specific biomarkers for different organisms which are representative in like manner for the total biomass of these organisms; that is, they have to be very similar in their chemical structures and thus their stabilities, and the rest of the cell biomass has to have

a similar composition, which is essentially given when 2 phytoplankton taxa are compared. Since degradabilities of biogenous Si and C differ largely, and C as such is not specific for any organism, information derived from Si/C measurements would be very difficult to interpret. 19′-oxyfucoxanthines, DMSP, O-methylated sugars and chlorophyll c_3 can be regarded as being specific for *Phaeocystis* spp. in certain cases, and can thus be a physical proof for the abundance of *Phaeocystis* spp.-derived organic matter (e.g. di Tullio et al. 2000); however, fucoxanthin, chl c_{1+2} (Jeffrey 1989), glucose (Janse et al. 1996) and DMSP (Baumann et al. 1994a) can be very abundant in both diatoms and *Phaeocystis* spp. so that their origin is uncertain if both phytoplankton taxa are abundant.

As fatty acids and sterols were used as biomarkers, the use of formaldehyde to fix the material in the sediment traps was suitable. In contrast to other fixatives such as $HgCl_2$ or sodium azide, formaldehyde hardens the bodies of swimmers, which probably limits leakage of zooplankton markers during the sampling period, and especially during the removal of swimmers (Knauer et al. 1984). While we cannot exclude a small amount of leakage from the swimmers in the sediment traps, the similarity of biomarkers in fecal strings from the experiment and in sediment trap material suggests that the contribution of swimmers to the biomarker composition in the sediment traps was not significant. However, while abundant in the surface, other potentially useful biomarkers to distinguish between *Phaeocystis* spp. and diatom biomass, such as chlorophylls c_1, c_2 and c_3 (Jeffrey 1989), were not detected in the sediment traps (Hamm unpubl. data), although chlorophyll *a* was still abundant. We suspect that the lack of the hydrophobic phytol residue (Borriss & Libbert 1984) increases the susceptibility of chl *c* to chemical reactions with formaldehyde compared to that of chlorophyll *a*; additionally, the chl *c*s, being (peripheral) antenna pigments, are more exposed and thus more sensitive to alteration by chemicals than the core pigment chl *a* in the less accessible reaction centres (B. Kroon pers. comm.).

The fact that it was possible to produce very similar fatty acid and sterol patterns at the chl max. and in the sediment traps from the patterns of isolated phytoplankton and individual krill suggests that besides these dominating plankton groups little other material was abundant in the water column, and that the biomarker patterns were conservative in space and time in the dominant taxa. Thus, apparently simple biomarkers of low specificity can give valuable information on the contribution of different phytoplankton taxa to the vertical flux of POC.

We found 3 sterols almost uniquely present in *Phaeocystis pouchetii*, *Thalassiosira decipiens*, and *Thysanoessa raschii*, respectively. The fatty acids in the dominant organisms were more numerous, which improved the characterization of the surface phytoplankton composition qualitatively, and enabled us to compare complex fatty acid patterns in the traps with those which were calculated from the proportions of the selected fatty acids of the key organisms. Differing stabilities of individual fatty acids and similar abundances in the key organisms forced us to select 1 fatty acid per organism for a characterization of the degraded sediment-trap material. Instead of 18:4 (n-3), which is widely used as a marker for flagellates in general, we used 18:2 (n-3), which, because of its chemical structure, was more useful to compare with 16:1 (n-7) in degraded matter. Also, it was more specific than 18:4 (n-3), which occurred in similar amounts (between 10 and 20%) in all 3 key organisms. Another advantage to using fatty acids as biomarkers is that the fatty acid composition of zooplankton reflectes the diets of the zooplankton (sensu Graeve et al. 1994).

Since it was not possible to find fatty acids with the same number of *cis*-doublebonds for *Phaeocystis pouchetii* and the Thalassiosiraceae, the interpretation of the biomarker patterns in the sediment traps and the experiment were greatly facilitated by the fact that the sterols were similar in their stability: 24-methylcholesta-5,22*E*-dien-3β-ol used for *P. pouchetii* and 24-methylcholesta-5,24(28)-dien-3β-ol used for the diatoms were degraded at the same rate during a phytodetritus degradation experiment (Harvey & Macko 1997).

In our study, a contribution of bacteria to 18:1 (n-7) (sensu Nichols et al. 1989) in the sediment-trap material was probably insignificant, because fatty acids which are commonly found in bacteria (e.g. 15:0 and 17:0, Bertone et al. 1996) were only present in trace amounts. Also, the presence of substantial amounts of bacterial fatty acids should have impaired the possibility of reconstructing the fatty acid pattern in the sediment-trap material from the isolated patterns of the 3 key organisms. The fatty acid composition of adult *Calanus finmarchicus* indicated that, like the krill, it ingested both *Phaeocystis pouchetii* and Thalassiosiraceae, since 16:1 (n-7) and the polyunsaturated C_{18}-fatty acids were present (sensu Graeve et al. 1994, data not shown). This observation is consistent with other feeding studies of *Calanus hyperboreus* and *C. finmarchicus* on *P. pouchetii* colonies and diatoms (Huntley et al. 1987, Hansen et al. 1990). This and the fact that fecal material was largely dominated by krill fecal strings (Fig. 3) indicate that the increasing importance of diatom biomarkers with depth was not caused by copepod activity, for instance by copepods feeding selectively on diatoms. Cholesta-5,24-dien-3β-ol, which is commonly found in copepods (Ikekawa 1985), was present in low amounts, and reflected the low abun-

dance of copepods at the chl max. and confirmed the efficient removal of copepods from the sediment-trap material.

In the experiment we used *Thysanoessa raschii* as a model for both *T. raschii* and *T. inermis* species. Feeding habits and biochemical compositions of *T. raschii* and *T. inermis* differ significantly during autumn and winter, when *T. inermis* contains large amounts of wax esters and smaller amounts of triacylglycerides and vice versa. In contrast, storage lipids (wax esters and triacylglycerols) are very low, and feeding habits and biochemical composition are very similar in both species, i.e. largely herbivorous, during the peak of the phytoplankton bloom in April (Falk-Petersen et al. 1981). Thus, we expect the biochemical composition of fecal material from both *Thysanoessa* species to have been very similar during our study.

In the isolated *Phaeocystis pouchetii* colonies and cultured *Thalassiosira decipiens*, much higher concentrations of polyunsaturated fatty acids (PUFAs) were measured than in the suspended matter of the water column, in blooms observed elsewhere (Claustre et al. 1990), or in the *P. antarctica* cultures of Nichols et al. (1991). In contrast to the suspended matter, our isolated *P. pouchetii* colonies were not subject to the lengthy filtration procedure which may increase the percentage of saturated fatty acids due to oxidation of unsaturated fatty acids. Further evidence that high percentages of saturated fatty acids are not characteristic of growing *Phaeocystis* spp. cells is provided by reports on fatty acid patterns in many other prymnesiophytes such as species of *Emiliania* or *Prymnesium*, which have patterns similar to those of the purified colonies in the present study (Okuyama et al. 1992, Conte et al. 1994).

The fatty acids and sterols used here as markers for the sedimentation of *Phaeocystis pouchetii* biomass are only derived from the *P. pouchetii* cells, since no lipids were found in the colony matrix and envelope (Hamm et al. 1999). The question as to which percentage of the total colony biomass is situated in the cells has not been resolved satisfactory; estimates range from 10% (Rousseau et al. 1990) to over 90% (van Rijssel et al. 1997) for large colonies. Although the krill in Balsfjorden apparently ingested whole *P. pouchetii* colonies, so that the cells and the extracellular material, whatever its nature and proportion, were ingested, the lack of knowledge about the extracellular material hampers estimations on its partition between assimilation and sedimentation in fecal strings.

In crustaceans, mechanical disruption of phytoplankton cells makes lipids, carbohydrates and proteins in like manner accessible to the enzymatic digestive processes (Dall & Moriarty 1983). Thus, in our study, where digestion caused the ratio between the biomarkers of *Phaeocystis pouchetii* and diatoms to shift in favor of the diatoms (Fig. 8), it might be suspected that the ratio between the total cell biomasses of these organisms shifted in the same direction. However, as extracellular, refractory carbon is an important component of *Phaeocystis* spp. colonies, the contribution of *P. pouchetii*-derived POC to the POC in the sediment traps may have been larger than the biomarkers indicate (although extracellular diatom-derived POC may have counteracted such an effect). Also, it is not likely that the biomarkers typical for *Thysanoessa raschii* are representative for the total POC derived from these organisms in the sediment traps. While a contribution of zooplanktonic lipophilic substances to fecal material is probably a physiological necessity (digestive enzymes are voided into the lumen of the digestive gland by exfoliation of B-cells (Nott et al. 1985), we know little of the contributions of zooplanktonic carbohydrates or proteins to fecal material (Cowie & Hedges 1996). Still, if we assume that the krill in Balsfjorden fed on and assimilated a diet dominated by *P. pouchetii* in the weeks before our study, when the phytoplankton composition was comparable to that shown in this study, it follows that most of the 'zooplanktonic' carbohydrates, proteins and lipids in the sediment traps had been also originally assimilated by *P. pouchetii*.

Conclusion

The phytoplankton composition of Balsfjorden in April 1996, which was dominated by *Phaeocystis pouchetii* and the Thalassiosiraceae, was clearly reflected in the sterol- and fatty acid composition of the POC. As shown experimentally, *P. pouchetii* was actively ingested by *Thysanoessa raschii*, which showed no significant preference for co-occurring diatoms. Thereby, gut passage in *T. raschii* modified but did not destroy the fatty acid and sterol signal from the food ingested. As a result, analysis of sediment-trap material, which was dominated by krill fecal strings, allowed inferences regarding the origin of the POC which sank to the sediment traps. The transition of biomarker patterns due to gut passage in *T. raschii* closely resembled the biomarker transition from the surface bloom to material in sediment-traps at 40 to 170 m depth. In both cases, a decrease in *P. pouchetii* biomarkers relative to diatom biomarkers was observed, which suggests that *P. pouchetii* was digested more efficiently than the diatoms. Still, our study did show a case where sedimentation of *P. pouchetii*-derived POC in krill fecal string was substantial. We hypothesize that if krill are abundant, POC derived from *Phaeocystis* spp. blooms generally has the potential to sink effectively to deeper

layers, although a large part of the ingested biomass may be assimilated by krill and eventually move on to higher trophic levels.

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