Paper VI

Does an input of ice algal phytodetritus to the sea floor automatically lead to an increase in sedimentary pigments?

Nathalie Morata[1,*], Michel Poulin[2], Paul E. Renaud[1,3]

In preparation

[1] Department of Marine Sciences, University of Connecticut, 1080 Shennecossett Road, Groton, CT 06340 USA
[2] Canadian Museum of Nature, Division Research, Ottawa, ON K1P 6P4 Canada
[3] Akvaplan-niva, Polar Environmental Centre, N-9296 Tromsø, Norway

[*] Corresponding author: nathalie.morata@gmail.com; tel: (860) 405-9167; fax: (860) 405-9153

Abstract

In ice-covered areas in the Arctic, production by ice algae 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 of ice algal production in Franklin Bay from January/February to April/May 2004 was found to be accompanied by an increase in benthic oxygen demand (Renaud et al. 2007). However sedimentary chlorophyll *a*, which is usually an indicator of inputs of "fresh" organic matter to the sea floor, did not increase. Consequently, it was asked what was the fate of ice algal phytodetritus arriving at the sea floor? In order to answer that question, photosynthetic pigments from the sea ice, particulate organic matter, and sediment, and diatom frustules in the sediment, were studied from January to May 2004. The ratio of sedimentary chlorophyll *a* to phaeopigments, as well as ice algal diatom cells in the sediment, showed an increase in April/May, confirming the 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 the enhanced benthic activities. Finally, the decrease of 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 algae input can be studied at different levels and it is the combination of these studies that allows understanding the overall fate of phytodetritus in the benthic compartment.

Keywords: Arctic, Beaufort Sea, diatoms, sedimentary pigment, pelagic-benthic coupling, ice-algae, carbon cycle, HPLC

1. Introduction

Marine primary production in the Arctic is based primarily on phytoplankton in the water column and microalgae associated with ice (Sakshaug 2004). Sea-ice microalgae are associated with ice cover, generally occurring in the bottom of the ice-sheet, in contact with the underlying sea water (Michel et al. 1996, Nozais et al. 2001, Arrigo 2003, Lizotte 2003). Ice-algal production increases during spring due to the seasonal increase in irradiance at the ice bottom (Wassmann et al. 2006). Although primary production rates by sea-ice algae are generally low compared to phytoplankton, sea-ice algae have been found to contribute considerably to the total productivity in polar seas (Legendre et al. 1992, Gosselin et al. 1997). It can be the main source of carbon for the food web (Gosselin et al. 1997, Nozais et al. 2001, Arrigo 2003) and is usually dominated by diatoms in Arctic seas (von Quillfeldt et al. 2003, Hill et al. 2005). Variations in ice-cover indirectly impact organic matter inputs by influencing ice-algal production.

Grazing by zooplankton can have a strong impact on pelagic-benthic coupling by shaping the magnitude and composition of the vertical particle flux (Olli et al. 2002, Wexels Riser et al. in press). The match or mismatch of zooplankton with regard to phytoplankton blooms determines the fate of the carbon produced, which can be either retained in the water column or exported to the bottom (Wassmann 1991, Wassmann et al. 1996). Grazing by ice fauna has been found to inefficiently control ice-algae biomass (Werner 2000, Michel et al. 2002) and herbivorous zooplankton grazers are usually scarce in the spring. This lead Carroll and Carroll (2003) to suggest a mismatch scenario in ice-covered seas, resulting in strong vertical fluxes of undegraded particulate organic matter to the benthos.

Sedimentary pigments have been used in short-term and long-term studies of marine ecosystem changes. Sedimentary chlorophyll *a* (chl *a*) is a marker of the “freshness” of the algal matter inputs to the sediment (Boon & Duineveld 1996). Degradation products indicate physiological status and nature of chlorophyll processing that has been undergone (Mantoura & Llewellyn 1983, Villanueva & Hastings 2000). Sedimentary accessory pigments are often specific for different algal groups and can be used as taxonomic markers (Gieskes & Kraay 1984, Jeffrey & Vesk 1997). However ice-algae and phytoplankton diatoms have the same pigment signature, and must be distinguished by microscopic analysis of the species composition. Frustules of ice algal diatoms have been found 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 be present due to high contents in the sediment of chl *a* and/or fucoxanthin, a pigment maker of diatoms (Schewe & Soltwedel 2003, Morata & Renaud in press, Pirtle-Levy et al. in press, Morata et al. submitted). Moreover, recent studies have indicated that benthic organisms can derive energy directly from ice algae (Hobson et al. 1995, McMahon et al. 2006).

The seasonal evolution of the pelagic-benthic coupling in the Franklin Bay (southeastern Beaufort Sea) was followed from January to May 2004 during the Canadian Arctic Shelf Exchange Study (CASES) overwintering program. Ice algae biomass, downward fluxes of particulate organic material and sediment oxygen demand increased from the winter to the spring (Renaud et al. 2007). When organic matter reaches the sea floor, it can be stored as benthic biomass, respired, or buried. The sediment oxygen demand (SOD) has been used as an estimation of the carbon going through the benthic communities. In Franklin Bay, SOD has been found to increase in April, as a response to an increase of ice algal phytodetritus inputs (Renaud et al. 2007). Previous studies in the Arctic have correlated sedimentary pigments with overlying production (Pfannkuche & Thiel 1987, Grebmeier et al. 1988, Grant et al. 2002, Bessière et al. 2007). Conversely, in Franklin Bay, no increase in sedimentary chl *a* was observed with the increase in ice algal production, leading to the title question: “Does an input of ice algal phytodetritus to the sea floor automatically lead to an increase in sedimentary pigments?” Three hypothetical responses can be foreseen. (H1) The arrival of fresh ice-algal phytodetritus to the sea floor leads to changes in surface sedimentary biomarkers (i.e. change in stable isotope composition, increase in sedimentary chl *a*, fucoxanthin, chl *a*/phaeopigments (chl *a*/phaeo) and fucoxanthin/degraded fucoxanthin ratios), as well as an increase in ice-algae in the sediment.

(H2) Alternatively, the increase of food inputs to the sediment stimulates the benthos, which consumes it quickly, and results in an increase of benthic activity, bioturbation, and an increase of pigment degradation products. (H3) Finally, the benthic response changes because the fresh input favors only one part of the community (e.g. macrofauna).

2. Methods

2.1 Study area

This study was conducted in the southeast Beaufort Sea from January to May 2004 on board the Canadian Research Icebreaker CCGS *Amundsen*. The ship was frozen into the annual landfast ice in western Franklin Bay (70°02′N, 126°18′W) at a water depth of 231 m (Figure 1).

2.2 Ice and water column sampling

Ice samples were collected six times, in an undisturbed area approximately 1.5 km NE from the ship (70°04′N, 126°26′W). Ice thickness increased from 1.31 m in February to a maximum of 2.00 m at the end of May. Ice cores were collected with a manual corer (Mark II coring system, 9 cm internal diameter; Kovacs Enterprises). The bottom 4-10 cm of the cores were cut and melted in 1-5 L of 0.2 µm filtered surface sea water to minimize osmotic stress (Garrison & Buck 1986). Four to 10 L of water from the water column chlorophyll max (15 m) were collected six times by a rosette through the “moon pool”, an opening in the ship's hull that allowed sampling from within the ship while it was frozen into the ice. Melted ice cores and water from the water column were filtered onto Whatman GF/F filters. Filters were frozen at -20°C prior to pigment analysis by high pressure liquid chromatography (HPLC).

2.3 Sediment sampling

Sediment was sampled four times (13 January, 11 February, 27 April, 7 May) from a box corer (45 cm x 45 cm) and one time on 6 April, from a piston corer. Due to difficulties in sampling logistics, a single core was taken at each sampling date and sub-cores were taken from the same box corer. Multiple sub-samples (5 cm diameter x 10 cm deep) for sedimentary pigments were taken from each station. The cores were extruded and sliced at 1 cm intervals under diminished light conditions. Each interval slice was divided in two, half for pigment analysis by fluorometry, and half for pigment analysis by HPLC, although HPLC analysis were only performed on the top 2 surface layers. Both sub-samples were wrapped in foil and frozen directly after slicing in order to avoid pigment degradation. Sub-samples for the two first cm for stable isotopes and diatom frustules were taken with a truncated syringe (1.4 cm diameter). Samples for stable isotope analysis were directly frozen. Samples for diatom frustule analysis were placed in a scintillation vial and fixed with 20 mL of buffered formaldehyde 3.7%.

2.4 Fluorometric analysis

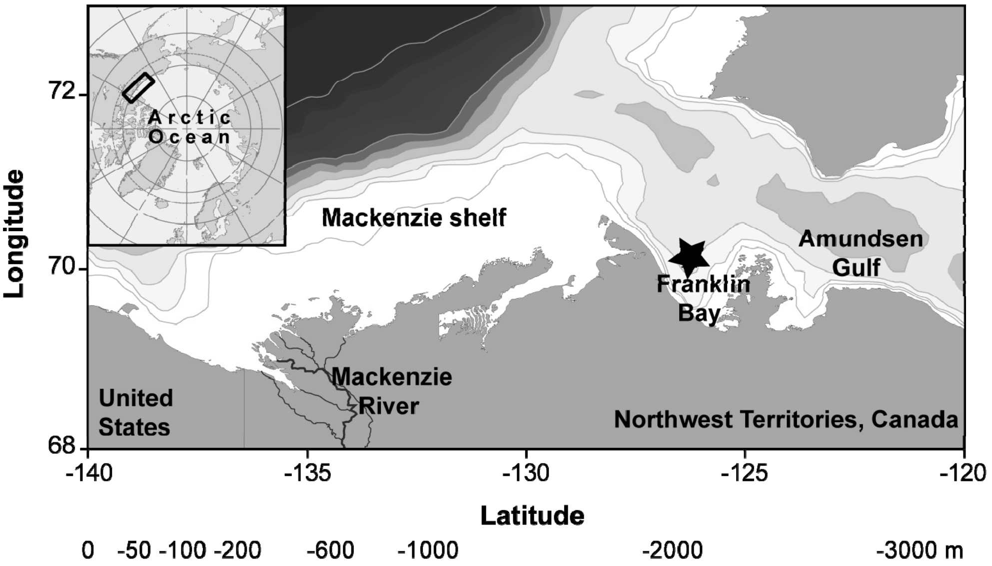

Figure 1. Study area. Overwintering station is indicated by a star in the Franklin Bay.

Within two weeks, sub-samples were analysed by fluorometry. The samples 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 fluorometry analysis, the sediment was centrifuged at 4000 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*, phaeo and chl *a*/phaeo ratio.

2.5 HPLC analysis

Ice algae, POM and sediment samples were extracted and analysed for pigment composition as described in Morata et al. (submitted). 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 mL of the sediment extracts were reconcentrated by blowing to dryness under nitrogen and redissolving in 250 µl of 90% acetone. Two hundreds µl of each sample were injected through a guard column to a reverse phase Alltech Absorbsphere C18 column (5 µm particle size; 250 x 4.6 nm i.d.), 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 is usually related to grazing and phaeophytin to various processes including microbial degradation. The accessory pigments used as a marker of diatoms is fucoxanthin. Moreover allomeres of fucoxanthin, considered as degraded fucoxanthin, were identified (similar spectrum, but different retention time) and were quantified using the RF of fucoxanthin.

2.6 Carbon and nitrogen stable isotope analysis

Frozen sediment samples for stable isotope analysis were dried at 60°C overnight. In order to decalcify sub-samples for carbon analysis, about 2 g of dry, homogenised sediment were placed in a crucible, where 2 mL of 1 N HCl was added, and then dried 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. This decalcified sediment was used for %C and $\delta^{13}C$ determination, and undecalcified samples were used for %N and $\delta^{15}N$ analysis. Stable isotope analysis of sediments was performed by the Environmental Geochemistry Laboratory, Department of Geology, Bates College, U.S.

2.7 Diatom frustule analysis

Diatom frustules were extracted from the sediment using Ludox/Colloidal Silica (L. Cooper, pers. comm). 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 were placed in a 15 ml polypropylene centrifuge tube. Sediment was first rinsed by adding water, centrifuging at 2200 rpm for 8 minutes and removing the supernatant. This procedure was repeated 4 times. In order to have a 3 to 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 1800 rpm. The thin "milky" layer of diatoms was transferred to a new tube. In order to rinse the remaining silica, 10 ml of distilled water was added to the tube, and centrifuged for 8 min at 2200 rpm. The supernatant was removed, and the procedure was repeated 4 times. The 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".

3. Results

3.1 Ice algae and water column pigments

An increase of pigment concentrations was observed at the bottom of the sea ice and at 15 m in the water column from winter to spring (Figure 2a,b,c,d). For both ice and water samples, the chl *a* concentration and chl *a*/phaeo ratio increased from January/February to April/May. This tendency is similar for accessory pigments. Fucoxanthin, a marker of diatoms, and fucoxanthin/degraded fucoxanthin ratio increased in April.

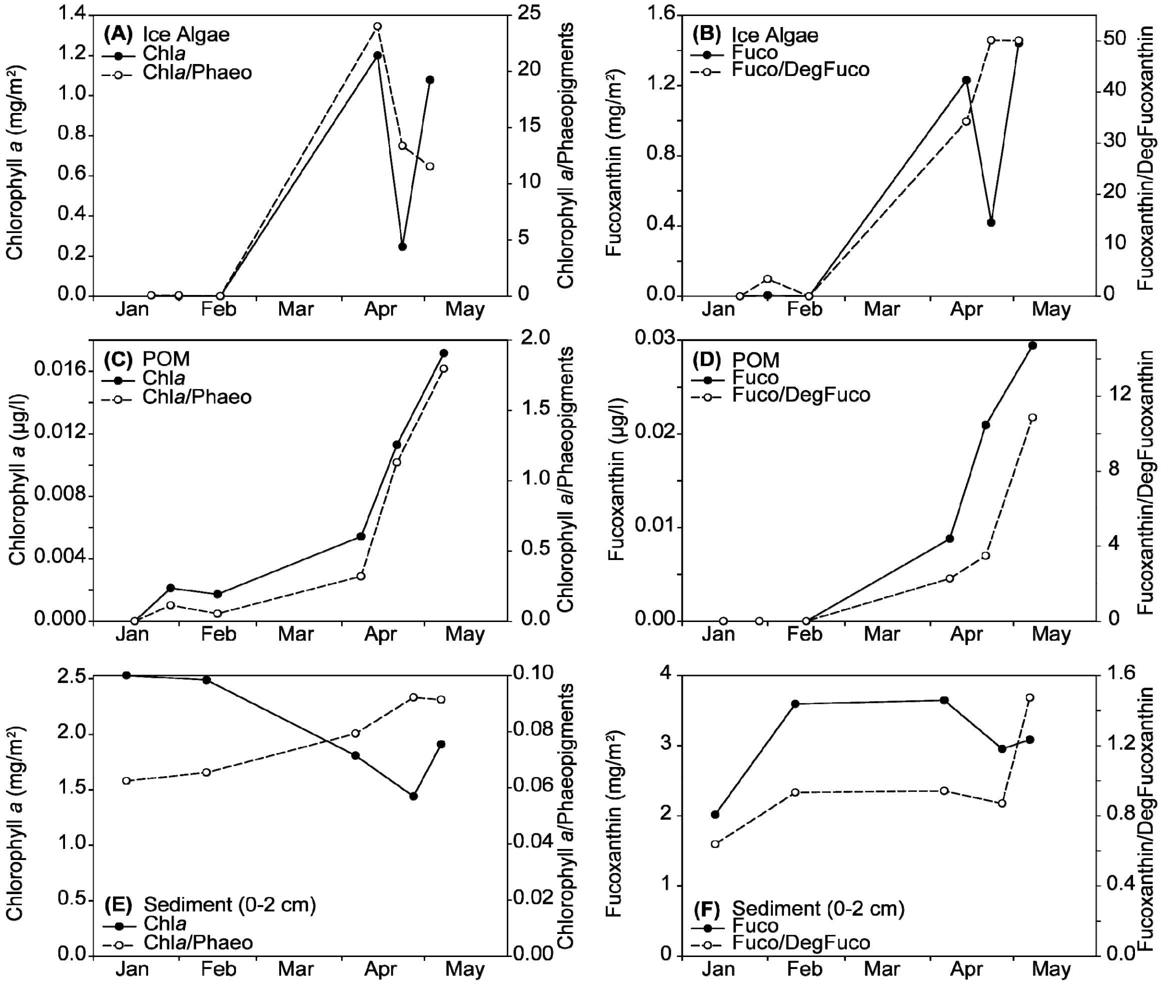

Figure 2. Temporal variations of the concentrations of chlorophyll *a* and accessory pigments in (a,b) ice , (c,d) particulate organic matter, and (e,f) sediment.

3.2 Surface sedimentary pigments and stable isotopes

Although chl *a* and fucoxanthin increased in ice and POM in April, they did not show an increase in the first two cm of sediment (Figure 2e,f). Chl *a* seemed to even decrease, and ranged from 0.014-0.031% d.w. sediment. However the chl *a*/phaeo ratio increased continuously over the study period, and the fucoxanthin/degraded fucoxanthin ratio increased in May. When studying degradation products of chl *a*, the chl *a*/phaeophorbide ratio showed a decrease in April while the chl *a*/phaeophytin ratio tended to increase (Figure 3). Stable isotopes and %N and %C in surface sediment did not change from January to April (Figure 4a,b). Since the %C ranged from 1.28-1.33% d.w. sediment, chl *a* represented only 1-2% of the total sedimentary organic carbon.

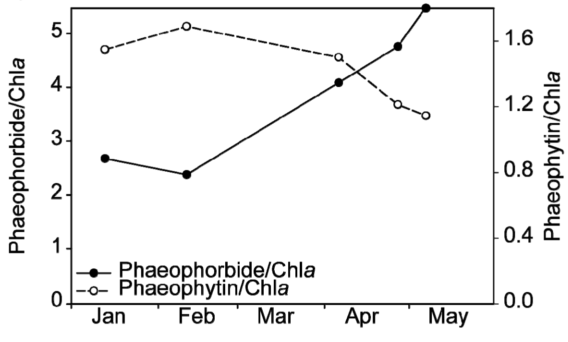

Figure 3. Variations of the ratios phaeophorbide/chl *a* and phaeophytin/chl *a*.

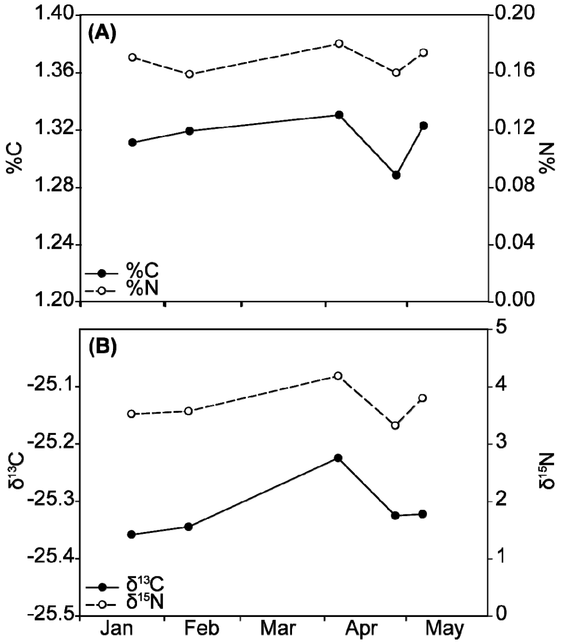

Figure 4. (a) Percentage of organic carbon (%C) and nitrogen (%N) in the sediment. (b) Sedimentary stables isotopes $\delta^{13}C$ and $\delta^{15}N$ composition.

3.3 Sedimentary pigment profiles

Concentrations of sedimentary chl *a* and chl *a*/phaeo were higher in the surface than in deeper layers in January/February. In April/May, the profiles were more homogeneous (Figure 5), suggesting an increase of sediment bioturbation in April. Chl *a* content in the first 1 cm decreased from 0.13 µg m^{-2} on 14 January to 0.5 µg m^{-2} on 27 April. However, when averaging over the first 5 cm and 10 cm, the chl *a* concentration remained more stable throughout time (Figure 6).

3.4 Diatom frustules

The number of both total pennates and living pennate diatoms showed an increase over the sampling period (Figure 7). Pennate diatoms identified at the species level were mainly (98-100%) ice algae species.7). The three dominant species were *Nitszchia frigida*, *Navicula* sp. and *Fragilariopsis cylindrus*.

4. Discussion

4.1 Inputs of ice-algae phytodetritus to the sea floor

The first hypothesis (H1) entails an increase of non-degraded surface sedimentary pigments following the increase of phytodetrital inputs to the sea floor. Previous studies on Arctic ecosystems have suggested local autochthonous primary production as a major factor determining sedimentary chl *a* (Pfannkuche & Thiel 1987, Grebmeier et al. 1988, Boetius & Damm 1998, Grant et al. 2002, Schewe & Soltwedel 2003, Clough et al. 2005, Bessière et al. 2007). In ice-covered regions, production by sea-ice algae, especially diatoms, can be a main source of carbon for the food web (Gosselin et al. 1997, Nozais et al. 2001, Arrigo 2003). In the present study, both chl *a* and fucoxanthin increased in the ice and in the water column from January/February to April/May (Figure 2a,b,c,d), indicating an increase of ice-algae and diatom biomass. Ice algal biomass in the region was dominated by the two pennate diatoms *Nitzschia frigida* and *Navicula* spp. and increased from February to May (M. Rozanska Pers. Comm.). The presence of sea-ice exopolymeric substances (EPS) has also been observed by Riedel et al. (2006) and Juul-Pedersen et al. (in press). However the very low chl *a* concentrations (<0.02) in the water column (Figure 2a) confirm the dominance of ice-algal biomass as main source of carbon for the rest of the food web. Vertical fluxes of particulate organic matter (POM) increased in the upper 25 m of the water column from mid March (Juul-Pedersen et al. in press). The sinking of algal cells also increased in the spring, dominated by the same two pennate diatoms in trap samples as found in the ice: *Nitzschia frigida* and *Navicula* spp. (A. Tatarek Pers. Comm.). Similarly, POM fluxes at 200 m in the area increased in the spring and ice algae were suggested to be an important part of it (Forest et al. in press).

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. in press). However, some authors found that copepods do not feed at chl *a* < 1µg/l (Frost 1972, Gamble 1978, Saunders et al. 2003). In the present study, chl *a* concentration in the subsurface chl *a* max never reached this level. Seuthe et al. (2007) observed an increase of zooplankton fecal pellet production during this period, but suggested it was probably due to additional unpigmented sources of food such as microzooplankton. No grazing degradation products were indentified during grazing experiments (Morata, unpublished data). All of this suggests that grazing might not significantly impact the

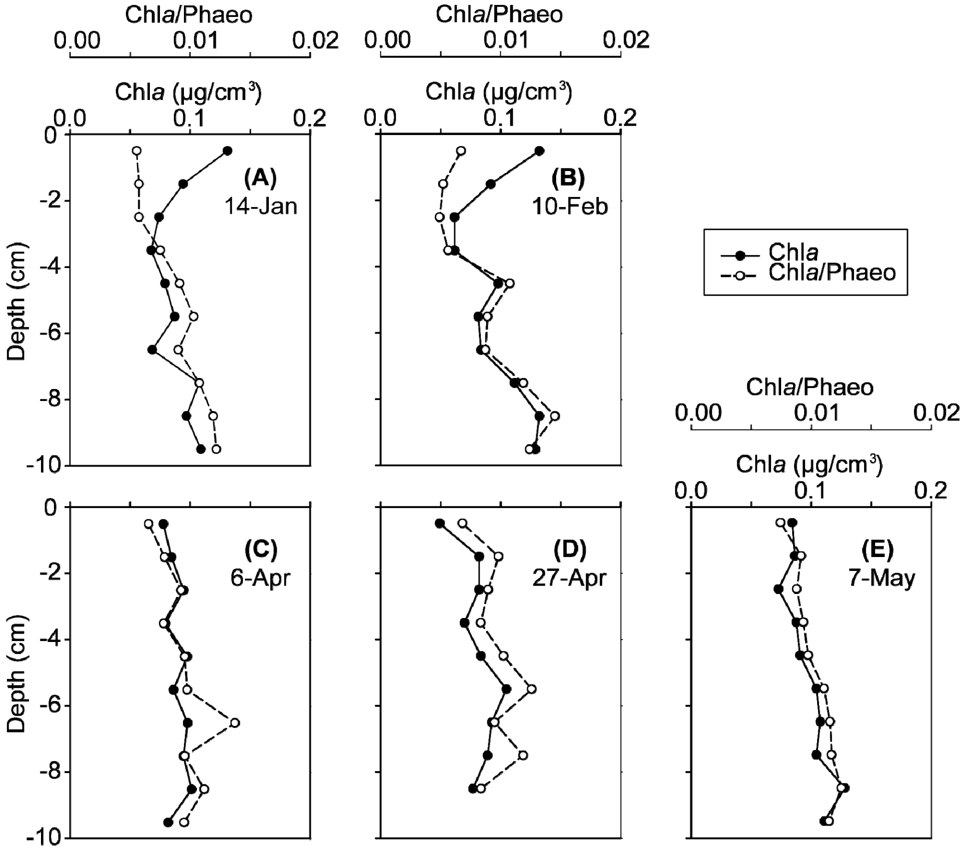

Figure 5. Profiles of sedimentary chlorophyll *a* (chl *a*) and ratio of chlorophyll *a* to phaeopigments (chl *a*/phaeo) over the first 10 cm, from January to May.

biomass, and is probably not a source of input of degraded material to the sea floor. Consequently, the decrease of sedimentary chl *a*/phaeophorbide *a* is likely due to higher inputs of fresher algal material.

The increase of ice algal biomass throughout the spring and the inefficient control of ice-algal biomass by grazers may be expected to lead to higher inputs of fresh organic matter to the benthos in April/May Carroll & Carroll (2003). Frustules of ice algae have been found 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 be present due to observation of high contents of chl *a* and/or fucoxanthin (Schewe & Soltwedel 2003, Morata & Renaud in press, Pirtle-Levy et al. in press, Morata et al. submitted). Here, the percentage of total pennate and living pennate diatoms increased (Figure 7) and, as in both surface ice algal assemblages and sediment traps (M. Rozanska and A. Tatarek,

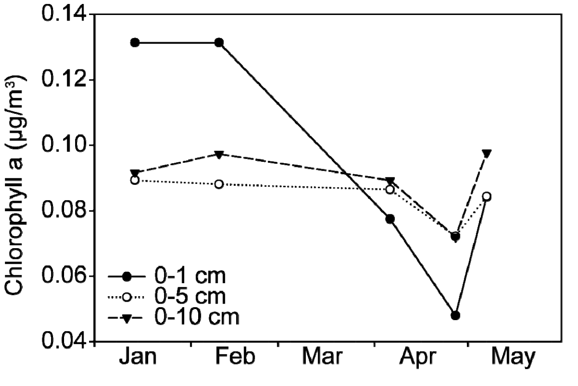

Figure 6. Chlorophyll *a* concentration in the first cm of sediment, and average chlorophyll *a* concentration in the first 5 and 10 cm of sediment from January to May.

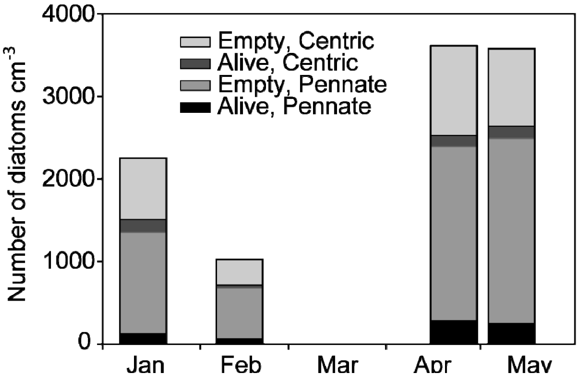

Figure 7. Relative percentage of empty, full (viable), pennate and centric diatoms in the sediment.

pers. comm.), *Nitzschia frigida* and *Navicula* sp. dominated the diatom composition of sediment samples. The ratio of sedimentary chl *a*/phaeo also increased, reflecting the higher inputs of sinking algae as "fresher" phytodetritus; however the chl *a* and fucoxanthin did not increase. Sedimentary pigments, then, only reflected the increase in the "quality" and not the quantity of phytodetritus. Only the number of diatoms cells showed the increase in quantity.

Stable isotopes have been applied in marine systems to estimate inputs of terrestrial and marine organic carbon to the sediment (Naidu et al. 1993, Goni et al. 2000) and to trace pathways of energy from different sources of primary production (including ice algae) through the food web (Hobson et al. 1995, Tamelander et al. 2006, 2007). Ice algal POM is usually more enriched than planktonic POM (i.e. ice algal $\delta^{13}C$ ranged from -15 to -20‰ in Tamelander et al. 2006). Stable isotopes, %N, and %C did not show variations from January/February to April/May (Figure 4), and $\delta^{13}C$ values remained between -25.22 and -25.35‰. Stable isotopes and percentages of carbon and nitrogen integrate the signal of the overall organic matter present in the sediment and did not show a clear influence of the ice-algae signal. Organic carbon represented about 1.3% of the sediment d.w., while sedimentary chl *a* represented <0.03% of the sediment d.w. Changes in the signal of sedimentary phytodetritus is therefore lost when studying the entire bulk sediment.

Hypothesis 1 is thus partially confirmed. Only diatom frustules (total numbers, total 'viable' cells) and chl *a*/phaeo ratio reflected the increase of ice-algal phytodetritus to the sea floor. Only the overall increase of phytodetritus quality can be studied using detailed pigment analysis, and not with biomarkers of bulk organic material.

4.2 Benthic activity

The second hypothesis response (H2) suggested that a quick increase of benthic activity lead to a degradation of the food as soon as it reached the sea floor. The sediment community has been observed to quickly respond to pulses of phytodetritus at the sea floor by increasing their consumption of oxygen (Witte et al. 2003, Renaud et al. in press).In the study area, high values of sediment oxygen demand (SOD) have been observed in April/May by Renaud et al. (2007) as a possible consequence of increase of ice algal inputs.

An increase in available food can lead to increased foraging activity by benthic animals (refs), which can influence sediment profiels of pigments and other consitutents. When bioturbation is low, sedimentary chl *a* profiles exhibit an exponential decrease with depth. Irregular profiles can occur due to non diffusive mixing by benthic organisms (Sun et al. 1994). Sedimentary pigment profiles (Figure 5) went from an exponential decrease with depth in January/February (Figure 5a,b) to a more homogeneous distribution in April/May (Figure 5c,d,e). The change in chl *a* profile can also be observed when comparing chl *a* in the first cm with the average in the first 5 cm and in the first 10 cm (Figure 6). The chl *a* concentration in the first cm decreases over time, while the average over the first 5 and 10 cm remains more stable. This suggests that in April/May, mixing of the surface chl *a* in the first 5 cm increases. While the exact calculation of bioturbation rate would require sedimentation and decomposition rate values, the change in sedimentary chl *a* content with depth suggests an increase of particle mixing, and thus of bioturbation.

The enhanced SOD in April/May may have lead to higher bioturbation as organisms increase burrowing activities. Although harder to explain, the lack of an increase in sedimentary chl *a* concentration can be a result of the rapid use of phytodetrital inputs due to higher benthic activity combined with a mixing of sedimented material to depth. Hypothesis 2 is mainly confirmed, although it remains uncertain how the fresh inputs of ice algae are degraded, as, for example, uncolored chl *a* degradation products, are not indentifiable by HPLC.

4.3 Benthic community composition

The hypothesis 3 (H3) suggested a switch of the community response, i.e. from micro- to macro- fauna dominance. Compared to temperate areas, Arctic macrobenthos has been found to have an enhanced role in benthic carbon cycling relative to meio- and micro- fauna (Piepenburg et al. 1995, Rowe et al. 1997, Clough et al. 2005, Witte et al. 2003, Grebmeier et al. 2006). Partitioning of benthic metabolism, however, has shown seasonal variations in the North Water Polynya, where meio- micro- benthos dominated oxygen consumption in the spring and macro- fauna dominated oxygen consumption in the summer (Grant et al. 2002).

Both macrozooplankton and macrobenthos have been found to remove the phytol chain of chl *a* during grazing (Prahl et al. 1984, Harvey et al. 1987), resulting in the creation of the phaeophorbide degradation products (Leavitt 1993). Microzooplankton or bacteria cannot efficiently remove the phytol chain of chl *a*, resulting in the creation of phaeophytin *a* instead of phaeophorbide *a* (Verity & Vernet 1992, Leavitt 1993).

From January/February to April/May, the total SOD increase ten times while the minivial showed only an increase of two time (Renaud et al. 2007), suggesting an increase of the macrofauna oxygen demand. Moreover the ratio chl *a* phaeophorbide *a* also decreased (Figure 3), confirming the enhancement of macrofauna activity. The present results suggest the confirmation of the hypothesis 3. Macrobenthic activity is enhanced by the pulse of ice algae phytodetritus.

5. Conclusion

The present study tested three hypothetical responses of sedimentary pigments to an input of ice algae to the seafloor. Hypothesis 1 was partially refuted. Although an increase of ice algae frustules was observed, as well as an increase in the chl *a*/phaeo ratio , the arrival of fresh ice-algal detritus did not lead to an increase in sedimentary chl *a* or fucoxanthin. Hypothesis 2 and 3 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 react to the pulse of ice algae. It is consequently important to consider the three types of responses, instead of focusing only on one, when using sedimentary pigments to study benthic response to a pulse of organic matter to the seafloor.

6. Acknowledgements

This work would not have been possible without the efforts of the captain G. Tremblay, officers, and crew of the CCGS Amundsen. We would like especially to thank chief scientists J. Deming, T. Papakyriakou and L. Fortier, and all the CASES scientists, especially the ones who helped with the gigantic task of cutting the ice for deploying the box corer. Many thanks are due to A. Aitken, S. Brugel, T. Connelly, G. Darnis, A. Forest, M. Gosselin, C. Guignard, T. Juul-Pedersen, M. Lizotte, C. McClelland, P. Massot, L. Michaud, J. Payet, A. Riedel, M. Rozanska, A. Tatarek and J. Wiktor. We are extremely grateful to J. Perl (San Diego State University Research Foundation) for providing pigment standards. Thank you very much to L. Cooper (University of Tennessee) for sharing results and methods with us. Thanks are also due to P.B. Hamilton (Canadian Museum of Nature) for his precious help and insights on diatom study. This research was funded by grants from the National Science Foundation (OPP-0326371) and Connecticut Sea Grant to PER. This work is a contribution to the research programs of the Canadian Arctic Shelf Exchange Study.

7. References

Ambrose WG, von Quillfeldt C, Clough LM, Tilney PVR, Tucker T (2005) The sub-ice algal community in the Chukchi sea: large- and small-scale patterns of abundance based on images from a remotely operated vehicle. Polar Biology 28:784-795

Arrigo KR (2003) Primary Production in Sea Ice. In: Black KD, Shimmield GB (eds) Sea Ice: An introduction to its Physics, Chemistry, Biology and Geology. Blackwell Publishing, Oxford, p 143-183

Bessière A, Nozais C, Brugel S, Demers S, Desrosiers G (2007) Metazoan meiofauna dynamics and pelagic-benthic coupling in the Southeastern Beaufort Sea, Arctic Ocean. Polar Biology 30:1123-1135

Blanchard G, Chretiennot-Dinet M-J, Dinet A, Robert J-M (1988) Méthode simplifiée pour l'extraction du microphytobenthos des sédiments marins par le gel de silice Ludox. Biologie Marine 307(3) :569-576

Boetius A, Damm E (1998) Benthic oxygen uptake, hydrolytic potentials and microbial biomass at the Arctic continental slope. Deep-Sea Research I 45:239-275

Boon AR, Duineveld GCA (1998) Chlorophyll a as a marker for bioturbation and carbon flux in southern and central North Sea sediments. Marine Ecology Progress Series 162:33-43

Carroll ML, Carroll J (2003) The Arctic Seas. In: Black KD, Shimmield GB (eds)

Biogeochemistry of Marine Systems. Blackwell Publishing, Oxford, p 126-156

Clough LM, Renaud P, Ambrose WG (2005) Impact of water depth, sediment pigment concentration, and benthic macrofauna biomass on sediment oxygen demand in the Western Arctic Ocean. Canadian Journal of Fisheries and Aquatic Sciences 62:1756–1765

Cremer H (1999) Spatial distribution of diatom surface sediment assemblages on the Laptev Sea shelf (Russian Arctic). In: Kassens H, Bauch HA, Dmitrenko I, Eicken H, Hubberten K-W, Melles M, J.Thiede, Timokhov L (eds) Land-Ocean Systems in the Siberian Arctic: Dynamic and History. Springer-Verlag, Berlin, p 533-551

Djinoridze RN, Ivanov GI, Djinoridze EN, Spielhagen RF (1999) Diatoms from surface sediments of the Saint Anna Trough (Kara Sea). In: Kassens H, Bauch HA, Dmitrenko I, Eicken H, Hubberten K-W, Melles M, J.Thiede, Timokhov L (eds) Land-Ocean Systems in the Siberian Arctic: Dynamic and History. Springer-Verlag, Berlin, p 553-560

Forest A (in press) The annual cycle of particulate organic carbon export in Franklin Bay (Canadian Arctic): environmental control and food web implications. Journal of Geophysical Research-Oceans

Frost BW (1972) Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnology and Oceanography 17:805-815

Gamble JC (1978) Copepod grazing during a declining spring phytoplankton bloom in the northern North Sea. Marine Biology 49:303-315

Garrison DL, Buck KR (1986) Organism losses during ice melting: A serious bias in sea ice community studies. Polar Biology 6:237-239

Goni MA, Yunker MB, Macdonald RW, Eglinton TI (2000) Distribution and sources of organic biomarkers in arctic sediments from the Mackenzie River and Beaufort Shelf. Marine Chemistry 71:23-51

Gosselin M, Levasseur M, Wheeler PA, Horner RA, Booth BC (1997) New measurements of phytoplankton and ice algal production in the Arctic Ocean. Deep-Sea Research II 44:1623-1644

Grant J, Hargrave B, MacPherson P (2002) Sediment properties and benthic-pelagic coupling in the North Water. Deep-Sea Research II 49:5259-5275

Grebmeier JM, Cooper LW, Feder HM, Sirenko BI (2006) Ecosystem dynamics of the Pacific-influenced Northern Bering and Chukchi Seas in the Amerasian Arctic. Progress in Oceanography 71:331-361

Grebmeier JM, McRoy CP, Feder HM (1988) Pelagic-benthic coupling on the shelf of the northern Bering and Chekchi Seas. I. Food supply source and benthic biomass. Marine Ecology Progress Series 48:57-57

Hamilton PB, Proulx M, Earle C (2002). Enumerating phytoplankton with an upright compound microscope using a modified settling chamber. Hydrobiologia 444: 171-175

Hamilton SK, Sippel SJ, Bunn SE (2005) Separation of algae from detritus for stable isotope and ecological stochiometry studies using density fractionation in colloidal silica. Limnology and Oceanography: Methods 3:149-157

Harvey HR, Eglinton G, O'Hara SCM, Corner EDS (1987) Biotransformation and assimilation of dietary lipids by *Calanus* feeding on a dinoflagellate. Geochimica et Cosmochimica Acta 51:3031-3040

Hill V, Cota G, Stockwell D (2005) Spring and summer phytoplankton communities in the Chukchi and Eastern Beaufort Seas. Deep Sea Research II 52:3369-3385

Hobson KA, Ambrose WG, Renaud PE (1995) Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: Insights from delta C-13 and delta N-15 analysis. Marine Ecology Progress Series 128:1-10

Jeffrey SW, Mantoura RFC, Wright SW (1997) Phytoplankton Pigments in Oceanography, UNESCO Publishing

Juul-Pedersen T, Michel C, Gosselin M, Seuthe L (in press) Seasonal changes in the sinking export of particular material, under first-year sea ice on the Mackenzie Shelf (western Canadian Arctic). Marine Ecology Progress Series

Leavitt PR (1993) A review of factors that regulate carotenoid and chlorophyll deposition and fossil pigment abundance. Journal of Paleolimnology 9:109-127

Legendre L, Ackley SF, Dieckmann GS, Gulliksen B, Horner R, Hoshiai T, Melnikov IA, Reeburgh WS, Spindler M, Sullivan CW (1992) Ecology of sea ice biota: 2. Global significance. Polar Biology 12:429-444

Lizotte MP (2003) The Microbiology of Sea Ice. In: Black KD, Shimmield GB (eds)

Biogeochemistry of Marine Systems. Blackwell Publishing, Oxford, p 185-209

McMahon KW, Ambrose Jr WG, Johnson BJ, Sun M-Y, Lopez GR, Clough LM, Carroll ML (2006) Benthic community response to ice algae and phytoplankton in Ny Ålesund, Svalbard. Marine Ecology Progress Series 310:1-14

Michel C, Legendre L, Ingram R, Gosselin M, Levasseur M (1996) Carbon budget of sea-ice algae in spring: Evidence of a significant transfer to zooplankton grazers. Journal of Geophysical Research-Oceans 101:18345-18360

Michel C, Nielsen TG, Nozais C, Gosselin M (2002) Significance of sedimentation and grazing by ice micro- and meiofauna for carbon cycling in annual sea ice (northern Baffin Bay). Aquatic Microbial Ecology 30:57-68

Morata N, Renaud PE (in press) Sedimentary pigments in the western Barents Sea: a reflection of the pelagic-benthic coupling? Deep-Sea Research II

Morata N, Renaud PE, Brugel S, Hobson KA, Johnson BJ (submitted) Spatial and seasonal variations in the pelagic-benthic coupling of the southeastern Beaufort Sea revealed by sedimentary biomarkers.

Naidu AS, Scalan RS, Feder HM, Goering JJ, Hameedi MJ, Parker PL, Behrens EW, Caughey ME, S.C. J (1993) Stable organic carbon isotope in sediments of the north Bering-south Chukchi seas, Alaskan-Soviet Arctic Shelf. Continental Shelf Research 13:669-691

Nozais C, Gosselin M, Michel C, Tita G (2001) Abundance, biomass, composition and grazing impact of the sea-ice meiofauna in the North Water, northern Baffin Bay. Marine Ecology Progress Series 217:235-250

Olli K, Riser CW, Wassmann P, Ratkova T, Arashkevich E, Pasternak A (2002) Seasonal variation in vertical flux of biogenic matter in the marginal ice zone and the central Barents Sea. Journal of Marine Systems 38:189-204

Pfannkuche O, Thiel H (1987) Meiobenthic stocks and benthic activity on the NE-Svalbard shelf and in the Nansen Basin. Polar Biology 7:253-266

Piepenburg D, Blackburn TH, Vondorrien CF, Gutt J, Hall POJ, Hulth S, Kendall MA, Opalinski KW, Rachor E, Schmid MK (1995) Partitioning Of Benthic Community Respiration In The Arctic (Northwestern Barents Sea). Marine Ecology Progress Series 118:199-213

Pirtle-Levy R, Grebmeier JM, Cooper LW, Larsen IL, DiTullio GR (in press) Seasonal variation of chlorophyll a in Arctic sediments implies long persistence of plant pigments. Deep-Sea Research II

Polyakova YI (2003) Diatom assemblages in surface sediments of the Kara Sea (Siberian Arctic) and their relationship to oceanological conditions. In: Stein R, Fahl K, Futterer DK, Galimov AM, Stepanets OV (eds) Siberian river run-off in the Kara Sea: Characterisation, quantification, variability and environmental significance, Vol 6. Elsevier, Amsterdam, p 375-399

Prahl FG, Eglinton G, Corner EDS, O'Hara SCM (1984) Copepod fecal pellets as a source of dihydrophytol in marine sediment. Science 224:1235-1237

Renaud PE, Riedel A, Michel C, Morata N, Gosselin M, Juul-Pedersen T, Chiuchiolo A (2007) Seasonal variation in benthic community oxygen demand: A response to an ice algal bloom in the Beaufort Sea, Canadian Arctic? Journal of Marine Systems 67:1-12

Renaud PE, Morata papier cabanera

Riedel A, C M, Gosselin M (2006) Seasonal study of sea-ice exopolymeric substances on the Mackenzie shelf: implication for transport of sea-ice bacteria and algae. Aquatic Microbial Ecology 45:195-206

Rowe GT, Borland GS, Escobar Briones EG, Cruz-Kaegi ME, Newton A, Piepenburg D, Walsh I, Deming J (1997) Sediment community biomass and respiration in the Northeast Water Polynya, Greenland: a numberical simulation of benthic lander and spade corer data. Journal of Marine Systems 10:497-515

Sakshaug E (2004) Primary and Secondary Production in the Arctic Seas. In: Stein R, Macdonald RW (eds) The Arctic Carbon Cycle in the Arctic Ocean. Springer, Berlin, p 57-81

Sancetta C (1981) Diatoms as hydrographic tracers: Example from Bering Sea Sediment. Science 211:279-281

Saunders KM, Deibel D, Stevens CJ, Rivkin RB, Lee SH, Klein B (2003) Copepod herbivory rate in a large Arctic polynya and its relationship to seasonal and spatial variation in copepod and phytoplankton biomass. Marine Ecology Progress Series 261:183-199

Schewe I, Soltwedel T (2003) Benthic response to ice-edge-induced particle flux in the Arctic Ocean. Polar Biology 26:610-620

Seuthe L, Darnis G, Wexels Riser C, Wassmann P, Fortier L (2007) Winter–spring feeding and metabolism of Arctic copepods: insights from faecal pellet production and respiration measurements in the southeastern Beaufort Sea. Polar Biology 30:427-436

Sun MY, Aller RC, Lee C (1994) Spatial and temporal distributions of sedimentary chloropigments as indicators of benthic processes in Long-Island Sound. Journal of Marine Research 52:149-176

Taghon GL, Jumars PA (1984) Variable ingestion rate and its role in optimal foraging behavior of marine deposit feeders. Ecology 65:549-558

Tamelander T, Reigstad M, Hop H, Carroll ML, Wassmann P (in press) Pelagic and sympagic contribution of organic matter to zooplankton and vertical export in the Barents Sea marginal ice zone. Deep-Sea Research II

Tamelander T, Renaud PE, Hop H, Carroll ML, Ambrose WG, Hobson KA (2006) Trophic relationships and pelagic-benthic coupling during summer in the Barent Sea Marginal ice Zone revealed by stable carbon and nitrogen measurement. Marine Ecology Progress Series 310:33-46

Verity PG, Vernet M (1992) Microzooplanton grazing, pigments, and composition of plankton communities during late spring in two Norwegian fjords. Sarsia 77:263-274

von Quillfeldt CH, Ambrose WG, Clough LM (2003) High number of diatom species in first-year ice from the Chukchi Sea. Polar Biology 26:806-818

Wassmann P, Slagstad D, Wexels Riser C, Reigstad M (2006) Modelling the ecosystem dynamics of the Barents Sea including the marginal ice zone II. Carbon flux and interannual variability. Journal of Marine Systems 59:1-24

Werner I (2000) Faecal pellet production by Arctic under-ice amphipods - transfer of organic matter through the ice/water interface. Hydrobiologia 426:86-96

Wexels Riser C, Wassmann P, Reigstad M, Seuthe L (in press) Vertical flux regulation by zooplankton in the northern Barents Sea during Arctic spring. Deep-Sea Research II, special volume on the Barents Sea Cabanera project

Witte U, Wenzhöfer F, Sommer S, Boetius A, Heinz P, Aberle N, Sand M, Cremer A, Abraham W-R, Jørgensen BB, Pfannkuche O (2003) In situ experimental evidence of the fate of a phytodetritus pulse at the abyssal sea floor. Nature 424