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ORIGINAL PAPER

A multiple biomarker approach to tracking the fate of an ice algal bloom to the sea floor

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Abstract In ice-covered Arctic seas, the ice algal production can be the main input of organic matter to the ecosystem. Pelagic–benthic coupling is thought to be particularly tight in those areas. The increase in ice algal production in Franklin Bay from January/February to April/May 2004 paralleled an increase in benthic oxygen demand. However, sedimentary chlorophyll *a*, which is usually an indicator of "fresh" organic matter inputs to the sea floor, did not increase. Consequently, it was asked what was the fate of the ice algal phytodetritus arriving at the sea floor? To answer this question, photosynthetic pigments from the sea ice, water column particulate organic matter, and sediment, as well as diatom frustules in the sediment, were studied from January to May 2004. The number of ice diatom cells in the sediment showed an increase in April/May, confirming higher inputs of fresh ice algae to the sediment. Changes in sedimentary pigment profiles in the first 10 cm suggested an increase in bioturbation due to enhanced benthic activities. Finally, the decrease in the ratio of chlorophyll *a* to phaeophorbide *a* implied an increase in macrobenthic activity. Benthic macrofauna consumed some of the deposited material and mixed some within the top five cm of sediment. The response of sedimentary pigments to an ice algal input can be studied at different levels and it is only the combination of these studies that will allow an understanding of the overall fate of phytodetritus in the benthic compartment.

Keywords Arctic · Beaufort Sea · Diatoms · Sedimentary pigment · Pelagic–benthic coupling · Carbon cycle

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Introduction

Marine primary production in the Arctic is primarily due to phytoplankton in the water column and microalgae associated with ice (Sakshaug 2004). Ice algae are generally found in the bottom layers of the ice sheet, in contact with the underlying sea water (Michel et al. 1996; Arrigo 2003; Lizotte 2003), and are represented by diatoms in Arctic and Antarctic seas (Günther and Dieckmann 1999; von Quillfeldt et al. 2003; Różańska et al. 2009). Ice algal production increases during spring due to the seasonal increase in irradiance (Wassmann et al. 2006). Although primary production rates by ice algae are generally low compared to phytoplankton, they contribute up to 57% of the total productivity in the central Arctic basin (Gosselin et al. 1997) and between 3 and 25% on Arctic shelves (Legendre et al. 1992). Ice algae can be the main source of carbon for the pelagic food web (Gosselin et al. 1997; Nozais et al. 2001; Arrigo 2003); however, variations in the extent of the sea-ice cover indirectly impact the inputs of organic matter to both pelagic and benthic food webs by influencing the ice algal production.

Grazing by ice fauna has been found to inefficiently control ice algal biomass (Werner 2000; Michel et al. 2002), and herbivorous zooplankton grazers are usually scarce in the spring. Thus, Carroll and Carroll (2003) suggested a mismatch scenario in ice-covered seas, resulting in strong vertical fluxes of undegraded particulate organic matter (POM) from the sea ice to the benthos. Moreover, recent studies have indicated that benthic organisms can derive energy directly from ice algae (Hobson et al. 1995; McMahon et al. 2006).

Sedimentary pigments have been used in short- and long-term studies assessing marine ecosystem change. Sedimentary chlorophyll *a* (chl *a*) is a marker of the "freshness" of the algal material flux reaching the sediment (Boon and Duineveld 1996). The presence of pigment degradation products in the sediments indicates the algal physiological status and the nature of processing that the chlorophyll pigment has undergone (Mantoura and Llewellyn 1983; Villanueva and Hastings 2000). Accessory pigments, which are light-absorbing compounds working in conjunction with chl *a*, are often specific for different algal groups and can be used as taxonomic markers (Gieskes and Kraay 1984; Jeffrey and Mantoura 1997). However, ice algae and phytoplankton diatoms have the same pigment signature, which means they can only be distinguished by a microscopic analysis of their respective communities. The direct study of diatom frustules in the sediment of Arctic shelves has revealed the presence of ice-associated diatom species under seasonally ice-covered waters (Sancetta 1981; Cremer 1999; Djinoridze et al. 1999; Polyakova 2003; Ambrose et al. 2005).

Previous studies in the Arctic have noted a positive correlation between sedimentary pigments and overlying production (Pfannkuche and Thiel 1987; Grant et al. 2002; Bessière et al. 2007). Since primary production varies greatly throughout the year, it has been hypothesized that inputs of organic matter to the sea floor also vary seasonally, in particular during the spring. When fresh organic matter reaches the sea floor, it can be stored as benthic biomass, respired, or buried.

The evolution of pelagic–benthic coupling in Franklin Bay in southeastern Beaufort Sea (Fig. 1) was followed from January to May 2004 during the Canadian Arctic Shelf Exchange Study (CASES) overwintering program. Ice algal biomass and downward fluxes of particulate organic material increased from the winter to the spring season (Riedel et al. 2006; Różańska et al. 2009). Sediment oxygen demand (SOD), a measure of labile carbon processed by the benthic community, also increased in April, as a response to an increase in ice algal phytodetritus inputs (Renaud et al. 2007). Unexpectedly, no increase in sedimentary chl *a* was observed, leading to the question of whether an input of ice algal phytodetritus to the sea floor always leads to an increase in sedimentary pigments.

The main objective of this study was to understand the complex fate of ice algal inputs to the sea floor. Three possible non-exclusive responses can be foreseen. (H1) The inputs of fresh ice algal phytodetritus to the sea floor increases ice algae in sediment and change surface sediment biomarkers. (H2) The increase in food inputs to the sediment stimulates the benthos, which consumes it quickly, resulting in an increase in benthic activity, bioturbation, and pigment degradation products. (H3) Finally, some groups of organisms are stimulated by fresh inputs more than others (macrofauna vs. bacteria).

Methods

Study area

Sampling was conducted six times from January to June 2004 at a field station on first-year landfast ice in Franklin

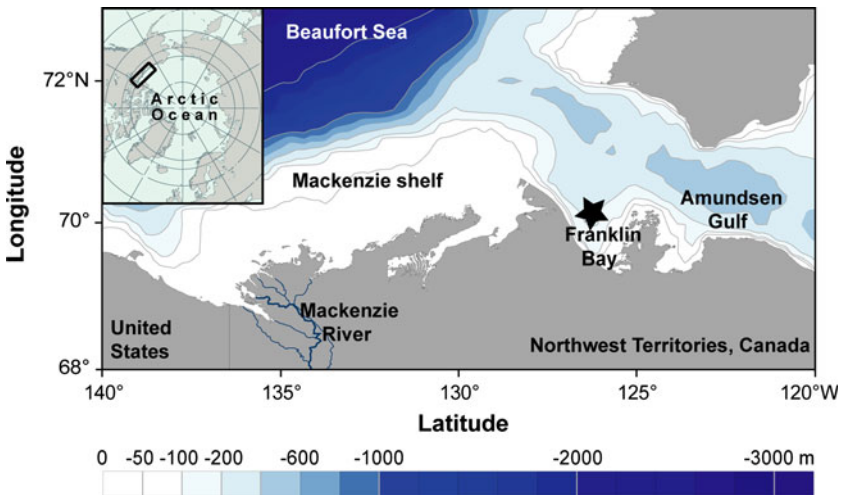

Fig. 1 Canadian Beaufort Sea showing the position of the overwintering station in Franklin Bay (indicated by a *star*)

Bay (70°04′N, 126°26′W; water depth ca. 250 m), southeastern Beaufort Sea, Northwest Territories, Canada (Fig. 1). The station was 1.5 km northeast of the overwintering site of the research icebreaker CCGS *Amundsen*. Ice thickness increased from 1.3 m in February to a maximum of ca. 2 m at the end of May.

Ice and water column sampling

Ice samples were collected three times in January/February and three times in April/May. Three ice cores per sampling date were collected manually with a Mark II ice corer (9 cm internal diameter; Kovacs Enterprises). The bottom 4–10 cm of each ice core was cut off and melted together in 1–5 L of 0.2-μm-filtered surface sea water to minimize osmotic stress (Garrison and Buck 1986). Four to 10 L of water (15 m) was collected on the same dates as for ice sampling in triplicates by a rosette through the ship's moon pool. Melted ice core and water samples were filtered onto Whatman GF/F filters, which were frozen at −20°C prior to pigment analysis by high-pressure liquid chromatography (HPLC).

Sediment sampling

Sediment was sampled on four occasions (13 January, 11 February, 27 April, 7 May) from a box corer (45 cm × 45 cm) and one more time on 6 April, from a piston corer. Due to difficulties in sampling logistics, the coring instrument was deployed only once at each sampling date. Three sub-cores (5 cm diameter × 10 cm deep) were taken from the same box corer for sedimentary pigment. For all sampling dates, no fluff layer was observed, but the sediment–water interface appeared to be intact, even when sampled with the piston corer. The cores were extruded and sliced at 1-cm intervals under reduced light conditions. Each interval was divided in two, half for pigment analysis by fluorometry and half for pigment analysis by HPLC, although HPLC analysis was only performed on the top 2 surface layers. Both subsamples were wrapped in aluminum foil and frozen at −20°C directly after slicing in order to avoid pigment degradation. Subsamples for the two first cm for stable isotope and diatom frustule analyses were taken with a truncated syringe (1.4 cm diameter). Samples for stable isotope analysis were directly frozen at −20°C. Samples for diatom frustule analysis were stored in a scintillation vial and preserved with 20 mL of buffered 3.7% formaldehyde.

Fluorometric analysis

Within 2 weeks, sediment subsamples were analyzed by fluorometry. Subsamples were placed in 60-mL centrifuge tubes and 20 mL of 100% acetone was added. Tubes were stored at –20°C in the dark for 48 h and shaken periodically. Prior to fluorometric analyses, the tubes were centrifuged at 4,000 rpm for 10 min at 0°C. The supernatant was analyzed in a Turner Designs Model 10-AU fluorometer before and after acidification with 5% HCl in order to determine chl *a* and phaeopigments (phaeo), respectively. Phaeo correspond to the total of chl *a* degradation products and include phaeophorbide *a* and phaeophytin *a*. Pigment concentrations were calculated according to Holm-Hansen et al. (1965).

HPLC analysis

Ice algae, POM and sediment samples were extracted and analyzed for pigment composition as described in Morata et al. (2008). In summary, ice algae and POM samples were extracted in 2 mL of 100% HPLC-grade acetone for 12–24 h, while 1–3 g of freeze-dried sediment was extracted in 8 mL of 80:20 HPLC-grade acetone:methanol. Five milliliters of the sediment extracts were reconcentrated by blowing to dryness under nitrogen and redissolving in 250 μL of 90% acetone. Two hundred microliters of each sample were injected through a guard column to a reverse-phase Alltech Absorbsphere C18 column (5 μm particle size; 250 × 4.6 nm id), using the program of Chen et al. (2001). Carotenoids were identified and quantified on the photodiode array (PDA) detector at 438 nm, while chlorophylls and phaeopigments were quantified on the fluorometer detector. The quantification of each pigment was determined using response factor (RF) of pigment standard (DHI Water and Environment, Denmark). Chl *a* is a marker of living algal cells while its degradation products, phaeophorbide *a* and phaeophytin *a*, are usually related to grazing and various processes, including microbial degradation, respectively (Leavitt 1993). The accessory pigment used as a marker for diatoms is fucoxanthin. In addition, fucoxanthin allomeres, considered as degraded fucoxanthin, were identified (similar spectrum, but different retention time) and quantified using the response factor of fucoxanthin.

Carbon and nitrogen stable isotope analysis

Frozen sediment subsamples for stable isotope analysis were dried at 60°C overnight. To decalcify subsamples for carbon analysis, about 2 g of dry, homogenized sediment was placed in a crucible, where 2 mL of 1 N HCl was added and then dried at 80°C overnight. This operation was repeated three times or until the sediment did not show a clear bubbling due to the conversion of carbonate to carbon dioxide gas. Decalcified sediment subsamples were used for %C (organic carbon) and δ^{13}C determination, while non-decalcified subsamples were used for %N and δ^{15}N

analysis. Stable isotope analysis of sediments was performed by the Environmental Geochemistry Laboratory, Department of Geology, Bates College, Lewiston, Maine, using a ThermoFinnigan Delta V coupled to a Costech EA Conflo III combustion interface. All stable carbon isotope values are reported in delta (δ) notation, in units of per mille (‰), where $\delta = [(\text{Rsample}/\text{Rstandard}) - 1] \times 1{,}000$. $R = {}^{13}C/{}^{12}C$ and ${}^{15}N/{}^{14}N$, and the standards are Vienna Peedee belemnite (VPDB) and air for carbon and nitrogen, respectively. The reproducibility on the bulk sediment was ±0.2‰, as determined by the standard deviation of multiple analyses.

Diatom frustule analysis

Diatom frustules were extracted from the sediment using Ludox/Colloidal Silica (L. Cooper, personal communication). Ludox has been previously used to separate algal material and microphytobenthos from detritus and sediment (Blanchard et al. 1988; Hamilton et al. 2005). Here, the centrifugation of sediment, Ludox, and distilled water creates a density gradient, allowing diatoms to aggregate in a layer at the interface between the Ludox-sediment and water layers. The 3.07 cm^3 of sediment sample was placed in a 15-mL polypropylene centrifuge tube. Sediment was rinsed with water, centrifuged at 2,200 rpm for 8 min, and the supernatant was removed. This procedure was repeated four times. In order to have a 3–1 Ludox to sediment ratio, 9 mL of Ludox was added to the tube, which was then gently inverted a few times. Distilled water (2.5 mL) was placed on top of the Ludox-sediment mixture, and the tube was centrifuged 5–7 min at 1,800 rpm. The thin milky-like layer of diatoms was transferred to a new tube. In order to rinse the remaining Ludox, 10 mL of distilled water was added to the tube and centrifuged for 8 min at 2,200 rpm. The supernatant was removed, and the procedure was repeated four times. Diatoms present in the extract were counted using the method of Hamilton et al. (2002). When the cytoplasm remained in the cells, diatoms were counted as potentially viable cells. When more than half of the cytoplasm was missing, the cells were counted as empty.

Results

Ice algae and water column pigments

Increases in pigment concentrations were observed at the bottom of the sea ice and in the water column POM at 15 m from winter to spring (Fig. 2a–d). Chl *a* concentration and chl *a*:phaeo ratio increased for both ice and POM from January/February to April/May. This trend was similar for accessory pigments. Fucoxanthin concentration and fucoxanthin:degraded fucoxanthin ratio increased in April.

Surface sedimentary pigments and stable isotopes

Although chl *a* and fucoxanthin concentrations increased in the bottom ice and POM in April, there was no similar increase in pigments in the top 2 cm of sediment (Fig. 2e, f). Chl *a* concentrations seemed to even decrease during the sampling period although the chl *a*:phaeo ratio increased continuously and the fucoxanthin:degraded fucoxanthin ratio started to increase in May. Relative concentrations of degradation products of chl *a* changed during the year: the chl *a*:phaeophorbide *a* ratio showed a decrease in April, while the chl *a*:phaeophytin *a* ratio tended to increase (Fig. 3a). In order to compare pigment degradation products with benthic activities, the ratio of total community SOD to bacteria/meiofaunal oxygen demand ("minivial" SOD) was calculated from Renaud et al. (2007). While the total SOD increased by an order of magnitude from January/February to April/May, the minivial SOD only varied by a factor of two (Fig. 3a in Renaud et al. 2007). The overall ratio of the total SOD:minivial SOD increased through time (Fig. 3b). Stable isotopes and %N and %C in surface sediment did not change from January to April (Fig. 4a, b). Since the %C ranged from 1.28 to 1.33% dry weight sediment, the carbon from chl *a* represented only 1–2% of the total sedimentary organic carbon.

Sedimentary pigment profiles

Vertical profiles of chl *a* concentration in the sediment showed a sub-surface maximum in January/February (Fig. 5a, b) which disappeared in April/May (Fig. 5c–e). Chl *a* concentration in the first 1 cm decreased from 0.13 μg cm^{-3} on 14 January to 0.05 μg cm^{-3} on 27 April. However, when averaging over the first 5 cm and 10 cm, chl *a* concentrations remained relatively stable throughout the sampling period (Fig. 6a). Finally, the chl *a*:phaeo ratio, an indicator of the freshness of organic matter, generally increased with time, especially in the top 5 cm and was always higher when averaged over the entire section (0–10 cm) than in the top first centimeter (Fig. 6b).

Diatom frustules

The abundance of both empty and viable pennate diatoms showed an increase of 170–300% over the sampling period (Fig. 7). Most of the pennate diatoms identified at the species level (98–100%) were represented by sea-ice algae (Table 1), and the three dominant taxa were *Fragilariopsis cylindrus*, *Navicula* spp. and *Nitzschia frigida*.

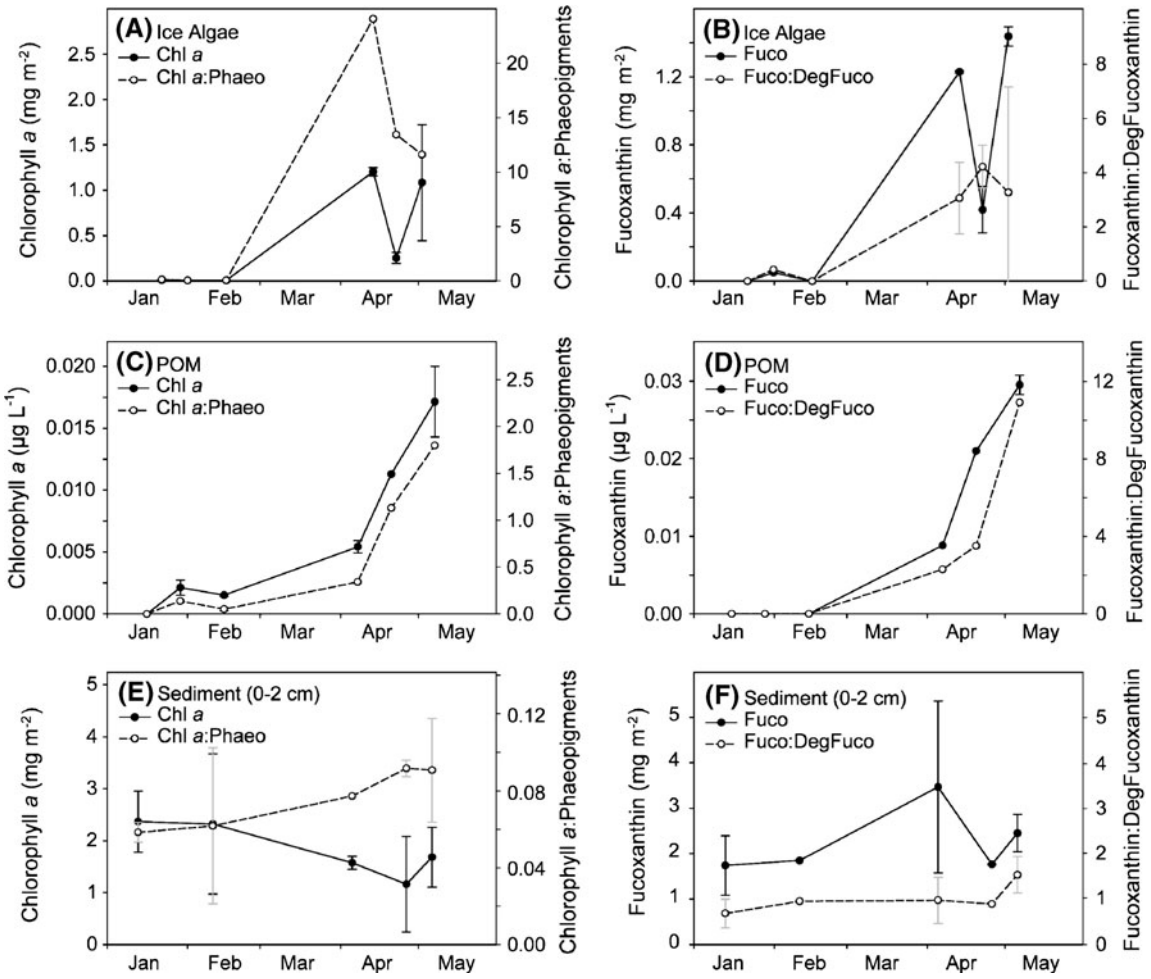

Fig. 2 Temporal variations of (**a**, **c**, **e**) chlorophyll *a* (chl *a*) concentration and ratio of chl *a* to phaeopigment (phaeo), and (**b**, **d**, **f**) fucoxanthin (Fuco) concentration and ratio of fuco to degraded fucoxanthin (DegFuco) in (**a**, **b**) the bottom ice, (**c**, **d**) water column particulate organic matter at 15 m and (**e**, **f**) top 2 cm of surface sediment in Franklin Bay from January to May 2004. Mean values ± SD are shown

Discussion

The present study confirms that inputs of ice algae to the sediment increased from January/February to April/May and are a source of organic matter to the benthos, as suggested by Renaud et al. (2007). The following discussion in organized as an evaluation of the three hypotheses.

H1: Inputs of fresh ice algal phytodetritus to the sea floor increase ice algae in sediment and change surface sediment biomarkers

Previous studies on Arctic ecosystems have suggested local autochthonous primary production as a major factor determining sedimentary chl *a* (Pfannkuche and Thiel 1987; Boetius and Damm 1998; Grant et al. 2002; Schewe and Soltwedel 2003; Clough et al. 2005; Bessière et al. 2007). In the Bering and Chukchi seas, increases in sedimentary chl *a* have been reported following breakup of the spring ice algal bloom (Cooper et al. 2009; Pirtle-Levy et al. 2009). However, to our knowledge, correlations between phytoplankton or ice algal production with sedimentary pigments have not been studied throughout the ice-covered season. In polar regions, the production by sea-ice algae, especially diatoms, can be the main source of carbon for pelagic and benthic food webs (Gosselin et al. 1997; Nozais et al. 2001; Arrigo 2003).

In the present study, both chl *a* and fucoxanthin concentrations increased in the bottom ice layer and the water column from January/February to April/May (Fig. 2a–d), indicating a biomass increase in ice algae and more specifically, diatoms. The ice algal community in Franklin Bay was dominated by the pennate diatoms *Nitzschia frigida*, *N. promare* Medlin, *Navicula* sp. 6 and *N. pelagica*, which increased steadily from February to May (Różańska et al. 2009). However, the very low chl *a* concentrations (<0.02 mg L^{-1}) in the water column (Fig. 2a) confirmed the dominance of ice algae as the main carbon source for the

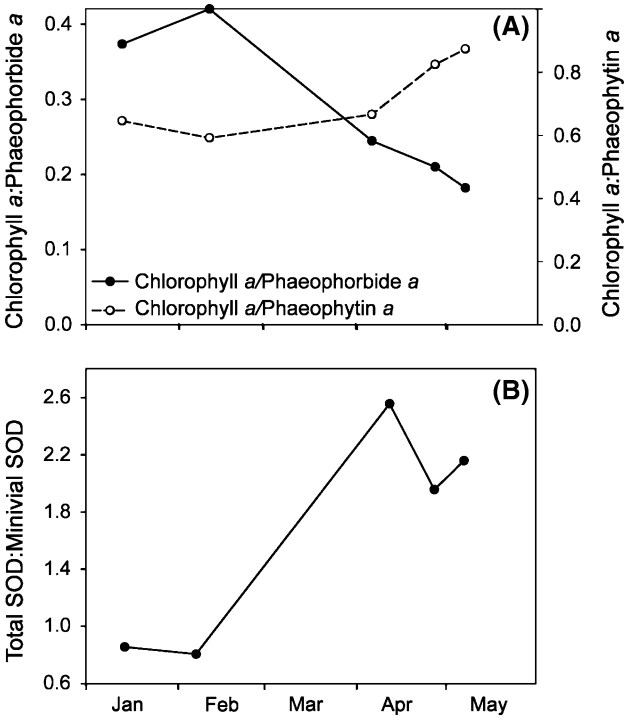

Fig. 3 Temporal variations of **a** ratios of sedimentary chlorophyll *a* (chl *a*) to phaeophorbide *a* and chl *a* to phaeophytin *a*, and **b** ratio of total sediment oxygen demand (SOD) to minivial SOD in Franklin Bay from January to May 2004. SOD data were from Renaud et al. (2007). Ratio < 1 in January/February is due to methodological overestimation of minivial SOD (see Grant et al. 2002 for further information)

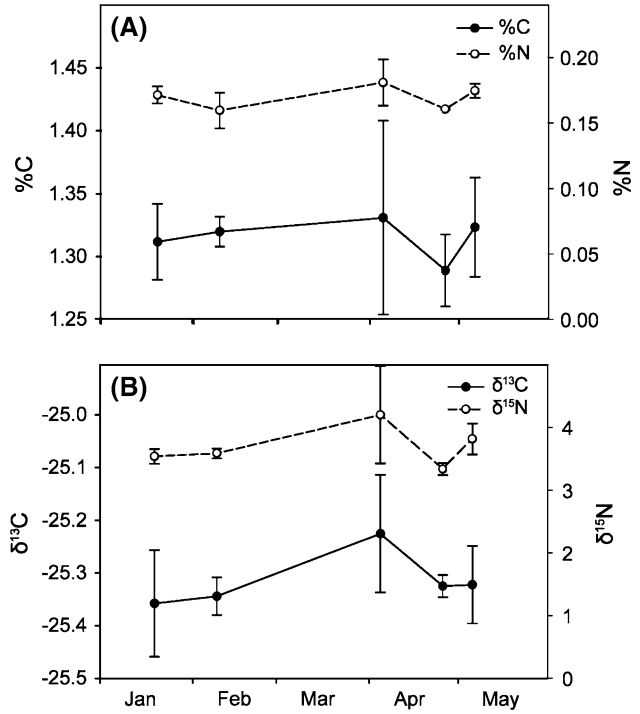

Fig. 4 Temporal variations of **a** percentage of organic carbon (%C) and nitrogen (%N) in the sediment, and **b** sedimentary stable isotope δ^{13}C and δ^{15}N composition. Mean values ± SD (n = 3) are shown

pelagic and benthic food web. Vertical fluxes of POM increased in the upper 25 m of the water column from mid-March (Renaud et al. 2007; Juul-Pedersen et al. 2008). During the spring, the sinking of algal cells also increased, and cells were mainly the same sea-ice pennate diatoms recorded in trap samples (i.e. *Nitzschia frigida* and *Navicula* spp., A. Tatarek personal communication). Similarly, POM fluxes at 200 m in Franklin Bay increased in the spring, and ice algae likely contributed significantly to this increase (Forest et al. 2008).

Grazing by zooplankton can strongly impact downward fluxes of POM produced in the surface layer of the water column (Olli et al. 2002; Wexels Riser et al. 2008). A higher degradation of fresh algal biomass is expected to increase the relative amount of chlorophyll degradation products (Welschmeyer 1985), which can be detected in the sediment by a change in the chl *a*:phaeo ratio. However, some studies have reported that copepods do not feed at chl *a* concentration <1 μg L^{-1} (Frost 1972; Gamble 1978; Saunders et al. 2003). In the present study, at the deep chl *a* maximum, no such chl *a* concentrations were attained. Seuthe et al. (2007) observed an increase in the zooplankton fecal pellet production during this same period but they suggested that this was probably due to additional non-pigmented sources of food, such as microzooplankton. No grazing degradation products were identified during fecal pellet production experiments (N. Morata, unpublished data). All of these suggest that the grazing occurring in the water column may not significantly impact the algal biomass during the early spring and it is probably not a source of input of degraded material to the sea floor. Consequently, the increase in sedimentary chl *a*:phaeophorbide *a* ratio is likely due to higher inputs of fresher algal material.

The increase in ice algal biomass throughout the spring and the inefficient control of the ice algal biomass by pelagic grazers may contribute to higher inputs of fresh organic matter to the benthos in April/May. Frustules of ice algae have been previously recorded in the sediment of Arctic shelves (Sancetta 1981; Cremer 1999; Djinoridze et al. 1999; Polyakova 2003; Ambrose et al. 2005) or have been suspected to occur due to observations of high concentrations of chl *a* and/or fucoxanthin (Schewe and Soltwedel 2003; Morata and Renaud 2008; Morata et al. 2008; Pirtle-Levy et al. 2009). Here, the percentage of empty and viable pennate diatoms increased (Fig. 7), and *Nitzschia frigida* and *Navicula* spp. dominated the diatom composition in ice algal communities and sediment traps (Różańska et al. 2009; A. Tatarek, personal communication) as well as in sediment samples. The ratio of sedimentary chl *a*:phaeo also increased, reflecting higher inputs of sinking algae as

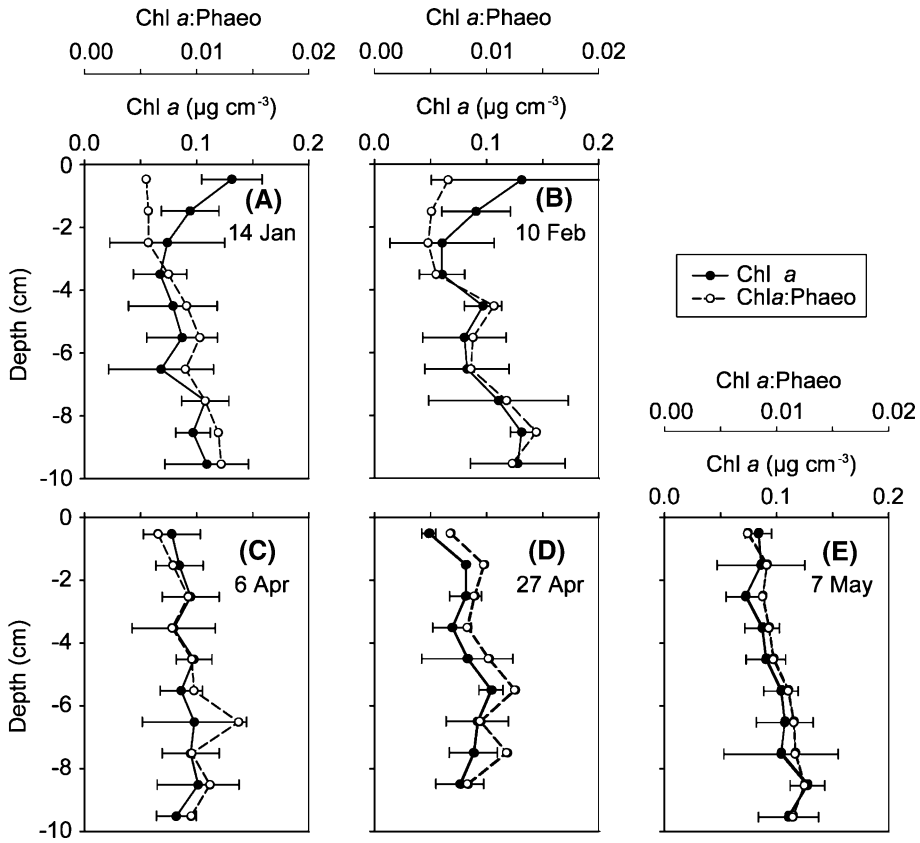

Fig. 5 Vertical profiles of sedimentary chlorophyll *a* (chl *a*) and ratio of chl *a* to phaeopigment over the first 10 cm of sediment in Franklin Bay from January to May 2004. Mean values ± SD ($n = 3$) are shown

fresher phytodetritus; however, the chl *a* and fucoxanthin concentrations showed no increase. Sedimentary pigments, then, only reflected the increase in the "quality" and not the quantity of phytodetritus. Only the number of diatom cells showed the increase in quantity (Table 1; Fig. 7).

Stable isotopes have been used in marine systems to estimate the inputs of terrestrial and marine organic carbon to the sediment (Naidu et al. 1993; Goni et al. 2000) and to trace the energy pathways from different sources of primary production (including ice algae) through the pelagic food web (Hobson et al. 1995; Tamelander et al. 2006, 2008). In the present study, stable isotopes, %N, and %C did not show substantial variations from January to May (Fig. 4). Stable isotopes and percentages of carbon and nitrogen integrate the signal of the overall organic matter present in the sediment over a period of months and thus are probably not good indicators of short-term changes in the vertical flux of the organic material to the sea floor in Franklin Bay. Organic carbon represented about 1.3% of the dry weight sediment, while sedimentary chl *a* only represented <0.03% of the dry weight sediment. Changes in the signal of the sedimentary phytodetritus may, therefore, be lost when studying bulk sediment parameters. Our first hypothesis is thus partially confirmed. The abundance of diatom frustules (empty and viable cells) and chl *a*:phaeo ratio reflected the increase in ice algal phytodetritus to the sea floor, but the data from other biomarkers were inconclusive. Consequently, in Franklin Bay, only the overall increase in the phytodetritus quality can be studied using detailed pigment analysis but not with biomarkers of bulk organic material.

H2: The increase in food inputs to the sediment stimulates the benthos, resulting in a quick increase in benthic activity, bioturbation, and pigment degradation products

Sediment communities have been reported to quickly respond to pulses of phytodetritus reaching the sea floor by increasing their consumption of oxygen (Witte et al. 2003; Renaud et al. 2008). High SOD values have been recorded in April/May in Franklin Bay by Renaud et al. (2007) as a possible consequence of increasing ice algal inputs.

Increasing food availability can increase foraging activity by benthic animals (Jumars and Wheatcroft 1989; Maire et al. 2006), which can affect sediment profiles of pigments and other constituents. Moreover, chl *a*:phaeo ratios can be used as indicators of the degradation of organic matter (Boon and Duineveld 1996). In Franklin Bay, the lowest chl *a*:phaeo ratios were always measured in the top centimeter of the sediment (Fig. 6b) compared to the average values over the 5 or 10 top centimeters. As fresh phytodetritus is always introduced to the sediment, these lower chl *a*:phaeo ratios suggest a rapid use of the surface organic

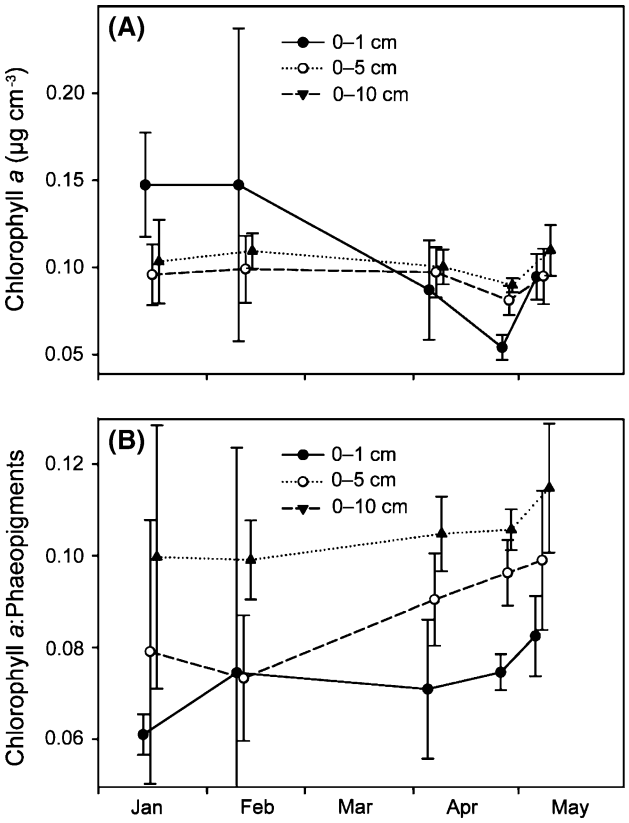

Fig. 6 Temporal variations of **a** chlorophyll *a* concentration and **b** ratio of chlorophyll *a* to phaeopigment in the 0–1, 0–5 and 0–10 cm of sediment in Franklin Bay from January to May 2004. Mean values ± SD are shown

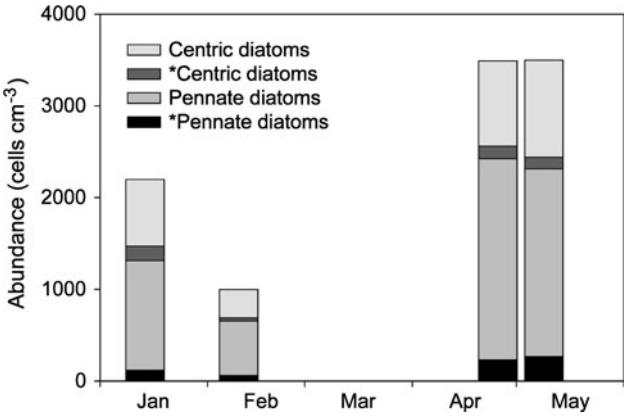

Fig. 7 Temporal variations in the relative abundance of viable (with chloroplasts) and empty centric and pennate diatoms in the sediment in Franklin Bay from January to May 2004. * Indicates viable species

matter, a quick burial of the fresh phytodetritus underneath the surface sediment, or both.

In low bioturbation conditions, sedimentary chl *a* concentrations exhibit an exponential decrease with depth, whereas irregular pigment profiles can occur due to non-diffusive mixing by benthic organisms (Sun et al. 1994). Sedimentary pigment profiles (Fig. 5) changed in Franklin Bay from a decrease with depth in January/February (Fig. 5a, b) to a more homogeneous distribution in April/May (Fig. 5c–e). The change in sedimentary chl *a* profile can also be observed when comparing the top cm with the average values for the first 5 and 10 top centimeters (Fig. 6a). Chl *a* concentration in the top first cm decreased over time, while the average values over the first 5 and 10 top centimeters remained more stable, suggesting a transport of the sedimentary pigments in April/May compared to January/February. While the calculation of bioturbation rate would require sedimentation and decomposition rate values, the change in sedimentary chl *a* concentrations with depth, and the increase through time of the chl *a*:phaeo ratio in the top 5 cm, suggest an increase in particle mixing.

In Franklin Bay, the fauna consists of a mud-associated community mainly dominated by the deep burrowing polychaete *Maldane sarsi* Malmgren and other common species, including other polychaetes (*Tharyx kirkegaardi* Blake + *T. marioni* St. Joseph, *Lumbrineris impatiens* (Claparède), *Prionospio cirrifera* Wiren + *P. steenstrupi* Malmgren), ostracods (Podocopid 1a, *Philomedes brenda* (Baird)) and bivalves (*Thyasira flexuosa* (Montagu), *Portlandia* spp.) (Conlan et al. 2008). The polychaete *Maldane sarsi* is a deep burrowing, head-down, non-selective deposit feeder that defecates at the surface and, therefore, is probably important in non-local sediment mixing, pore water oxygenation and surface nutrient replenishment (Holte 1998). Enhanced benthic activity (SOD) in April/May may have contributed to higher bioturbation as many benthic organisms increase burrowing activities. Previous studies have shown that the benthos can use rapidly ice algae as food source (McMahon et al. 2006; Sun et al. 2009). The lack of an increase in sedimentary chl *a* concentration in the present study may, then, be a result of the rapid use of phytodetrital inputs due to a higher benthic activity, as suggested in Renaud et al. (2007), combined with a reworking and burial of the sedimented organic material. We can consider our second hypothesis as being mostly confirmed even though it remains uncertain how the vertical inputs of fresh ice algae are degraded, as, for example, the uncolored chl *a* degradation products are not identifiable by HPLC.

H3: Some groups of organisms are stimulated by fresh inputs more than others (macrofauna vs. bacteria)

Compared to temperate regions, the Arctic macrobenthos has an enhanced role in benthic carbon cycling relative to the meio- and microfauna (Piepenburg et al. 1995; Clough et al. 2005; Renaud et al. 2008). Partitioning of benthic metabolism, however, has been found to vary seasonally depending on the trophic conditions of the system, i.e. oligotrophic

Table 1 Abundance of viable (with chloroplasts) and empty diatoms in cells cm^{-3}, with their relative proportion in parenthesis, in the first 2 cm of sediment under first-year landfast ice in Franklin Bay in winter and spring 2004

	14 Jan cm^{-3} (%)	10 Feb cm^{-3} (%)	29 Apr cm^{-3} (%)	9 May cm^{-3} (%)
Diploneis spp.	0	0	314 (9.0)	139 (4.0)
**Fossula arctica* Hasle, Syvertsen & von Quillfeldt	0	0	0	69 (2.0)
Fossula arctica	0	16 (1.6)	46 (1.3)	0
Fragilariopsis cylindrus (Cleve) Frenguelli	303 (13.8)	202 (20.2)	661 (18.9)	939 (26.8)
Fragilariopsis oceanica (Cleve) Hasle	41 (1.9)	0	0	0
**Navicula pelagica* Cleve	52 (2.4)	24 (2.4)	216 (6.2)	0
**Navicula vanhoeffenii* Gran	0	12 (1.2)	0	0
Navicula spp.	70 (3.2)	47 (4.7)	111 (3.2)	233 (6.7)
Nitzschia frigida Grunow	169 (7.7)	79 (7.9)	111 (3.2)	57 (1.6)
Nitzschia neofrigida Medlin	23 (1.1)	0	0	0
Nitzschia spp.	47 (2.1)	16 (1.6)	39 (1.1)	0
Pseudogomphonema arcticum (Grunow) Medlin	146 (6.6)	43 (4.3)	105 (3.0)	44 (1.3)
*Unidentified pennate cells	94 (4.3)	36 (3.6)	177 (5.5)	163 (4.7)
Unidentified pennate cells	367 (16.7)	166 (16.6)	635 (17.0)	617 (18.1)
Chaetoceros spp.	29 (1.3)	16 (1.6)	0	0
**Leptocylindrus minimus* Gran	58 (2.7)	0	0	0
**Melosira arctica* Dickie	29 (1.3)	12 (1.2)	33 (1.0)	0
**Thalassiosira* spp.	82 (3.7)	0	79 (2.3)	69 (2.0)
Thalassiosira spp.	641 (29.2)	206 (20.6)	615 (17.6)	737 (21.1)
*Unidentified centric cells	17 (1.0)	35 (3.6)	59 (1.7)	82 (2.4)
Unidentified centric cells	23 (1.1)	87 (8.7)	314 (8.9)	321 (9.4)

Only species representing more than 1% of the total cell numbers at a given date are presented

* Indicates viable species

vs. meso–eutrophic (Gooday 2002). In the North Water Polynya in the eastern Canadian Arctic, the meio- and microbenthos dominated oxygen consumption in the spring, while the macrofauna was responsible for the greatest oxygen consumption in the summer (Grant et al. 2002).

From January/February to April/May, the total SOD increased 10 times, while the minivial SOD showed only two time increase (Renaud et al. 2007). The minivial incubations overestimated the bacterial activity since the sediment exposure to oxygenated waters can break up nutrient microgradients and redox conditions, therefore, possibly enhancing bacterial oxygen demand (Grant et al. 2002). However, the increase in the total SOD:minivial SOD ratio over time suggested an increase in the macrofaunal oxygen demand.

Both macrozooplankton and macrobenthos remove the phytol chain of chl *a* during grazing (Prahl et al. 1984; Harvey et al. 1987), resulting in the creation of phaeophorbide *a* degradation products (Leavitt 1993). Conversely, the microzooplankton or the bacteria cannot efficiently remove the phytol chain of chl *a*, resulting in the creation of phaeophytin *a* instead of phaeophorbide *a* (Verity and Vernet 1992; Leavitt 1993). During our study, the chl *a*:phaeophorbide *a* ratio decreased while chl *a*:phaeophytin *a* increased (Fig. 3). Although phaeophorbides were used to trace grazing processes in both the water column (Jeffrey 1974; Carpenter et al. 1986; Spooner et al. 1994) and the sediment (Brotas and Plante-Cuny 1998; Riaux-Gobin et al. 2000), it has recently been argued that they may not always be a relevant indicator of herbivorous activities (Villanueva and Hastings 2000; Ford and Honeywill 2002). The chl *a*:phaephorbide *a* ratio by itself does not allow to conclude to a relative enhancement of the macrofauna activities. However, combined with the SOD results, the present study suggests that the macrobenthic activity is enhanced by the pulse of ice algal phytodetritus to a greater extent than bacteria and microfauna, therefore supporting our third hypothesis.

Conclusion

The present study tested three non-exclusive hypotheses explaining the responses of sediment communities to an input of ice algae to the sea floor. The first hypothesis was partially refuted; although an increase in the abundance of ice diatom frustules and the chl *a*:phaeo ratio was observed, the arrival of fresh ice algal phytodetritus did not lead to a measurable increase in sedimentary chl *a* or fucoxanthin. The second and third hypotheses were mainly confirmed.

When more and fresher ice algal phytodetritus reached the sea floor, the macrobenthos was stimulated, and increased its respiration and sediment bioturbation, leading to changes in pigment profiles and degradation of pigments. None of the three hypotheses can by itself explain how sedimentary pigments would reflect the pulse of ice algae. In highly productive ecosystems, the signal of freshly deposited material may not be affected by the partial loss of this signal to benthic activities. However, when studying less productive non steady-state ecosystems, such as some Arctic seas during the ice-covered spring bloom, it is thus important to consider the three types of responses and choose the right biomarkers or indicators. Studying single traditional parameters of the quality of organic matter to the sea floor, such as sedimentary chl *a* or stable isotopes, carbon and nitrogen contents, might not be sufficient. Multiple biological and biochemical biomarkers that indicate sources, mixing, and fate must be employed if questions about complex processes are to be solved.

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