Sedimentary Pigments as Biomarkers of Spatial and Seasonal Variations in Arctic Pelagic-Benthic Coupling

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Abstract

The Arctic Ocean is characterized by broad continental shelves, which have high rates of primary productivity. In some areas, much of this production falls to the bottom, supplying rich and active communities of benthic organisms. Benthic-pelagic coupling over much of the Arctic shelves is thought to be particularly tight. Moreover in areas covered by ice, ice algae can be the main source of carbon for the food web, and thus for the benthos.

Sedimentary pigments have demonstrated their usefulness in studies of ecosystem changes, and especially changes of organic matter inputs to the benthos. In order to characterize variation in pelagic-benthic coupling in the Arctic, sedimentary pigments were studied in the oligotrophic Beaufort Sea (CASES project) and in the more productive Barents Sea (CABANERA project). During 7 cruises from 2003 to 2005, sediment cores, water column POM and ice algae samples have been collected, representing a significant spatial coverage and seasonal variations.

Sedimentary pigments reflected changes in environmental factors, sources of primary productivity, food web structure, and benthic activity. The Beaufort Sea and Barents Sea showed very different pelagic-benthic coupling, reflecting the important contrast between the two ecosystems of primary productivity, secondary production, and hydrography. In the Barents Sea, spatial changes were highly influenced by currents while in the Beaufort Sea, spatial changes were due to depth and river influence. Physical parameters seemed more responsible of spatial changes. From a seasonal point of view, productivity regime, especially ice-algal production and the match/mismatch of grazing, seemed important in shaping organic matter inputs to the benthos. In the spring, ice-algal production largely influenced organic matter inputs to the benthos in both the Barents and Beaufort Seas. In the summer, grazing was responsible for inputs of degraded material in both ecosystems. In addition to biological parameters, environmental factors were also important in summer and/or fall. In the Barents Sea during summer, the different currents lead to phytoplankton taxonomy variations, and in the Beaufort Sea during fall, riverine inputs were found to be responsible for presence of allochtonous material in the sediment.

APPROVAL PAGE

Doctor of Philosophy Dissertation

Sedimentary Pigments as Biomarkers of Spatial and Seasonal Variations in Arctic Pelagic-Benthic Coupling

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To the memory of Mimi and André Labarrère, Maire de Pau.

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List of papers

This thesis is based on the following papers, which are referred to by their Roman numerals I-VI and are presented as appendices.

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

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

III. Renaud PE**, Morata N**, Carroll ML, Denisenko SG, Reigstad M (in press) Pelagic-benthic coupling in the western Barents Sea: processes and time scales. Deep-Sea Research II

IV. Renaud PE, **Morata N**, Ambrose WG, Bowie JJ, Chiuchiolo A (2007) Carbon cycling by seafloor communities on the eastern Beaufort Sea shelf. Journal of Experimental Marine Biology and Ecology 349:248-260

V. 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

VI. **Morata N**, Poulin M, Renaud PE (in preparation for Polar Biology) Does an input of ice-algal phytodetritus to the sea floor automatically lead to an increase in sedimentary pigments?

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1. Introduction and background

1.1 Climate change and carbon cycling in the Arctic Ocean

Effects of global warming are expected to be enhanced in the polar regions, especially the Arctic. Mitchell et al. (1995) predicted temperature increase of 3-4°C in the Arctic during the next 50 years, which would lead to a substantial retreat of Arctic ice cover. From a permanently ice-covered region with multiyear ice, the Arctic Ocean would become ice-free during the summer (ACIA 2005, IPCC 2007). The sea ice cover is an important component of both the global and the Arctic climate system, modulating the exchange of heat and moisture between ocean and atmosphere, as well as stratification and winter deepwater formation (Johannessen & Miles 2000). Changes in ice cover will restructure some of carbon cycling pathways in the Arctic Ocean by affecting primary production.

Recent studies (Wheeler et al. 1996, Chen et al. 2002, Klein et al. 2002, Tremblay et al. 2002, Vidussi et al. 2004) have shown that primary production is much higher in the Arctic than previously believed. Total primary production in the Arctic Ocean contributes >329 Tg C y^{-1} and most of it, 279 Tg C y^{-1}, occurs in the shelf areas (Sakshaug 2004). Ice algae contribute a large fraction of primary production in some areas on the Arctic (Gosselin et al. 1997, Arrigo 2003). A reduction in ice cover as a result of global warming will increase the relative importance of phytoplankton production.

Because of the ice-dependent character of Arctic primary production (see section 1.2 for more details), climate change is expected to affect both primary production and vertical fluxes by favouring phytoplankton production over ice algae (Carroll and Carroll 2003).

In addition to primary production, terrestrial organic matter is an important source of organic matter for the Arctic Ocean. The Arctic Ocean, on a volume basis, has the highest terrestrial input of freshwater and organic matter (10% of the global river discharge and 8% of the total global organic carbon flux, Maybeck 1993, Dittmar & Kattner 2003). Climate models suggest that global warming will affect riverine fluxes by intensifying the hydrological cycle (Peterson et al. 2002, Wu et al. 2005). The increased riverine organic matter fluxes will affect the entire Arctic carbon cycle.

In addition to the role of the continental margin as a source of terrestrial organic matter, the continental shelf is an important site for organic matter sedimentation and burial. Thirty percent of the world's continental shelves are found within the Arctic region (Macdonald et al. 1998), while the Arctic Ocean comprises only 1% of the global ocean area (Dittmar & Kattner 2003). These huge continental shelves represent an important sink of carbon, since 70% of the total sediment input is accumulating there, and 7 to 11% of the world ocean organic carbon burial occurs in the Arctic Ocean (Stein & Macdonald 2004). The amount and composition of particulate organic matter preserved in the sedimentary records of the continental shelves are controlled by factors such as terrigenous input, primary production, transformation processes in the water column and at the seafloor as well as bulk sedimentation (Stein and Macdonald, 2004). Each of these factors can be affected by global warming, leading to changes in organic carbon burial.

1.2 Primary production and fluxes

Marine primary production in the Arctic is based principally on phytoplankton in the water column and microalgae associated with ice (Sakshaug 2004). Sea-ice microalgae generally occur at 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). Although the primary production rate by sea-ice algae is generally low compared to pelagic phytoplankton, it can be a main source of carbon for the food web in ice-covered regions (Gosselin et al. 1997, Nozais et al. 2001, Arrigo 2003).

Ice can also regulate primary production in the water column in other ways. Phytoplankton blooms are commonly associated with ice retreat in marginal ice zones (Froneman et al. 1997, Murphy et al. 1998, Goffart et al. 2000, Olli et al. 2002, Wassmann et al. 2005). When ice melts, the high input of fresh water increases stratification. These stable conditions, and the abundance of nutrients brought to the surface during winter mixing create optimal conditions for phytoplankton growth. Production at ice edges can be very high (Engelsen et al. 2002). Thus, ice margins and polynyas are highly productive ecosystems (Stirling 1981, Savidge et al. 1996, Rat'kova & Wassmann 2002, Reigstad et al. 2002, Leventer 2003, Ferreyra et al. 2004).

Although primary production determines the maximum concentration of organic carbon potentially available for the system, the flux of this energy toward higher pelagic trophic levels and toward the seafloor can be highly controlled by zooplankton grazing. Match and mismatch of zooplankton biomass with primary production rates can be responsible for variations in vertical flux of organic carbon, which might not always be proportional to primary production rates. When phytoplankton blooms and large zooplankton stocks coincide in space and time (i.e. match scenario), the grazing efficiency is high and sedimentation of intact phytoplankton cells is low. Conversely, when phytoplankton blooms and large zooplankton stocks are separated in time and space (i.e. mismatch scenario), grazing efficiency is lower and sedimentation large.

It has been suggested that ice abundance may influence whether there is a "match" or "mismatch" relation between primary production rate and grazing. The early ice-algal production and the episodic character of production in the Arctic (Wassmann et al. 1996), lead Carroll & Carroll (2003) to suggest a matching scenario in the case of limited ice, where carbon is mainly used and recycled in the water column. In the second scenario of abundant ice, primary production is dominated by ice algae, and herbivorous grazers and ice fauna are scarce. Ice fauna grazing has been suggested to inefficiently control ice-algal biomass (Werner 2000, Michel et al. 2002) resulting in higher vertical fluxes of organic matter, representing a potential food source for the benthos.

1.3 Pelagic-benthic coupling

The continental shelves of the various Arctic seas (Figure 1) can be sites of high production (Sakhaug 2004), and in some areas, much of this production falls to the bottom. In areas where conditions (light, nutrients) do not support local benthic primary production, benthic organisms depend primarily on organic matter derived from the euphotic zone. Some of the incoming organic matter is stored in benthic biomass and utilized for growth and maintenance of benthic populations, while some part is respired and remineralized by the benthos into CO_2, dissolved organic carbon (DOC), and nutrients. In addition, a residual part of the carbon reaching the sea floor may be buried in the sediment and sequestered for millions of years (Figure 4).

The quality and abundance of particulate organic matter (POM) available for Arctic benthic communities is highly variable in space and time. Due to the importance of Arctic rivers (Figure 1), most of the POM reaching the sea floor on Arctic continental shelves is terrestrially derived and considered to be refractory, poor in nutritional quality (Dittmar & Kattner, 2003). However, in some areas where lateral transport and riverine input are negligible, the metabolism of the benthic community depends on local primary production (Klages et al. 2004). Surprisingly, the benthic carbon remineralization rates found on Arctic continental shelves are similar to those of lower latitudes (Glud et al. 1998, Rysgaard et al. 1998; Glud et al. 2000; Grant et al. 2002, Clough et al. 2005), suggesting that benthic remineralization is regulated primarily by the availability of organic matter and not by temperature. Moreover, in some regions, high benthic abundance, biomass and production reflect the production patterns of the overlying water column (Grebmeier et al. 1988, Ambrose & Renaud 1995, Piepenburg et al. 1997b). This significant transfer of organic matter and the efficient assimilation by the benthic community (Grebmeier et al. 1988, Grebmeier & Barry 1991, Ambrose & Renaud 1995, Klages et al. 2004) suggest a tight pelagic-benthic coupling in Arctic ecosystems.

In summary, the amount and composition of organic matter preserved in the sedimentary record are controlled by factors such as terrigenous input, primary production, sedimentation rate, and transformation processes in the water column and in the sediment (e.g. anoxia, abundance of fauna). All these factors are highly variable and depend on the region, and are responsible for spatial and seasonal variations in pelagic-benthic coupling.

Figure 1. Map of the seas, major rivers and major polynyas in the Arctic Ocean. NEW: Northeast Water Polynya, NOW: North Water Polynya, CBP: Cape Bathurst Polynya. Adapted from AMAP (1998) and University of Texas Perry-Castaneda Library map collection.

2. Aim of this study

Global warming is expected to affect organic carbon production and cycling and, thus, the entire Arctic ecosystem. Characterizing and understanding factors responsible for variations in pelagic-benthic coupling is a key to better understanding the effects of global warming on Arctic ecosystems.

The overall goal of this dissertation was to use biomarkers of the origin and nutritional quality of POM to study its transfer from the water column to the benthos as a function of environmental and biological factors, such as ice conditions (presence/absence of ice), riverine input, and productivity regime. The main biomarkers were pigments, which are expected to reflect POM sources and degradation pathways. In addition, other biomarkers were also studied (stable carbon and nitrogen, percentages of carbon and nitrogen, diatom frustules), and sediment oxygen demand was used as indicator of benthic carbon cycling. This is the first time such a study was performed in the Arctic, and these different techniques helped addressing the following hypotheses:

H_1: Qualitative and quantitative differences in sedimentary pigments reflect changes in algal source and variation in organic matter flux to the seafloor.

*This hypothesis was addressed for the Barents Sea in Papers **I**, for the Beaufort Sea in Paper **II** and for the winter/spring season in Paper **VI**.*

H_2: Benthic carbon cycling depends on inputs of phytodetritus from overlying water.

*This hypothesis was addressed for the Barents Sea in Papers **III**, for the Beaufort Sea in Paper **IV**, for the winder/spring season in Paper **V**.*

H_3: Environmental factors (ice, current and river) and biological parameters (primary and secondary production) shape pelagic-benthic coupling differently in the Barents and Beaufort Seas

This hypothesis was addressed in all papers, in order to identify these factors. They are summarized in the present synthesis.

3. Study sites

This study included two study areas (Figure 2a). The southeast Beaufort Sea was studied four times (October/November 2003, January/February 2004, April/May 2004 and July/August 2004) during the Canadian Arctic Shelf Exchange Study (CASES) project funded primarily by Canada (Figure 2b). The Barents Sea was studied three times (summer 2003 and 2004, and spring 2005) during the Norwegian/EU funded “CArbon flux and ecosystem feedback in the northern BAreNts sea in an ERA of climate change (CABANERA)” project (Figure 2c).

3.1 Southeastern Beaufort Sea

The Beaufort shelf receives the outflow of the Mackenzie River, the fourth largest Arctic river in terms of freshwater discharge, and the largest in the world in terms of sediment supply (Macdonald et al. 1998). Much of this material is either buried or recycled on the wide continental shelf (Macdonald et al. 1998). Primary production rates are usually low and the area is mainly considered to be oligotrophic (Arrigo & Van Dijken 2004, Carmack et al. 2004). Although the area is generally ice-free from May to early October, the spring Cape Bathurst polynya and ice-associated algae could be a source of early-season primary production. In summary, carbon input to the southeast Beaufort Sea seafloor derives primarily from three sources: marine biological production, the Mackenzie plume, and coastal and seabed erosion (O'Brien et al. 2006).

The CASES project had 2 major components. The first included studies of the Mackenzie shelf, slope, Amundsen Gulf and Franklin Bay during fall 2003 and late spring/summer 2004. The second component followed the evolution of the system through an entire year. This was achieved by freezing an icebreaker into the annual shore-fast ice in western Franklin Bay (station 200, Figure 2b) over the winter at a water depth of 231 m, when this area is usually not accessible for regular scientific cruises. To allow sampling while frozen into the ice, the icebreaker was equipped with a “moon pool”, an opening in the ship's hull. The project was international and covered physical, biological, chemical and geological oceanography.

3.2 Western Barents Sea

The western Barents Sea is influenced by Atlantic waters in the south and west, while Arctic waters penetrate from the north and east (Wassmann et al. 2006). Different water masses have different phytoplankton (Rat'kova & Wassmann 2002, Reigstad et al. 2002) and zooplankton (Colebrook 1985) compositions. Primary production in the Barents Sea is one of the highest among the Arctic shelf systems (Sakshaug & Slagstad 1992), and pelagic-benthic coupling may be particularly tight (Wassmann et al. 2006). As much as 50% of the primary production is exported from the surface and represents potential food for benthic organisms (Wexels Riser et al. in press). Much of the Barents Sea is a marginal ice zone (MIZ), which is defined as "that part of the ice cover which is close enough to the open ocean boundary to be affected by its presence" (Wadhams 1986). Therefore, inputs of organic matter to the benthos will vary spatially and temporally as a function of physical processes influencing patterns of ice melt in the region (Reigstad et al. 2002).

The CABANERA project focused on the Barents Sea continental shelf (200-500 m). The goal was to investigate how primary production, the biological pump, and pelagic-benthic coupling are regulated in spring and summer.

3.3 Comparison of the two sites

The Barents Sea represents a strong contrast to the Beaufort Sea. Primary production is expected to be higher in the Barents Sea than in the Beaufort Sea and to be strongly influenced by surrounding currents. In contrast, the Beaufort Sea is expected to be more oligotrophic than the Barents Sea and to be influenced by the Mackenzie River (Macdonald et al. 1998). However, both systems should show strong seasonal and spatial variations of POM inputs to the benthos. An important element of seasonal variation is expected to be due to productivity regime (phytoplankton vs. ice algae), while the riverine influence, currents and water depth might be responsible for spatial variations.

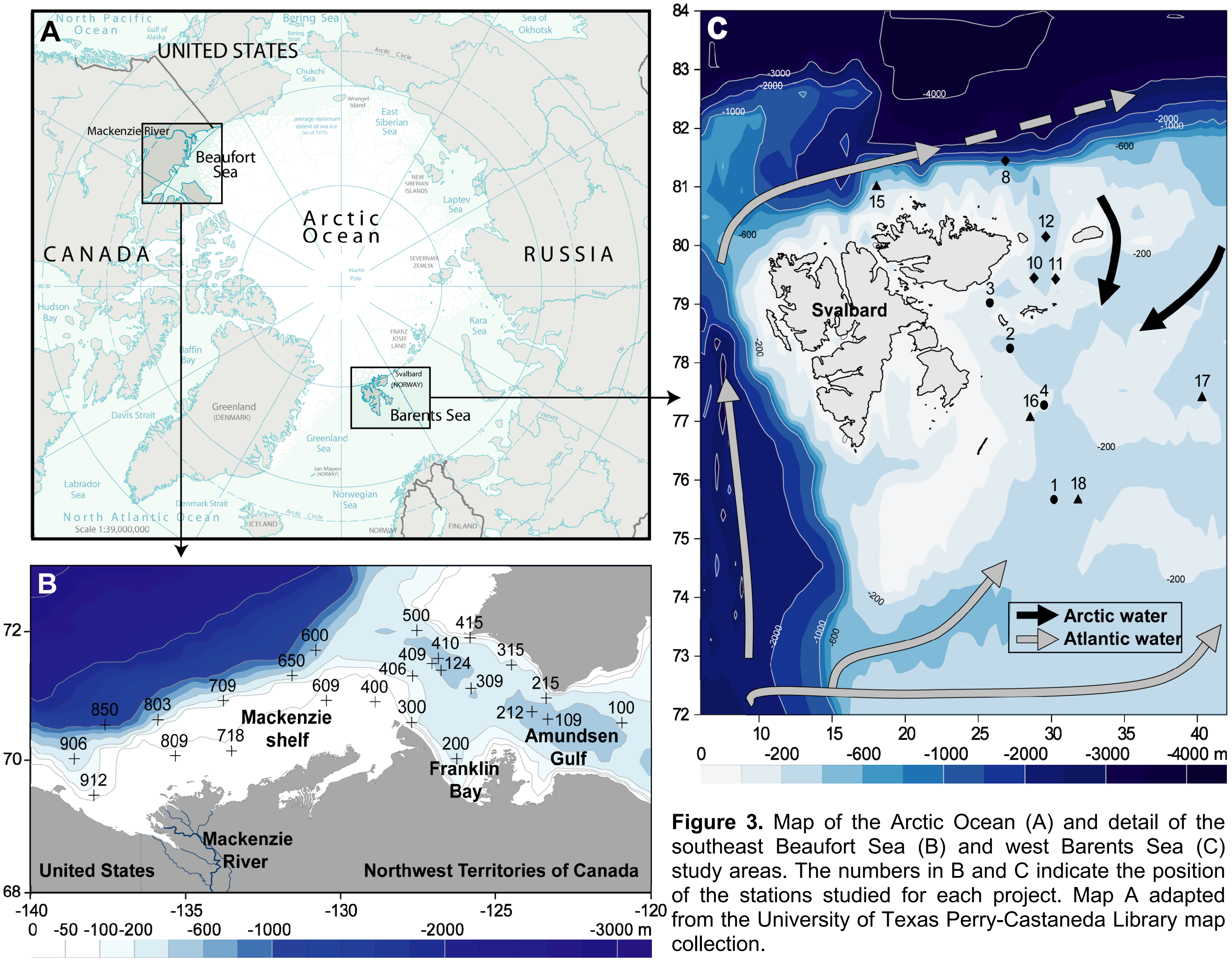


Figure 3. Map of the Arctic Ocean (A) and detail of the southeast Beaufort Sea (B) and west Barents Sea (C) study areas. The numbers in B and C indicate the position of the stations studied for each project. Map A adapted from the University of Texas Perry-Castaneda Library map collection.

4. Methods

For both study sites, samples for biomarker analysis (pigments and isotopes) were collected in the water column and ice when present (Table 2). At each station, when possible, sediment was sampled for biomarker analysis (pigments and isotopes), for benthic community composition, and for sediment oxygen demand (SOD).

Table 2: Type of samples and method used in each study.

Method	Sample	Paper						Reference
		I	**II**	**III**	**IV**	**V**	**VI**	
Pigment	Ice	√	√				√	Wright et al. (1991)
	Water column	√	√				√	Wright et al. (1991)
	Sediment (HPLC)	√	√				√	Chen et al. (2001)
	Sediment (Fluo)	√	√	√	√	√	√	Holm-Hansen et al. (1965)
Stable isotope	Water column		√					Hobson et al. (1995)
	Sediment		√				√	Hobson et al. (1995)
Sediment O_2 Demand	Total			√	√	√		e.g. Clough et al. (2005)
	Macrofauna free				√	√		Grant et al. (2002)
Diatom frustule	Sediment						√	Adapted from Hamilton et al. (2005)

4.1 Ice, water column and sediment sampling for biomarker analysis

Suspended particulate organic matter was determined in the following manner: water from the water column chlorophyll maximum determined by an in vivo fluorescence probe was filtered onto precombusted (5 h at 500°C) Whatmann GF/F filters. Filters were stored at -20°C prior to pigment and isotope analysis. During the CASES program, 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). The melted cores were then filtered onto GF/F filters as for POM. During the CABANERA program, ice algae and ice detritus (IPOM) were collected from the underside of the ice by SCUBA divers using an electric suction pump as described by Tamelander et al. (2007). IPOM was filtered onto GF/F filters as described previously for POM.

Samples for organic carbon and nitrogen percentages (%C and %N), and stable isotope ($\delta^{15}N$ and $\delta^{13}C$) analysis were collected with a truncated syringe from the top 2 cm of the sediment column. Samples were immediately frozen. Sediment cores (5 cm diameter×10 cm deep) were collected for determination of of sedimentary pigment concentration and composition profiles. Immediately after sampling, the sediment cores were extruded and sliced at 1 cm intervals under low light conditions. Each interval was divided in two, half to be used for an estimate of chlorophyll *a* and total chloropigment concentration by fluorescence and half for determination of individual pigment concentration by high pressure liquid chromatography (HPLC). See section 4.4 for detail pigment analysis methodology. Both pigment sub-samples were wrapped in foil and frozen immediatly after slicing in order to avoid pigment degradation. The overall slicing procedure did not exceed 1-2 hours.

4.2 Sediment oxygen demand and benthic community composition

SOD was used as an indicator of benthic activity. Sediment cores (10 cm diameter×20–25 cm deep with as much overlying water preserved as possible, 3–12 replicates per station) for SOD were collected with a multicorer during the CABANERA program, and sub-sampled from a spade corer (45 cm×45 cm) during the CASES program. Sediment cores were topped off with oxygenated bottom water and incubated in a cold room (<4°C). The measurement of SOD after addition of O_2 to reach 100% can be seen as measurement of the "potential sediment oxygen demand". However near-bottom oxygen concentrations were never below 2 ppm (i.e. hypoxia) and so differentiating potential from in situ sediment oxygen demand is probably not relevant in this study. Oxygen was monitored every 2-8 hours using a microelectrode (Unisense, A/S; Aarhus, Denmark) until 15-30% had been consumed (usually 24-48 h). The slope of the linear relationship between time and oxygen concentration was used as estimation of the SOD. In some cores, common large epifauna species were added in order to evaluate the oxygen consumption of individual organisms. Control cores with only bottom water were also incubated under the same conditions. After the end of incubations, sediment cores were sieved (1 mm) and macrofauna fixed in buffered 5% formalin in seawater and later preserved in 70% ethanol. Faunal composition of CABANERA samples was determined by taxonomic experts at the Russian Academy of Sciences Zoological Institute, St. Petersburg.

In order to estimate how much of the whole-core respiration was due to micro- and meio- fauna, additional incubations (minivials) were performed following procedures of Grant et al. (2002). Approximately 24 sub-cores (1.4 cm diameter×2 cm deep) were collected at each station with a truncated syringe. Visible macrofauna were removed as the sediment was transferred into pre-cleaned 24 mL glass scintillation vials. Vials were checked again afterward and replicates with macrofauna were rejected. Vials were filled with filtered (0.45 μm) near-bottom water and the oxygen concentration in half the vials was determined using a microelectrode. The remaining vials were incubated in a cold room for 48–56 h (drop in O_2: 2-28%), after which the oxygen concentrations were determined. The difference between readings at the beginning and end of the incubation was attributed to oxygen consumption by meiofauna, protozoa and bacteria. It is however important to keep in mind that these minivial incubations have been found to overestimate bacterial activity since exposure of the sediment to oxygenated waters can lead to break up of nutrient microgradients and redox conditions, and possibly enhance bacterial oxygen demand (Aller & Aller 1998, Dauwe et al. 2001, Grant et al. 2002). Once the minivial incubations were complete, samples were fixed for diatom-frustule analysis by withdrawing 2 mL of water and adding 2 mL of 37% buffered formaldehyde. Sedimentary diatom analyses were performed at the Canadian Museum of Nature, under the supervision of Dr. Michel Poulin, using an adaptation of the method of Hamilton et al. (2002).

Because estimates of epifaunal density are difficult to obtain from classical methods (i.e. sediment sieving), pictures of the surface sediment were taken during CASES. The underwater digital camera (Benthos, 1.2 megapixel resolution) and two strobes were mounted on a 1×1 m frame, equipped with a bottom-triggered shutter release. Organisms were identified and counted, and densities were scaled to values per square meter.

4.3 Stable isotopes and CHN analysis

Stable isotope analysis of the suspended particulate organic matter (i.e. POM filters) were performed after acidification for removing inorganic carbon, by the National Hydrology Research Institute in Saskatoon, Saskatchewan, Canada, using the method of Hobson et al. (1995). 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, 2 mL of 1 N HCl was added, and the sample was dried overnight. The operation was repeated 3 times, or until no bubbling occurred after acid addition. In order to avoid the carbon isotopic signature of carbonate, the decalcified sediment was used for %C and δ^{13}C determination. However, since acidification can alter the nitrogen isotope composition, undecalcified samples 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, U.S. Some of the decalcified sub-samples were also used for CHN analysis on a Fisons model 1108 CHN Analyzer with acetanilide as a standard.

4.4 Pigment analysis

Concentrations of individual pigments in POM and ice samples were determined by HPLC (Wright et al. 1991). Concentrations of sedimentary pigments were determined using both HPLC (Chen et al. 2001) and fluorometry (Holm-Hansen et al. 1965). Ice samples and POM filters were extracted in 2 mL of 100% HPLC-grade acetone for 12-24 h. Extracts were filtered through 0.2-µm-pore-size nylon syringe filters. Freeze-dried sediment (1-3 g) was transferred to a 50 mL polypropylene centrifuge tube where 8 mL of 80:20 (v:v) HPLC grade acetone:methanol was added. The mixture was sonicated for 5 minutes in an ice bath and extracted in the freezer overnight. Extracts were separated from the sediment by centrifugation (10 min, 2000 rpm) and 5 mL of the supernatant was filtered through a 0.2-µm-pore-size syringe filter. Extracts were blown to dryness under nitrogen, and then redissolved in 250 µl of 90% acetone in water.

Quantitative analysis of all pigments was conducted with a Waters HPLC equipped with an online photodiode array (Waters 996 PDA) and fluorescence detector (Waters 616) with excitation set at 440 nm and emission at 660 nm. Two hundred µl of each sample were injected through a guard column to a reversed-phase Alltech Absorbsphere C18 column (5 µm particle size; 250×4.6 nm i.d.). The 3-step gradient program was a modification of Wright et al. (1991) as described by Chen et al. (2001) for enhancing the separation of chlorophyll degradation products, also called phaeopigments.

Identification of pigments was performed by comparing retention time and spectra from photodiode array (PDA) detector of samples (See Appendix 7 for an example) with standards (DHI Water and Environment, Denmark, Appendices 8 and 9). Carotenoids were quantified using absorbance at 438 nm using the PDA detector, while chlorophylls and phaeopigments were quantified on the fluorescence detector (excitation 440 nm, emission 660 nm). The response factor (RF) was determined for each pigment from single run of each pigment standard.

Within two weeks of sample collection, total pigment concentrations were determined in sub-samples of sediment 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 48h, and shaken periodically. Prior to fluorescence determination, the sediment was centrifuged (4000 rpm for 10 minutes at 0°C). The fluorescence of the supernatant was determined using a Turner Designs Model 10-AU fluorometer (excitation 440 nm, emission 660 nm) before and after acidification with 5% HCl (Holm-Hansen et al. 1965), in order to determine chlorophyll *a* (chl *a*) and phaeopigments (phaeo).

5. Pigments as biomarkers

5.1 Photosynthetic pigments

Pigments are bound in pigment-protein complexes. Chlorophylls are a combination of cyclic complexes with a magnesium ion in the center (also called Mg-phorbin ring) and a long-chain isoprenoid alcohol ester group (also referred to as phytol chain, Figure 3a). Carotenoids are hydrocarbons consisting of eight isoprenoid units (carotenes) and their oxygenated derivatives (xanthophylls) (Figure 3b).

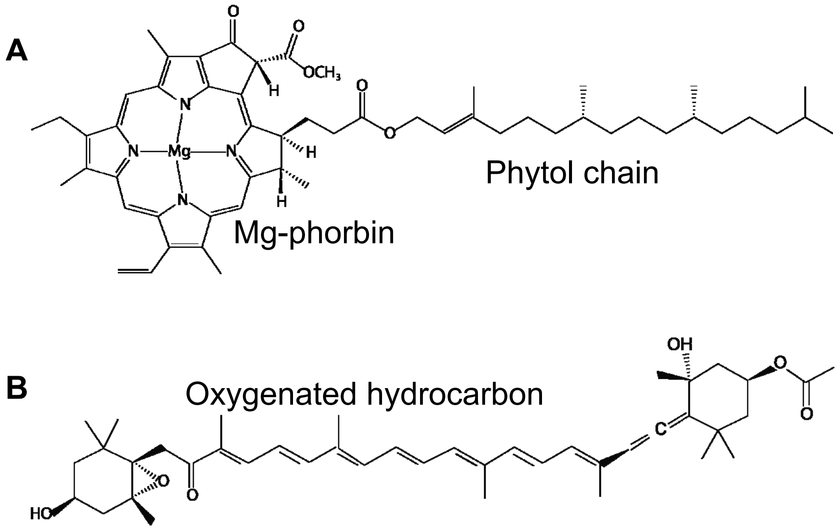


Figure 3. Chemical structure of (A) chlorophyll *a* and (B) fucoxanthin (carotenoid).

Pigments are present in all photosynthetic organisms and function primarily as light-harvesting agents for photosynthetis and for photo-protection (Porra et al. 1997). Chl *a* is the most common pigment, but other kinds of closely related chlorophylls and carotenoids also exist. While chl *a* is common to all algal species, many other accessory pigments are present in the different organisms and often have a restricted taxonomic distribution (Table 1). Thus pigments are useful as biomarkers of the algal groups responsible for primary production due to their taxonomic specificity (Jeffrey et al. 1997).

Preservation of pigments in sediment is generally favored by high plankton production, high sedimentation rates, and anoxia, the three main features of eutrophic basins (Schulte et al. 1999, Kowalewska et al. 2004). Thus, sedimentary pigments have been used in short-term and long-term studies of marine ecosystem changes, such as changes in organic matter production (Harris et al. 1996), eutrophication (Chmura et al. 2004, Kowalewska et al. 2004), and cyanobacterial blooms (Bianchi et al. 2000, Poutanen & Nikkilä 2001), as well as in larger-scale studies of sea level (Squier et al. 2003) and hydrodynamic changes (Zhao et al. 2000, Kowalewska 2001). In the Arctic, production can be very high, major phytoplanktonic groups can change spatially and seasonally, and downward fluxes can also be high. This makes pigments good candidates for studying pelagic-benthic coupling dynamics in Arctic systems. HPLC techniques represent the best way to study sedimentary pigments, since they allow separation of various chlorophylls, carotenoids and their degradation products (Sun et al. 1991, Sun et al. 1994, Kowalewska 1995, Bianchi et al. 1997, Kowalewska et al. 1998, Kowalewska et al. 2004). Few studies have investigated sedimentary chl *a* and phaeopigments by fluorometry in the Arctic (see summary in **Paper I**). The study of other pigments by HPLC has, to my knowledge, never been performed in Arctic marine sediments.

Table 1. Summary of pigments recovered in the water column and in sediment and their provenance. Compiled from Jeffrey et al. (1997) and Leavitt & Hodgson (2001). The relative degree of chemical stability and preservation is ranked from most (1) to least (4) stable. Pigments with the least stability are rarely found in the sediment. The predominant source is identified as planktonic (P), littoral (L), terrestrial (T) or sedimentary (S, post-depositionnal derivatives); upper case letter indicates the quantitatively more important sources, while lower case a less important source. - = not determined.

Pigment	Major groups or process	Stability	Source
Chlorophylls			
Chlorophyll *a*	All photosynthetic algae, higher plants	3	P L
Chlorophyll *b*	Green algae, euglenophytes, higher plants	2	P L
Chlorophyll *c* family	Dinoflagellates, diatoms, chrysophytes	1	P l
Carotenoids			
β-Carotene	Most algae and plants	1	P L t
Fucoxanthin	Diatoms, prymnesiophytes, chrysophytes, raphidophytes, several dinoflagellates	2	P L
Peridinin	Dinoflagellates	4	P
Alloxanthin	Cryptophytes	1	P
19'But-fucoxanthin	Prymnesiophytes, chrysophytes	-	P L
19'Hex-fucoxanthin	Prymnesiophytes	-	P
Zeaxanthin	Cyanobacteria, prochlorophytes, rhodophytes, chlorophytes	1	P l
Chlorophyll degradation products			
Phaeophytin *a*	Chlorophyll *a* derivative (general)	1	P L t s
Phaeophytin *b*	Chlorophyll *b* derivative (general)	2	P L t s
Phaeophorbide *a*	Grazing, senescent diatoms	3	P l s
Pyro-phaeo(pigment)	Derivatives of *a* and *b*-phaeopigments	2	L S

5.2 Flux and degradation of pigments

Pigments are degraded in the aquatic environment by biological processes (Figure 4), as well as chemical and photochemical processes, and in the water column (Cuddington & Leavitt 1999) and following deposition in the sediment (Hodgson et al. 1998). Chlorophylls contain nitrogen and are therefore more prone to degradation than carotenoids. Within the water column, pigment degradation is usually very rapid and extensive (hours to weeks, Figure 4). In the sediment, chl *a* has a half life of several weeks (Graf et al. 1995).

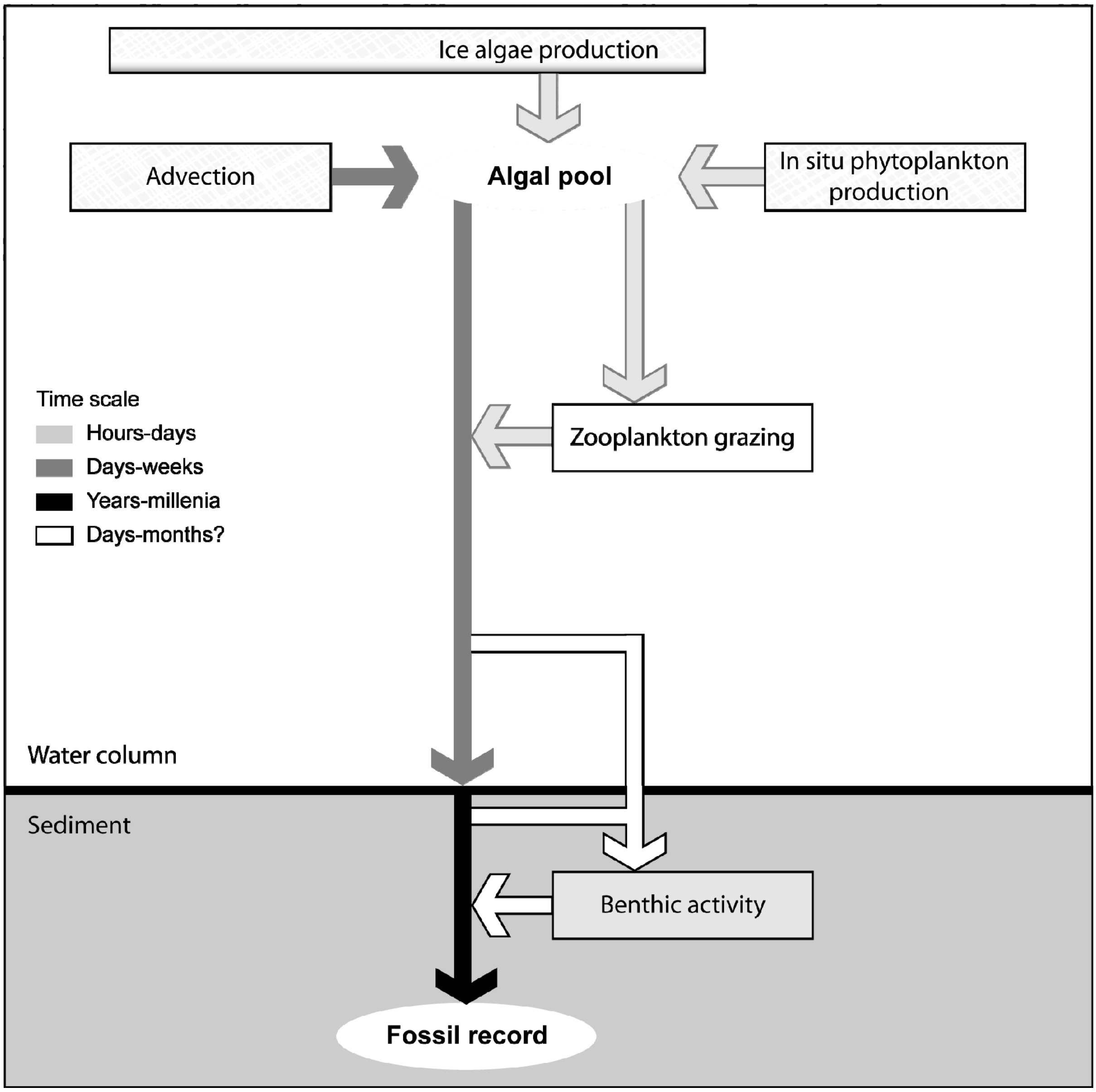


Figure 4. Main biological pathways of pigment production in the "algal pool", transformation and degradation in the Arctic marine ecosystem. Most degradation of pigments occurs during deposition through the water column and in the surface sediments. Note that the scale of the effect of benthic activity is not well defined, and is addressed in this study.

The fate of pigments in Arctic sediments is not fully understood. Smith et al. (in press) suggested the existence of a "foodbank" for Antarctica. This foodbank consists of organic matter maintained in the sediment throughout the year, and thus available to the benthos during low depositional periods. Another explanation consists of fast response to POM inputs, especially to spring ice-algae inputs, as discussed in **Paper V**. The benthic activity increases as soon as fresh POM reaches the sea floor. A third option would be a combination of the two previous hypotheses, where the benthos responds quickly to inputs, but a part of the carbon arrival is stocked in the sediment and can be use through the entire year, as suggested in **Papers II** and **VI**.

Different pathways of pigment degradation affect the integrity of the Mg-phorbin ring, the phytol chain, or both, and result in different degradation products (Figure 5). Formation of phaeophorbide is mainly due to herbivore activity, chlorophyll is degraded to chlorophyllide by chlorophyllase during cell senescence, and phaeophytin is formed during herbivory, cell senescence, and microbial degradation.

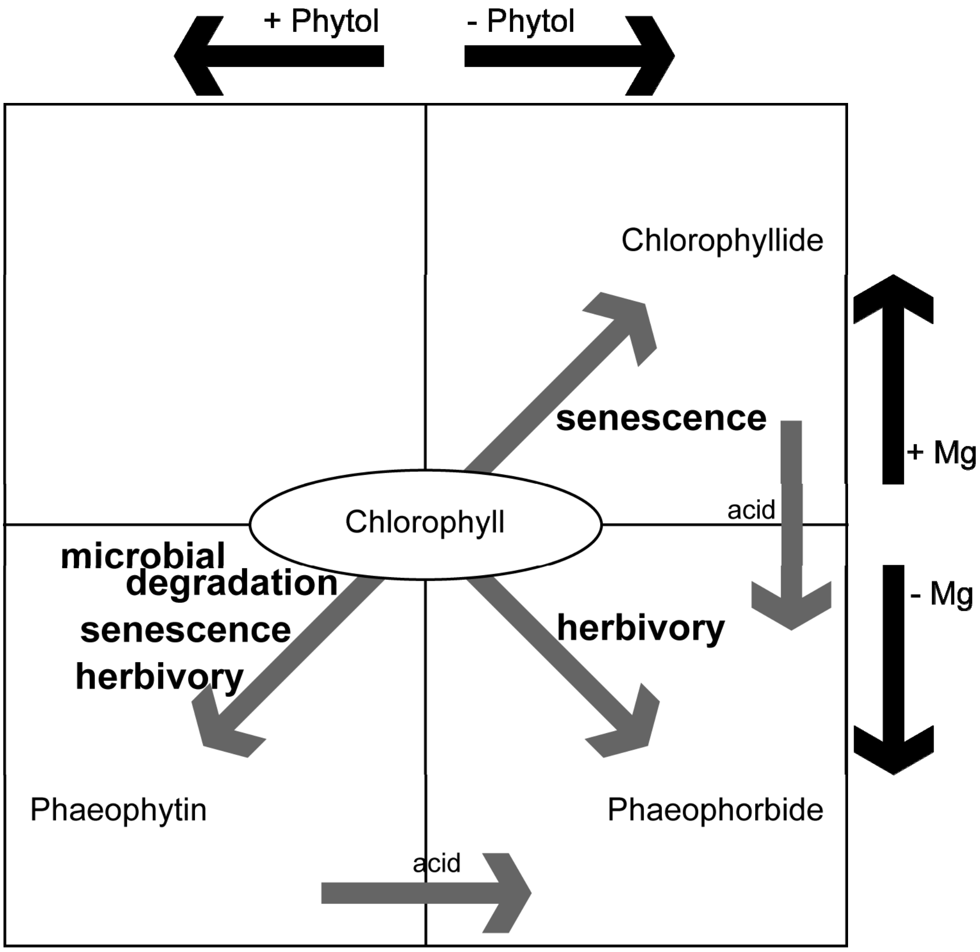


Figure 5. Production of the 3 main colored chlorophyll derivatives under oxic conditions: chlorophyllide, phaeophytin and phaeophorbide. Adapted from Leavitt (1993).

To summarize, relative abundance of sedimentary chl *a* is a marker of the freshness of algal matter inputs to the sediment (Boon & Duineveld 1996), sedimentary accessory pigments specific for different algal groups can be used as taxonomic markers (Gieskes & Kraay 1984, Jeffrey & Vesk 1997), and degradation products indicate physiological status and nature of chlorophyll processing organic matter has undergone (Mantoura & Llewellyn 1983, Villanueva & Hastings 2000).

5.3 Results obtained in this study

As expected, the study of sedimentary pigments by HPLC allowed the separation of various chlorophylls, carotenoids, and pigment degradation products. The chl *a* results from the HPLC method correlated strongly with the results from the fluorometric method (Figure 6, **Papers I, II and VI**).

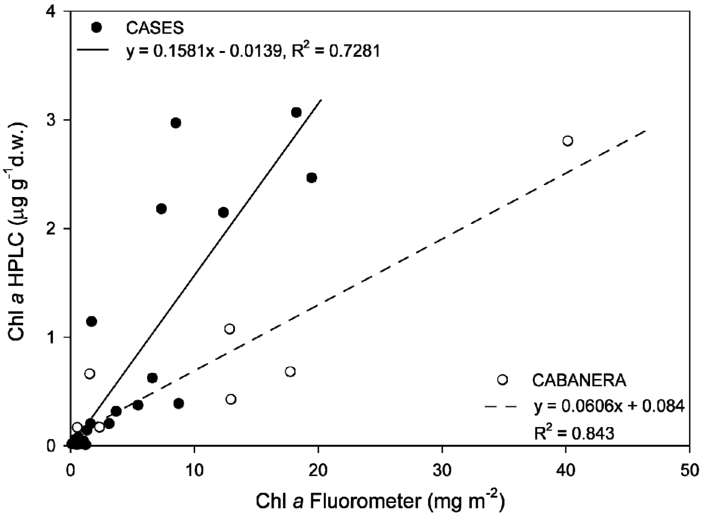


Figure 6: Comparison of the results of sedimentary chlorophyll *a* content (0-2 cm) by Fluorometer and HPLC analysis for the Beaufort (CASES) and Barents (CABANERA) seas.

The main sedimentary accessory pigments found in all studies were chlorophyll *b* (chl *b*), a marker of green algae, and fucoxanthin, a marker of diatoms (**Papers I, II and VI**). Other accessory pigments were also found in the sediment, and an even larger number of pigments were identified in water column and ice (**Papers I and II**). The large number of pigments found in water and ice samples is likely due to the fact that in the water column and ice, degraded pigments were usually not very abundant, while in the sediment, degradation products were sometimes extremely abundant, and could have masked other pigment signals. This is illustrated in the Figure 7, where, for the same station, the chromatogram of the water column POM presents distinct peaks, and easily identifiable spectra, while the chromatogram in the two first cm of sediment presents many more peaks of unidentified degradation products.

Sedimentary chl *a* abundance showed strong correlations with local primary production and fluxes (**Papers I, II, III and IV**), and was inversely correlated with depth (**Papers II, III and IV**). Moreover chl *a* abundance was also correlated with benthic activities (**Papers III and IV**). The ratio of chl *a* to total phaeopigment concentrations (chl *a*/phaeo) was also used as an indicator of the freshness of sedimentary organic matter.

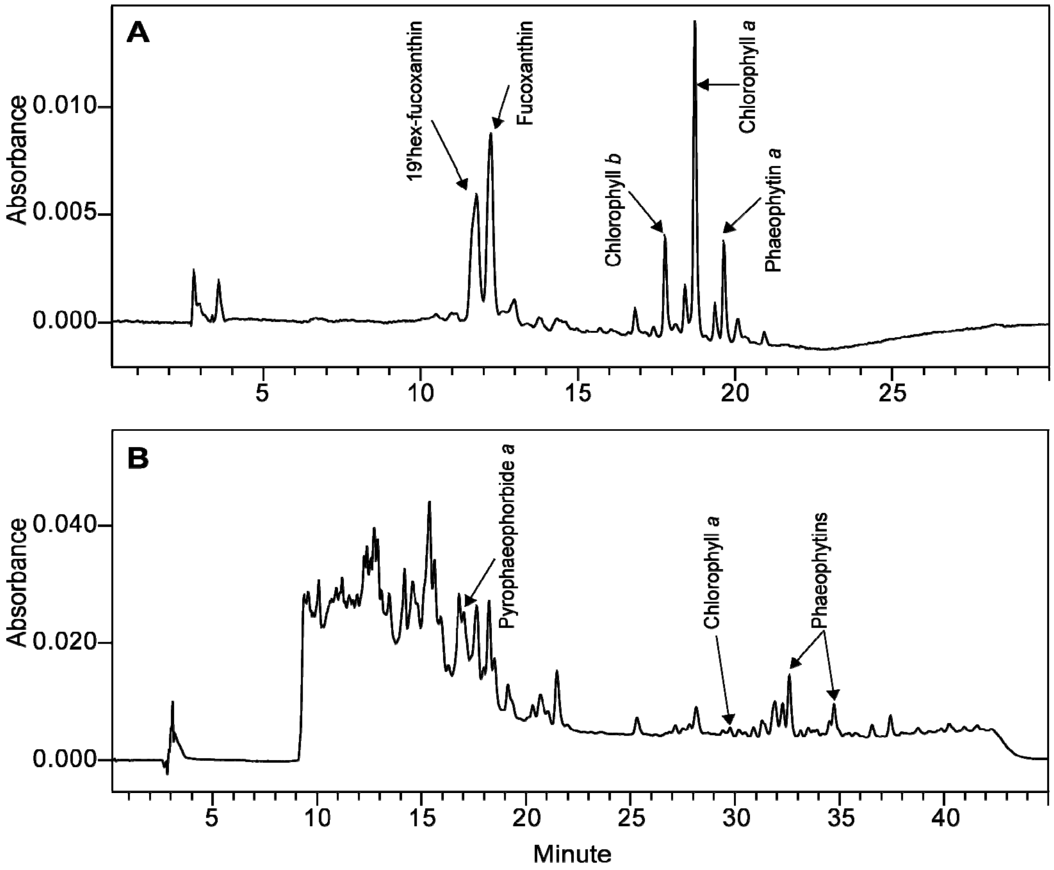


Figure 7. Characteristic pigment chromatogram from (A) a POM sample and (B) a 0-1 cm sediment slice from station 100, CASES, fall 2003. In the POM sample, main peaks are easily identifiable. In contrast, in sediment, peaks overlap and the chromatogram includes many unidentified degradation products. Absorbance signals were detected at 438 nm using a PDA detector. Note that the retention time for the same compounds differ between the chromatograms, because different gradients were used.

Fucoxanthin, a marker of diatoms, was by far the most abundant accessory pigment found in ice, water column, and sediment. Although it is impossible to differentiate ice-derived diatoms from phytoplankton diatoms from their similar pigment signature, it was hypothesized in **Papers I** and **II** that a part of sedimentary fucoxanthin derived from ice. **Paper VI** suggested that this hypothesis was valid as fresh intact ice-algal cells were found in the surface sediment of the Beaufort Sea when ice-algal biomass increased in the spring.

Other accessory pigments were used as taxonomic markers of various phytoplankton groups. Moreover the use of the CHEMTAX program (Mackey et al. 1996) allowed us to relate the water column pigment composition to phytoplankton taxonomic composition. In the Beaufort Sea for example, the three major phytoplanktonic groups (>90% total groups) determined by CHEMTAX were diatoms, green algae (prasinophytes + chlorophytes classes) and haptophytes (prymnesiophytes). In the cell counts, the major classes found were diatoms, prasinophytes, prymnesiophytes and flagellates (Poulin et al. pers. comm.). Lovejoy et al. (2007) found that *Micromonas*-like picoprasinophytes were very abundant in the Western

Arctic, which suggests that an important part of the flagellates found in the Beaufort Sea could be prasinophytes. Paired t-tests between the CHEMTAX and cell-count results showed no significant difference ($p>0.05$) of the total percentages of diatoms and green algae in summer and fall, and no difference for the haptophytes in the summer. Haptophyte percentages were however significantly different in the fall. A part of the cell count might have ignored some haptophytes counted as "flagellates". The comparison of CHEMTAX with cell counts is hard to perform because of the difference of the different limitations of identification for each group and class for both techniques. However, although the use of CHEMTAX is somewhat controversial, the results obtained in both the Barents and Beaufort Seas (**Papers I and II**) gave similar results as microscope cell counts for the major groups.

Both pigment signature and CHEMTAX results showed that small flagellated cells such as prasinophytes and prymnesiophytes were important during the fall in the Beaufort Sea (**Paper II**). In the Barents Sea, green algae (which includes prasinophytes) and prymnesiophytes were influenced by the predominant water-mass (Arctic or Atlantic water were the predominant water mass) (**Paper I**). Degradation products of chl *b* were used to track riverine influence (**Paper II**).

Finally, phaeophorbide and carotenol chlorine esters (CCE) were used as markers of macrozooplankton and macrobenthos grazing (**Papers I, II and VI**). CCE are created during grazing processes by a combination of carotenoid and phaeophorbide (Goericke et al. 1999, Soma et al. 2001, Chen et al. 2005), and were only recently identified. It was thus extremely interesting to find them in the sediment of the Barents Sea as a marker of diatom grazing (**Paper I**). It is important to note that although phaeophorbides have been used to trace grazing processes in both the water column (Jeffrey 1974, Carpenter et al. 1986, Spooner 1994) and the sediment (Brotas and Plante-Cuny 1998, Riaux-Gobin 2000) it has recently been argued that it might not always be a relevant indicator of herbivorous activities (Villanueva and Hastings 1999, Ford and Honeywill 2002). However the correlation of phaeophorbide with CCE in the Barents Sea (**Paper I**) and with macrozooplankton fecal pellets in the Beaufort Sea (**Paper II**) confirmed the reliability of this pigment as marker of grazing.

This work found sedimentary pigments to reflect changes in environmental factors, in sources of organic matter, in food web structure, and in benthic activity. Although useful information is gained from the pigment patterns alone, the addition of other biomarkers, such as stable isotopes and diatoms frustules, allowed further elucidation of factors influencing spatial and seasonal changes in pelagic-benthic coupling.

6. Effects of environmental factors

The present study in the Beaufort and Barents Seas highlighted three major abiotic factors affecting pelagic-benthic coupling: water depth, water masses, and riverine input. Not surprisingly, these factors had very different impacts in the two ecosystems. Depth and riverine inputs were important n the Beaufort Sea (**Papers II, IV and VI**) while in the Barents Sea, oceanic source waters seemed more important in determining organic matter inputs to the benthos (**Papers I and III**).

6.1 Water depth

Previous studies pointed out the importance of depth for determining the quality and quantity of organic matter reaching the benthos in marine systems, both polar (e.g., Grebmeier 1993) and temperate (e.g., Suess 1980). In the Arctic, increasing depths have been correlated with decreasing sedimentary chl *a* (Ambrose & Renaud 1995, Grahl et al. 1995, **Paper II**), decreasing SOD (Pfannkuche & Thiel 1987, Ambrose & Renaud 1995, Piepenburg et al. 1995, Glud et al. 2000, Clough et al. 2005, **Paper IV**), and changes in benthic community composition (Grebmeier et al. 1988, Clough et al. 1997, Piepenburg 2005, Conlan et al. in press). Shallower depths seemed to be associated with shorter pelagic food chain (Grebmeier et al. 2006), probably allowing greater inputs of organic matter of better quality. Indeed, sedimentary chl *a*, chl *a*/phaeo ratio, and SOD were higher in the shallower Mackenzie shelf than in the surrounding deeper environment (Tables 2, 3, **Papers II and IV**). For a given water depth, sediment type and water column nutrient regime, benthic macrofaunal biomass in the Arctic appears to be greater than at lower latitudes (Petersen & Curtis 1980, Rowe 1983), suggesting a stronger pelagic-benthic coupling in the Arctic.

Pronounced depth zonation has been found in the composition and distribution of benthic assemblages, leading Piepenburg (2005) to separate 3 distinct zones: shelf, slope, and basin. This concept was used in **Paper II**. However, even though the study areas are defined by water depths, differences are not the result of just one single factor, but several direct and indirect depth-dependent ecological processes (Carney et al. 1983). Indeed, water depth can have an influence on factors such as mixed layer depth, current speed, ice cover, primary production, bacterial degradation, and sea floor sediment properties, which are often interrelated (Piepenburg et al. 2001). This means that although pressure, directly related to water depth, can impact benthic organisms (Somero et al. 1983), it is most likely the inverse relationship between water depth and sedimentation rates that explains the fundamental influence of water depth on the quality and quantity of organic matter reaching the sea floor (Graf 1992). Surprisingly, in the Barents Sea, depth did not seem to be an important factor for determining benthic activity and sediment properties (**Papers I and III**), depth range was too narrow to make correlations (200-350 m, station 8 was at 500 m).

6.2 Water masses and currents

In addition to depth zonation, current regime has been found to be the most prominent feature in the distribution of some Arctic assemblages (Piepenburg 2000). Currents can directly influence carbon source and fate by bringing allochthonous organic matter to the system in water (Feder et al. 1994) or ice (Reimnitz et al. 1993). Alternatively, currents can export organic material, making it unavailable for the local benthos. Allochthonous terrestrial inputs have been found to balance the overall carbon demand in the Laptev Sea (Schmid et al. 2006), and off-shelf export has been suggested to feed communities of the deep Arctic basin during some seasons (Moran et al. 2005). Thus, the prevailing water masses and currents in the area are important in determining the potential characteristics of food deposition to the benthos and can have significant impacts on local and regional carbon cycling pathways.

As noted, the Barents Sea is influenced by warm Atlantic Water in the south and by Arctic Water in the north (Figure 2c). These water masses have different phytoplankton compositions (Rat'kova & Wassmann 2002, Reigstad et al. 2002), which were reflected in the sedimentary pigment composition (**Paper I**). The effect of dominant water mass on phytoplankton composition has also been observed in the Chukchi Sea where changes in phytoplankton species and water-column pigment composition due to water mass variations (Hill et al. 2005) were apparent in the sedimentary pigment composition (Pirtle-Levy et al. in press).

In the Beaufort Sea, an upwelling off Cape Bathurst is suspected to be responsible for areas of elevated benthic biomass (Conlan et al. in press). Sedimentary chl *a* concentrations and the chl *a*/phaeo ratio were higher in this area (see Figure 2 a,c, station 300 of **Paper II**). This increase of benthic biomass in upwelling areas is similar to sites in the Chukchi Sea, where upwelling of nutrient-rich waters causes high primary production and sustained high benthic biomass (Grebmeier et al. 1988, Grebmeier & Barry 1991).

6.3 Riverine inputs

As mentioned previously, about 10% of the global river discharge enters the Arctic Ocean, which is only 1% of the world ocean water (Dittmar & Kattner 2003). Despite pronounced seasonal patterns, organic matter concentrations in Arctic rivers are generally among the highest in the world, while nutrient concentrations are among the lowest (Dittmar & Kattner 2003). Terrigenous organic carbon inputs into the Arctic Ocean are mainly due to the particulate organic carbon discharged by river (80% of total organic carbon flux). Coastal erosion contributes about 15% of the terrigenous organic carbon, with the rest due to underground water discharge, sea-ice input, and eolian deposition (Rachold et al. 2004). The Barents Sea did not show markers of riverine inputs (**Papers I and III**), probably because river inputs and sediment load are substantially lower in the Barents Sea than on other Arctic shelves (Rachold et al. 2004). Isotopic signatures typical of terrestrial organic matter and freshwater algae have been found in the sediment of the Kara Sea (Fernandes & Sicre 2000, Fahl et al. 2003, Polyakova 2003, Stein et al. 2004), Laptev Sea (Cremer 1999, Matthiessen et al. 2000), and Beaufort Sea (**Paper II** and references within), influenced by the Yeniseya and Ob', the Lena, and the Mackenzie Rivers, respectively (Figure 1). Moreover, the sedimentary pigment composition (chl *b* degradation products) corroborated the terrestrial isotope signature in the Beaufort Sea (**Paper II**). However, most of the imported fluvial organic matter is usually fairly degraded (Stein 1996, Fahl et al. 2001, **Paper II**), and likely represents low-quality food for the benthos. Thus, although riverine inputs are important for the pelagic-benthic coupling and impact bulk organic inputs to the sediments, they do not seem to be an important food resource for benthic communities in the Arctic (Klages et al. 2004).

7. Effects of biotic factors

Environmental factors often control variations in biological factors. In the Barents Sea, for example, water masses seemed to play an indirect role in pelagic-benthic coupling by influencing phytoplankton composition in the summer. However, biological parameters including primary production, phytoplankton taxonomy, and zooplankton grazing seemed to predominate in shaping pelagic-benthic coupling over time.

7.1 Local water-column production

Previous studies on Arctic ecosystems have suggested local autochthonous primary production as the major factor determining sedimentary chl *a* and SOD (Pfannkuche & Thiel 1987, Ambrose & Renaud 1995, Piepenburg et al. 1997a, Grant et al. 2002, Bessière et al. 2007). In the deep Arctic Ocean, sedimentary chl *a* and SOD were lower than on the Arctic shelves (Clough et al. 2005). They are also lower than on the NE-Atlantic abyssal plain (Pfannkuche 1992), reflecting limited primary production under the permanent ice cover (Boetius & Damm 1998, Soltwedel & Schewe 1998).

Although sedimentary chl *a* and SOD were not correlated with depth in the Barents Sea, they were correlated with overlying biomass of primary producers and vertical fluxes in both the Barents and Beaufort Seas (**Papers I, II and III**). For similar depths (>200 m), sedimentary pigments and SOD were usually higher in the Barents Sea (**Papers I and III**) than in the Beaufort Sea (**Papers II and IV**). Primary production rates in the Barents Sea and the Bering/Chukchi Sea are among the highest in the Arctic (see review by Sakshaug 2004), and sedimentary pigments reflect this by exhibiting high contents of chl *a* and high chl *a*/phaeo ratios (Table 3). Although sedimentary chl *a* and SOD at depths >200 m in the southeastern Beaufort Sea were lower than in more productive ecosystems, values in the shallower areas of the Mackenzie shelf were comparable with other Arctic shelves (Table 3).

An important feature of primary production in the Arctic Ocean is its strong episodic character (Wassmann et al. 1996), leading to important temporal/seasonal variations in addition to the spatial variations addressed previously. Seasonal variations in abundance and composition of sedimentary pigments were observed in both the Barents and Beaufort Seas (**Papers I, II and VI**). In the Beaufort Sea, the chl *a*/phaeo ratios were higher in the summer compared to the fall, representing a material less degraded and thus “fresher”. In the spring study (**Paper V**), SOD increased through time, while chl *a* did not. Other sedimentary pigments, markers of phytoplankton taxonomy (section 7.2) and pigment degradation

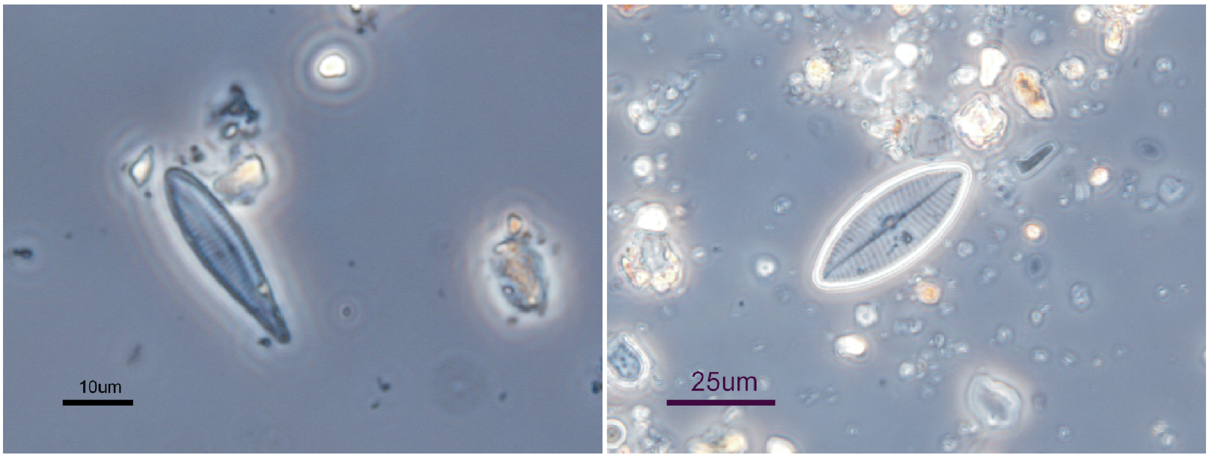
(Section 7.3), provided insights regarding the benthic response to the spring pulse of organic matter (**Paper VI**). In the Barents Sea, chl *a* and SOD did not show significant differences between spring and summer, although accessory-pigment composition reflected seasonal changes in productivity regime (section 7.2).

Seasonal variations are often due to changes in ice-associated production and this will be discussed below. Chl *a* and SOD can reveal spatial variations in pelagic-benthic coupling due to changes in total algal biomass. However in order to track changes in primary producers, the only study of chl *a* and SOD is not sufficient and other pigments have to be identified by HPLC.

7.2 Productivity regime (phytoplankton vs. ice algae)

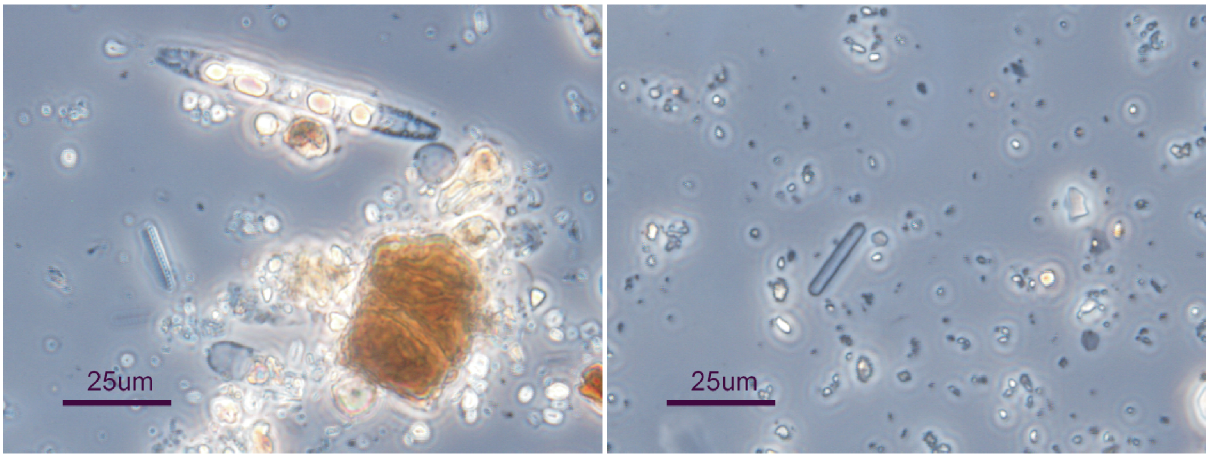
Variation in ice cover indirectly impacts organic matter inputs by its influence on ice-algal production. Sea-ice algae have been found to contribute considerably to total primary production in polar seas (Legendre et al. 1992, Gosselin et al. 1997) and to be dominated by diatoms (von Quillfeldt et al. 2003, Hill et al. 2005). Sea-ice algal production is particularly favoured in the spring, when sea ice has not melted yet and light is sufficient. It can also indirectly impact the overall water column production. The release of ice algae into the water column by ice melt is commonly associated with phytoplankton blooms (Leventer 2003) suggesting that sea-ice algae may serve as the seeding population for bloom onset (Syvertsen 1991, Gradinger 1999). In the present study, primary producers occurring directly within the ice and in the underlying water due to ice-algae inoculums are referred to as "ice-associated algae".

Ice-associated algae can sink, representing a potential source of food for the benthos. Frustules of ice-associated algae have been found in the sediment of Arctic shelves (Sancetta 1981, Cremer 1999, Djinoridze et al. 1999, Polyakova 2003, Ambrose et al. 2005, **Paper VI**, Figure 8) or their presence has been indicated by high concentrations of chl *a* and/or fucoxanthin (Schewe & Soltwedel 2003, Pirtle-Levy et al. in press, Papers I, II, VI). Moreover, indications that benthic organisms can derive energy directly from ice algae have been observed (Hobson et al. 1995, McMahon et al. 2006, Papers V, VI). However, while SOD correlated with increased ice-algal production (**Paper V)**, it was unclear how sedimentary pigments were reflecting this episodic input of ice algae to the sediment of the Beaufort Sea, and this will be discussed in section 7.4.



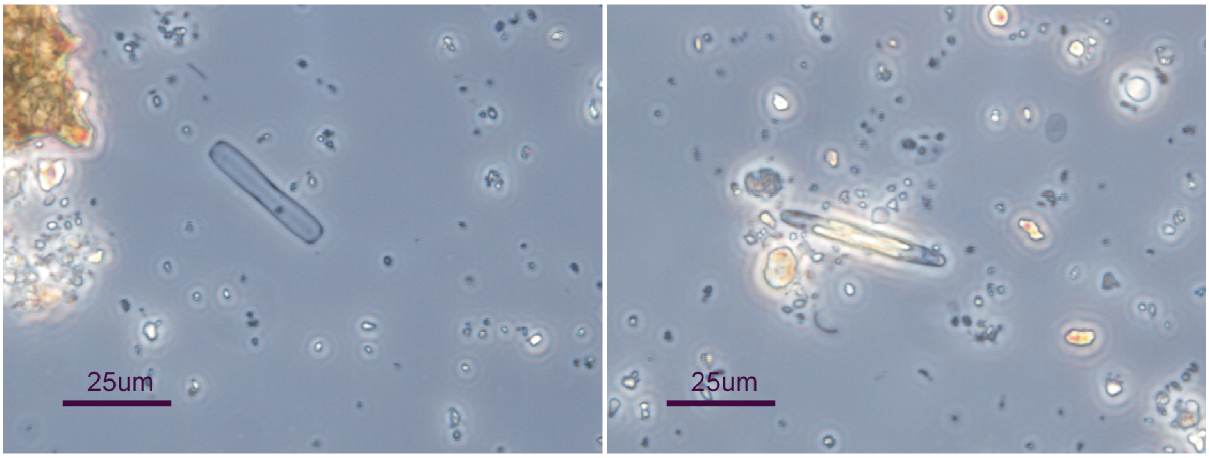
A. January 14, *Pseudogomphonema arcticum*

B. April 29, *Navicula valida*



C. April 29, *Nitzschia frigida*

D. May 9, *Fragilariopsis cylindrus*



E. May 9, *Navicula pelagica*

F. May 9, *Fossula arctica*

Figure 8. Photography of ice-algae frustules found in the sediment of Franklin Bay during CASES overwintering.

The importance of diatoms in the ice-associated algal community was noted earlier. They are also major producers throughout the Arctic (Hill 2005), and were found to dominate in the summer on the Mackenzie shelf (**Paper II**), and associated with sea ice in the Barents Sea (**Paper I**). The significance of diatoms during the summer was indicated by the high levels of fucoxanthin in the Beaufort Sea (**Paper II**), Barents Sea (**Paper I**), and in the Bering/Chukchi Sea (Pirtle-Levy et al. in press). It was interesting, however, to find that in the summer, other phytoplankton species were important in the Amundsen Gulf area and the Beaufort Sea (**Paper II**). As discussed earlier, the different phytoplankton taxonomy in the Barents Sea can be largely attributed to the influence of variations in the dominant water-mass. Atlantic waters contain more prymnesiophytes (Wassmann et al. 2005), whereas Arctic waters contain more green algae (Not et al. 2005). In the Cape Bathurst polynya (Figure 2b), early melting of ice probably leads to an earlier growing season as in other polynyas (Smith et al. 1997). Thus, in the summer, although the surrounding areas are at their peak of production with diatoms as dominant group, the Cape Bathurst polynya is already in post-bloom condition, with smaller cells.

In the fall, small algal cells seem to predominate algal population in Arctic waters. Traditionally, Arctic marine production has been thought to be dominated by large phytoplankton (von Quillfeldt 1997). However, recent studies have shown that picophytoplankton can be abundant in late summer/fall (Not et al. 2005, Lovejoy et al. 2006). Indeed, haptophytes and prasinophytes were dominant in the water column of the Beaufort Sea (**Paper II**). This was also found in the accessory pigment composition in the sediment. Interestingly, and contrary to previous thoughts, small cells seem to sink relatively fast (Richardson & Jackson 2007, **Paper II**), and might be a significant late-season source of food for the benthos.

7.3 Grazing and bacterial degradation

The match or mismatch of high zooplankton biomass with phytoplankton blooms determines the fate of the produced organic carbon, which can be either retained in the water column or exported to the bottom (Wassmann 1991, Wassmann et al. 1996). Thus 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). Large copepods of the genus *Calanus* are important grazers on phytoplankton in all Arctic seas. Grazing by macro- and meso- zooplankton has been found to degrade chl *a* to phaeophorbide *a*, so sedimentary phaeophorbide *a* was used in the present study to estimate abundance of zooplankton-degraded organic matter. In the Barents Sea sediment, phaeophorbide *a* was the most abundant phaeopigment (**Paper I**), and input of grazed material was the highest in the summer. The stations where fecal pellets represented the highest proportion of carbon flux (Wexels Riser et al. in press) also had the highest sedimentary phaeophorbide *a* content. Moreover, the presence of CCE, a combination of phaeophorbide and fucoxanthin, suggested the importance of grazing on diatoms, and perhaps on ice-associated diatoms. In the spring, material reaching the benthos had higher chl *a*/phaeo ratio, and thus a higher nutritional quality (**Paper I**). SOD was also higher (**Paper III**), suggesting that the mismatch of zooplankton and phytoplankton in the spring allows inputs of higher quality organic matter to the sea floor, where the benthos responds by increasing activity.

In the Beaufort Sea, higher macrozooplankton grazing in the summer (Forest et al. 2007) also resulted in higher sedimentary phaeophorbide *a* (**Paper II**). In the fall, however, grazing activity by macro- and meso- zooplankton was lower and fecal pellets were mainly from microzooplankton (Forest et al. 2006). Indeed, the sedimentary phaeopigment composition switched from a clear phaeophorbide *a* signal to a less clear phaeopigment composition. In the spring, phaeophorbide *a* increased from January to April. However, grazing in the water column did not seem to be responsible for this increase, instead, the increase in phaeophorbide *a* was attributed to increased of benthic macrofaunal activity (**Paper VI**).

Although inputs of grazing-degraded organic matter to the sea floor can be estimated by the identification of phaeophorbide *a*, microbial degradation is much harder to estimate using pigment composition. No specific marker of microbial degradation was identified in the present study. Phaeophytin is created during herbivory (grazing), microbial degradation and cell senescence (see section 5.2), and thus microbial degradation was mainly implied when no proof of grazing was found. In the Amundsen Gulf, the importance of sedimentary phaeophytin *a* relative to other phaeopigments was observed (**Paper II**), suggesting that less grazing by macro- and meso- zooplankton occurred and therefore relatively more microbial degradation.

7.4 Benthic communities

SOD has been used as an estimate of carbon going through the whole benthic community (Table 4), while minivial incubations and bottom photography allowed partitioning of carbon degradation between epifauna, macrofauna, and microfauna/bacteria to be assessed (Table 5). The relationship between the whole benthic community activity and the environmental and biological factors has been discussed in the previous sections. Depth and downward carbon fluxes seemed to be the most important factors in determining SOD. Moreover, sedimentary chl *a* concentrations correlated strongly with SOD (**Papers I, II, III**

and IV), and availability of high quality food (i.e., higher chl *a* content and chl *a*/phaeo ratio) has been found to correlate with SOD also on other Arctic shelves (Grant et al. 2002, Clough et al. 2005, Dunton et al. 2005). As a further indicator of the robustness of the positive correlation between chl *a* and SOD, sedimentary chl *a* has been accepted for use in models as a predictor of SOD in steady state systems (Sun et al. 1991).

However, as episodic organic matter inputs to the benthos occur, SOD and chl *a* may not be sufficient to explain the benthic response, necessitating additional parameters. Although SOD increased, the higher inputs of ice algae in the spring did not lead to higher sedimentary chl *a* (**Paper V**). This lead us to carry out a further detailed study of sedimentary pigments and diatom frustules (**Paper VI**). From January to May, the phaeophorbide *a* to chl *a* ratio increased at the Franklin Bay overwintering site, as did sediment bioturbation. This suggests that macrobenthos activity was enhanced by fresh detrital inputs, increasing bioturbation. The rapid use of phytodetritus lead to a quick degradation of the chl *a* to its grazing degradation products. Compared to temperate areas, Arctic macrobenthos have 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, Grebmeier et al. 2006). In the Beaufort Sea, microbial oxygen demand varied from 25-90% (average 60%). In the Barents Sea, when comparing total SOD (from **Paper III**) with microbial oxygen demand determined by Vandieken et al. (2006), it appeared that 38-62% (average 52%) of the total SOD was due to microbial activity. Although the minivial incubation technique is thought to overestimate oxygen consumption, in both studies, macro- and micro- fauna seemed to have similar contributions to oxygen demand. However, as suggested in other Arctic studies, these macrofauna oxygen-demands appear to remain higher than in studies of non-polar ecosystems (Boucher & Clavier 1990, Mahaut et al. 1995, Heip et al. 2001).

In some Arctic areas, epifauna can reach very high abundances and ophiuroids are among the most abundant megafauna on Arctic continental shelves (Piepenburg 2000). The results in the Beaufort Sea confirmed this tendency, where ophiuroids were abundant in the shallow shelf area and contributed an important part, up to 41%, of the SOD (**Paper IV**). The importance of ophiuroids in the Arctic Ocean is due to flexibility of their feeding mode (Piepenburg 2000) and considerable mobility, allowing a rapid response to episodic food pulses (Smith 1986), which are common in the Arctic.

Different groups of the sediment community respond in different ways and on different time scales to the deposition of phytodetritus (Pfannkuche et al. 2000). Some previous studies have found a time lag between the pulse of organic matter to the seafloor and the benthic response. In contrast, the present study shows that the benthos can quickly respond to these inputs. Benthic macrofauna seems to be particularly efficient in degrading carbon. This has also been previously suggested by Witte et al. (2003). Consequently, the benthic faunal composition (epi-, macro-, or micro- fauna) can determine the fate of organic matter reaching the sea floor.

Table 3. Summary of sedimentary pigments in the Arctic. Chl *a*: Chlorophyll *a*; CPE: ChloroPlastic Equivalent (Chlorophyll *a* + Phaeopigments); Chl *a*/Phaeo: ratio chlorophyll *a* to total phaeopigments. Note that the units used and the sediment depth differs in the various studies, and are indicated in the columns "Units" and "Sediment depth (cm)" respectively.

Location	**Date**	**Water depth (m)**	**Chl *a***	**CPE**	**Units**	**Chl *a* / Phaeo**	**Sediment Depth (cm)**	**Study**
Western Barents Sea	May	206-340	0.3-30	2-90	mg m^{-2}	0.2-0.4	1	**Paper I**
	Jul-Aug	195-503	0.2-1	5-13	mg m^{-2}	0.03-0.2	1	
Northern Barents Sea	Jul-Aug	226-405	1-4	7-23	mg m^{-2}	0.16-0.2	5	Pfannkuche & Thiel (1987)
(Svalbard Shelf)		854-3920	<1-1	1-7	mg m^{-2}	0.16	5	
Barents Sea slope	Jul	1400		66-102	mg m^{-2}	0.07-0.1	10	Thomsen et al. (1995)
Mackenzie shelf	Jul-Aug	32-82	1-14	13-37	mg m^{-2}	0.09-0.7	1	**Paper II**
	Oct-Nov	45-86	0.8-3.5	15-27	mg m^{-2}	0.06-0.3	1	
Southeastern	Jul-Aug	180-440	0.2-3.7	5-22	mg m^{-2}	0.03-0.2	1	**Paper II**
Beaufort Sea	Oct-Nov	395-420	0.06-0.7	5-11	mg m^{-2}	0.06-0.07	1	
Laptev Sea	Aug-Sep	50	45	100	mg m^{-2}	0.8	1	Boetius & Damm (1998)
(Eurasian Arctic)		1000-3500	<2	10-40	mg m^{-2}	0.05-0.1	1	
	Sep-Oct	37-107		2-13	µg cm^{-3}		1	Grahl et al. (1995)
		213-3427		0.6-3	µg cm^{-3}		1	
	Jul-Aug	39-140		3-5	µg cm^{-3}		1	
		264-3831		0.2-3	µg cm^{-3}		1	
Bering/Chukchi Sea	May-Jun	34-170	1-19		mg m^{-2}		1	Cooper et al. (2005)
		202-523	2-15		mg m^{-2}		1	
	July Aug	46-185	9-31		mg m^{-2}		1	
		189-478	2-37		mg m^{-2}		1	
Chukchi Sea	Jul	40-600	0.07-2.8	1-26	µg cm^{-3}	0.03-0.3	1	Clough et al. (2005)
Western Arctic	Jul-Aug	540-3648	0-0.01	0.03-0.3	µg cm^{-3}	0-0.07	1	Clough et al. (2005)*

Fram Strait	Jul-Aug	750-3020	0.03-0.9	2-6	µg cm^{-3}	0.01-0.2	1	Schewe & Soltwedel (2003)
Ellesmere Island- W Greenland (NOW)	Apr-May	247-680	0-2	4-30	mg m^{-2}	0-0.07	1	Grant et al. (2002)
	Jul		<1-5	11-42	mg m^{-2}	0.01-0.1	1	
NE Greenland (NEW)	Jul-Aug	150-515		9-46	mg m^{-2}		1	Ambrose & Renaud (1995)
	May-Aug	290-340	<1-3	12-44	mg m^{-2}	0.07-0.1	1	Ambrose & Renaud (1997)
	Sept	183-774		6-33	mg m^{-2}		1	Brandt & Schnack (1999)
		1098-1965		3-7	mg m^{-2}		1	
Central Arctic Ocean	Jul-Aug	68	<1	7	mg m^{-2}	<0.16	2	Clough et al. (1997)
		540-4190	0	<1	mg m^{-2}		2	
	Aug-Sep	1055-4180		1-12	mg m^{-2}		1	Soltwedel & Schewe (1998)

* Barrow Canyon station not included due to its extremely high pigment content

Table 4. Summary of SOD values determined in the Arctic (modified from Clough et al. 2005).

Location	Water depth (m)	SOD mmol O_2 m^{-2} day^{-1}	Study
Barents Sea	195-503	2.3-10.4	**Paper III**
	80-1000	1.6-2.8	Piepenburg et al. (1995)
Eastern Svalbard	226-320	3.2-11.9	Pfannkuche & Thiel (1987)
	170-240	3.9-11.2	Hulth et al. (1994)
Mackenzie shelf	42-82	3.2-9.4	**Paper IV**
Southeastern Beaufort Sea	167-420	2-6.5	**Paper IV**
	234	4.9-20.2 (over winter-spring)	**Paper V**
Laptev Sea continental slope	200-1000	0.5-7.8	Boetius & Damm (1998)
Eastern Chukchi Sea	40-600	0.7-13.2	Clough et al. (2005)
Bering Shelf-Anadyr Water	49-68	10.3-20.7	Clough et al. (2005)
Northern Bering-Chukchi Seas			
Alaskan Coastal Water	20-55	0.6-19.4 (mean 8.7)	Grebmeier & McRoy (1989)
Bering Shelf-Anadyr Water	20-55	1.8-45.6 (mean 19.2)	Grebmeier & McRoy (1989)
Northern Bering-Chukchi Seas	11-48	7.4-18	Devol et al. (1997)
Western Arctic Ocean	540-3648	0.3-1.4	Clough et al. (2005)
Young Sound, Greenland	36	5-13 (over year)	Rygsgaard et al. (1998)
	20-163	4-20	Glud et al. (2000)
Northeast Greenland Shelf	250-350	1.4-2.6	Rowe et al. (1997)
Resolute Bay, Canadian Arctic	16	2-18 (over year)	Welch et al. (1997)
Baffin Bay	300-680	1.7-4.1	Grant et al. (2002)

Table 5. Summary of oxygen-demand partitioning between macro- and epi- fauna in the Arctic (modified from **Paper IV**).

Location	Depth (m)	Macrofauna (%)	Epifauna (%)	Study
Barents Sea	198-503	38-62 (avg 47)*		**Paper III**, Vandieken (2006)
	<200	14-75 (avg 17)	20-94 (avg 21)	Piepenburg et al. (1995)
	>200	5-75 (avg 21)	2-4 (avg 3)	
Beaufort Sea	38-440	33-50	0.1-41	**Paper IV**
Chukchi Sea	30-280	Up to 61		Grebmeier & McRoy (1989)
	29-213		0-26	Ambrose et al. (2001)
Young Sound	<40		17.5	Rysgaard & Nielsen (2006)
	>40		26	
NOW	250-570	0-70 (spring) 70-80 (summer)		Grant et al. (2002)

8. Concluding remarks

The study of sedimentary pigments by HPLC confirmed Hypothesis 1 showing quantitative and qualitative changes in algal sources of organic matter and in organic matter fluxes, and thus allowed the identification of different variables affecting the pelagic-benthic coupling in the Arctic. Changes in primary production were accompanied by changes in abundance of chl *a* and accessory pigments; changes in food web structure were indicated by changes in abundance of phaeopigments (i.e. phaeophorbide due to grazing); changes in environmental factors (depth and riverine influence) were reflected in changes in the chl *a*/phaeo ratio and abundance of chl*b* degradation products.

Pigment analysis also helped confirm Hypothesis 2, indicating that SOD was strongly dependent on inputs of organic matter from overlying waters. Moreover the combination of sedimentary pigments with SOD and other biomarkers, such as stable isotopes and diatom frustules, allowed a better assessment of the pelagic-benthic coupling.

As suggested by Hypothesis 3, the present study highlighted some spatial and seasonal changes in the pelagic-benthic coupling of the Barents and Beaufort Seas (Table 6), emphasizing the important contrast between the two ecosystems (primary production, secondary production, and hydrography). In the Barents Sea, spatial changes were highly influenced by currents (**Paper I**) while in the Beaufort Sea, spatial changes were due to water depth and river influence (**Papers II and IV**). Physical factors seemed to be responsible for spatial variability.

From a seasonal point of view, productivity regime, especially ice-algal production and match/mismatch of grazing with primary production, seemed to impact the organic matter inputs to the benthos. In the spring, ice-algal production largely influenced organic matter inputs to the benthos in both the Barents and Beaufort Seas (**Papers I, V and VI**). In the summer, grazing was responsible for inputs of degraded material in both ecosystems (**Papers I and II**). In addition to biological factors, environmental factors were also important in summer and/or fall. In the Barents Sea, during the summer, the different currents lead to phytoplankton taxonomy variations (**Paper I**), and in the Beaufort Sea, during the fall, riverine inputs were found to be responsible for the presence of allochthonous material in the sediment.

Table 6. Summary of the environmental and biological factors shaping the pelagic-benthic coupling in the Beaufort and Barents Seas.

	Beaufort Sea	Barents Sea
Ice algae	spring and summer	spring and summer
Phytoplankton	seasonal variation	spatial variation in summer
Grazing	summer	summer
River input	√	
Current		√
Water depth	√	
Benthic activities	marine (gulf) terrestrial (shelf)	overlying productivity

Both environmental and biological factors were found to affect seasonal and spatial variations in pelagic-benthic coupling. Physical variables such as water depth, riverine inputs and dominant water mass, seemed to impact spatial variations, while biological factors such as primary production, grazing, and composition of benthic communities, seemed to mainly impact seasonal variations.

Global warming is expected to directly or indirectly affect each factor shaping the Arctic pelagic-benthic coupling, and thus will most likely lead to large changes in organic matter cycling on Arctic shelves.

9. Overall significance and perspectives

This is the first time sedimentary pigments have been studied by HPLC technique in the Arctic, allowing identification and quantification of various pigments and degradation products in the Barents and Beaufort Seas. This provided the opportunity to assess multiple factors (spatial, temporal, biotic, abiotic) simultaneously affecting POM inputs to the sea floor. Biotic and abiotic factors shaping pelagic-benthic coupling have usually been addressed individually (i.e. study of macrozooplankton grazing, study of primary production, study of currents). The new approach used in this work is unique in the sense that it increased the knowledge of pelagic-benthic coupling the Barents and Beaufort Seas by including many components of the ecosystem, environmental factors and biological parameters.

However, although this method allowed the relative comparison of factors such as input from the river or grazing, it was not possible to quantify the effects of each factor on the quality and quantity of POM inputs to the sediment. As outlined below, some improvements in this approach could allow creating POM-fluxes models using only concentration and composition of sedimentary pigments.

Firstly, in order to use pigments as markers of particulate organic carbon (POC) flux to sediment, it is important to know the ratio between photosynthetic pigments and POC. Measuring this ratio under different conditions would allow determination of quantitative relationships between pigment and POC fluxes.

Secondly, a better understanding of pigment degradation in both the water column and the sediment would make it possible to estimate the relative contribution of the different secondary producers to pigment degradation. Compounds derived from a specific degradation process could be studied in laboratory experiments where one single process occurs (i.e. zooplankton grazing, benthos grazing, bacterial degradation in the water column and in the sediment, photooxidation). However the evaluation of the results from such an experiment is complicated since some pigments are degraded to colorless compounds and some pigments have multiple degradation products. The degradation products could be identified by nuclear magnetic resonance spectroscopy (NMR), which identifies functional groups, or by HPLC coupled with a mass spectrometer (HPLC-MS), which gives the composition of the compound by measuring the mass-to-charge ratio of ions.

Third, in order to differentiate phytoplankton diatoms from ice-associated diatoms, it would be necessary to use another marker, such as lipid composition. Although the pigment composition itself (i.e. fucoxanthin) is not different between phytoplankton diatoms and ice-associated diatoms, the degradation products may be different. For example, ice-algal diatoms are closer to the water surface and thus their pigments may be more photodegraded. The degradation products of fucoxanthin could differ between ice algal and phytoplankton diatoms and could be identified, as mentioned previously, either by NMR or HPLC-MS.

Finally, in order to assess the quality of POM derived from ice algae reaching the seafloor and understand if the quality of ice algae is higher than phytoplankton, the degradation products of fucoxanthin could be used. This could actually explain the tighter coupling of the benthic response in the ice covered scenario of Carroll and Carroll (2003).

10. References

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Paper I

Sedimentary pigments in the western Barents Sea: a reflection of pelagic-benthic coupling?

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Abstract

Local pelagic and sympagic primary production are usually the base of the Arctic food webs, and can be the main inputs of organic matter to the benthos. In order to characterize the major sources of production and understand the fate of organic matter to the benthos, water column, ice, and sedimentary pigments of the Barents Sea were studied by HPLC analysis at 12 stations during the summer 2003, summer 2004, and spring 2005, in the framework of the CABANERA project. Chlorophyll *a* (chl*a*) concentration in surface sediments correlated significantly with total chl*a* integrated throughout the water column as well as the chl*a* fluxes measured at 1 m and 90 m water depth. This suggests that local water column and ice associated algae production are the main sources of fresh organic matter to the benthos. In the sediment, water column, and ice, the major accessory pigment found was fucoxanthin, the marker pigment of diatoms, particularly dominant in spring. In summer, chlorophyll *b*, a marker of green algae, was found in stations influenced by Arctic waters, while 19'hex-fucoxanthin, a marker of prymnesiophytes, was found in stations influenced by Atlantic waters. The source of organic matter inputs to the benthos is thus highly dependent of the water masses influences in the summer. The ratio of sedimentary chl*a* to total phaeopigments (chl*a*/phaeo) was higher in the spring, and the total of phaeopigments in the sediment was correlated with water column phaeopigments and with sedimentary phaeophorbide *a*, a pigment typical of grazing by zooplankton. This suggests that in the summer, organic matter reaching the sediment has already been degraded through grazing, while in spring, more fresh material reaches the sediment. The chl*a*/phaeo ratio was correlated with benthic oxygen demand measured by other researcher in this project, suggesting the importance of the quality of the organic matter reaching the sediment for benthos activities. Our results confirm a close pelagic-benthic coupling in both spring and summer over the entire study area.

Keywords: Arctic, Barents Sea, marginal ice zone, sedimentary pigments, benthic-pelagic coupling, carbon cycle, HPLC

1. Introduction

The Arctic Ocean is characterized by broad continental shelves (51% of its surface area), many of which have high rates of primary production (Sakshaug, 2004). In some areas, much of this production falls to the bottom, supplying rich and active communities of benthic organisms (Piepenburg *et al.*, 1997). In areas covered by ice, ice algae can be a major source of carbon for the food web (Gosselin *et al.*, 1997; Nozais *et al.*, 2001), and, therefore, can be an important source of nutrition for benthic communities (Klages *et al.*, 2004). It is now generally accepted that global warming effects are expected to be enhanced in the Arctic (Mitchell *et al.*, 1995; ACIA, 2004). Modification of ice distribution and seasonality due to global warming is expected to lead to a drastic shift of the productivity regime (phytoplankton vs. ice algae), and thus to an entire restructuring of the food web. It is therefore very important to characterize organic matter pathways to the sea floor across the Arctic.

The primary productivity in the Barents Sea is high for Arctic shelf systems, about 100 g C m^{-2} yr^{-1} (Sakshaug and Slagstad, 1992), and pelagic-benthic coupling may be particularly tight (Wassmann *et al.*, 2006). The western Barents Sea is influenced by Atlantic waters in the south and west, while Arctic waters penetrate from the north and east (Wassmann *et al.*, 2006). Different water masses are found to have different phytoplankton (Rat'kova and Wassmann, 2002; Reigstad *et al.*, 2002) and zooplankton compositions (Colebrook, 1985). Moreover variations in the inflow of warm and saline Atlantic waters determine the sea-ice distribution (Wassmann *et al.*, 2006). A marginal ice zone (MIZ) is defined as "that part of the ice cover which is close enough to the open ocean boundary to be affected by its presence" (Wadhams, 1986). The Barents Sea MIZ plays an important role in timing, development and magnitude of phytoplankton bloom (Wassmann *et al.*, 1996). The match or mismatch of zooplankton with regard to phytoplankton blooms determines the fate of the produced carbon, which can be either retained in the water column or exported to the bottom (Wassmann, 1991; Wassmann *et al.*, 1996). In the Barents Sea, as much as 50% of the primary production is exported from the surface and may represent potential food for the benthic organisms (Wexels Riser, in press).

Sedimentary pigments have demonstrated their usefulness in short-term and long-term studies of ecosystem changes, such as changes in organic matter production (Harris *et al.*, 1996), eutrophication (Chmura *et al.*, 2004; Kowalewska *et al.*, 2004), and cyanobacterial blooms (Bianchi *et al.*, 2000; Poutanen and Nikkilä, 2001), as well as larger scale sea-level (Squier *et al.*, 2002) and hydrodynamic changes (Kowalewska, 2001; Zhao *et al.*, 2000). HPLC (High Pressure Liquid Chromatography) analysis allows the identification of various chloropigments and carotenoids (Sun *et al.*, 1991; Sun *et al.*, 1994; Kowalewska, 1995; Bianchi *et al.*, 1997; Kowalewska *et al.*, 1998; Kowalewska *et al.*, 2004). The advantage of HPLC analyses over fluorometric methods is that it allows identification of these accessory pigments and of degradation pigments. Many of the accessory pigments are specific for certain algal groups and can be used as taxonomic markers (Gieskes and Kraay, 1984; Jeffrey and Vesk, 1997). Chl*a* is a pigment present in all photosynthetic organisms. Thus, sedimentary chl*a* is a marker of the “freshness” of the algal matter inputs to the sediment (Boon and Duineveld, 1996), while its degradation products are markers indicating physiological status and the processes they went through (Mantoura and Llewellyn, 1983; Villanueva and Hastings, 2000). Very few studies have investigated the sedimentary chlorophyll *a* (chl*a*) and its derivatives (phaeo) in the Barents Sea (Pfannkuche and Thiel, 1987; Thomsen *et al.*, 1995) and, to our knowledge, there are no other published studies of using HPLC to investigate sedimentary pigments anywhere in the Arctic.

By studying sedimentary pigments during the CABANERA (Carbon flux and ecosystem feedback in the northern Barents Sea in an era of climate change) program, we addressed the following questions: How do sedimentary pigment composition and concentration vary seasonally and spatially? Do the sedimentary pigments reflect the local production and processes in the water column and the ice? What are the main processes responsible for degradation of pigments in the sediment?

2. Methods

2.1 Study area and sampling techniques

The Barents Sea is permanently ice-free in the south, seasonally ice-covered in the center and the east and has a more or less permanent ice-cover above 80°N. The North Atlantic Current coming from the southwest separates into two branches while the Arctic waters come from the northern Barents Sea (Figure 1). The northwestern Barents Sea region was investigated in summer 2003 (benthic stations 1, 2, 3, 4) and 2004 (benthic stations 8, 10, 11, 12), and spring 2005 (benthic stations 15, 16, 17, 18), during the CABANERA project, onboard the R/V *Jan Mayen* (Figure 1 and Table 1). For each station where sediment was collected, 2-6 l of water from the water column chlorophyll maximum determined by a CTD (Sea-bird Electronics) were collected and filtered through GF/F filters. Hodal et al. (this issue) determined that all stations were in bloom phase. When ice was present, samples of ice algae and detritus were collected by SCUBA diving below the ice, using a 20 µm mesh net mounted in electrical suction pump. Samples were then filtered through GF/F filters (0.7 µm). POM and ice algae filters were stored at -20°C prior HPLC analysis.

At stations 3 and 10, fecal material was collected from pelagic and sympagic crustaceans to investigate pigments characteristic of degradation due to grazing. About 50 pelagic copepods (*Calanus* spp.) and sympagic amphipods (*Gammarus wilkitzkii*) were placed in separated chambers with filtered sea water. Animals in the overlying water were separated from the bottom by a mesh, so the fecal pellets were isolated from the animals. After 24-48 h, animals were retired and the water was filtered on GF/F filters. Filters were frozen for HPLC analysis.

Sediment was sampled by replicate deployments of a box corer (45 cm x 45 cm) or multicorer. Multiple sub-samples (5 cm diameter x 10 cm deep) for sedimentary pigments were taken from each station. Each sub-core was extruded and the two first cm were sliced. Each slice was divided in two, half for pigment analysis by fluorometer, half for pigment analysis by HPLC. Both sub-samples were wrapped in foil and frozen directly after slicing in order to avoid pigment degradation.

2.2 Pigment analysis

HPLC Analysis

POM and ice algae filters were extracted in 2 ml of 100% HPLC-grade acetone for 12-24 h. Extracts were filtered through 0.2 µm nylon syringe filters. Freeze-dried sediment (1-5 g) was transferred to a 50 ml polypropylene centrifuge tube where 15 ml of 100% HPLC grade methanol was added. The mixture was sonicated

Table 1: Location, date, depth, ice coverage and water column chlorophyll *a*. Tchl*a* represents the total of chlorophyll *a* integrated over the entire water column (data from Hodal and Kristiansen, this issue). Flux 1 m is the surface flux of chlorophyll *a* determined in traps at 1 m while flux 90 m is the flux of chlorophyll *a* determined by traps placed at 90 m. Fluxes data are from Reigstad et al. (this issue). * Fluxes at station 15 were not measured, but station 14 was close and in similar condition so fluxes data are from station 14.

Station	Date	Depth (m)	Ice cover (%)	Tchl*a* ($mg\ m^{-2}$)	Flux 1 m ($mg\ m^{-2}\ d^{-1}$)	Flux 90 m ($mg\ m^{-2}\ d^{-1}$)
1	11 Jul 03	348	40-70	40.38	0.06	0.11
2	14 Jul 03	320	40-70	239.48	0.15	2.94
3	16 Jul 03	198	50-70	158.14	0.30	1.63
4	19 Jul 03	222	40-70	62.99	1.60	0.68
8	28 Jul 04	503				
10	29 Jul 04	303	40	68.78		1.84
11	1 Aug 04	195	30	207.57		2.48
12	2 Aug 04	286				
15	21 May 05	311	30	471.86*	20.97*	6.22*
16	26 May 05	206	80-90	548.32		3.48
17	29 May 05	208	60-70	131.24	2.04	0.98
18	30 May 05	340	Open water	213.48		13.58

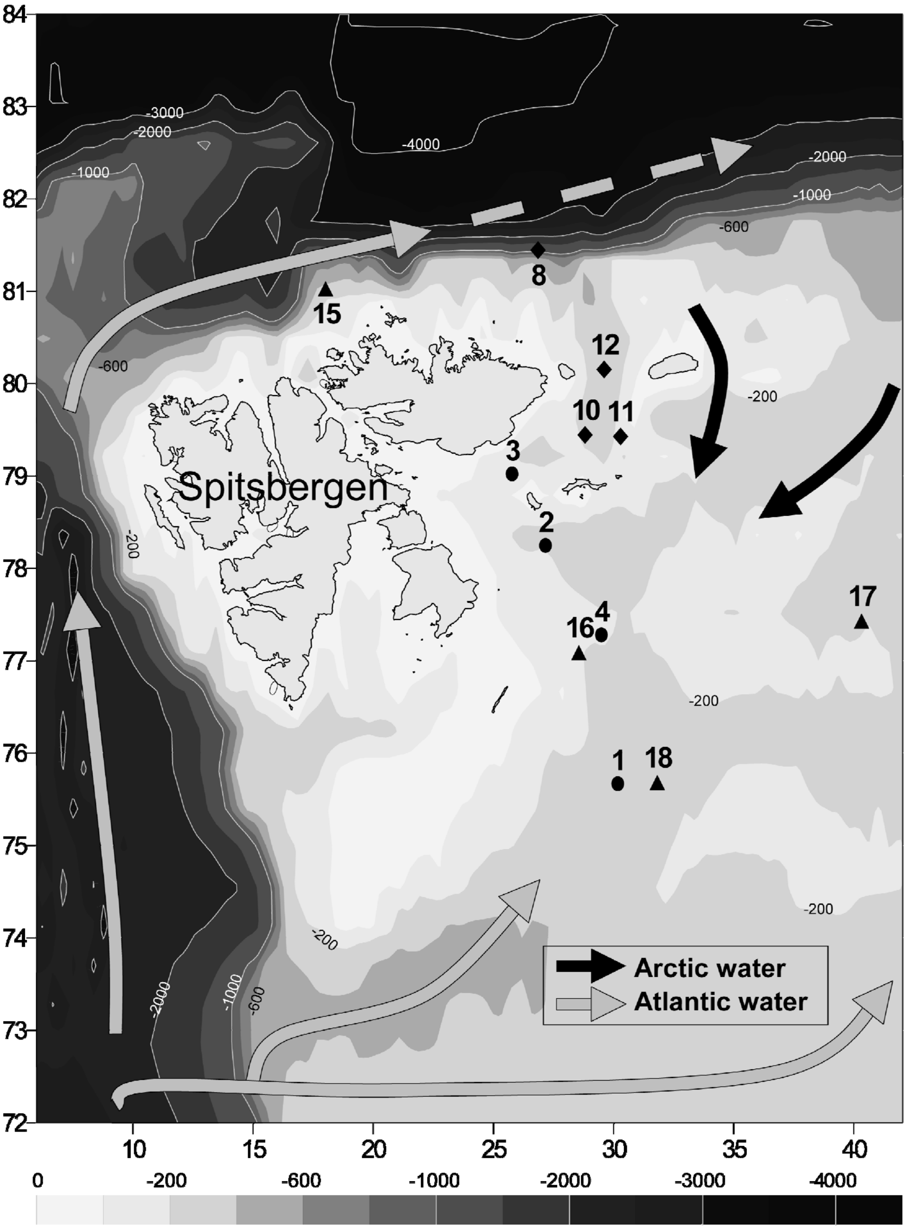

Figure 1: Map of the CABANERA study area. The stations where sedimentary pigments were sampled are represented by dots (CABANERA I, July 2003, stations 1, 2, 3, 4), diamonds (CABANERA II, July-August 2004, stations 8, 10, 11, 12) and triangles (CABANERA III, April 2005, stations 15, 16, 17, 18). Arctic and Atlantic waters are represented by a black and a grey line respectively. The grey dash line represents Atlantic waters sinking underneath Arctic waters.

for 5 minutes in an ice bath and extracted in the freezer overnight. Extracts were separated from the sediment by centrifugation (10 min, 2000 rpm) and 10 ml of the supernatant was filtered through a 0.2 µm syringe filter. Extracts were blown to dryness under nitrogen, and then redissolved in 1 ml of 90% acetone.

Quantitative analysis of all pigments was conducted with a Waters HPLC equipped with an online photodiode array (Waters 996 PDA) and fluorescence detector (Waters 616) with excitation set a 440 nm and emission at 660 nm. Two hundred to 500 µl of the samples 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 ammonium acetate as buffer. The 3-steps gradient program was a modification of Wright et al. (1991) as described by Chen et al. (2001) for enhancing the separation of phaeopigments.

Identification of pigments was performed by comparing retention time and PDA spectra with standards (DHI Water and Environment, Denmark). Carotenoids were quantified on the PDA at 438 nm, while chlorophylls and phaeopigments were quantified on the fluorescence detector. The response factor (RF) was determined for each pigment by single run of each pigment standard. When no standard was available, RF from similar pigments was used. For chlorophylls breakdown products, RF of chl*a* and *b* were adjusted by the difference in molar mass (Reuss *et al.*, 2005).

Fluorometric analysis

Within a month, each sub-sample of sediment was analysed by fluorometry. The samples were placed on a 60 ml centrifuge tube, 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 fluorometer analysis, the sediment was centrifuged (4000 rpm for 10 minutes at 0°C). The supernatant was analyzed in a Turner Designs Model 10-AU fluorometer before and after acidification with 20% HCl, in order to determine the ratio of chl*a* to total phaeopigments (chl*a*/phaeo).

2.3 CHEMTAX and statistical treatment

The contribution of the 3 major algal groups (diatoms, haptophytes and green algae) was estimated using the CHEMTAX program (Mackey *et al.*, 1996). The ratios used were determined by Not *et al.* (2005), for the Barents Sea. The use of CHEMTAX as an estimation of the algal groups from pigments is controversial. It is often very hard to have accurate pigment ratios, which can vary highly depending on environmental conditions. The use of CHEMTAX in the present study is not intended to determine the exact proportion of the different algal groups, but to confirm the dominant species as suggested by pigment results.

Differences between summer and spring were assessed by t-test. Relationship between each pigment and between pigments and other data were determined by Pearson's product-moment correlation. The study of similarity and differences of the various sedimentary pigments found were performed by principal components analysis (PCA). Correlation analyses, t-tests, and PCA were performed using R (R Development Core Team 2005).

3. Results

3.1 Water column and ice pigments

Relative percentages of the major accessory pigments found at the chlorophyll maximum are represented in Figure 2a. Chl*a* and phaeopigments over the entire water column and in the sediment traps were studied by Hodal and Kristiansen and Reigstad *et al.* (both in this issue) and are presented in Table 1. The present study intended only to determine the proportion of the major accessory pigments, not the absolute concentration. The pigments studied are fucoxanthin (marker of diatoms and haptophytes), 19'-butanoyloxyfucoxanthin and 19'-hexanoyloxyfucoxanthin (markers of haptophytes), peridinin (marker of dinoflagellates), alloxanthin (marker of cryptophytes), zeaxanthin (marker of cyanobacteria) and chl*b* (marker of green algae and higher plants). Fucoxanthin was by far the most abundant pigment. The ratio of diatoms, haptophytes and green algae determined by the CHEMTAX program, confirmed that diatoms were the dominant species at most of the stations. For all but 3 stations, diatoms represented more than 80% of the species composition (Figure 2b). The 3 stations where diatoms were the less dominant were the same suggested by the pigment composition before the CHEMTAX transformation: stations 1, 8, and 17. Fucoxanthin was also the main accessory pigment found in the detritus collected at the water-ice interface at stations 7, 10, 17, confirming diatoms as dominant taxonomic component of ice algae.

During the grazing process, chl*a* in phytoplankton can be degraded to phaeophorbide *a* and phaeophytin *a*. These degraded pigments were found in the fecal material collected from zooplankton. However another peak was observed at 12.897 minutes, in the PDA and the fluorometer (Figure 3). This peak is a combination of phaeophorbide *a* and fucoxanthin, and was recently identified as a carotenol chlorin ester (CCE), a specific marker of diatom grazing (Goericke *et al.*, 1999; Chen *et al.*, 2003).

3.2 Sediment pigments

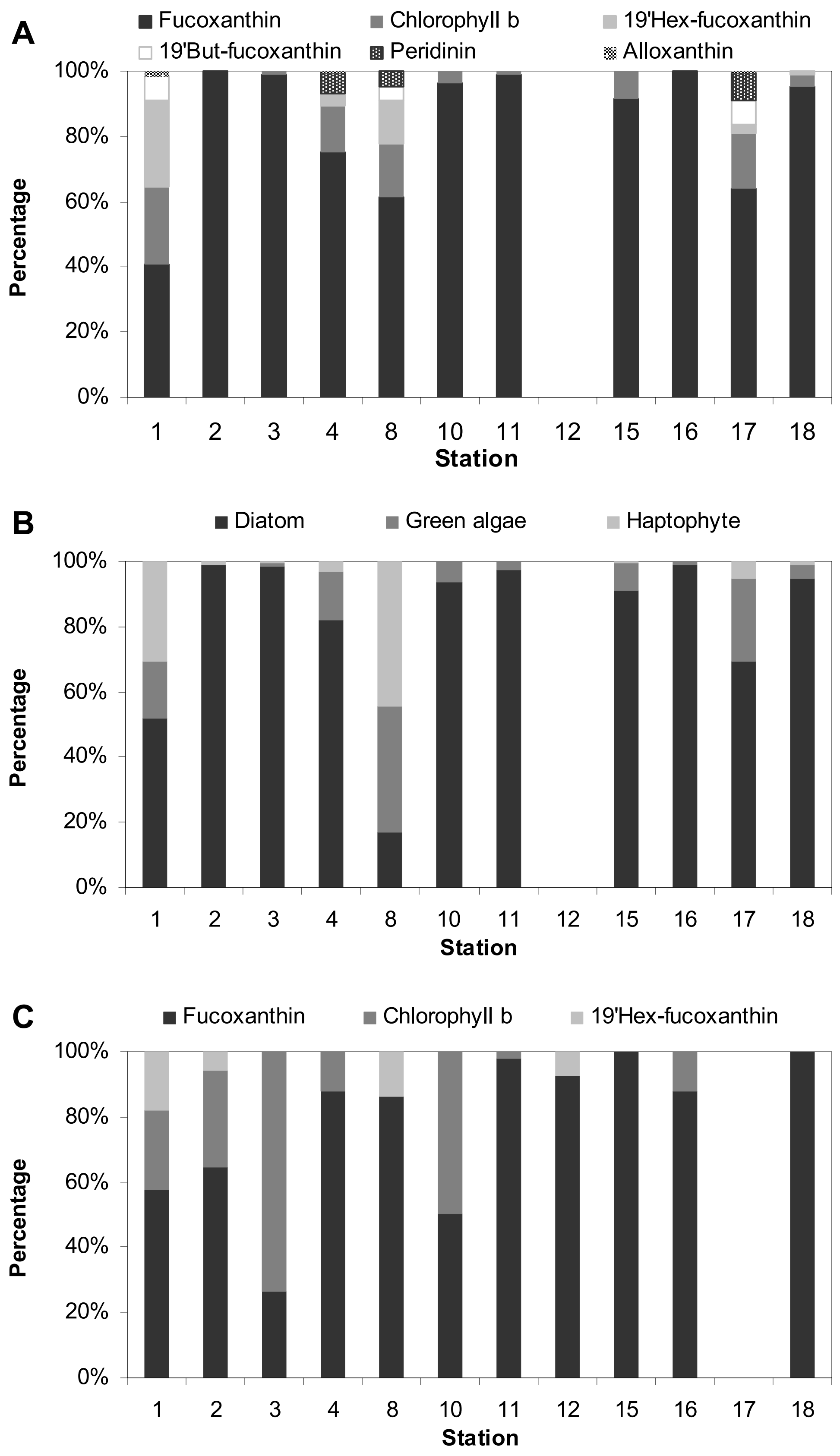

Figure 2: **A**. Relative proportion of water column accessory pigments for each station. **B**. Percentage of the 3 main algae groups (diatoms, green algae and haptophytes) determined by the CHEMTAX program from the previous pigments ratios. **C**. Ratios of the major accessory pigments found in the sediment. Note that no water column samples were collected for station 12, and no accessory pigments were found in the sediment in station 17.

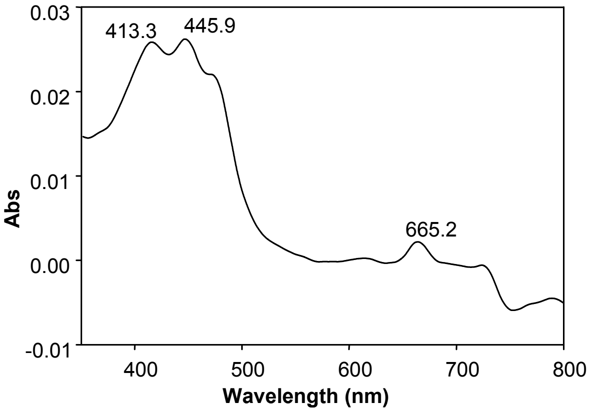

Figure 3: PDA spectrum (438 nm) at 12.897 minutes of the chromatogram of fecal material. This spectrum show a peak at 413.3 and 665.2, as phaeophorbide *a*, but also a peak at 445.9 nm, like fucoxanthin. This combination of phaeophorbide *a* and fucoxanthin appears to be a carotenol chlorine ester (see text).

Chl*a* and other sedimentary chlorophylls and carotenoids were determined by HPLC in the 2 first cm of sediments (Table 1). Sedimentary chl*a* and total phaeopigments in the same interval were determined by fluorometer in order to compare the HPLC and the fluorometer results, and to know the ratio of chl*a* over total phaeopigments (Table 2). Fluorometer and HPLC results for chl*a* strongly correlated significantly ($r = 0.93$, $p<0.05$). Chl*a* was determined by fluorometry at all stations, but was below the limit of HPLC detection at one station. 19'hex-fucoxanthin occurred at only four stations (1, 2, 8 and 12), while chlorophyll *b* was detected at seven stations (mainly in summer). All but two stations had fucoxanthin. All stations had phaeophytin *a* and all but three summer stations had phaeophorbide *a*.

Chl*a*, phaeophorbide *a*, CCE, and fucoxanthin determined by HPLC were strongly correlated with each other, as well as with the chl*a* determined with fluorometer (Table 3) Pyrophaeophorbide *a*, pyrophaeophytin *a* and 19'hex-fucoxanthin were not correlated to any other pigment.

Chl*a* concentrations varied from being undetectable (by HPLC method) at station 17, to comprising 2.8 μg of pigment per gram of dry sediment (μg g^{-1} dw) at station 15. As at station 15, station 11 had more than 1 μg g^{-1} dw, while all other stations had less. There was no significant difference (t-test>0.05) between the chl*a* concentrations at the spring stations (15, 16, 17, 18) and the summer stations (1, 2, 3, 4, 8, 10, 11, 12).

Phaeophorbide *a* and phaeophytin *a* were the main degradation products of chl*a*. Phaeophorbide *a* is usually considered as a degradation product of chl*a* issued from grazing while phaephytin *a* can also be due to senescence. The pyro- derivatives, pyrophaeophorbide *a* and pyrophaeophytin *a*

Table 2: Sedimentary pigments concentration by HPLC (in ug of pigment g^{-1} dw) in the two first centimeter. Chl*a*: chlorophyll *a*, Phorbid*a*: phaeophorbide a, Pphorbid*a*: pyrophaeophorbide *a*, Phytin*a*: phaeophytin *a*, Pphytin*a*: pyrophaeophytin *a*, CCE: carotenol chlorine ester, Fuco: fucoxanthin, Hex: 19'hex-fucoxanthin, Chl*b*: chlorophyll *b*, Chl*a*/Tphaeo is the ratio chlorophyll *a* / total phaeopigments both determined by fluorometer.

Station	Chl*a*	Phorbid*a*	Pphorbid*a*	Phytin*a*	Pphytin*a*	CCE	Fuco	Hex	Chl*b*	Chl*a*/Tpheo
1	0.464	0.296	0.006	1.090	0.142	0.075	0.133	0.041	0.056	
2	0.784	0.470	0.022	3.491	0.537		0.203	0.018	0.093	
3	0.064	1.202	0.015	0.962	0.218	0.037	0.004		0.010	
4	0.309	0.260	0.024	0.501	0.030	0.213	0.152		0.021	
8	0.166	0.081	0.006	0.152	0.026	0.240	0.081	0.013		0.197
10	0.163	0.795	0.039	1.451	0.189		0.024		0.024	0.046
11	1.069	0.633	0.025	1.142	0.159	0.337	0.404		0.010	0.420
12	0.656	0.113	0.016	0.666	0.527	0.036	0.288	0.023		0.073
15	2.801	1.810	0.024	0.245	0.251	1.649	1.541			0.507
16	0.676		0.011	0.134	0.032		0.127		0.017	0.595
17			0.065	0.040						0.140
18	0.421	0.010	0.454	0.171	0.013		0.163			0.591

Table 3: Correlations between sedimentary chlorophyll *a*, degradation products and accessory pigments (0-2 cm). Chl*a*: chlorophyll *a*, Phorbid*a*: phaeophorbide a, Pphorbid*a*: pyrophaeophorbide *a*, Phytin*a*: phaeophytin *a*, Pphytin*a*: pyrophaeophytin *a*, CCE: carotenol chlorine ester, Fuco: fucoxanthin, Hex: 19'hex-fucoxanthin, Chl*b*: chlorophyll *b*, Chl*a*Fluo: chlorophyll a determined by fluorometry, PhaeoFluo: phaeopigments determined by fluorometry. Significant correlation ($p<0.05$) are indicated by a "*" after the correlation coefficient

	Chl*a*	Phorbid*a*	Phytin*a*	CCE	Fuco	Chl*b*	Chl*a*F	PhaeoF
Chl*a*	1							
Phorbid*a*	0.65*	1						
Phytin*a*	-0.08	0.01	1					
CCE	0.95*	0.76	-0.49	1				
Fuco	0.98*	0.68	-0.19	0.97*	1			
Chl*b*	0.24	-0.48	0.82*	-0.4	0.07	1		
Chl*a*F	0.92*	0.80*	-0.26	0.98*	0.88*	-0.65	1	
PhaeoF	0.99*	0.86*	-0.1	0.97*	0.97*	-0.86*	0.96*	1

were less abundant and were not correlated with any other pigment. Phaeophorbide *a* was significantly correlated with chl*a* ($r = 0.65$, $p<0.05$) and CCE ($r = 0.91$, $p<0.05$). The total of phaeopigments determined by fluorometer was significantly correlated with the grazing pigments phaeophorbide ($r = 0.83$, $p<0.05$) and CCE ($r = 0.92$, $p<0.05$), while was not correlated with the other degradation products of chl*a* determined by HPLC. The ratio of chl*a* to total phaeopigments, was significantly higher (t-test: $p<0.05$) in the spring than in the summer.

The main accessory pigment found in the sediment was fucoxanthin (Figure 2c). Only 3 stations, station 1, 3 and 8, had less than 60% of fucoxanthin as a main accessory pigment. Fucoxanthin was found in each station but station 17, where almost no pigments were found. The station with the highest concentration of fucoxanthin was station 15, while stations 3, 10, and 17 had the lowest amounts.

3.3 Principal components analysis

The 1st and 2nd axis of the PCA explained 72% of the variance in sediment pigments among stations. Axis 1 (41% of variance) was largely defined by chl*a*, fucoxanthin, CCE, and phaeophorbide *a*, and served to separate stations 15 and 11 (high concentrations of these pigments) from the other stations (Figure 4). The second axis (31%) separates the remaining stations on the basis of high concentrations of the accessory pigments 19'hex-fucoxanthin and chlorophyll *b*, and the degradation pigments phaeophytin *a* and pyrophaeophytin *a* (stations 10, 12, 1 and 2), or high levels of pyrophaeophorbide *a* (stations 4, 16, 8, 17 and 18).

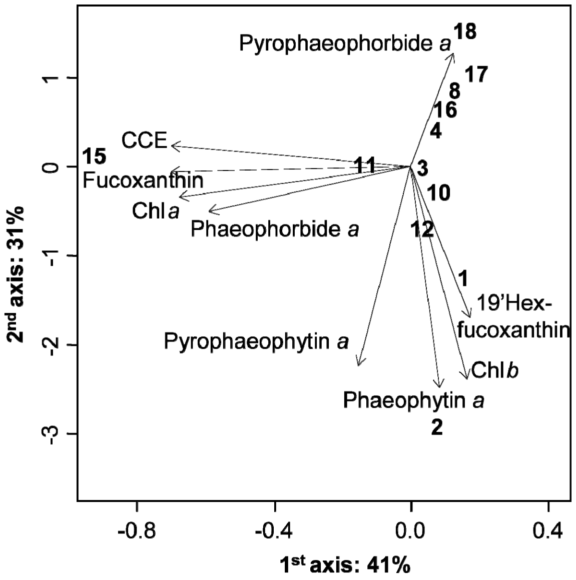

Figure 4: Principal Components Analysis of sedimentary pigments compositions from the 12 stations. The plot displays 72% of the total variability of the dataset.

4. Discussion

The study of sedimentary pigments by HPLC method allowed us to study sedimentary chl*a* and make a comparison with fluorometer values, but also to separate various chl*a* degradation products and some accessory pigments, especially fucoxanthin, 19'hex-fucoxanthin and chl*b*. This is, to our knowledge, the first time such a study has been realized in the Arctic Ocean. Sedimentary pigments have been studied by HPLC in various other ecosystems, especially in lacustrine, coastal, marine eutrophic and anoxic ecosystems, where inputs of organic matter are usually high (see review in Beaulieu, 2002). Sedimentary chl*a* in marine shallow or eutrophic environments show extremely high values, typically tens of µg g^{-1} dw. Kowalewska (2005) defined three zones in the Baltic Sea: in the permanently eutrophic area, sedimentary chl*a* in 0-1 cm is higher than 35 µg g^{-1}, in coastal area, chl*a* ranges from 8 to 35 µg g^{-1}, while in mesotrophic open sea, chl*a* is lower than 8 µg g^{-1}. Deep-sea oligotrophic ecosystems showed values <0.06 µg g^{-1} in the central equatorial Pacific (Smith *et al.*, 1996) and an average of 0.04 µg g^{-1} in the Indian sector of the Southern Ocean, with a maximum of 0.15 µg g^{-1} at the permanently open ocean zone (Riaux-Gobin *et al.*, 1997). Our data ranged from 0.06 to 2.80 µg g^{-1}, which is lower than previous studies in marine eutrophic systems, but higher than in deep-sea sediments. Despite the modest values, we are able to relate sedimentary chl*a* to water column inputs, use accessory pigments as markers of phytoplankton taxonomy, and relate degraded pigments to the source of degraded material and processes they went through.

4.1 Local chlorophyll *a* inputs

Local water column chl*a* is clearly the most determinant factor of sedimentary chl*a* concentration. Sedimentary chl*a* is significantly correlated with the total of chl*a* (Tchl*a*) integrated over the entire water column ($r = 0.69$, $p<0.05$) and the chlorophyll concentration at the chlorophyll *a* max ($r = 0.57$, $p<0.05$), measured by fluorometry by Hodal and Kristiansen (this issue). Sedimentary chl*a* is even better correlated to fluxes of chl*a* in the water column determined by fluorometry by Reigstad (this issue). It is highly correlated to the surface (1 m) chl*a* fluxes ($r = 0.96$, $p<0.05$) and deep fluxes (90 m) ($r = 0.86$, $p<0.05$, excluding the station 18). These correlations between sediment and water column pigments are similar to those found by Renaud et al. (this issue) in the same region. All but one station (station 18) had ice presence on the surface. Even though no significant correlation were found between percent ice cover and sedimentary chl*a* (see below), the strong correlation between sedimentary chl*a* and surface (1 m traps) chl*a* fluxes suggests that ice-associated production plays a key role in the input of fresh organic matter to the benthos.

The relationship between sedimentary chl*a* and Tchl*a* is not significantly different in the spring than in the summer, suggesting that sedimentary chl*a* depends on short-term local production and vertical flux. Phytoplankton blooms tend to be highly localized in space and time and occur as episodic events from early spring to late autumn in the Barents Sea (Codispoti *et al.*, 1986; Wassmann *et al.*, 1996) when sufficient light and nutrients are available (Hegseth, 1997, 1998). However, Engelsen *et al.* (2002) found that a large bloom is most likely to occur 2 weeks after the ice edge has receded from a given area. Thus we could have expected to find in the spring more chl*a* in the water column, and thus in the sediment than in the summer. In the spring, very high water column chl*a* values were observed at two of the four studied stations by Hodal and Kristiansen (this issue). Sedimentary chl*a* does not show higher concentration in the spring than in summer, however the ratio of chl*a*/phaeo is higher in the spring, suggesting an input of "fresher" material.

Previous studies (Grahl *et al.*, 1995) pointed out the correlation between the sedimentary chl*a* and water depth. These two parameters are not correlated in the present study. This is probably a result of our small water depth range, 198 to 503 m. Sedimentary pigments are also not significant related to the percentage of ice cover. Wassmann *et al.* (1996) explained that sea-ice cover does not directly control the pelagic-benthic coupling in the Barents Sea, but is a factor in the episodic character of vertical fluxes.

4.2 Phytoplankton and ice algae species

In this study, we used fucoxanthin as a marker of diatoms, 19'hex-fucoxanthin as a marker of prymnesiophycae (which include *Phaeocystis pouchetii*) and chl*b* as a marker of green algae. Typically, diatoms and prymnesiophytes are dominant producers in the spring, while flagellates are more important in the summer (Luchetta *et al.*, 2000; Rat'kova and Wassmann, 2002). Moreover different water masses in this area are found to have different phytoplankton compositions (Rat'kova and Wassmann, 2002; Reigstad *et al.*, 2002). Atlantic waters contain more prymnesiophytes (Wassmann *et al.*, 2005) while Arctic waters contain more green algae especially *Micromonas pusilla* (Not *et al.*, 2005). Our pigment composition and taxonomic results from the water column support this. The spring stations (15, 16, 17 and 18) show a high percentage of diatoms, while the stations 1 and 8, with Atlantic water inflow, show high percentage of haptophytes, and station 17, under Arctic water inflow, show high amount of green algae.

Sakshaug (2004) pointed out the dominance of diatoms in waters mixed to <40 m. Due to the relatively low silicate concentrations in the Barents Sea, the proliferations of diatoms is reduced when compared to Chukchi Sea or North Atlantic (Wassmann *et al.*, 2006). However, in our study in the western Barents Sea, fucoxanthin is by far the most dominant pigment in the sediment as well as in the water column and ice. Diatoms are especially abundant in spring stations and summer stations in bloom stage (2, 3, 10 and 11). Hancke *et al.* (this issue) found similar dominance of diatoms in the water column when studying the effects of light on pigments compositions. Diatoms are an important producer in the water column, and are usually the most common algal group in ice algae (Lizotte, 2003; Riaux-Gobin *et al.*, 2000; Von Quillfeldt *et al.*, 2003). The high levels of fucoxanthin found in our ice-detritus samples confirm the importance of diatoms in ice algae, and thus ice-associated diatoms are likely to be an important part of trap material from 1 m. It is impossible to differentiate ice-algae diatoms from phytoplankton diatoms by HPLC, Ice algae diatoms have previously been observed in Arctic sediment (Sancetta, 1981; Ambrose *et al.*, 2005). Moreover, ice algae can play an important part of vertical fluxes of organic matter in some stations in the Barents Sea (Tamelander *et al.*, this issue). The important proportion of diatoms in surface (under-ice) fluxes and the high correlation between sedimentary fucoxanthin and chl*a* fluxes at these stations ($r = 0.99$, $p<0.05$) suggest the important role of ice-associate production as a source of fresh organic matter inputs to the benthos.

Interestingly, summer stations determined in peak-bloom phase (stations 2, 3, 10 and 11) showed the highest percentage of diatoms in the water column. However, even if they also showed important percentage of fucoxanthin in the sediment, they also revealed the presence of chl*b*. Chl*b* is a marker of green algae, which are common in Arctic waters (Not *et al.*, 2005). The half-life of chlorophyll pigments is approximately three weeks in polar sediments (Graf *et al.*, 1995). Thus sedimentary chlorophylls integrate inputs of fresh organic matter from the water column over several weeks to a few months. While sedimentary chl*a* was clearly related to the water column chl*a* measured during the cruise time, other, less abundant pigments might integrate events that occurred at a longer time scale. The presence of sedimentary chl*b* in the summer in stations influenced by Arctic Waters shows that green algae can be also a source of fresh organic matter input to the benthos.

In the summer, the northernmost and southernmost stations (stations 1 and 8) show an important contribution of prymnesiophytes, reflected by the presence of 19'hex-fucoxanthin, in both the water column and the sediment. These stations are influenced by Atlantic water (Figure 1, Sundfjord *et al.* 2007), where *Phaeocystis pouchetii* is often abundant (Wassmann *et al.*, 2005). Prymnesiophytes are an important source of organic matter inputs to the benthos at these stations.

In the summer, the type of water (Atlantic vs. Arctic) influences the water column production and thus the type and degradation stage of organic matter reaching the sediment. Alternately, the spring stations showed a high percentage of fucoxanthin in the water column as well as in the sediment, regardless of their influence by Atlantic or Arctic waters.

The PCA indicated diatom-dominated inputs at stations 15 and 11, while the presence of accessory pigments is important at stations 1, 2, 10 and 12, suggesting significant inputs of other algal groups at these stations (Figure 4). The differences in primary producer taxonomy were reflected in sedimentary pigments and may represent a difference in quality of algal detritus reaching the benthos.

4.3 Input of grazed material

Total sedimentary phaeopigments correlate significantly to the phaeopigments fluxes at 90 m ($r = 0.70$, $p<0.05$, excluding station 18) but this relationship is weaker than the correlation between sedimentary chl*a* and chl*a* fluxes at 90 m ($r = 0.87$, $p<0.05$, excluding station 18). This suggests that even though degraded pigments in the sediment can come from the overlying waters the relationship may also depend on processes occurring within the sediment.

The highly significant relationship between both phaeophorbide *a* and CCE and the total phaeopigments in the sediment ($r = 0.86$ and 0.97 respectively, $p<0.05$), as well as their significant relationship with the total phaeopigments in the water column (r = 0.85 and 0.94 respectively, $p<0.05$), clearly suggest that the main input of degraded pigments from the water column in grazed material. The summer stations showed the highest amount of grazed pigments in the sediment. Moreover, in the summer, the stations with the highest amount of phaeophorbide *a* with respect to the chl*a* in the sediment (stations 3 and 10) are the same stations determined by Wexels Riser (in press) as having the highest proportion of carbon flux as fecal pellets flux.

Faecal material has been found to be an important part of the sinking organic matter in the Barents Sea (Wassmann *et al.*, 1996), especially in the summer (Wexels Riser *et al.*, 2002). However in the spring, the mismatch between primary producers and consumers (Rat'kova and Wassmann, 2002) can lead to fluxes of ungrazed material. Moreover zooplankton tends to graze on large cells such as diatoms. In our study, the higher ratio of chl*a*/phaeo in the spring and the presence of CCE suggest the input of “fresher” organic matter to the benthos in the spring, while in the summer, organic matter reaching the sediment is more degraded, especially by grazing.

Because of the few-week-long half-life of chlorophyll pigments in polar sediments and the rapid consumption by benthic organisms (Graf *et al.*, 1995; Renaud *et al.*, this issue), sedimentary chl*a* relates relatively short term water column inputs, while degraded pigments represent a longer time scale of accumulation and additional processing. PCA confirmed that highly degraded pigments, such as pyrophaeophorbide, can be important at stations where inputs are low (as stations 17) or inputs are highly processed (as station 16). Inputs of fresh organic matter can be quickly processed (Ritzrau and Thomsen, 1997; Renaud *et al.*, this issue). The ratio of chl*a*/phaeo is significantly (r = 0.90, $p<0.05$) correlated to the sediment oxygen demand determined by Renaud *et al.* (this issue) suggesting an increase of benthic activities during inputs of fresher material. Moreover the sediment oxygen demands are significantly higher (t-test $p<0.05$) in the spring than in the summer. Thus benthic community activities are particularly enhanced by inputs of fresher, not degraded, material, and probably play an important role in the benthic degradation of organic matter and pigments.

4.4 Comparison with other Arctic shelves

Sedimentary pigments are useful indicators of organic matter inputs to the sediment (Sun et al., 1991) and have been used previously to characterize food deposition to Arctic benthos (Table 4). However previous studies used fluorometry methods, which only detect chla and total phaeopigments. It is impossible to directly compare our HPLC chla results with previous studies in the Arctic, but chla values determined by fluorometer were highly correlated to chla determined by HPLC in our study, and ranged from 0.6 to 40 mg m-2, with total chloropigments ranging from 5 to 120 mg m-2 in the first 2 cm. The chla values are slightly higher than in studies at similar water depth in the North Water (Grant et al., 2002) and the Northeast Water (Ambrose and Renaud, 1995, 1997) polynyas, and much higher than in the central Arctic Ocean determined by Soltwedel and Schewe (1998), where primary production is particularly low. The Barents Sea and the Bering Sea have the highest rates of primary production among the Arctic shelves (see review in Sakshaug, 2004), the Bering Sea having higher rates (Wang et al., 2005). Interestingly, despite the higher production in the Bering Sea respect to the Barents Sea, sedimentary chla contents have similar ranges and are the highest of the Arctic shelves for similar depths. Moran et al. (2005) proposed that 20% of the production in the Bering Sea, at some times of the year, is directly exported out of the production area to the deep Arctic basin. The ratios chla/phaeo are the highest in the Barents Sea suggesting fresher material than in other Arctic shelves reaching the benthos. This might suggest that a higher percentage of local production reached the bottom of the Barents Sea. Pelagic-benthic coupling in Arctic marginal ice zones is particularly tight (Carmack and Wassmann, 2006), and seems as tight in the Barents Sea as than anywhere else in the Arctic.

5. Conclusion

Because of the episodic character of water column events, it is hard to study temporal or spatial variations in the Barents Sea. However our first attempt to use sedimentary pigments to characterize pelagic-benthic coupling variation allowed us to observe spatial and seasonal variations. Local primary production by phytoplankton and ice algae is clearly the main

Table 4: Chlorophyll *a* (Chl*a*), total of chlorophyll *a* + phaeopigments also called chloropigment equivalent (CPE), and ratio chlorophyll *a* / total phaeopigments (Chl*a*/Phaeo) in offshore Arctic sediment. The depths of surface sediment of the integrated pigments are variable and are presented in the sediment depth column. Most studies' values are for the upper 1 cm. Our data are presented for the upper 1 cm and 2 cm integration depths.

Location	Date	Water depth (m)	Chl*a* (mg m^{-2})	CPE (mg m^{-2})	Chl*a* Phaeo	Sediment depth (cm)	Study
Western Barents Sea	May	206-340	0.3-30	Feb-90	0.18-0.42	1	This study
			0.7-40	5-120	0.14-0.59	2	
	July-Aug	195-503	0.2-1	13-May	0.03-0.16	1	
			0.6-13	14-44	0.05-0.42	2	
Northern Barents Sea	July-Aug	226-405	4-Jan	23-Jul	0.16-0.2	5	Pfannkuche and Thiel (1987)
(Svalbard Shelf)	July-Aug	854-3920	<1-1	7-Jan	0.16	5	
Barents Sea slope	July	1400		66-102	0.07-0.1	10	Thomsen *et al.* (1995)
Bering Sea	May-June	202-523	15-Feb			1	Cooper *et al.* (2005)
	July Aug	189-478	Feb-37			1	
Ellesmere Island-	Apr-May	247-680	0-2	30-Apr	0-0.07	1	Grant *et al.* (2002)
W Greenland (N Water)	July		<1-5	Nov-42	0.01-0.1	1	
NE Greenland (NE Water)	July-Aug	150-515		Sep-46		1	Ambrose and Renaud (1995)
NE Greenland (NE Water)	May-Aug	290-340	<1-3	Dec-44	0.07-0.1	1	Ambrose and Renaud (1997)
NE Greenland	Sept	183-774		Jun-33		1	Brandt and Schnack (1999)
		1098-1965		7-Mar		1	
Laptev Sea	Aug-Sept	50	45	100	0.82	1	Boetius and Damm (1998)
(Eurasian Arctic)		1000-3500	<2	Oct-40	0.05-0.11	1	
Arctic Ocean section	July-Aug	68	<1	7	<0.16	2	Clough *et al.* (1997)
		540-4190	0	<1		2	
Central Arctic Ocean	Aug-Sept	1055-4180		12-Jan		1	Soltwedel and Schewe (1998)

source of organic matter to the benthos. In the spring, fresher (ungrazed) material, mainly composed of diatoms, reaches the benthos, while in the summer, inputs are more degraded (especially by grazing), and other phytoplanktonic groups are important.

Pelagic-benthic coupling is tight in both spring and summer. The correlation between benthic activities and chla, and also with the ratio chla/phaeopigments shows that not only the quantity of organic matter reaching the sediment is important for the benthos, but also its stage of degradation. Any climate-induced change in productivity or water mass position will likely be immediately reflected in quality and quantity of carbon input to the benthic ecosystem, potentially leading to changes in the benthic carbon cycling.

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Paper II

Spatial and seasonal variations in the pelagic-benthic coupling of the southeastern Beaufort Sea revealed by sedimentary biomarkers

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Abstract

Photosynthetic pigments and stable isotopes from suspended particulate organic matter (POM) and surface sediment of the southeast Beaufort Sea, including the Mackenzie shelf and the Amundsen Gulf, were studied during the fall 2003 and the summer 2004. This multiple-biomarker approach led to an increased understanding of spatial and seasonal variation in pelagic-benthic coupling, as these two biomarkers reflect inherent differences in the time scales over which they integrate. Sedimentary pigments highlighted the importance of local water-column production as a source of phytodetrital inputs to the sea floor. In the summer, dominance of diatoms in the water column was reflected in the sediment by the abundance of fucoxanthin, a pigment broadly found in diatoms. In the fall, a more eclectic suite of sedimentary pigments reflected inputs from smaller cells such as haptophytes and prasinophytes. While stable isotope composition of the POM showed seasonal variations, i.e. a more marine signature in the summer and a more terrestrial signature in the fall, sedimentary stable isotopes revealed geographical differences. Sediment on the Mackenzie shelf suggested a terrestrial source of organic matter, while on the Amundsen Gulf, sources of organic matter had a more marine origin. Finally, benthic community compositions and activity (sediment oxygen demand) seemed affected by both spatial and seasonal variations in organic matter inputs to the benthos. This study stresses the importance of both physical factors (water depth and riverine inputs) and biological production (primary productivity and secondary production) in the determination of organic matter inputs to the benthos.

Keywords: Arctic, Beaufort Sea, sedimentary pigment, pelagic-benthic coupling, stable isotope, carbon cycling, HPLC

1. Introduction

While the Arctic Ocean represents only 1% of the global ocean, it accounts for 25% of the world's continental shelves (Dittmar & Kattner 2003). These shelves represent an important sink of carbon: the average organic carbon burial corresponds to 7 to 11% of the global budget (Stein & Macdonald 2004). Organic fluxes to the sea floor depend on production and processes in the overlying water column. In particular, the quality as well as the quantity of biogenic matter fluxes can be determined by zooplankton grazing which have been found to have a strong impact on pelagic-benthic coupling (Olli et al. 2002, Wexels Riser et al. in press). The inputs to the sea floor are not always directly buried, and can be used by the benthos. In some areas, much of the overlying production falls to the bottom, supplying rich and active communities of benthic organisms (Piepenburg *et al.*, 1997). Recent studies (Wheeler et al. 1996, Chen et al. 2002, Klein et al. 2002, Tremblay et al. 2002, Vidussi et al. 2004) have shown that primary production is much higher in the Arctic than previously believed and in areas covered by ice, ice algae can be a major source of carbon for the food web (Gosselin et al. 1997, Nozais et al. 2001). Ice algae can thus also be an important source of nutrition for benthic communities (Dayton 1990, Klages et al. 2004, Renaud et al. 2007b).

The Arctic Ocean is, on a volume basis, the ocean with the highest terrestrial input in terms of freshwater and organic matter (Dittmar & Kattner 2003), and thus terrestrial inputs can be an important source of organic matter to the benthos. The Mackenzie River is the fourth largest of all river systems discharging into the Arctic (Macdonald et al. 1998). Carbon input to the southeast Beaufort Sea, adjacent to the Mackenzie River, is derived primarily from three sources: marine biological production, the Mackenzie plume, and coastal and seabed erosion (O'Brien et al. 2006).

Climate models suggest that global warming effects in the Arctic are expected to be disproportionately higher than in temperate regions, and to change riverine fluxes by intensifying the hydrological cycle (Peterson et al. 2002, Wu et al. 2005). Moreover, modifications of ice distribution and seasonality are expected to have an effect on primary production, probably favouring phytoplankton to the detriment of ice-algae production, affecting the entire food web and leading to changes in pelagic-benthic coupling (Carroll & Carroll 2003). It is therefore very important to characterize organic matter pathways to the shelf of the Arctic basin. This study explores the nature of the organic matter supplied to the southeast Beaufort Sea, as a function of environmental factors, including productivity regime, riverine inputs and ice conditions.

The study of sedimentary pigments is valuable for understanding spatial and seasonal variations of organic matter inputs to Arctic benthos (Morata & Renaud in press). Chlorophyll *a* (chl *a*), a pigment present in all photosynthetic organisms, has a half-life of approximately three weeks in polar sediments (Graf et al. 1995). Thus, sedimentary chl *a* is a good indicator of the "freshness" of the algal matter inputs to the sediment (Boon & Duineveld 1996), while its degradation products (phaeophorbides, phaeophytins and their pyro-derivatives), also called phaeopigments, are markers indicating physiological status of phytoplankton and decomposition pathways, such as herbivory grazing or bacterial degradation (Mantoura & Llewellyn 1983, Villanueva & Hastings 2000). Moreover, since chlorophyll *b* (chl *b*) is largely found in higher terrestrial plants and has a shorter half-life than chl *a*, its degradation products (phaeophytin *b* and phaeophorbide *b*), can be used to investigate inputs of terrestrial material. Many of the accessory pigments (e.g. fucoxanthin) are specific for certain algal groups and can be used as taxonomic markers (Gieskes & Kraay 1984, Jeffrey & Vesk 1997).

The particulate organic matter (POM) within water column is comprised of all suspended material > 0.45 µm, and is usually dominated by various types of phytoplankton (including ice algae) and detritus (Sakshaug 2004). Stable isotopes and C:N values may be used to determine the relative importance of ice algae, phytoplankton and terrestrial sources in the POM (McMahon et al. 2006). C:N values are helpful for differenciating marine and terrestrial organic matter (Redfield et al. 1963, Takahashi et al. 1985, Andersen & Sarmiento 1994). In sediments, isotopic fractionation results from decomposition such that the data may become more difficult to interpret.

The present study combined pigment and stable isotope analysis, and measurement of elemental composition of POM and sedimentary organic matter to trace the sources and fate of organic matter in the southeast Beaufort Sea. We address the following questions: What is the importance of local production for inputs of organic matter to the benthos? Is the Mackenzie River an important source of terrestrial organic material to the entire area? Are the spatial and seasonal variations of organic matter inputs to the benthos affecting benthic activities?

2. Methods

2.1 Study area and sampling techniques

This study was conducted in the southeast Beaufort Sea (Figure 1) during the fall 2003 (20 October to 19 November 2003) and summer 2004 (26 June to 31 July 2004) on board the Canadian Research Icebreaker CCGS *Amundsen* (See Figures 2a, 2b). The study area includes the Mackenzie shelf, the Amundsen Gulf, and Franklin Bay. While the entire area is ice-covered in the winter, the Cape Bathurst Polynya opens during spring in the Amundsen Gulf and along the continental slope, and by summer, the entire area is usually ice-free. All the summer stations were ice-free, but during the fall, ice was present at some stations.

Figure 1: Map of the major seas and rivers of the Arctic Ocean. The study area is indicated by a rectangle in the Beaufort Sea.

In the fall, sediment was collected at 7 stations, and water column samples were collected at 11 stations; in the summer, there were 20 sediment and 11 water column stations (Figures 2a, 2b). To collect particulate organic matter (POM), water from the water column chlorophyll maximum (from 10 to 50 m) determined by in vivo fluorescence probe attached to the CTD was filtered onto precombusted Whatmann GF/F filters (5 h at 500°C). Filters for POM analysis were stored at -20°C prior to HPLC and isotope analysis. Since many stations did not exhibit a phytoplankton bloom, the chlorophyll max was sometimes poorly defined. Thus, the total chlorophyll *a* (Tchl *a*) over the entire water column was also measured by sampling several depths and integrating for the entire depth. Comparison of the POM chl *a* and Tchl *a* showed a significant correlation in both summer and fall; however, Tchl *a* was significantly correlated with the sedimentary chl *a* while the POM chl *a* concentration was not, suggesting that the sedimentary chl *a* reflects the entire chl *a* of the water column and not only at the chlorophyll maximum. For that reason, when comparing sedimentary biomarkers with water column pigments, Tchl *a* is used instead of POM chl *a*.

Sediment was sampled by replicate deployments of a box corer (45 cm x 45 cm). Multiple sub-samples (5 cm diameter x 10 cm deep) for sedimentary pigment and stable isotope analysis were taken from each station. The top 2 cm of sediment were extruded and sliced under diminished light conditions. Each interval slice was divided in two, half for pigment analysis by fluorimetry (Holm-Hansen et al. 1965), and half for pigment analysis by HPLC (Wright et al. 1991, Chen et al. 2001) and stable isotope analysis (Hobson et al. 1995). Both pigment sub-samples were wrapped in foil and frozen directly after slicing in order to avoid pigment degradation.

2.2 Fluorometry analysis

Within two weeks, every sub-sample of sediment was analysed for chloropigment content by fluorimetry (Holm-Hansen et al. 1965). 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 48h, and shaken periodically. Prior to fluorometer analysis, the sediment was centrifuged (4000 rpm for 10 minutes 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 the ratio of chl *a* to total phaeopigments (chl *a*/phaeo).

2.3 HPLC analysis

POM filters were extracted in 2 ml of 100% HPLC-grade acetone for 12-24h. Extracts were filtered through 0.2 µm nylon syringe filters. Freeze-dried sediment (1-3 g) was transferred to a 50 ml polypropylene centrifuge tube where 8 ml of 80:20 HPLC grade acetone:methanol was added. The mixture was sonicated for 5 minutes in an ice bath and extracted in the freezer overnight. Extracts were separated from the sediment by centrifugation (10 min, 2000 rpm) and 5 ml of the supernatant was filtered through a 0.2 µm syringe filter. Extracts were blown to dryness under nitrogen, and then redissolved in 250 µ ml of 90% acetone.

Quantitative analysis of all pigments was conducted with a Waters HPLC equipped with an online photodiode array (Waters 996 PDA) and fluorescence detector (Waters 616) with excitation set at 440 nm and emission at 660 nm. 200 µl of each sample were injected through a guard column to a reverse phase Alltech Absorbsphere C18 column (5 µm particle size; 250x4.6 mm i.d.). The 3-step gradient program modified after Wright et al. (1991) and described by Chen et al. (2001) for enhancing the separation of phaeopigments.

Identification of pigments was performed by comparing retention time and PDA spectra with standards (DHI Water and Environment, Denmark). Carotenoids were quantified at 438 nm on the PDA detector, while chlorophylls and phaeopigments were quantified on the fluorometer detector. The response factor (RF) was determined for each pigment by single run of each pigment standard. In the POM, the pigments identified for determining the phytoplankton composition through CHMETAX were chl *a*, peridinin, 19'but-fucoxanthin, fucoxanthin, prasinoxanthin, 19'hex-fucoxanthin, alloxanthin, zeaxanthin, chlorophyll b, dinoxanthin, chlorophyll c_2. In the sediment, chl *a*, phaeophorbide *a* and *b*, phaeophytin *a* and *b* and some accessory pigment were identified. The accessory pigments identified were: fucoxanthin as marker of diatoms, 19'but-fucoxanthin and 19'hex-fucoxanthin as markers of haptophytes, alloxanthin as marker of cryptophytes, prasinoxanthin and chl *b* as a marker of green algae (prasinophytes+chlorophytes), peridinin as marker of dinoflagellates and zeaxanthin as marker of cyanobacteria.

2.4 Carbon and nitrogen stable isotopes analysis

Stable isotope analysis of POM filters were performed after acidification by the National Hydrology Research Institute in Saskatoon, Saskatchewan, Canada, using the method of Hobson et al. (1995). 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 3 times, or until the sediment did not show a clear bubbling due to the conversion of carbonate to carbon dioxide gas. The decalcified sediment was used for %C and $\delta^{13}C$ determinations, and undecalcified sediment was 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. using a ThermoFinnigan Delta V coupled to a Costech EA Conflo III combustion interfaces. All stable carbon isotope values are reported in delta (δ) notation, in units of per mil (‰), where $\delta = [((R)_{sample} / (R)_{standard}) - 1] * 1000$, and $R = {}^{13}C/{}^{12}C$ and ${}^{15}N/{}^{14}N$ and the standards are 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.

2.4 CHEMTAX and statistical treatment

The contributions of the 6 major algal groups (diatoms, haptophytes, cryptophytes, green algae, dinoflagellates and cyanobacteria) were estimated from the pigment ratios determined by HPLC, using the CHEMTAX program (Mackey *et al.*, 1996). The use of CHEMTAX as an estimation of the algal groups from pigments is controversial, as it is often hard to establish accurate pigment ratios, and these may vary depending upon environmental conditions; however, the results obtained with CHEMTAX followed the tendency observed in the raw pigments ratios, i.e. high percentage of dinoflagellates when abundant peridinin (see 2.3

for the main pigment marker of taxonomic groups). Moreover the relevance of CHEMTAX for estimating major algal group contribution in the present study was confirmed by comparison with microscopic algal counts (S. Brugel, pers. observation).

Seasonal differences between summer and fall, and spatial differences between the Gulf and the Mackenzie shelf were analysed by t-test when data were normal and variances equal, and by Mann-Whitney Rank Sum test (MW test) when data failed normality and equal-variance tests. It is important to note that the stations studied in summer and in fall were not always the same. This could introduce a confusing bias while trying to make seasonal comparisons (see Discussion). Linear relationships between environmental factors (depth, distance to river, Tchl *a*), sediment oxygen demand (data from Renaud et al. 2007a), and biomarkers were analyzed by Pearson's product-moment correlation. Correlation analyses, Mann-Whitney Rank Sum test and t-tests were performed using SigmaStat 3.5 (2006 Systat Software, Inc).

3. Results

3.1 Phytoplankton species and water column isotopes

Chlorophyll *a* integrated over the entire water column (Tchl *a*) is presented in Figures 2c and 2d. Values were higher in the summer than during the fall (MW test, $p<0.05$). Tchl *a* values were higher closer to the coast, particularly near the Mackenzie River delta and may reflect an increase in primary productivity associated with increased nutrient delivery to the nearshore zone. Analysis of pigment distributions using CHEMTAX indicates significant seasonal and spatial differences in phytoplankton distributions (Figures 2e, 2f). In the summer, diatoms dominate (avg. 51%±30), particularly in the shelf region, whereas smaller cells, such as haptophytes and green algae, are more abundant in the Gulf. In the fall, diatoms decreased significantly (avg. 15%±10, t-test, $p<0.05$); haptophytes and green algae dominate (both combined represent avg. 80%±17).

The C:N ratio in POM in the fall was higher than in the summer (t-test, $p<0.05$). In the fall, C:N values ranged between 9.3 at station 718 and 17.1 at station 309, and were higher in the Gulf than the shelf, while most of summer C:N data were between 6.7 and 9.5. $\delta^{13}C$ values in POM were significantly lower in the fall than in the summer (t-test, $p<0.05$). $\delta^{13}C$ varied from -26.6 ‰(station 410) to -28.5 ‰ in the fall, and from -21.0 ‰ (station 912) to -26.8 (station 200) in the summer. $\delta^{15}N$ value of POM varied from 0 ‰ (station 100) to 4 ‰ (station 709) in the Gulf and are more variable and more enriched along the shelf, particularly in the summer (Figures 3, 6a).

3.2 Sedimentary pigments and isotopes

Sedimentary chl *a*, as determined by fluorometer and by HPLC, were significantly correlated ($r=0.8$, $p<<0.05$). Sedimentary chl *a* determined by HPLC ranged from <0.01 in the Amundsen Gulf to a maximum of 3 $\mu g\ g^{-1}$ on the shelf. Sedimentary chl *a* determined by fluorometer ranged from 0.16 to 19.52 $mg\ m^{-2}$ (Figures 4c, 4d). Highest sedimentary chl *a* values are found close to the Mackenzie River delta. Although the difference in chl *a* was not significant between the fall and the summer, the difference between the Gulf and the shelf was significant in the summer (MW test, $p<0.05$) and showed a similar tendency in the fall (MW test, $p=0.05$). The chl *a*:phaeo ratio(Figures 4a, 4b), an indicator of the freshness of the organic matter reaching the benthos, showed similar results for the summer, with higher ratios (fresher material) on the shelf (MW test, $p<0.05$). Sedimentary accessory pigments varied spatially and seasonally (Figures 4e, 4f). In the summer, sedimentary fucoxanthin was the most abundant accessory pigment on the continental shelf, and chl *b* in the Gulf, while in the fall, the pigment composition was more heterogeneous, and indicated a substantial contribution from small cells on the sediment surface.

No significant difference was observed between the fall and the summer for the sedimentary isotopes (Figures 5, 6b), however, significant differences in both $\delta^{15}N$ and $\delta^{13}C$ values were observed between the Amundsen Gulf and the shelf area (MW tests, $p<0.05$). $\delta^{15}N$ values were highest in the Gulf area (6.8 ‰ at station 100 in the fall, and 6.7 ‰ at station 212 in the summer) and lowest on the shelf (2.1 ‰ at station 300 in the fall and 1.9 ‰ at station 809 in the summer). $\delta^{13}C$ values were also the highest in the Gulf area (-22.8 ‰ station 100 and 124 in the fall and -21.1 ‰ at station 212 in the summer) and lowest on the shelf (-26.2 ‰ station 300 in the fall and -25.8 ‰ at station 809 in the summer). The C:N ratio did not show clear seasonal or spatial variation. The minimum (8.5) was observed at station 124 in the summer and the maximum (15) at station 300 in the fall.

3.3 Environmental factors and biomarker correlations

The percentage of nitrogen in POM samples showed a significant inverse correlation with the distance to the river mouth during the fall ($r=-0.93$, $p<0.05$), but no other significant relationship was found between the depth and distance to river and either POM, isotopes, or Tchl *a*. In the fall, the percentage of haptophytes was significantly correlated with the distance to the river ($r=0.86$, $p<0.05$), and the percentage of green algae was significantly inversely correlated ($r=-0.78$, $p<0.05$) with the distance to the river. The $\delta^{15}N$ and $\delta^{13}C$ and C:N values showed seasonal differences in the POM stable isotope composition (Figure 6a). Fall stations had a more terrestrial (i.e. depleted) signature while summer stations had a more marine and mixed (i.e. enriched) signature.

Although environmental factors did not seem to influence summer POM constituents, correlations between depth, distance to the river mouth and total water column production with sedimentary biomarkers (Table 1) showed the importance of these factors for sediment isotopes and pigments for both seasons. The amount of sedimentary chl *a* and the ratio chl *a*:phaeo were always significantly inversely correlated to the depth. In the fall, depth is significantly positively correlated with the sedimentary carbon and nitrogen isotopes, however only $\delta^{13}C$ correlates positively significantly with depth in the summer. In the fall, degraded chl *b* (phaeophytin and phaeophorbide *b*) is inversely correlated with depth and distance to the river. During the summer, total phaeopigments correlated significantly with phaeophorbide *a* ($r=0.64$, $p<0.05$), while in the Gulf area, total phaeopigments correlated with phaeophytin *a* ($r=0.61$, $p<0.05$).

In the summer, sedimentary $\delta^{13}C$ and $\delta^{15}N$ values were significantly correlated with the distance to the river mouth while the correlation was only significant for $\delta^{13}C$ values in the fall. Geographical differences in sediment isotopes were also found when ploting $\delta^{13}C$ with $\delta^{15}N$ values (6b).

4. Discussion

The use of multiple biomarkers for both water column and sediment analysis in the southeast Beaufort Sea allowed delineation of sources of carbon and confirmed the strength of pelagic-benthic coupling. The approach also allowed an understanding of the relative importance of time and space for both the sources of organic matter and its fate. Local water-column inputs to the benthos were also identified as well as the geographical differences based on the Mackenzie River influence, and how changes in organic matter inputs to the sea floor can impact the benthos.

4.1 Importance of local water- column inputs

The significant correlation between Tchl *a* and sedimentary chl *a* ($r=0.6$, $p<0.05$) indicates that local primary production plays an important role in the inputs of fresh organic matter to the

Table 1: Correlation between environment factors (water depth, distance to river, water column total integrated chlorophyll *a* noted Tchl *a* and sediment carbon demand noted SCD) and sedimentary biomarkers during fall 2003 and summer 2004. Significant correlation (p<0.05) are indicated by an asterisk. SCD data from Renaud et al. (2007).

		$\delta^{15}N$	$\delta^{13}C$	Chl *a* Phaeo	Chl *a*	Phaeoph-orbide *a*	Phaeo-phytin *a*	Chl *b* degraded
Depth	Fall	**0.95***	**0.94***	**-0.77***	**-0.82***	0.56	-0.2	**-0.82***
	Summer	0.02	0.05	**-0.50***	**-0.52***	-0.43	0.38	-0.01
Distance to river	Fall	0.69	**0.93***	-0.68	-0.6	0.08	-0.56	**-0.92***
	Summer	**0.79***	**0.78***	-0.34	-0.29	-0.17	0	0.07
Tchl *a*	Fall	**0.79***	**0.98***	-0.63	**-0.79***	0.2	-0.03	**-0.32***
	Summer	0.03	-0.06	0.36	**0.63***	0.42	-0.23	0.01
SCD	Fall	**-0.89***	**-0.89***	0.52	**0.78**	-0.68	-0.19	0.23
	Summer	-0.23	0.09	**0.70**	**0.73**	-0.17	0.29	0.24

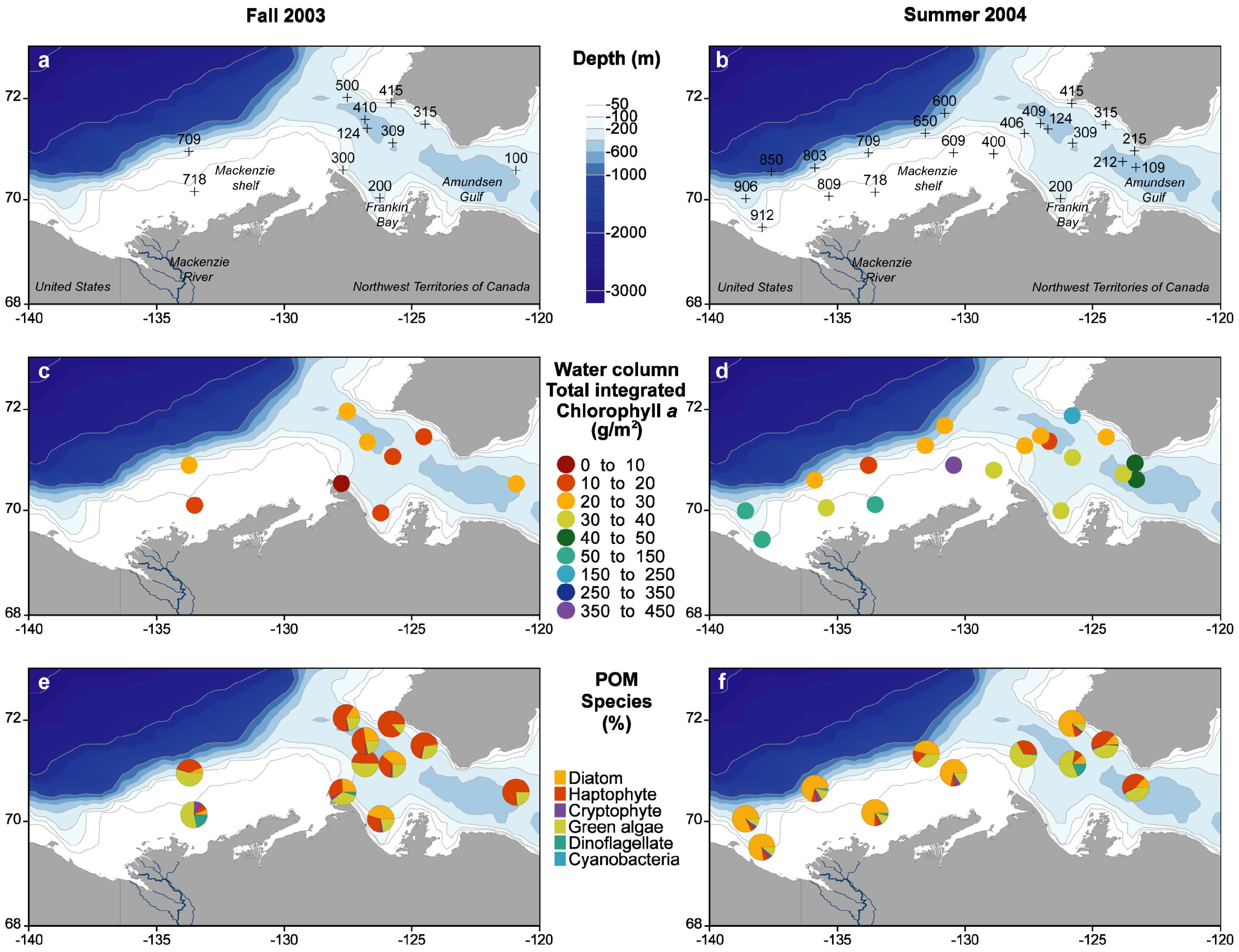

Figure 2: (a and b) Positions of the fall and summer stations. (c and d) Water column integrated chlorophyll a. Note: Increment of 10 until 50, and of 50 after. (e and f) Phytoplankton species composition at the chlorophyll maximum depth.

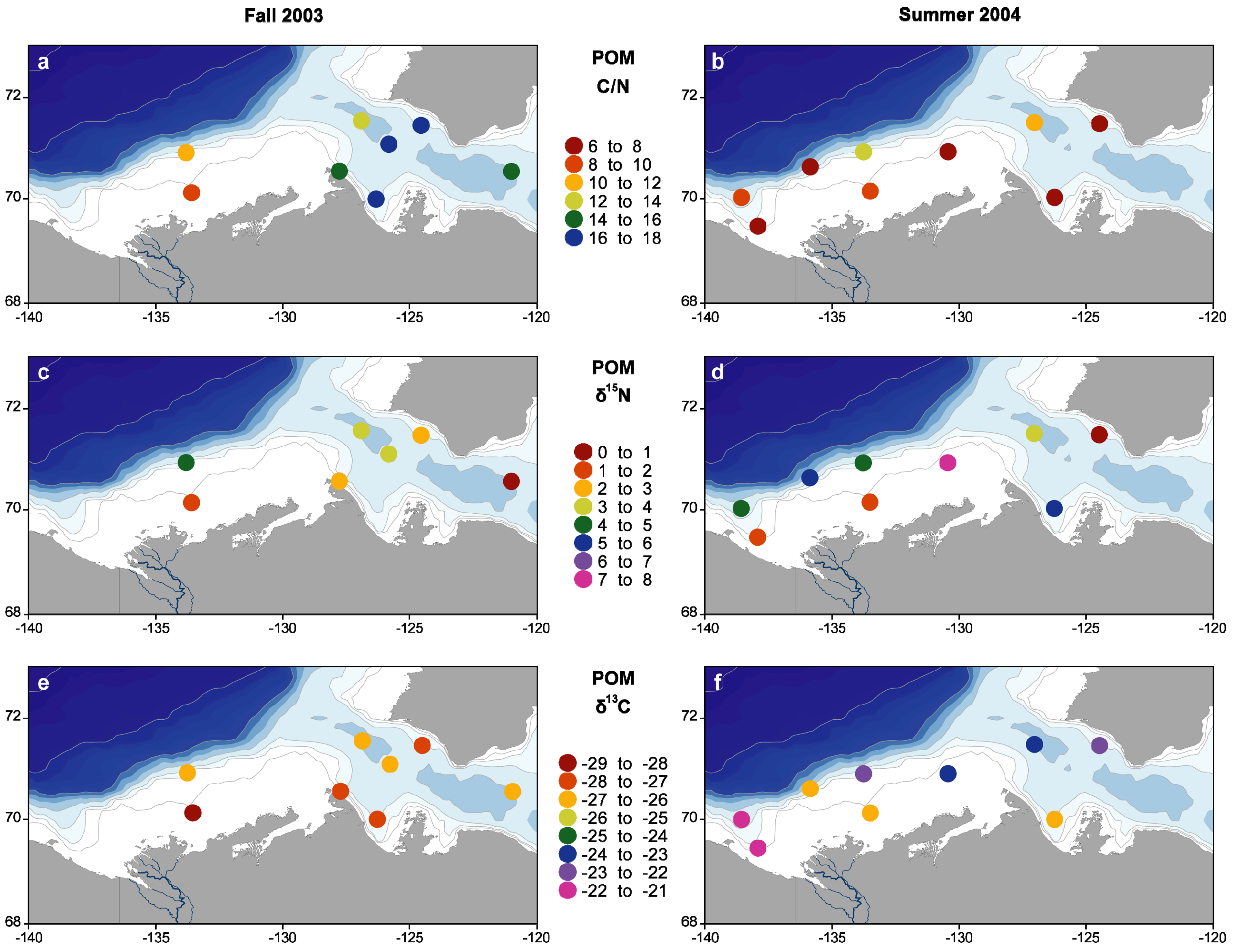

Figure 3: Stable isotope (‰) and elemental composition of the particulate organic matter at the depth of the chlorophyll maximum. (a and b) C:N ratio. (c and d) δ^{15}N. (e and f) δ^{13}C.

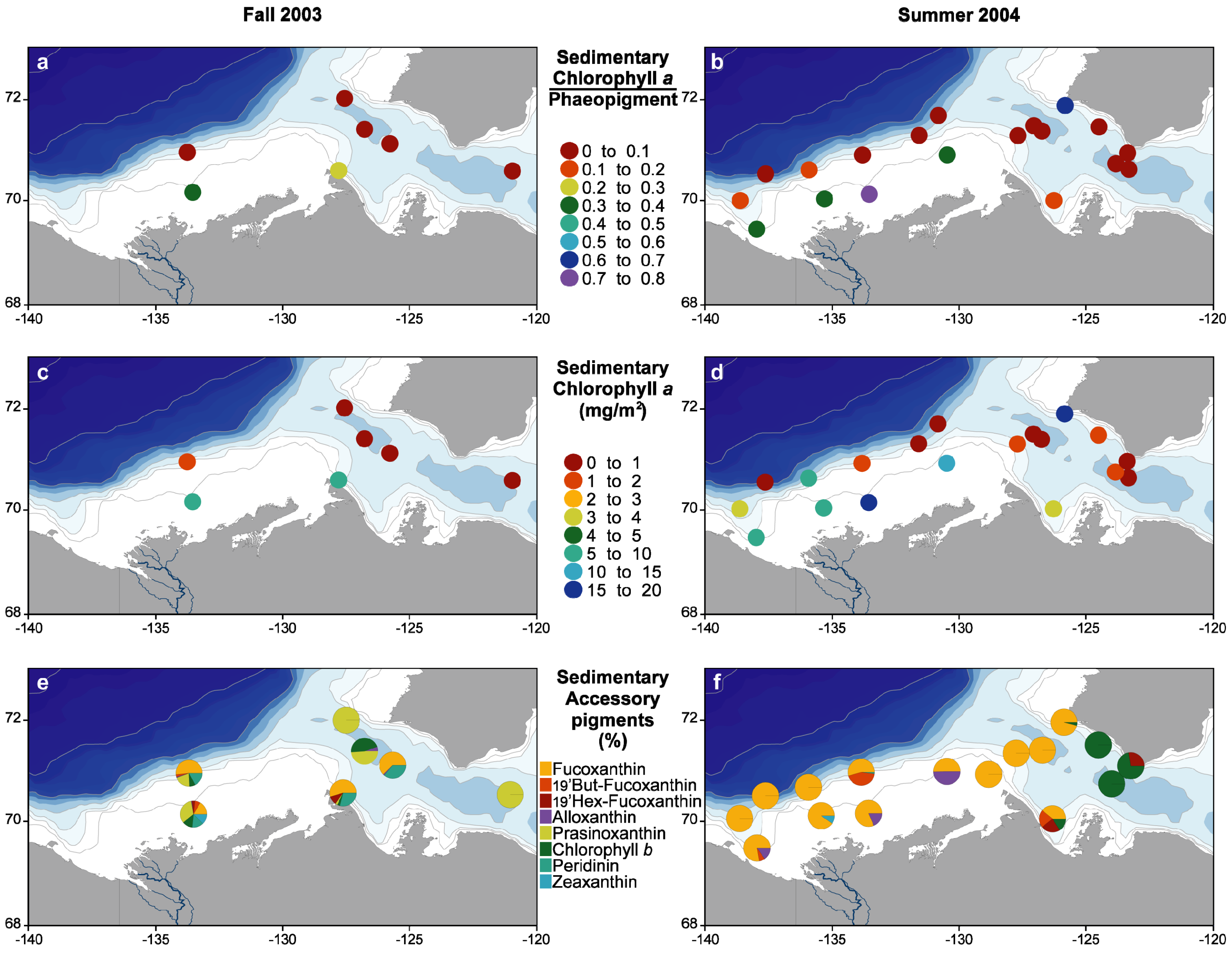

Figure 4: Sedimentary pigment composition in the top first 2 cm. (a and b) ratio chlorophyll *a*/phaeopigment. (c and d) Concentration in chlorophyll *a*. Note: Increment of 1 until 5, and of 5 after. (e and f) Accessory pigment composition in percentage.

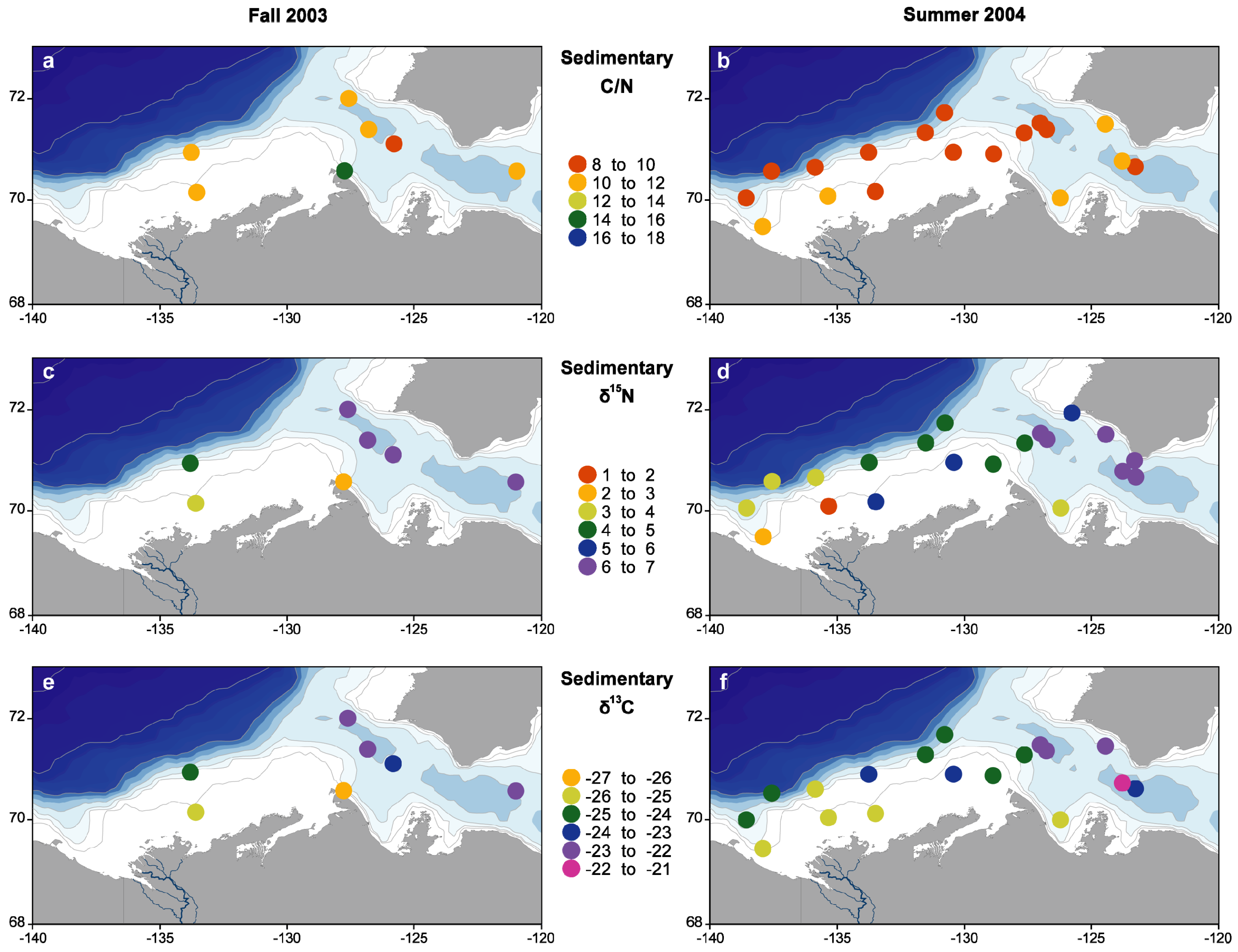

Figure 5: Sedimentary stable isotope (‰) and elemental composition in the top first 2 cm. (a and b) C:N ratio. (c and d) δ^{15}N. (e and f) δ^{13}C.

benthos in all areas. The southeast Beaufort Sea is commonly thought to be oligotrophic (Carmack et al. 2004, Walsh et al. 2005) and the inputs of fresh organic matter to the benthos minimal. Deep-sea oligotrophic ecosystems showed sedimentary chl *a* values <0.06 µg g^{-1} in the central equatorial Pacific (Smith et al. 1996) and an average of 0.04 µg g^{-1} in the Indian sector of the Southern Ocean, with a maximum of 0.15 µg g^{-1} at the permanently open ocean zone (Riaux-Gobin et al. 1997). On the shelf area, our sedimentary chl *a* averaged 1.7±1 µg g^{-1} and was clearly higher than in those systems, but was similar to values found in the Bering Sea (Pirtle-Levy et al. in press). In the Gulf area, the average (0.05±0.07 µg g^{-1}), showed similar values to the Northeast Water and North Water polynyas (Ambrose & Renaud 1997, Grant et al. 2002, respectively). These values are lower than in more productive systems such as in the Bering and the Barents Seas for similar depths (Cooper et al. 2005, Morata & Renaud in press, respectively) but still emphasize the importance of water column productivity for sedimentary chl *a* in Arctic ecosystems.

Not only has the total chl *a* in the water column been shown to determine the sedimentary chl *a*, but the composition of phytoplankton was also reflected in the sedimentary pigment composition in other Arctic ecosystems (Morata & Renaud in press, Pirtle-Levy et al. in press). In our study, the importance of diatoms in the summer was reflected in the sediment by the importance of fucoxanthin, while in the fall, pigments of smaller cells (haptophytes, prasinophytes) were found in the sediment. It is commonly thought that picoplankton is recycled within the food web and only larger phytoplankton is exported. Recently, Richardson & Jackson (2007) suggested that picoplankton, despite their small size, can play an important role in inputs of organic matter to the equatorial Pacific benthos. Traditionally, the Arctic marine production has been thought to be dominated by large phytoplankton (von Quillfeldt 1997); however, recent studies have shown that picophytoplankton can play an important role in late summer (Not et al. 2005, Lovejoy et al. 2006), including in the Beaufort Sea (Lovejoy et al. 2007). These small cells seem to sink relatively fast and be a source of inputs of organic matter inputs to the benthos in the fall.

In the Amundsen Gulf area, the importance of green algae in the water column is reflected in the sediment by the presence of chl *b*. Arctic waters tend to have high amounts of green algae (Suzuki et al. 2002, Not et al. 2005) and thus in the summer, the strong signal of chl *b* in the Gulf may indicate greater importance of Arctic water in this region than on the shelf.

Sedimentary fucoxanthin was found broadly in the shelf area in the summer. Diatoms are important primary producers in the Arctic for both phytoplankton and ice algae (von Quillfeldt 2000 and references within, Hill 2005). Ice algae diatoms have been previously found in Arctic sediment (Sancetta 1981, Cremer 1999, Djinoridze et al. 1999, Polyakova 2003, Ambrose et al. 2005) and were also found in the station 200, studied over the winter/spring (Morata, pers. observation). While chlorophylls are in general more labile and have shorter half lives (2-3 weeks in the Arctic, Graf et al. 1995), carotenoids can be very persistent in the sediment (Buchaca & Catalan 2007). Sedimentary fucoxanthin found in the summer could reflect remaining inputs from the spring ice-associated algae. Ice algae has been found to be quickly processed by benthic fauna (McMahon et al. 2006, Renaud et al. 2007b). Resting cells of diatoms, however, can remain in the sediment from months to years (McQuoid et al. 2002), and Smith et al. (2006) suggested the idea of a “foodbank” in Antarctica, where phytopigments can be stored and remain available through the year. The high amounts of sedimentary fucoxanthin in the summer may indicate that, while benthic communities quickly utilize newly deposited ice algae, some phytopigments remain for a longer period. These results raise questions similar to those of Pirtle-Levy et al. (in press) who also found significant concentrations of fucoxanthin in the sediment of the Bering Sea. Alternatively, the POM data (Tchl *a*, δ^{13}C, C:N) imply rapid rates of primary production in the summer months on the shelf, which might increase the flux of fucoxanthin into the sediment record. Although it is impossible to differentiate ice algae diatoms from phytoplankton diatoms using pigment analysis, it would be interesting in the future to assess the importance of inputs from ice algae in the sediment by other techniques such as direct cell identification and counting or lipid biomarker analysis (McMahon et al. 2006).

While both sedimentary chl *a* and phaeopigments reflect inputs of fresh organic matter, the presence of phaeopigments also indicates degradation processes (Mantoura &

Llewellyn 1983, Villanueva & Hastings 2000) since phaeophorbide *a* is a marker a herbivory digestion (Bianchi et al. 1988) and phaeophytin *a* can be due to microzooplankton or microbenthos grazing (Bianchi et al. 1988, Verity & Vernet 1992), bacterial degradation (Leavitt & Carpenter 1990) or cell senescence (Louda et al. 1998). During the summer, intact faecal pellets of large herbivorous copepods and appedicularians were found in sediment traps, while in the fall, pellets were more degraded (Forest et al. 2006). The correlation of total sedimentary phaeopigments with sedimentary phaeophorbide *a* in the summer (Table 1) underlines the importance of macro- and meso-zooplankton grazing as a main degradation factor of material reaching the benthos; however, in the fall, the very low chl *a*:phaeo ratios suggested that the material reaching the benthos was highly processed and it is hard to relate chl *a* degradation products to their sources. Spatially, for both seasons, the total phaeopigments in the Gulf area were correlated with phaeophytin *a* (Table 1), highlighting complex degradation processes, since phaeophytin *a* can be created by microbial degradation, grazing, and cell senescence. On the shelf area, no clear correlation was found. Carroll & Carroll (2003) suggested two scenarios of arrival of organic matter to the sea floor as a function of the amount of ice. In ice-limited areas, such as in polynyas, primary production is expected to be used within the water column while in ice-abundant areas, more production sinks to the benthos.

The significant correlation between phaeopigments with phaeophytin *a*, the lowest chl *a*:phaeo ratios, and the enriched $\delta^{15}N$ and $\delta^{13}C$ values, suggest that in the Gulf area, material reaching the sediment has been heavily degraded, especially by microbial degradation. This could be explained by enhanced microbial degradation in the polynya (Lovejoy et al. 2002, Sherr et al. 2003, Wassmann et al. 2006), but the greater water depth could also be a factor. Sedimentary chl *a* has been found to be inversely correlated to depth (Table 1, Ambrose & Renaud 1995, Grahl et al. 1995) suggesting that over a deeper water column, material has more time to be degraded and recycled by bacteria, and thus a smaller, and more degraded, fraction of the overlying production reaches the seafloor. It remains impossible, however, to determine the relative importance of these two mechanisms.

4.2 River influence

In order to determine material origin in the sediment in the Beaufort Sea, Parsons et al. (1989) determined the stable isotope composition ($\delta^{15}N$ and $\delta^{13}C$), and delimited approximate maximum values for marine and terrestrial sources of organic material. These amounts are represented in Figure 6. For the POM, the origin differed between seasons (fall was more terrestrial, summer was more marine), while in the sediment, the spatial position seems a more important factor in determining the matter origin since the Gulf area has a more marine signature and the shelf area a more

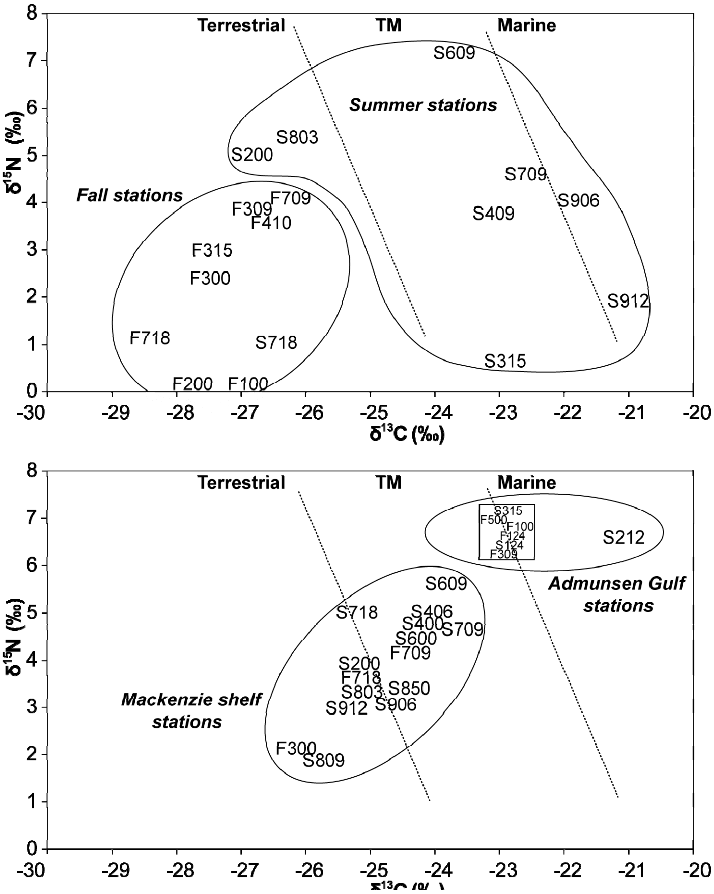

Figure 6: Stable isotopes composition (‰) in (a) the particulate organic matter at the depth of chlorophyll max, and in (b) the sediment. Dash lines represent Parsons' delimiting lines for separating terrestrial origin (noted R) from marine origin (noted M). RM represents an area of mixing between terrestrial and marine origin.

terrestrial signature.

The autochtonous marine signature of the POM in the summer was also confirmed by C:N ratios of 6-7 (Figure 3a), which are typical of marine phytoplankton (Redfield et al. 1963, Daly et al. 1999). It is important to note that the POM samples were sampled at the chl *a* max determined by the CTD, between 10 and 50 m; however, at some stations, elevated levels of chl *a* were also observed in the surface waters (S Brugel, pers. observation), where the water properties over the first 5 meters showed a lower salinity typical of the Mackenzie River. Previous studies have reported the spread of the Mackenzie plume across the shelf region as a shallow lens, especially later in the summer and fall (Carmack & MacDonald 2002, Carmack et al. 2004), but this seemed to have a low direct influence on composition of deeper POM (Figure 3); however, nutrients delivered by the Mackenzie River might be stimulating primary productivity in the nearshore zone. Previous studies have suggested that, although a heterotrophic food web based on riverine organic carbon exists near the Mackenzie River mouth, the offshore community is more marine/oceanic (Parsons et al. 1988, O'Brien et al. 2006). Although the stations studied in summer and fall were different which, as mentioned previously, might lead to a bias during comparison, POM had a more terrigenous signature in the fall, as also suggested by other POM biomarkers studies (Yunker et al. 1995) and sediment trap studies (Forest et al. 2006, O'Brien et al. 2006) and the presence of allochtonous bacteria on the shelf (Wells et al. 2006).

While the river influence on the POM was seasonal, with maximal direct influence in the fall, sedimentary isotope values showed more of a spatial difference between the Gulf and the shelf (Figure 6b). The higher δ^{15}N and δ^{13}C values suggested that during the summer, in the Gulf area (furthest from the river), material reaching the benthos is more marine and/or degraded. Conversely, the shelf had more terrestrial signature (terrestrial δ^{13}C values -26.5 to -27‰ for the Beaufort area, Goni et al. 2000, Naidu et al. 2000). The difference in isotopic signature between the Mackenzie shelf vs. Amundsen Gulf was confirmed when plotting δ^{13}C and δ^{15}N values for sediments (Figure 6b), highlighting the geographic position as the main factor influencing sedimentary stable isotopes values.

Although stable isotopes measurements did not show seasonal variations, chl *b* degradation products (phaeophytin *b* and phaeophorbide *b*) are more abundant in the fall. Chl *b* occurs mainly in green algae and terrestrial plants (Kowalewska 2005) and is less stable than chl *a* (Kowalewska & Szymczak-Zyla 2001), however, degradation products of chlorophylls are usually very persistent in sediment records (Scheer 1991). Freshwater green algae have been used as a marker of river runoff in the Beaufort, Laptev and Kara Seas (Matthiessen et al. 2000) and high sedimentary chl *b* contents have been attributed to intensive influence of riverine fresh water (Kowalewska et al. 1996, Matthiessen et al. 2000). In the fall, the high levels of chl *b* degradation products and the strong negative correlation of chl *b* degradation products with distance from the river suggest that, as for the POM, the influence of degraded material from the Mackenzie River is high, especially on the shelf; however, this material is probably a small portion of the total organic matter present in the sediment, and this signal is lost when studying stable isotopes in the bulk sediment. Sedimentary stable isotopes values integrate signals at a longer time scale, and showed clear spatial variations, but no seasonal variations.

To date, our knowledge of the influence of Arctic rivers on POM and sedimentary stable isotope composition has been based on rivers such as the Laptev Sea influenced by the Lena River (Rachol & Hubberten 1999), and the Kara Sea, influenced by the Ob and Yenisei (Kahl et al. 2003). These studies found depletion in ^{13}C next to the river mouth, implying high amounts of terrigenous detrital input, while enriched ^{13}C values are found in regions less influenced by rivers such as the Chukchi, Bering, and Barents Seas (Naidu et al. 1993, Dunton et al. 2006, Tamelander et al. 2006). Although sedimentary isotopes might not reflect by themselves changes in organic matter origin at a short time-scale, combined with sedimentary pigment, they should allow the tracking of changes of influence of the Mackenzie in the Beaufort Sea.

4.3 Seasonal and spatial variations in the inputs of organic matter to the benthos

Benthic community response to inputs of fresh phytodetritus has been found to be rapid (Graf 1989, Renaud et al. 2007b) and sediment oxygen demand (SOD) has been found to be correlated with sedimentary chl *a* (Clough et al. 2005, Renaud et al. 2007a, Renaud et al. in press). The present study shows that not only the sedimentary chl *a* correlates with SOD, but also the ratio chl *a*:phaeo, an indicator of the "freshness" of the organic matter (Table 1). Moreover, the percentage of organic carbon in the sediment (%C) is significantly correlated with SOD in the summer while stable isotope measurements correlate with SOD in the fall. Stable isotope measurements of the bulk sediment relate the total contents of organic matter in sediment, not only the fresh inputs as pigments. This suggests that in the summer, benthic activities depend on arrival of fresh organic matter, characterized by high amount of chl *a*, high ratio chl *a*:phaeo and high %C, while in the fall, since material reaching the sediment is more degraded and less important, benthic activities depend more on the bulk of organic matter. Inputs of phytodetritus have been found to also have an impact on the meiofauna in the southeast Beaufort Sea (Bessière et al. 2007), where highest meiofauna densities in the summer on the Mackenzie shelf and Franklin Bay are attributed to high inputs of fresh organic matter. Meiofauna composition changed in relation to their affinity to phytodetritus: nematodes seemed to be more adapted to degraded phytodetritus, while turbellarians and kinorhynchs were correlated with fresh phytodetritus in the summer.

Although the meiofaunal composition seemed to be influenced by seasonal variations of organic matter inputs to the benthos, the southeast Beaufort Sea macrofaunal community composition showed spatial variations (Conlan et al. in press) between the Mackenzie shelf and the Gulf area, even though the difference was not explained by the presence of the polynya. Macro- and mega- benthic animals have been reported to respond more to environmental forcing than micro- and meio- fauna (Gage & Tyler 1991) and so their distribution and structure are expected to integrate variations at longer time scale (Piepenburg 2005). Interestingly, SOD also showed spatial variations and was lower in the Gulf than in the shelf (t-test, $p<0.05$). As seen previously, the Gulf area shows more degraded pigments and a stable isotopic composition typical of marine origin. Benthic activities (SOD) and community compositions might reflect these differences in organic matter inputs.

5. Conclusion

The combination of sedimentary pigments and stable isotope measurements allowed us to identify spatial and seasonal variations of organic matter inputs to the benthos of the eastern Beaufort Sea. Sedimentary pigments reflected seasonal variations in the pelagic-benthic coupling. In the summer, inputs of "fresh" organic matter to the benthos were related to the overlying production. The main degradation process is through zooplankton grazing. In the fall, there is evidence of rapid deposition of small algal cells to the sea floor, with material also being generally more degraded. Inputs from the river were also an important source of arriving material in the fall. Sedimentary pigments also suggested that in the Gulf area, most material reaching the sea floor was heavily degraded, probably due to microbial degradation. Stable isotopes highlighted spatial differences between the shelf and the Gulf area. The shelf area is under terrestrial inputs influence, while in the Gulf, material reaching the sea floor is from a more marine origin.

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Paper III

Pelagic-benthic coupling in the western Barents Sea: Processes and time scales

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Abstract

The link between pelagic and benthic systems has been suggested to be particularly strong on Arctic continental shelves. Differing sampling strategies and the multitude of pelagic and benthic parameters that have been compared, however, make it difficult to determine the limitations of this important ecosystem concept. We sampled across multiple gradients in water mass characteristics, ice cover, productivity regimes, and seasons to test the generality of the pelagic-benthic coupling paradigm during a 3-year study (2003-2005) in the Barents Sea. While benthic community structure varied among stations, biomass was not significantly correlated with sediment oxygen demand (SOD), a finding contrary to some published studies. Average SOD varied from 2.3 – 7.3 mmol O_2 m^{-2} d^{-1}, and was (positively) correlated as well with sediment pigments, as it was with the vertical flux of pigments and carbon measured by sediment traps deployed at 90 m. Export flux was also strongly coupled with our measure of benthic carbon cycling (SOD), suggesting that both processes vary on similar, short time-scales (days to weeks). In contrast, processes responsible for patterns in benthic biomass reflect a response over longer time scales (several years), and are thus not well coupled with SOD. We conclude that conflicting results of studies assessing pelagic-benthic coupling may not necessarily be due to general inconsistencies in the fundamental relationship, but instead to improper comparisons of parameters or processes that vary over different scales. These findings are particularly relevant for evaluating system processes in ecosystem modeling studies.

Keywords: Arctic, Barents Sea, benthos, benthic-pelagic coupling, carbon cycling, continental shelf, sediment oxygen demand, temporal patterns, vertical flux

1. Introduction

Research performed on Arctic continental shelves over the past 25 years has suggested that benthic and pelagic systems may be more tightly coupled here than in warmer seas (Petersen and Curtis 1980, Grebmeier and Barry 1991, Ambrose and Renaud 1995, Hobson et al. 1995, Piepenburg 2005). Mechanisms proposed to explain this include reduced importance of the microbial loop, mismatch of zooplankton and phytoplankton population cycles, highly pronounced seasonality, persistent low temperatures, and rapid sinking of pelagic or sympagic (ice-associated) algae (Eilertsen et al. 1989, Graf 1992, Piepenburg et al. 1997, Wassmann et al. 2003). Despite the apparent generality of this emerging paradigm, some areas have been suggested to be relatively uncoupled (Sauter et al. 2001, Gooday 2002, Grebmeier et al. 2006b, Tamelander et al 2006), raising the question of whether the paradigm may be an artifact of timing or location of sampling (e.g. initial focus on productive areas), or if there are fundamental geographical differences in how benthic systems function on Arctic shelves. Since the benthos plays an important role in carbon cycling and nutrient regeneration on these shelves (Grebmeier et al. 1989, Glud et al. 2000, Grant et al. 2002, Renaud et al. 2006), and Arctic shelves have been suggested to be particularly vulnerable to climatic change (ACIA 2004, Carroll and Carroll 2003, Renaud et al. 2007a), these inconsistencies are not merely academic curiosities.

A wide range of benthic parameters describing both structure and function of Arctic shelf communities has been studied in the context of pelagic-benthic coupling. These include faunal abundance and biomass, community structure, food-web structure, feeding behavior, oxygen consumption and heat production, sedimentary geochemical profiles, and benthic faunal reproductive cycles (Graf 1989, Grebmeier and McRoy 1998, Ambrose and Renaud 1995, 1997, Hobson et al. 1995). Relationships have been tested among these parameters and data from the pelagic system, including primary production; nutrient concentration; ice cover; and sedimentation rates of carbon, nitrogen, and phytodetritus. Clearly, all of these variables reflect processes occurring over different temporal and spatial scales. For example, spatial patterns in benthic community structure are thought to represent a time-integrated response to food inputs over several years or more (e.g. Dunton et al. 2005); while primary production rates or feeding rates of benthic organisms may vary on the scale of hours. It is not clear how coherent different measurements of the strength of pelagic-benthic coupling will be when examined over a spatially heterogeneous range of water mass influence, ice conditions, and depths, compared to being studied within discrete oceanographic features (e.g. polynyas).

The Norwegian-funded CABANERA project (‘Carbon flux and ecosystem feedback in the northern Barents Sea in an era of climatic change’) investigated the spatial variability, temporal dynamics, and regulation of ecosystem processes during three field campaigns from 2003-2005 in the western Barents Sea. The area sampled spans the northern extent of Atlantic Water, through the Marginal Ice Zone, to primarily Arctic-water influence at the Arctic Ocean shelf-break. This area is known to exhibit high spatial and seasonal variability in terms of benthic communities (Zenkevitch 1963, Piepenburg et al. 1995), primary production rates, and vertical fluxes (Wassmann et al. 2006). Under these conditions, it should be possible to identify differences in functional relationships between the links among water-column and sea floor processes, thus testing the generality of the pelagic-benthic coupling paradigm.

We address both the structure and function (sediment oxygen demand: SOD) of benthic communities, properties presumed to respond to pelagic variability on different time scales, and ask: How does SOD vary in the western Barents Sea? What is the relationship between SOD and benthic faunal associations? and What is the nature of the coupling between benthic and pelagic processes across the range of conditions found in the western Barents Sea?

2. Methods

2.1 Study area and sampling techniques

The western Barents Sea (Fig. 1) was the study area for an intensive, multidisciplinary ecosystem study that was performed during 2-3 week cruises in July-August during 2003 and 2004, and in May-June 2005. Stations were sampled from the R/V Jan Mayen under conditions ranging from open water to more than

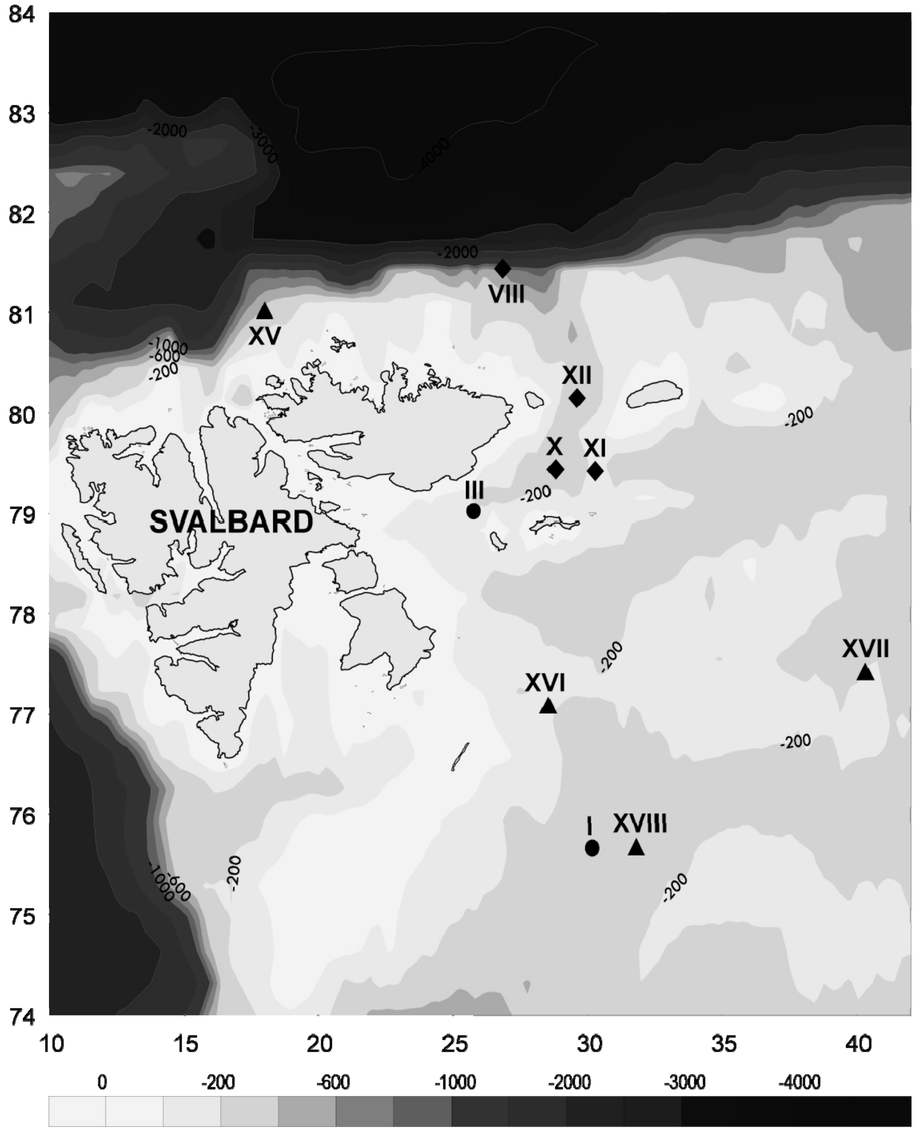

Figure 1. Map of western Barents Sea indicating sampling stations. Circles: sampled summer 2003; diamonds: sampled summer 2004; triangles: sampled spring 2005.

90% cover of primarily first-year ice. See Kivimäe et al. (2007) and Sundfjord et al. (2007) for a discussion of the general hydrography during this study. Depth ranged from 195 to 503 m (Table 1).

Benthic sampling was performed using replicate multicorer or box corer casts. Only cores with intact surface layers, indicated by surface 'fluff' or delicate epifauna, were used. Replicate sub-cores (10 cm diameter x 20-25 cm deep with as much overlying water preserved as possible) were taken from each cast for estimating the respiration of the entire infaunal sediment community. Additional subcores were taken for sediment pigment concentration, and these were sectioned into 1 cm intervals. While subcoring may be viewed as pseudoreplication (Hurlburt 1984), our analyses indicated that variance in respiration rates and chemical composition among subcores from the same box core deployment was not significantly different from the variance among cores from different deployments at the same station (unpub. data).

2.2 Oxygen demand measurements

Incubation cores (5-12 per station) were filled with bottom water collected using the ship's rosette, and bubbled for at least 2 h to saturate the overlying water with oxygen. Core tubes without sediment were filled with bottom water and bubbled, and acted as controls for methodological effects and for respiration of water-column biota. Cores were always kept in

Table 1. Location, depth and sampling dates for Barents Sea stations sampled for benthic process studies in 2003-2005.

Station No.	Location	Latitude °N	Longitude °E	Depth (m)	Date
I	Hopen Trench	75° 40.0’	30° 10.0’	345-352	11-July-2003
III	Erik Eriksenstredet	79° 01.2'	25° 46.3’	198	16-July-2003
VIII	N Kvitøya trench	81° 16.7’	26° 51.2’	503	28-July-2004
X	N. Kong Karlsland	79° 26.5’	28° 48.4’	303	29-July 2004
XI	NE Kong Karlsland	79° 56.6'	30° 17.0'	195	01-Aug-2004
XII	Kvitøya trench	80° 09'	29° 36.0'	286	02-Aug-2004
XV	Questrenna Shelf	81° 01.5’	18° 01.1’	311	21-May-2005
XVI	N. Hopen Trench	77° 05.2’	28° 33.0’	206	26-May-2005
XVII	E. Storbanken	77° 25.6’	40° 18.3’	208	29-May-2005
XVIII	Hopen Trench	75° 40.8’	31° 48.7’	340	30-May-2005

the cold room under reduced light at 0–2ºC. At the beginning of the oxygen-demand assays, cores were sealed using tops that provided constant stirring without sediment resuspension. Oxygen concentrations were monitored every 3-6 hours during the incubations using a polarographic oxygen probe (YSI) inserted into a small sampling port in the core top. Incubations were terminated when 15-30% of the oxygen had been consumed (usually after 30–48 h).

2.3 Faunal analysis

After incubations were completed, sediment cores were gently sieved on 1 mm mesh and the sieve residue was fixed with buffered 10% formaldehyde with Rose Bengal stain added. These samples were later sorted to coarse taxonomic groups and transferred to 70% ethanol. Experts at the Zoological Institute of the Russian Academy of Sciences identified all organisms to the lowest practical taxonomic level, usually species. Species lists were compared with data bases at Akvaplan-niva and the European Register of Marine Species (http://www.marbef.org/data/erms.php) to insure compatibility with other studies performed in this area. Blotted wet biomass was determined for each taxon in each sample. Shells are included in biomass values, but tube structures are not included for polychaetes or crustaceans.

2.4 Sedimentary pigment analysis

Triplicate sub-cores for sediment pigments (5 cm diameter) were taken from each station. Pigments from the top 2 cm were analyzed fluorometrically according to Holm-Hansen et al. (1965). In the laboratory, this sediment was thawed and 20 mL of 100% acetone was added. Pigments were extracted in the freezer in the dark, during which tubes were shaken periodically. After 48 h, sediment was centrifuged (4000 rpm for 10 minutes) and the supernatant was analyzed in a Turner Designs model 10-AU fluorometer before and after acidification with 10% HCl. In 2004, pigment content was determined 2-3 weeks following collection, while these values were measured on board in 2005. Pigment samples for fluorometric analysis were not taken in 2003.

2.5 Statistical treatment

Respiration rates were determined as the (negative) slope of the regression of oxygen concentration (mmol O_2) on incubation time (days) and scaled to 1 square meter (Clough et al. 2005). If control cores exhibited significant oxygen consumption ($p<0.05$), the mean of these values was subtracted from the slope of each sediment incubation core. Dry biomass of infauna (g DM m^{-2}) was calculated from: 1. family-level DW/WW (including shells, where applicable) conversion factors if available in the compiled list of conversion factors by Brey (2001), 2. the higher-taxonomic-level factors from Ricciardi and Bourget (1998) since most of these factors were determined from a larger number of taxa than those of Brey (2001), and 3. assuming dry mass to be approximately 20% of wet mass (Rowe et al. 1983) if the taxon was not available from either of the first two sources. SOD was normalized for infaunal biomass by dividing the SOD of each core by that core's computed dry biomass of macrofauna. Values of this ratio that are < 1 have been noted to be normal at many Arctic shelf sites at depths < 500m, a result suggested to indicate dominance of respiration by macrofauna (Clough et al. 2005).

Faunal communities were analysed using nonmetric multidimensional scaling (MDS) of the Bray-Curtis similarity matrix calculated from a species-abundance data file. Analyses were run on untransformed data and on the same data set following presence/absence transformation.

Comparison of the results is useful for assessing the relative importance of dominant or rare species in generating the observed patterns. An analysis of similarities (ANOSIM) was performed on the data to compare communities among stations. ANOSIM is a resampling technique that can identify significant differences in species composition among groups of samples (stations), after which pairwise comparisons can be conducted (Clarke and Gorley 2006). Similar analyses were performed for the species-biomass data. Faunal data were not available from station XI.

Linear correlation analyses were performed to investigate the relationships among sediment carbon, sediment pigments, sediment oxygen demand, infaunal biomass, and vertical flux estimates of carbon and chlorophyll. Vertical flux measurements were performed by Reigstad et al. (2007 – this volume), and we used data from 90 m traps, as this depth was common to all stations where we had SOD and other sediment data, it is sufficiently below the euphotic zone at all sites, and is far enough above the sea floor that resuspension is unlikely to have a major impact on estimates. Reigstad et al.'s flux data from station XIV were assumed to approximate flux at our nearby station XV, and were collected within 24 h of our sampling.

3. Results

3.1 Benthic faunal communities

Community structure based on species abundances was significantly different among all stations sampled (ANOSIM: p<0.001). The MDS plot (Fig. 2) visualizes the ANOSIM result, indicating that replicate cores were generally much more similar within a station than they were to cores from other stations. However, it is important to note that axes in the MDS plot are dimensionless so it is less clear how different they are. In fact, we sampled a similar bottom type (sandy mud to mud) within a relatively narrow depth range in the Barents Sea

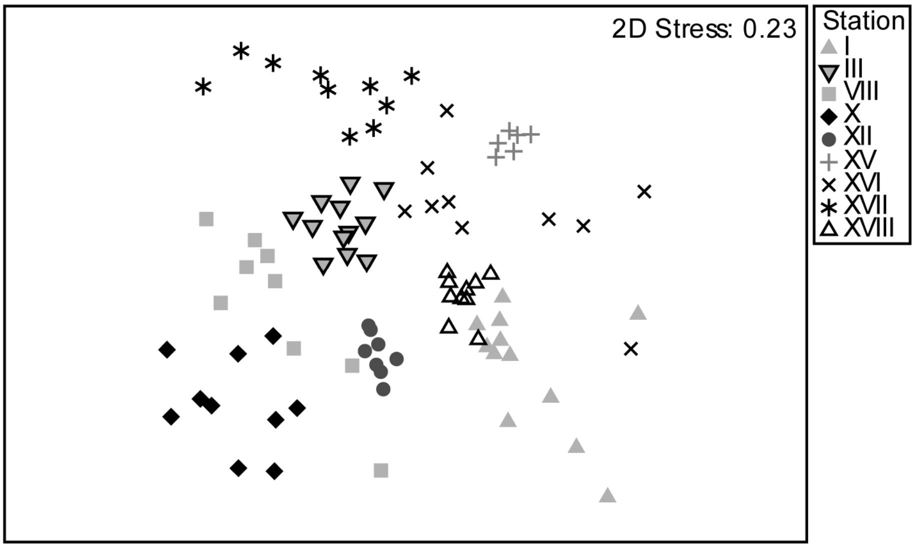

Figure 2. Multidimensional scaling of benthic macroinfaunal communities from Barents Sea stations during 2003-2005. Results are for untransformed abundance data, and each point represents an individual core. Stations indicated by each symbol are identified in the legend. All stations are significantly different from each other by ANOSIM at alpha = 0.05. Foraminiferans were excluded from data.

(Table 1), so it is somewhat surprising that stations were so distinct. Results for the untransformed and severely transformed data sets gave identical results (ANOSIM; $p < 0.001$), indicating that patterns are robust to biases against or for rare species in the different techniques. Only results for analysis of the untransformed data are presented here.

Biomass varied between 2.8 g DM m^{-2} on the eastern end of Storbanken to 13.5 g DM m^{-2} in the Kvitøya Trench (Table 2). Fauna was dominated by polychaetes, crustaceans and bivalves on both abundance and biomass bases. Parallel samples were taken for more detailed community analysis and are presented in Carroll et al. (this volume). MDS and ANOSIM based on faunal-biomass data indicated broad community differences among stations, just as it did for species-abundance data. Station pairs X/XII, X/XV, and XII/XV were not significantly different from each other, while all other pairs (32/35) were distinct (global ANOSIM: $p < 0.001$; pairwise ANOSIM: $p < 0.05$).

3.2 Sediment oxygen demand

Sediment oxygen demand (station means) varied by a factor of about 3, between 2.3 and 7.3 mmol O_2 m^{-2} d^{-1} (Table 2). Macrofaunal biomass was not an accurate predictor of sediment oxygen demand. Linear correlations of the two variables on either a per-core or a per-station basis were non-significant ($p >> 0.05$; Fig. 3). SOD also did not correlate significantly with depth ($p>>0.05$). For all stations, the biomass-normalized SOD was < 1 mmol O_2 consumed g-dry-mass^{-1} d^{-1} (0.22 - 0.93) (Table 2).

3.3 Coupling with sedimentary parameters and vertical flux

Sediment pigment concentration (chlorophyll a and phaeopigments in the top 2 cm) varied by more than an order of magnitude across all stations, from a low of 5.4 mg m-2 at station XVII to 119.5 mg m-2 at station XV (Table 2). Chlorophyll a comprised between 4% and 37% of the total pigment content. Variation in sediment pigment concentration explained half of the variability in sediment oxygen demand ($p < 0.05$), despite high core-to-core variability at each station (Fig. 4a). Pigment concentrations at the sediment surface were highly correlated with measured pigment flux at 90 m, even though total depths ranged from 195-503 m. Vertical flux at 90 m explained 87 and 96 % of the variability in sediment phaeopigments and chlorophyll a, respectively, when station XVIII (open symbols) was excluded (Fig. 4b; $p < 0.01$ for each).

The sediment community responded quickly to arrival of fresh food, or proxies thereof, from surface waters. Sinking chl a and carbon at 90 m

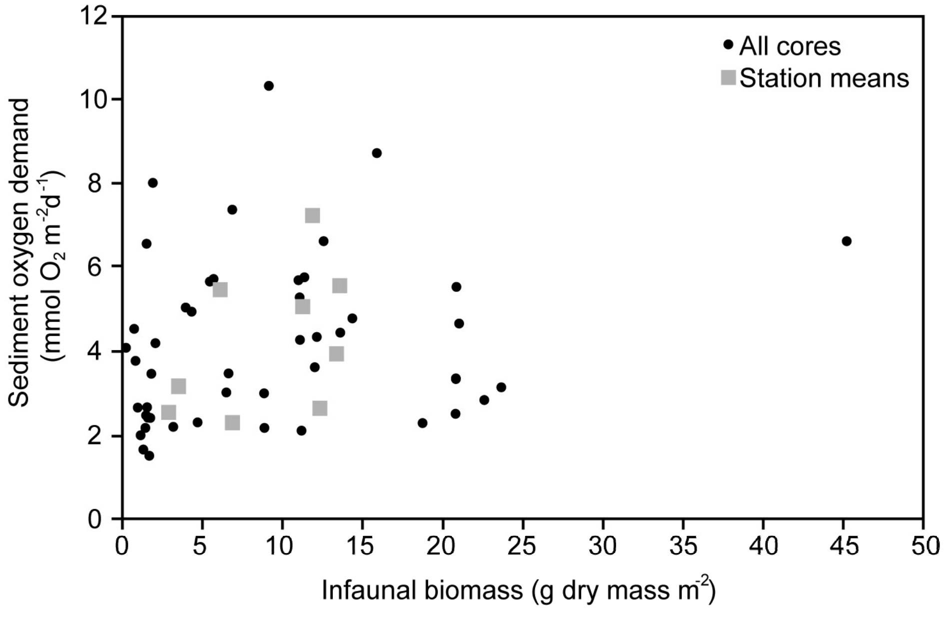

Figure 3. The relationship between biomass of macrofauna from incubation cores and sediment oxygen demand from those cores for all stations. Small triangles indicate values for individual cores while squares represent station means. Linear correlations for both sets of points are non-significant ($p >> 0.05$).

Table 2. Sediment oxygen demand (SOD) and other sediment parameters from benthic stations sampled for process studies. Data represent means (1 standard deviation). Pigment data are from the top 2 cm of sediment. Flux data are from Reigstad et al. (this volume). See text for sample size and other pertinent information.

Station	**SOD** (mmol O_2 m^{-2} d^{-1})	**Infaunal biomass** (g dry m-2)	**SOD/Biomass** (mmol O_2 g dry^{-1} d^{-1})	**Sediment Chlorophyll** (mg m^{-2})	**Sediment Phaeopigment** (mg m^{-2})	**Flux of Chlorophyll** (mg m^{-2} d^{-1})	**Flux of Phaeopigment** (mg m^{-2} d^{-1})	**Flux of Carbon** (mg m^{-2} d^{-1})
I	2.7 (0.6)	12.3 (6.3)	0.22	no data	no data	0.11 (0.01)	0.28 (0.01)	123 (31)
III	2.3 (0.5)	6.8 (9.1)	0.34	no data	no data	1.63 (0.12)	1.70 (0.24)	222 (24)
VIII	5.5 (1.9)	6.0 (8.4)	0.91	2.4 (2.7)	12.2 (7.7)	no data	no data	no data
X	2.6 (0.7)	2.8 (2.2)	0.91	0.6 (0.3)	13.1 (2.2)	1.85 (0.07)	2.98 (0.43)	117 (4)
XI	6.7 (4.9)	no data	no data	12.9	30.7	2.48 (0.26)	3.33 (0.49)	219 (9)
XII	5.6 (0.2)	13.5 (4.9)	0.41	1.6 (0.8)	21.8 (4.4)	no data	no data	no data
XV	7.3 (2.1)	11.8 (5.9)	0.61	40.2 (5.4)	79.3 (5.3)	6.22 (0.24)	4.44 (0.63)	351 (31)
XVI	5.1 (0.9)	11.2 (19.1)	0.45	17.8 (12.9)	29.9 (14.2)	3.48 (0.06)	3.15 (0.44)	208 (15)
XVII	3.2 (1.0)	3.4 (5.7)	0.93	0.7 (0.3)	4.7 (2.2)	0.98 (0.07)	2.02 (0.19)	80 (10)
XVIII	4.0 (0.8)	13.3 (6.5)	0.30	13.0 (2.1)	22.0 (4.6)	13.58 (0.13)	8.59 (0.15)	720 (51)

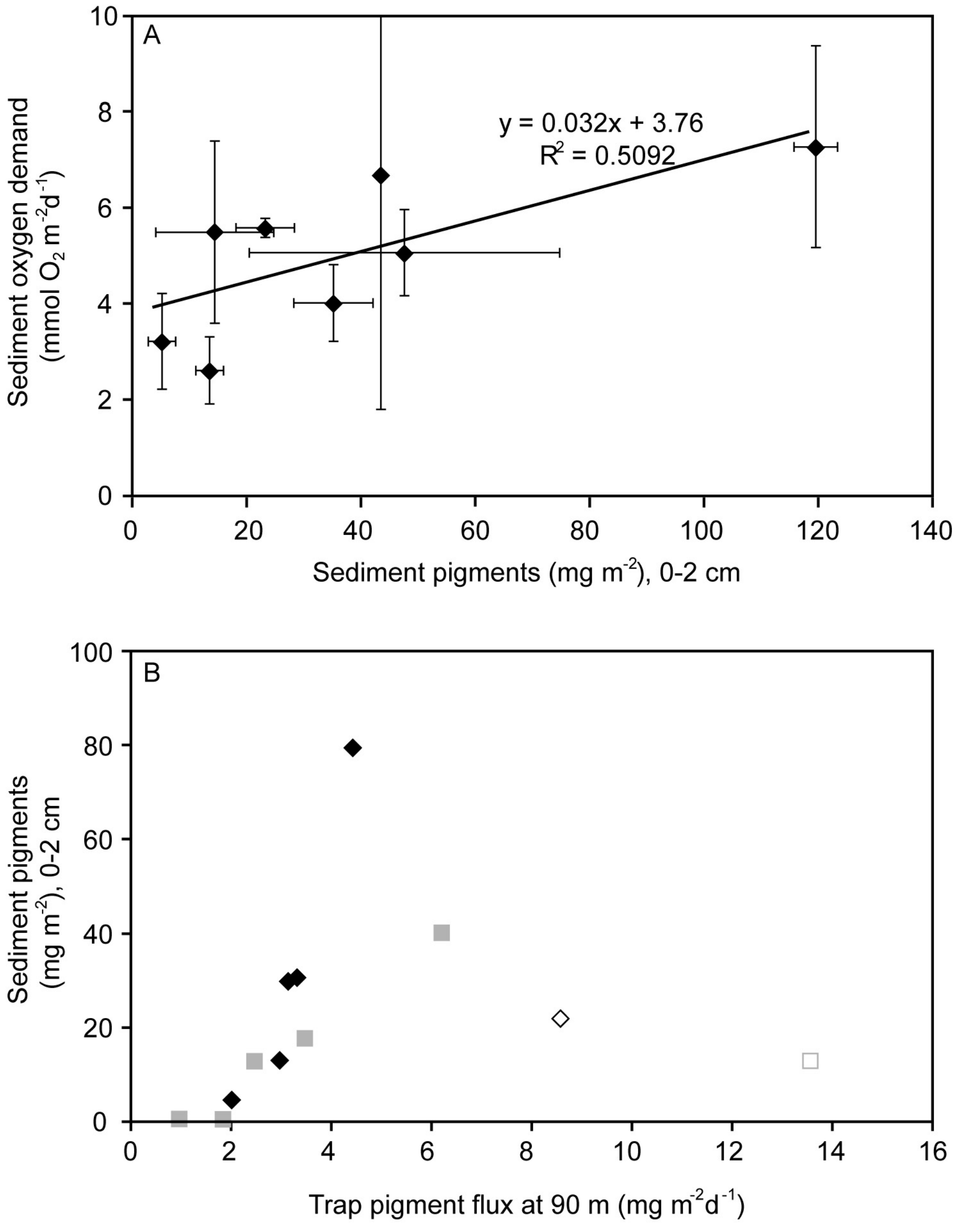

Figure 4. Regressions indicating the relationship between (a) sediment oxygen demand and sediment pigments (total from top 2 cm), and (b) sediment pigment concentration (from top 2 cm) and pigment flux calculated from sediment traps at 90 m. In (b) chlorophyll and phaeopigments are presented separately, and Station XVIII (open symbols) is excluded from the regression analyses. Regression lines not added in (b) to retain clarity, but see sec. 3.4 for more details of these statistically significant relationships. SOD values represent stations means of 4-12 replicates; pigment values are means of 2-3 replicates.

depth explained 58% and 47% of the sediment oxygen demand, respectively (Fig. 5a, b; $p < 0.03$ and 0.06, respectively). Again, station XVIII was excluded from these regressions (see sec. 4.3.1). A positive intercept of the y-axis in the regression of SOD on carbon flux indicates a tentative value for a 'baseline' respiration level of sediment community in the absence of any vertical flux (1.04 (+ 1.4) mmol O2 m-2 d-1, corresponding to a carbon remineralization rate of 0.88 mmol C m-2 d-1, assuming 1:1 stoichiometry and a respiration coefficient of 0.85; Smith 1978). This value needs to be further clarified from more stations from this region and around the Arctic.

4. Discussion

4.1 Patterns in SOD

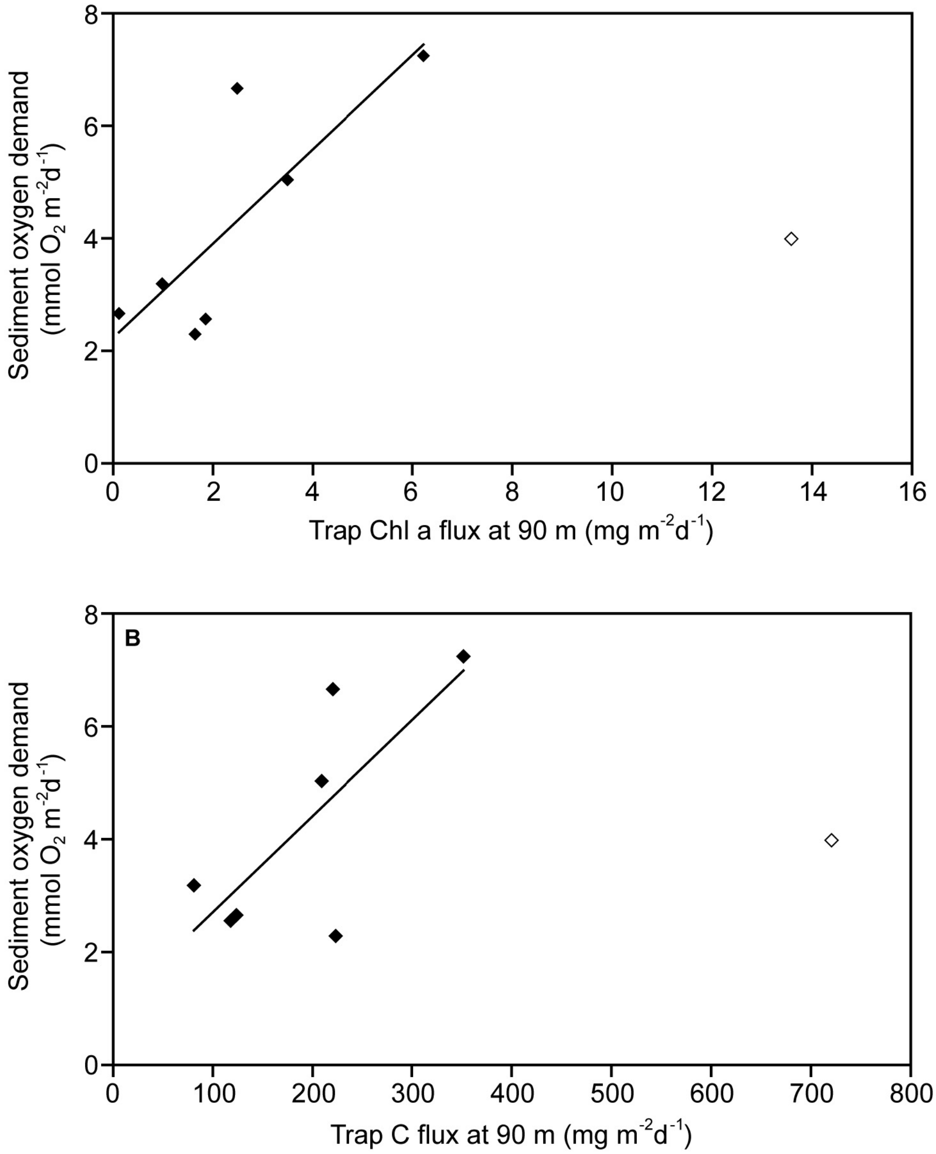

Figure 5. Regressions indicating the relationship between sediment oxygen demand and (a) chlorophyll a flux, and (b) carbon flux calculated from sediment traps at 90 m. Data for Station XVIII (open symbols) are presented but were omitted from regression analyses (see sec. 3.4 for details). SOD values represent stations means of 4-12 replicates.

Sediment oxygen demand measured over the range of biological and hydrographic conditions sampled in 2003-2005 in the western Barents Sea were within the range of values recorded for other shelf areas across the Arctic (Table 2; see also Clough et al. 2005, Grebmeier et al. 2006a). Higher (2-4 x) values have been found in 'hot spots' on shallow shelf areas well under 100m. Measured SOD values are underestimates of actual carbon mineralization by the sediment community as they do not take into account either metabolic activity by epifauna or anaerobic respiration. In the Barents Sea, epifauna can be abundant and may account for up to 75% of sediment community oxygen consumption (SCOC), although such values are usually restricted to depths shallower than 150 m (Piepenburg et al. 1995). Epifauna have also been found to be responsible for up to 25% of SCOC in the Chukchi Sea (Ambrose et al. 2001), and over 40% of SCOC in the Beaufort Sea (Renaud et al. 2007b). While we do not have epifaunal density estimates from the stations we sampled, most stations were deeper than 200 m. At these depths, Piepenburg et al. (2005) estimated the contribution of epifauna to be around 4% in the Barents Sea. The contribution to carbon mineralization by anaerobic bacteria has been shown to be important in Arctic fjords (Rysgaard et al. 1998, Glud et al. 2000), but less so in the open waters of the Barents Sea (Vandieken et al. 2006). Variability in SOD in time and space in the Arctic has been suggested to reflect an interaction among quality and quantity of carbon supply (Grebmeier and McRoy 1989, Piepenburg et al. 1997, Cooper et al. 2002, Renaud et al. 2006, Morata and Renaud 2007 – this volume), benthic community structure (Piepenburg et al. 1995), and sediment organic-carbon content (Grebmeier et al. 2006a). Other physical and biological parameters (ice cover, sediment grain size, integrated water-column chlorophyll, depth) act through one or more of the above parameters. Interannual variability in SOD has been suggested to be an indicator of climate-driven changes in ecosystem structure (Grebmeier et al. 2006b), although there has been little documentation of the temporal scales of variability in SOD (but see Renaud et al 2006 for a study at 230 m in the Beaufort Sea). A 7-year study at a deep (4100 m) station in the North Pacific showed considerable seasonal and interannual variability in SCOC (Smith and Kaufmann 1999). Renaud et al. (2006) have noted a 10-fold increase in SOD over a time span of several weeks at a single location, and Wenzhöfer and Glud (2004) observed a 7-fold variability over a diel cycle. These studies suggest that it is important to determine what is driving SOD, and over which time scales these drivers operate in benthic communities, especially if changes in SOD are to be used as indicators of climate change.

4.2 Role of faunal communities

The structure of benthic infaunal communities was distinct at each station (Fig. 2), despite sampling areas with similar sediment types on the Barents shelf. This was the case whether abundance data were transformed or not, and was also consistent if species-biomass data matrices were used instead of species-abundance matrices. A companion study using a VanVeen grab at the same stations revealed a similar biomass range; and these faunal community patterns are discussed in more detail, and in relation to environmental parameters at these stations, by Carroll et al. (this volume).

Communities with different composition and biomass may be expected to process food arriving at the sea floor in different manners. This has been shown in studies in the Bering and Chukchi Seas where SOD and macrofaunal biomass were significantly (positively) correlated (Clough et al. 2005, Grebmeier et al. 2006a). In this study, however, there is no direct statistical link between SOD and macrofaunal biomass, either on a per-core or per-station basis (Fig. 3). There are different arguments that can be used to explain this finding. It is possible, for example, that macrofauna are not responsible for the bulk of the oxygen consumption measured in our study (the Barents Sea). Multiple lines of evidence, however, suggest that macrofauna are, in fact, dominating SOD on some Arctic shelves (e.g. Piepenburg et al. 1995). Additionally, Clough et al. (2005) propose that biomass-specific respiration rate can be a useful indicator of the relative importance of macrofauna versus microbial processes, and suggest a value less than 1 indicates dominance by macrofauna. This metric is less than 1 for all stations sampled in our study (Table 2), indicating that macrofauna are likely to be important contributors to SOD. Grebmeier et al. (2006a) also suggest that macrofauna are dominating sediment oxygen consumption in their study area, citing several supporting works from that region. It seems likely, therefore, that macrofaunal respiration comprises the majority of the oxygen consumption on the Barents shelf. A second possible explanation is that this study samples from depths (approximately 200-500 m) where infauna are less important, and SOD is relatively low. This is probably important when comparing our results to those from areas of the highly productive and very shallow Chukchi Sea. As mentioned above, however, SOD measured in this study are similar to the general range found throughout the Arctic, including in shallow areas (< 200 m) of both the Beaufort and Laptev Seas (Schmid et al. 2006, Renaud et al. 2007, and references within).

We maintain that macrofauna are dominating SOD in our study, and that the published significant correlations between SOD and macrofaunal biomass on Arctic shelves with episodic deposition of phytodetritus do not reflect direct causal links between the two. We propose a modification to the current view of pelagic-benthic coupling on Arctic shelves. A change in macrofaunal community structure, including biomass, is a response to long-term (interannual) trends in organic carbon deposition (e.g. Blacker 1957, Grebmeier et al. 2006a), while SOD may respond rapidly to pulsed arrival of food to the sea floor (e.g. McMahon et al. 2006, Renaud et al. 2006). Therefore, finding a positive correlation between macrofaunal biomass and SOD may be a fortunate coincidence of sampling during a peak (or at least representative) time of deposition. Most stations in the Grebmeier et al. (2006a) study, and all shelf stations evaluated by Clough et al. (2005), were sampled in June-July, the time of highest primary production over the Chukchi shelf. The Barents Sea region is characterized by high variability in bloom conditions. Stations sampled in our study span a period of early to late phytoplankton bloom (Hodal and Kristiansen – this volume). It is likely, then, that many of the stations had not received their representative annual pulse in food supply. We suggest, then, that SOD and biomass respond to processes acting on significantly different time scales and should not be expected to correlate a priori. Admittedly, our findings are not conclusive, but are supported by both the stations sampled in this study and many of the studies for which relevant system-level data is available.

4.3 Pelagic-benthic coupling

Quantitative evidence: vertical flux, sediment inventories, and SOD

Correlation analysis suggested that half of the variability in SOD in our incubations can be explained by pigment concentrations in the top 2 cm of sediment (Fig 4A). This finding is consistent with other studies from the Arctic (Grant et al. 2002, Clough et al. 2005), and even from a tropical deep-sea site (Smith et al. 2002). Phytodetritus is the major carbon source to the benthos on Arctic shelves lacking significant riverine inputs, and processes affecting its delivery to the benthos are likely to be linked with benthic stocks and processes. Despite water depths at our stations being between 195 and 503 m, vertical pigment flux measured in traps 100-410 m above the sea floor explained over 85% of the variance in surface chl a and phaeopigments concentrations (Fig. 4B). This implies that material must be sinking quickly, and that the 90 m trap accurately estimates export production. Strong correlation of fluorometrically-determined chl a data with both chl a and fucoxanthin analyzed by HPLC (Morata et al. – this volume) suggests the majority of the phytodetrital input is from diatoms.

Wexels Riser et al. (2007), working at the same stations, found that 30% of the carbon flux at 90 m was in the form of fast-sinking fecal pellets from large copepods. Fast-sinking phytodetritus and a responsive benthic community suggest that these two processes are linked in both biological significance and in time scale. Not surprisingly then, both chl a and carbon flux measured in 90 m traps had strong relationships with SOD, each explaining more than 45% of the variance in this benthic process (Fig. 5). Clearly, the rate of delivery to the benthos will vary over the season depending on bloom stage, phytoplankton cell size, and pelagic grazing dynamics. Most of the flux, however, will occur during or around the spring bloom period, and approximately 45% of primary production during the spring bloom is exported below 90 m (Wexels Riser et al. 2007) and sinks with relatively little degradation from there to the sea floor. Although primary production by ice algae is considerably less than that by phytoplankton in the Barents Sea (Wassmann et al. 2006), ice algae can be a locally important additional food source for the benthos (McMahon et al. 2006, Tamelander et al. 2006), the more so as they presumably sink with greater efficiency than phytoplankton (Carroll and Carroll 2003). This suggests that a large part of net annual primary production sinks to the benthos in the productive Barents Sea and is rapidly processed by resident fauna.

We must point out several caveats in the interpretation of these data. Our results demonstrate statistical correlations and not direct causal relationships. Therefore, they do not necessarily indicate that chl a or carbon is the factor cuing benthic activity. Other biochemicals (amino acids, fatty acids, etc.) may stimulate benthic activity, and may even be the material immediately assimilated by deposit-feeding macrofauna. In addition, activity by bacteria and meiofauna, while assumed to represent a lower proportion of total oxygen demand on Arctic shelves than that by macrofauna (e.g. Piepenburg et al. 1995), may also respond to food inputs. In a study in the Beaufort Sea, however, meio- and micro- fauna increased their respiration rates by a factor of ~2 in response to ice algal deposition, while macrofaunal respiration increased by more than a factor of 10 (Renaud et al. 2006).

Finally, regressions involving trap data (Figs. 4B, 5) were performed excluding station XVIII where flux values were 2-3 times higher than at any other station. This is probably due to a 48 h storm that reached the station just after our arrival, completely homogenizing the previously stratified water column. Increased vertical transport estimates may be real, caused by increased flocculation and/or active transport, or an artifact of resuspension and/or lateral advection off nearby bank sediments. Since C:chl a and C:N ratios suggest trap material is fresh (Reigstad et al. - this volume), flocculation and active transport seem to be the most likely possibilities. Regardless, this event shows that while pelagic-benthic coupling is robust across a wide variety of water masses and bloom conditions, local dynamics may override its importance under some conditions.

Temporal and spatial scales

Time scales of benthic response to food inputs are not well studied, especially at high latitudes. Our evidence, and that by Renaud et al. (2006) from a January-July study in the Beaufort Sea, suggests that the benthic community is capable of rapid increases in activity (measured as SOD). Resolution of the time scale is difficult, but statistical links between vertical flux and both sediment pigments and SOD imply that response is on the order of days to a very few weeks. These scales agree with the days to weeks identified for faunal response to bloom sedimentation (Graf 1989, 1992) or experimental addition (McMahon et al. 2006), and the one-month lag between arrival and disappearance of a phytodetrital pulse on the sea floor off Northeast Greenland (Ambrose and Renaud 1997). In a review of benthic response to seasonal flux, Gooday (2002) grants that macrofauna may react quickly in productive waters of the continental margins. In the deep-sea, however, rapid response may be limited to smaller size fractions of the benthos (Gooday 2002), or may not be identifiable at all (Sauter et al. 2001).

A recent study around Antarctica tracked the seasonal signal of phytodetrital fluxes, sediment pigments, and sediment oxygen demand from shelf (to 600 m) environments (Smith et al. 2006). The authors found a strong seasonal pulse in vertical flux, but little response in SOD or sediment chl a integrated over the top 10 cm, and interpreted this as indicating that respiration responds to long-term trends in productivity, and sediment pigment inventories are evidence of poor coupling of benthic and pelagic processes. These results appear to be in sharp contrast to ours, and certainly the conclusions are divergent. As discussed above, benthic communities below a deeper water column may be expected to show less of a response to seasonal signals than those in shallow water (cf Gooday 2002). The depth of the Antarctic shelf may result in the most labile material being consumed during vertical transit. Additionally, POC flux may be intercepted by communities of epifaunal suspension feeders that Smith et al. (2006) observed feeding throughout most of the year. The sediment inventories of Smith et al. (2006) were considerably lower than those seen in our study: the largest concentration is less than half the smallest value that we found. It is unclear how such a low concentration could be seen as a buffer for the system (as they suggest) unless benthic fauna have particularly low food requirements. In fact, Stephens et al. (1997) found 43 – 89% of sediment pigment inventory to be "poorly degradable," perhaps bound to sediment particles (Keil et al.1994) and thus unavailable to consumers, despite appearing to be labile. The overwhelming majority (99%) of the flux material from the deep equatorial Pacific was found to have a half-life of days to a few months (Stephens et al. 1997). It is possible that the Antarctic shelf, especially at depths up to 600 m, operates in a fundamentally different manner than many other areas of the world ocean; and, clearly, different studies show different rates of benthic response to sedimenting organic material. It is left to further investigation, however, how respiratory processes should reflect a long-term supply process in communities of organisms generally considered to be opportunistic.

Perhaps what the contrasts between our study and that of Smith et al. (2006) best show is just how little spatial variability in patterns and process in the benthos has actually been investigated. Spatial patterns are difficult to identify as they are almost always accompanied by temporal (including, e.g. bloom stage: Tamelander et al. – this issue) variability. Still, over multiple studies, spatial patterns in benthic activity are identifiable (Grebmeier et al. 2006a), and these can be linked to pelagic processes on similar (meso-) scales.

Our findings of a tight link between benthic and pelagic processes highlight a second aspect of spatial scale. The high correlation ($r^2 > 0.85$) between vertical pigment flux at 90 m and surface-sediment pigments indicates a rapid sinking of some fraction of suspended particulate organic matter. Sinking matter does not fall straight downward, of course, but is advected laterally by currents. What our results indicate is that either vertical flux estimates are representative for a large area surrounding the study site, or trapped material sinks very quickly, or both. Similar results have been found on Arctic shelves (Ambrose et al. 2005, and see Renaud et al. 2006 for a longer discussion), suggesting that point measurements (opposed to time-integrated values) in surface waters are valid for assessing pelagic-benthic coupling at these depths.

4.4 Designing studies of pelagic-benthic coupling

A paradigm such as pelagic-benthic coupling is only valuable if we can use it as a tool to more effectively conduct research and make predictions about the functioning of ecosystems. This study points to the need for a common interpretation of the paradigm such that deviations from its predictions are interpretable and are neither dismissed as flawed nor used to invalidate a principle based on considerable data. What then is pelagic-benthic or benthic-pelagic coupling? Hargrave (1973) has described it as a fundamental relationship between the pelagic and benthic regions, while Gooday (2002; p. 312) defines it as "the deposition on the seabed of organic-rich particles originating in the upper water column." Already, these two quite general definitions differ importantly in that one points to the existence of a relationship, and the other describes a process by which this occurs. Pelagic-benthic coupling has been used synonymously with benthic-pelagic coupling by some, but the order of the wording should represent the predominant direction of transfer (in this case, pelagic productivity to benthic respiration would be pelagic-benthic coupling). Even within this context, pelagic-benthic coupling has also been used to describe the attenuation of vertical carbon flux in the top approximately 200 m of the water column without mention of a specific benthic stock or process this attenuation is impacting (Wassmann et al. 2003, Carmack and Wassmann 2006). We choose to use the more general definition for the relationship between benthic and pelagic processes (Hargrave 1973), and let each investigator decide which processes to study.

We maintain, however, that the only valid studies of pelagic-benthic coupling are those comparing processes (or stocks) that can reasonably be expected to vary on similar temporal and spatial scales. This study shows that benthic standing stock, a parameter that most investigators agree reflects an integrated response to food supply over interannual scales (e.g. Dunton et al. 2005), is not directly connected with SOD, a process varying on the scale of days to several weeks. SOD is, however, tightly linked to pelagic flux processes that vary over similar short time-scales.

We conclude that correlative studies investigating coupling of processes mismatched in temporal scale can lead to misinterpretation of observed patterns. Numerous examples exist in the literature (see reviews by Grebmeier and Barry 1991, Graf 1992, Piepenburg 2005), and a comprehensive reassessment of these studies may be enlightening. This revised view is not intended to discount the value of these studies, but to suggest a new perspective in which to view the results. The coherence of rates of water-column and sea-floor processes described in this study confirms the generality of the pelagic-benthic coupling paradigm since time scales are matched. Matching scales of time and space when looking for coupling may make studies more complex, but it will provide meaningful tests of where and when systems are coupled, and give useful insights into processes that may interfere with this fundamental relationship. Knowledge about potential influences of, for example, relative importance of pelagic consumption/retention of organic carbon, advection and vertical mixing events, benthic boundary-layer processes, or lag time in responses, are valuable in understanding ecosystem functioning and how it may vary in time and space. This is the ultimate value in using paradigms as conceptual models in ecological studies.

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Carbon cycling by seafloor communities on the eastern Beaufort Sea shelf

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Abstract

Tight pelagic–benthic coupling on Arctic shelves suggests that resident benthic communities may be particularly important in the cycling of carbon and regeneration of nutrients. We sampled 16 stations in the eastern Beaufort Sea during Autumn 2003 and Summer 2004 to determine spatial patterns in sediment community carbon demand, and the manner in which that demand was partitioned among epifauna, macroinfauna, and meio-/microfauna. Sediment carbon demand in this relatively oligotrophic area was similar to that measured in more productive Arctic shelf sites, and was largely related to the distribution of phytodetritus in surface sediments. Epibenthic megafaunal communities were dominated by echinoderms and exhibited peak abundance (up to 240 ind. m^{-2}) and biomass at stations in the 60–90 m depth range. Partitioning of the carbon demand revealed the local importance of megafauna, accounting for up to 41% of the community demand. Macrofauna accounted for on average between 25 and 69% of the carbon demand, while meio-/microfauna were responsible for 31–75% of the demand. Total community carbon demand by the benthos is estimated to account for approximately 60% of the annual new production in the region, suggesting the great ecosystem importance of benthic communities on the Beaufort shelf, and potentially across the Arctic. Our study region is strongly influenced by the Mackenzie River, and ongoing climate change is likely to result in altered productivity regimes, changes in quality and quantity of available food, and higher levels of sediment deposition. Impacts of these events on benthic community structure and function will likely have repercussions throughout the ecosystem.

Keywords: Benthos; Bottom photography; Climate change; Epifauna; Macrofauna; Sediment carbon demand

1. Introduction

While the central Arctic Ocean generally exhibits low biological activity, many shelf regions are hot spots of primary production. These areas of enhanced production may be associated with mesoscale oceanographic features, such as leads or polynyas, and develop

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due to a combination of factors including enhanced nutrient supplies from terrestrial sources or deep-mixing, consistently high light levels during the polar summer, and melt-water induced stratification (Stirling, 1980). The fate of organic carbon produced over Arctic shelves, however, is less understood. Clearly, abundant fish, seabird, and marine mammal populations in these areas suggest efficient links to higher trophic levels (Stirling, 1980). Other studies indicate high zooplankton grazing rates and recycling within the water column (Wassmann et al., 2006; Wexels Riser et al., in press), importance of the microbial loop (Sherr et al., 1997; Calbet and Landry, 2004), and off-shelf transport (Clough et al., 2005; Moran et al., 2005). Productivity of seafloor communities in the Arctic can be extremely high (e.g. Highsmith and Coyle, 1990; Grebmeier et al., 2006), indicating rapid deposition of considerable amounts of labile material to the seafloor. Studies of this pelagic–benthic coupling have determined that, in many areas of the Arctic, a large proportion of newly fixed carbon does, indeed, arrive at the seafloor relatively intact (Peterson and Curtis, 1980; Grebmeier and Barry, 1991; Piepenburg, 2005). How benthic communities process this material has significant consequences for ecosystem function, including carbon sequestration, nutrient regeneration, food web structure, and system sensitivity to environmental variability.

It is increasingly clear that seafloor communities in the Arctic can respond rapidly to seasonal food inputs (McMahon et al., 2006; Renaud et al., in press-a,c). On continental shelves around the world, bacteria and microfauna are thought to play a primary role in carbon cycling by the sediment community (Deming and Baross, 1993). Evidence from across the Arctic suggests that the macrofaunal component of the benthos can also be responsible for a significant, but variable, proportion of the total benthic activity (Grebmeier and McRoy, 1989; Piepenburg et al., 1995; Grant et al., 2002; Clough et al., 2005). Less well-documented, however, is the role of large, mobile epifaunal organisms. These organisms can be extremely abundant and account for the 20–94% of carbon processing in shallower areas (under 150 m) of Arctic shelf seas (Piepenburg et al., 1995; Ambrose et al., 2001). How benthic metabolism is partitioned among these three components of the community will affect the availability of organic carbon to consumers and, thus, determine the fate of carbon on Arctic shelves.

Arctic shelves may be particularly sensitive to the Earth's rapid climate change, which is nowhere more pronounced than in the Arctic (Intergovernmental Panel on Climate Change, 2001, 2007; Arctic Climate Impact Assessment, 2004). The direct and indirect effects of widespread warming are difficult to predict given the synergistic interactions of changing physical and chemical parameters, and the complex feedback mechanisms that may act. It is clear, however, that Arctic ecosystems will experience fundamental change in the coming decades. Possible impacts of climate warming on shelf benthos include change in community structure, increased sedimentation from riverine input, and altered sympagic (ice)–pelagic–benthic linkages due to new ice and water mass regimes (Arctic Climate Impact Assessment, 2004; Renaud et al., in press-b). It is arguable that shelf communities in areas of significant riverine discharge may experience the most intense changes.

The eastern Beaufort shelf is characterized by strong physical and biological gradients produced by the Cape Bathurst Polynya, the Mackenzie River, and a seasonally ice-covered shelf. Increased river flow and sediment loads are predicted consequences of climate change, and are expected to impact shallow areas of the shelf (Arctic Climate Impact Assessment, 2004). Additionally, coastal erosion caused by loss of ice cover, melting of permafrost, and more intense storms is already increasing. Predicting the effects of elevated loads of inorganic and organic material on the marine ecosystem requires an understanding of the present pathways of carbon processing by shelf benthos. We, therefore, sampled across the region during two seasons during the Canadian Arctic Shelf Exchange Study (CASES) and ask: What are the spatial patterns in sediment carbon demand on the eastern Beaufort shelf? What factors determine the distribution of epibenthic megafauna across the region? and How is carbon cycling partitioned among bacteria/microfauna, macrofauna, and epibenthic megafauna?

2. Methods

2.1. Sediment sampling and pigment analysis

Sediment was sampled from 16 stations during Autumn (20 October–19 November) 2003 (6 stations) and Summer (26 June–31 July) 2004 (11 stations), with one station being sampled during both seasons (Table 1, Fig. 1). Replicate spade corer (45 cm × 45 cm) deployments were made from the CCGS *Amundsen*, and only cores with intact surface layers were used. Sub-cores were taken for estimating the respiration of the entire infaunal sediment community, and for assessing sediment parameters. While sub-coring may be viewed as pseudoreplication, our analyses indicated that variance

Table 1
Depth, sampling date, and position for all stations sampled for benthic carbon consumption in the Beaufort Sea during this study

Station	Depth	Sampling date	Sampling position	
			Latitude (°N)	Longitude (°W)
Mud volcano	32	26-Jul-04	70.39	135.42
400	36	25-Jul-04	70.92	128.92
809	43	7-Jul-04	70.09	135.34
609	44	28-Jun-04	70.94	130.48
718F	45	20-Oct-03	70.17	133.54
718	42	11-Jul-04	70.17	133.54
300F	~50	15-Nov-03	70.59	127.74
415	54	21-Jul-04	71.90	125.87
912	55	6-Jul-04	69.49	137.94
403	56	25-Jul-04	71.11	128.31
709	86	21-Oct-03	70.95	133.75
206	90	1-Aug-04	70.32	124.84
406	180	24-Jul-04	71.31	127.71
315	221	20-Jul-04	71.48	124.54
200	234	17-Jul-04	70.05	126.30
803	241	9-Jul-04	70.64	135.89
650	244	13-Jul-04	71.32	131.58
906	271	5-Jul-04	70.05	138.58
500F	395	26-Oct-03	72.00	127.58
100F	~400	1-Nov-03	70.59	120.99
124F	~400	29-Oct-03	71.40	126.80
309F	420	13-Nov-03	71.12	125.80

These stations are listed in order of increasing depth, and are plotted on Fig. 1. Station numbers followed by an 'F' indicate those stations visited during Leg 2 (Fall 2003), and correspond with data presented by station number in Table 2 and Fig. 4.

in respiration rates among sub-cores from the same box core deployment was not different than the variance from different deployments at the same station (Renaud et al., in press-c).

Three sub-cores for sediment pigments (5 cm diameter × 10 cm deep) were taken from each station. Each sub-core was extruded and sliced at 1 cm intervals. Half of each slice was frozen in 60 mL centrifuge tubes, which were then wrapped in foil. Within 3 weeks, this sediment was thawed and 20 mL of 100% acetone was added. Pigments were analyzed fluorometrically (Holm-Hansen et al., 1965). Pigments were extracted in the freezer in the dark for 48 h, during which time tubes were shaken periodically. Sediment was then centrifuged (4000 rpm for 10 min at 0 °C) and the supernatant was analyzed (Turner Designs model 10-AU) before and after acidification with 20% HCl.

2.2. Oxygen demand measurements and estimates

Incubation cores (10 cm diameter × 20–25 cm deep with as much overlying water preserved as possible, 5–6 replicates per station) were topped off with bottom water collected using the ship's rosette and bubbled for at least 2 h to saturate the overlying water with oxygen. Control core tubes were filled with bottom water and bubbled. Cores were always kept in the cold room at 0–2 °C under very low light. All cores were sealed using tops that provided constant stirring. Oxygen concentrations were monitored during the incubations using a microelectrode (Unisense A/S; Aarhus, Denmark) inserted into a small sampling port in the core top. Incubations were terminated when 15–30% of the oxygen had been consumed (usually 30–48 h). Oxygen consumption rates were calculated as the (negative) slope of the regression line between oxygen concentration and time. If the slope of the regression for the control cores was significant, the mean value was subtracted. Rates were then scaled to a per m^2 basis.

Additional incubations (3–7 replicates) were performed to estimate the oxygen consumption of the most common large epifaunal species. The most abundant of these organisms observed in bottom photographs were collected using an epibenthic sled, and one average sized individual was added to each sediment core. Incubations were carried out exactly as for sediment cores above. Oxygen consumption by individuals was calculated by subtracting the whole sediment core means from the sediment plus added epifauna means, after accounting for control values. These values were then multiplied by mean densities (by species) determined from bottom photographs to arrive at oxygen consumption rates for the most common large epifaunal species for each station where photographs were taken.

To estimate how much of the whole-core respiration was due to micro- and meiofauna, we performed additional incubations ("minivials") according to Grant et al. (2002). Approximately 24 sub-cores (1.4 cm diameter × 2 cm deep) were taken at each station. Visible macrofauna were removed as the sediment was transferred into pre-cleaned 24 mL glass scintillation vials. Vials were filled with ultrafiltered (0.45 μm) near-bottom water to overflowing and sealed using caps with conical inserts to prevent air bubbles. All vials were shaken for 30 s and the oxygen concentration in half the vials was determined after 0.5–1 h using a microelectrode. This time allowed for settlement of sediment, as well as chemical oxidation of reduced mineral species present in the top 2 cm of sediment. The remaining vials were incubated for 48–56 h, after which the oxygen concentrations were measured. The difference between readings at the beginning and end of the incubation estimates the oxygen consumed by meiofauna, protozoa, and bacteria in the sediment. After eliminating vials where macrofauna were

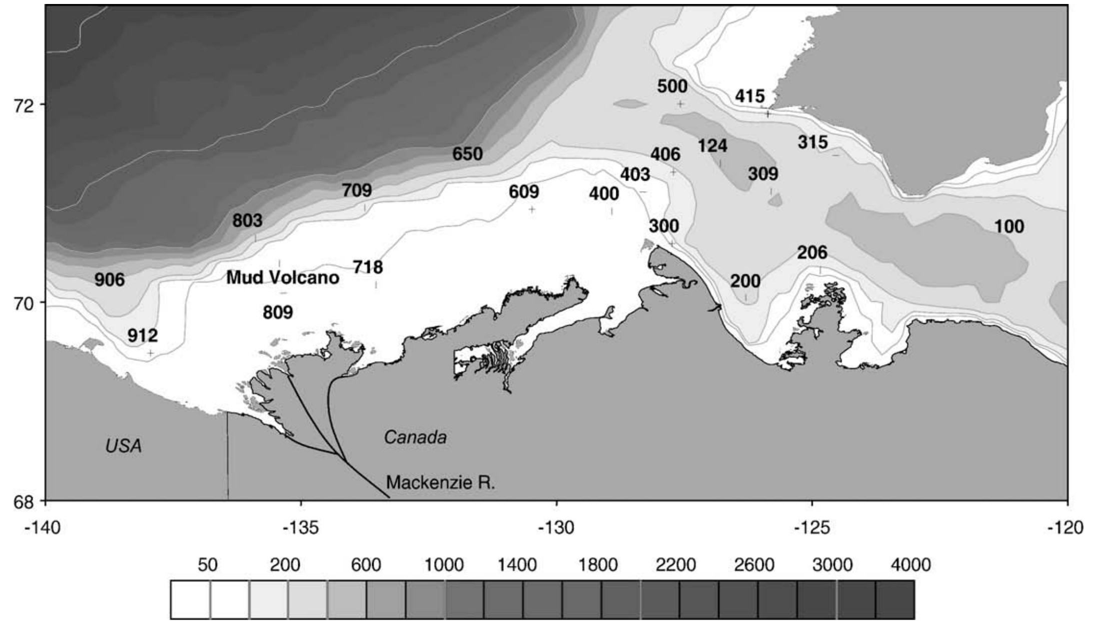

Fig. 1. Map of the eastern Beaufort Sea with station locations and numbers (or names) indicated. Shading indicates water depth. Latitude is in °N and longitude is negative (°W).

found after the incubation, sample sizes ranged from 5 to 12 vials per station. The entire procedure was performed in a cold room (0–2 °C) under very low light.

2.3. Bottom photography and analysis

An underwater digital camera (Benthos, 1.2 megapixel resolution) and two strobes were mounted 1.25 m above and centered within a 1 × 1 m frame which was equipped with a bottom-triggered shutter release. When the frame was lowered to the seafloor, a single photograph was taken. The system was raised several meters while the ship drifted, and 30 s later was again lowered to take another photograph. Up to 40 photographs were taken at each of the 12 stations sampled during Summer 2004. At one point, one of the strobes malfunctioned and, to compensate for the decreased light availability, the remaining strobe was remounted 0.5 m above the bottom of the frame. All photos were converted to jpeg format and processed using SigmaScan Pro Image Analysis (Jandel). Images with less than 30% of the area visible (due to stirring up of bottom sediments or to the benthic nepheloid layer) and frames that overlapped due to minimal ship drift were discarded, leaving between 8 and 30 usable images per station. The camera system could only be operated at depths less than 250 m.

Frame area was calculated using the frame bars visible in most images and varied somewhat among photographs. These bars also allowed for accurate measurement of animals present. Organisms were identified and counted, and densities were scaled to values per square meter. The most common organisms (mostly echinoderms) were measured (disk diameter and length × width, respectively) for estimation of biomass, which was then scaled to a m^2 basis as well. Estimation of biomass (ash-free dry mass: AFDM) from disk or test diameter was performed for only the three most common epifaunal taxa using published empirical relationships (Piepenburg and Schmid, 1996a for *Ophiocten sericeum* and *Ophiacantha bidentata*; Bluhm et al., 1998 for *Strongylocentrotus pallidus*). Densities of *Ophiopleura borealis* were low ($<0.5\ m^{-2}$), and, since no relationships were available from the literature, biomass of this taxon and of *Saduria sabini* (a locally abundant isopod) was not estimated.

2.4. Data treatment

Oxygen consumption rates were converted into carbon demand by assuming a 1:1 stoichiometric relationship between oxygen and carbon consumption, and then applying a respiratory coefficient of 0.85 (Smith, 1978). All values presented here use carbon demand as the currency for sediment community activity. Sediment carbon demand (hereafter used to describe carbon demand by *entire infaunal* sediment community) from whole-core incubations was partitioned between 'microfauna' and macrofauna by subtracting estimates of carbon demand from minivial incubations ('microfauna') from the rates derived from the whole-core incubation. Standard errors for resulting macrofaunal rates were determined by error propagation (calculating error estimates for derived values). Linear regressions were performed using the JMP-IN software package (SAS Institute), and adjusted r^2 values are presented.

3. Results

3.1. Sediment carbon demand

We sampled across a large range of depths on the Beaufort Sea continental shelf, from the 34 m deep mud volcano to 440 m at station 124. Sediment at most stations was fine silt with drop stones visible in many of the photographs. The percentage of fine sediment (silt-clay fraction) was less than 90% at only 4 (709, 300, 400 and 609) of the 16 stations (A. Aitken, U. Saskatchewan, pers. com.).

Sediment carbon demand was measured 17 times during the two cruises and varied from 1.3 to 5.2 mmol C m^{-2} d^{-1}, with rates at one station (300F) reaching 8.0 mmol C m^{-2} d^{-1} (Table 2). Sediment at this station contained numerous hyperbenthic amphipods, which undoubtedly were partly responsible for the high rates. Due to their frequent swimming behavior, these organisms cannot be strictly classified as infauna, and since hyperbenthic organisms were rare and possible to remove from other cores, this station was excluded from further statistical analyses.

Depth was significantly related to sediment carbon demand, with highest rates being found in shallow waters ($r^2 = 0.312, p < 0.05$; Fig. 2a). While depth explained 30% of the variability in sediment carbon demand, there was considerable scatter in the data. The range in sediment carbon demand was also much greater at stations of shallow and intermediate depth than the deepest stations, which all had very similar carbon demand.

Surface (0–2 cm) sediment pigment concentrations (chlorophyll *a* and phaeopigments) were much better

Table 2
Carbon demand (CD) by components of the sediment community presented as means (1 standard deviation, SD)

Station	SCD	Minivial CD	Macrofauna CD	Epifauna density	Epifauna biomass*	Epifauna CD
Mud volcano				2.7 (4.4)		0.17 (0.2)
400				7.1 (5.5)	310 (260)	0.11 (0.1)
809				1.2 (1.9)	24 (54)	0.04 (0.1)
609	5.2 (0.3)					
718F	3.2 (1.8)	3.7 (1.5)	−0.6 (2.3)			
718	4.8 (0.8)	10.9 (1.4)	−6.1 (1.4)			
300F	8.0 (4.3)					
415	4.9 (1.7)			19 (14)	4061 (1689)	0.07 (0.2)**
912	4.3 (0.4)					
403				91 (35)	1670 (550)	1.5 (0.6)
709	2.0 (0.6)			89	1251 (334)	1.5 (0.4)
206				243 (83)	2184 (638)	4.1 (1.4)
406	1.8 (0.3)	1.5 (0.3)	0.3 (0.4)	27(13)	396 (206)	0.4 (0.2)
315	2.1 (0.6)	1.5 (0.2)	0.6 (0.6)	12 (5.3)	429 (339)	0.2 (0.1)
200	4.9 (2.8)	2.8 (1.9)	2.0 (3.4)	11 (13)	159 (181)	0.2 (0.2)
803	3.2 (1.1)	1.8 (0.6)	1.4 (1.3)	0.7 (1.3)	54 (148)	0.01 (0.02)
650	1.3 (0.3)	0.4 (0.3)	0.9 (0.4)	0.4 (0.9)	0 (0)	0.01 (0.01)
906	3.9 (0.9)	2.0 (1.0)	2.0 (1.4)			
500F	2.3 (0.3)					
100F	1.5 (0.3)	1.2 (0.4)	0.3 (0.6)			
124F	1.9 (0.3)					
309F	2.2 (0.2)	2.4 (0.4)	−0.2 (0.5)			

Station numbers followed by 'F' indicate that it was sampled during the Autumn 2003 cruise. Other stations sampled during Summer 2004. Macrofaunal rates are calculated from whole-core incubation rates (sediment carbon demand, SCD) with minivial rates subtracted, with SD calculated from error propagation. This results in some values for Macrofauna CD to be negative. Abundance (ind. m^{-2}), biomass (mg ash-free dry mass m^{-2}), and CD data for epibenthic megafauna ('Epifauna') only include the three most common ophiuroid species, a sea urchin, and a single isopod species (see text Section 2.2 for details). Carbon demand data presented in mmol C m^{-2} d^{-1}. *Biomass not calculated for one species of ophiuroid or the isopod. **CD not calculated for sea urchins at Sta 415, but a possible range is included in the text (Section 4.2).

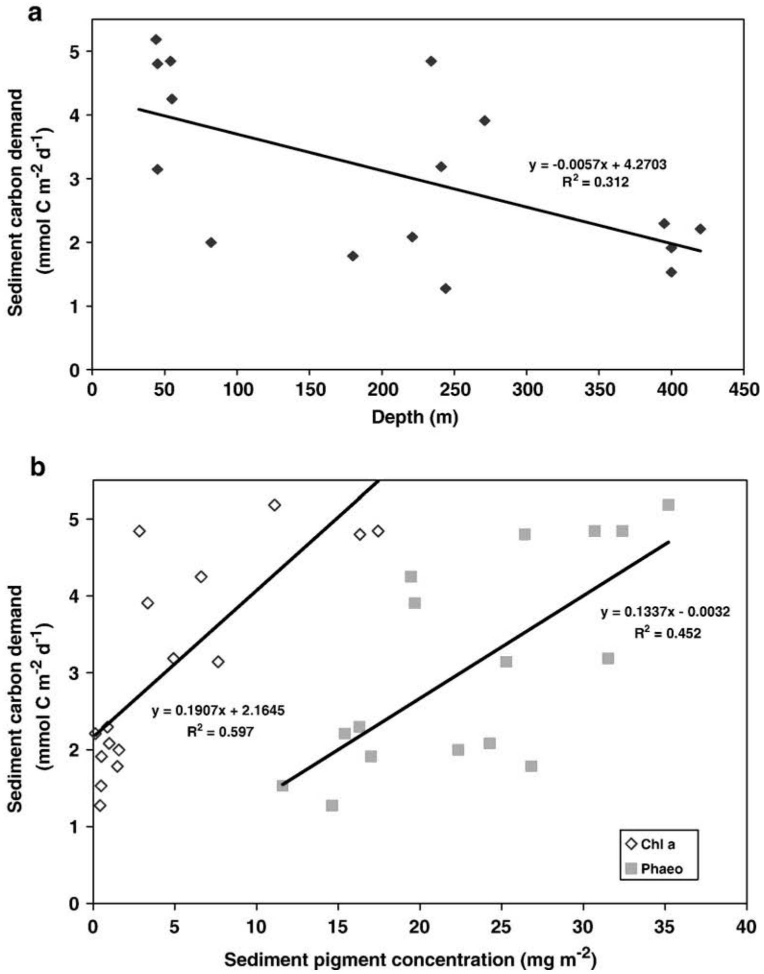

Fig. 2. Carbon demand (mmol C m^{-2} d^{-1}) from sediment core incubations plotted against (a) depth (m) and (b) sediment pigment concentration (chlorophyll *a* and phaeopigments) from the top 2 cm (mg m^{-2}). Regression lines are significant at $p<0.05$ and adjusted r^2 values are given.

predictors of sediment carbon demand than depth (Fig. 2b). These pigments alone explained between 45% (phaeopigments) and nearly 60% (chlorophyll *a*) of the variability in sediment carbon demand among stations. The strong positive relationship between chlorophyll *a* and sediment carbon demand should be interpreted with some caution, however, as half the stations had very low chlorophyll *a* concentrations and sediment carbon demand while the relationship at the remaining stations was much more variable. Taken together, however, the concentrations of chlorophyll *a* and phaeopigments were good predictors of sediment carbon demand among the stations sampled.

3.2. Epifaunal carbon demand

After excluding photographs with less than 30% of the image visible, 288 photographs were suitable for analysis and these had an average visibility of greater than 90% (range 66–99%). A total of 19 taxa were identified from bottom photographs from 12 stations, but the density and biomass was dominated by echinoderms: two common ophiuroids (*O. sericeum* and *O. bidentata*) and the sea urchin (*S. pallidus*). The large, conspicuous isopod, *S. sabini*, was also sufficiently common (station means as high as 3.2 m^{-2}) to be included in respiration estimates. The ophiuroids (primarily *Ophioctin*) were the most common large epifaunal organisms with over 240 individuals m^{-2} recorded at station 206. A third ophiuroid, *O. borealis*, was relatively uncommon. Density of each of these epifaunal species was highly and significantly positively correlated with its biomass ($r^2=0.93$). *S. pallidus* was present at only one station (415) and contributed 4022 mg AFDM m^{-2} to the total epifaunal biomass of 4061 mg AFDM m^{-2}. Since we did not conduct faunal respiration measurements with the urchin, we could not estimate the carbon demand for this species. Therefore, urchin biomass was subtracted from total epifaunal biomass in the statistical analyses described below.

The large range in density and biomass of large epifauna resulted in estimated carbon demand values that ranged over 2 orders of magnitude from a low of 0.01 mmol C m^{-2} d^{-1} at the deepest stations where photographs were possible (803 and 650) to 4.1 mmol C m^{-2} d^{-1} at a shallower station 206 (Table 2). By comparison, sediment carbon demand from whole-core incubations varied only by a factor of 6, and “microfauna” (minivials) carbon demand by only one order of magnitude. As with the epifauna, the lowest sediment and “microfauna’ carbon demands were recorded at station 650.

Maximum values of both epifaunal biomass and carbon demand were reached at stations located between approximately 60 and 90 m depth, with a sharp decline in both variables between 100 and 175 m deep (Fig. 3a, b). At very shallow and very deep stations, epifaunal carbon demand was less than 1.0 mmol C m^{-2} d^{-1} and often as low as 0.01 mmol C m^{-2} d^{-1} (Table 2, Fig. 3a). Epifaunal biomass was an excellent predictor of epifaunal carbon demand, with a strong positive linear relationship between the two variables ($r^2=0.862$, $p<0.001$; Fig. 3b).

3.3. Partitioning of carbon demand

It was possible to estimate the relative contributions of sediment and large epifauna to the sediment community carbon demand at 7 stations where both were measured (Table 2, Fig. 4). Sediment carbon demand dominated the community demand at all of these stations, but large epifauna accounted for 18% of total carbon demand at station 406, and 43% at 709. We

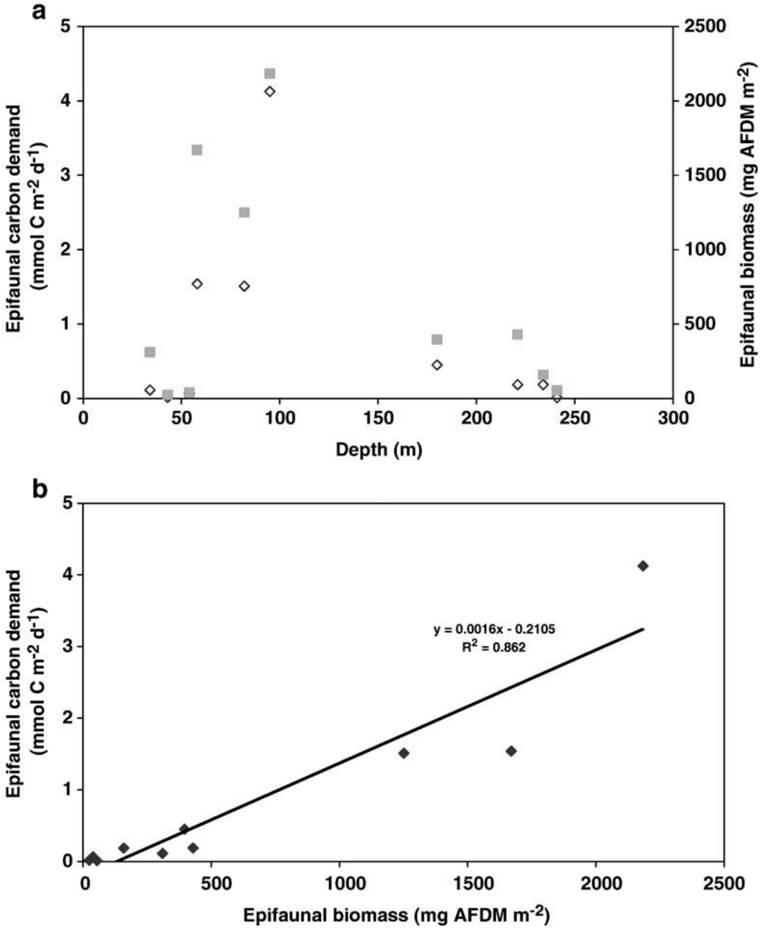

Fig. 3. (a) Scatter plots of epifaunal carbon demand (open diamonds, mmol C m^{-2} d^{-1}; left axis) and biomass (filled squares, mg AFDM m^{-2}; right axis) against depth (m). Station numbers for each point can be determined from Table 2. (b) Plot of epifaunal carbon demand (mmol C m^{-2} d^{-1}) against epifaunal biomass (g AFDM m^{-2}), indicating a statistically significant ($p<0.001$) positive relationship. Adjusted r^2 and linear equation provided.

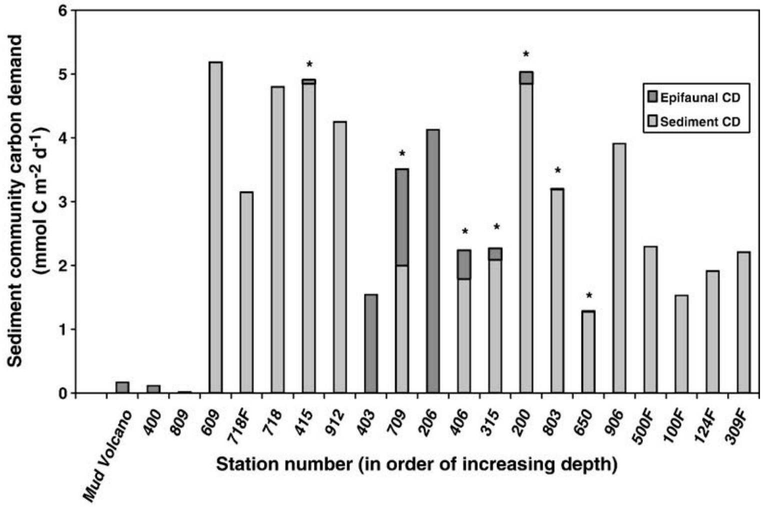

Fig. 4. Partitioning of carbon demand (CD; mmol C m^{-2} d^{-1}) between sediment (pale bars) and epifaunal (dark bars) components of the benthic community by station. Asterisks indicate stations where both measurements were made. Station information can be obtained in Table 1.

were not able to measure sediment carbon demand at the two stations with the highest epifaunal carbon demand (403, 206), but, assuming sediment carbon demand at these stations was similar to that at stations of similar depth, we suspect that epifauna would have been responsible for at least 40% of the community carbon demand at those stations (Table 2).

Minivial incubations were conducted at 10 stations, with rates ranging from 0.4 to 3.7 mmol C m^{-2} d^{-1} at 9 of the stations and a high of 10.9 mmol C m^{-2} d^{-1} at 718 (Table 2). Microfaunal carbon demand usually accounted for over half the sediment carbon demand, and exceeded that of macrofauna at most stations where both measurements were made (but not 650, Table 2). Microfaunal carbon demand was higher than the total sediment carbon demand at 3 stations (718F, 718, and 309F; Table 2). Carbon demand was estimated for all three components of the benthic community at 5 stations (406, 315, 803, 650, and 200) (Table 2). Partitioning of community carbon demand resulted in estimates of 0.3–18% for large epifauna, 14–69% for macrofauna, and 31–68% for microfauna. These values represent minimum ranges, however, as, for example, epifauna account for 43% of community carbon demand at station 709 where minivial incubations were not performed.

4. Discussion

4.1. Spatial patterns in sediment carbon demand

Sediment carbon demand measured over a range of depths and other environmental conditions across the eastern Beaufort Sea shelf revealed similar rates as those recorded elsewhere in the Arctic (Table 2, Clough et al., 2005; Renaud et al., in press-c). This is somewhat surprising considering that this area is thought to be relatively oligotrophic, especially compared with the more productive Chukchi and Barents Seas (Stein and Macdonald, 2004; Grebmeier et al., 2006). In addition, the influence of the Mackenzie River plume and its associated sediment load and refractory organic material may have been expected to result in lower carbon utilization rates. It is important to consider, however, that our measurements are snapshots taken during relatively productive periods (summer and fall) when labile material is expected to be arriving at the seafloor, at least at some of the stations. Recent studies have indicated tight coupling of benthic and pelagic processes and a rapid response by soft-sediment benthic communities in the Arctic to arrival of food (Renaud et al., in press-a,c). It is possible then, that annually integrated carbon demand is lower than in more productive shelf seas of the Arctic, but we do not have enough resolution to detect seasonal differences at all the stations sampled. Multiple mid-winter (January–March) measurements of sediment carbon demand at a single station (200) in this region (Renaud et al., in press-a) suggested an annual minimum rate of approximately 1.5 mmol C m^{-2} d^{-1}, similar to our lowest rates measured during the summer (Table 2).

The Beaufort shelf represents a complex of physical and chemical gradients. Depth explained around 30% of the variance in carbon demand, with higher rates found in shallower areas (Fig. 2a). Depth is a proxy for many variables, but on the Beaufort shelf, sediment grain size is not one of them. This is likely due to shallow regions being depositional areas in the Mackenzie delta region, instead of erosional areas as seen in the Barents Sea and northeast Greenland (Ambrose and Renaud, 1995; Piepenburg et al., 1995, 1997). A shallower water column may result in higher food inputs to the seafloor as sinking material has less time to be degraded or advected from the area. Finally, any nutrients regenerated by sediment communities may be more easily mixed into the euphotic zone in shallower areas, potentially leading to enhanced primary production. We are unable to discern among these or other potential ultimate factors responsible for the significant correlation between depth and sediment carbon demand. It is also difficult to test for an effect of the Mackenzie plume as the discharge is so great that it heavily influences much of the nearshore shelf area under 100 m, thus confounding depth effects with those of river inputs. Not surprisingly, therefore, we observed little difference in carbon demand at three stations along the shelf at depths from 42 to 55 m. Carbon demand at shallow stations 912, 718, and 609 (Fig. 1) ranged from 4.3 to 5.2 mmol C m^{-2} d^{-1} in the summer of 2004.

Availability of high quality food, particularly pigmented material indicative of phytodetritus, has proven to be the most reliable predictor of sediment carbon demand on Arctic shelves (Ambrose and Renaud, 1995; Piepenburg et al., 1997; Grant et al., 2002; Clough et al., 2005; Dunton et al., 2005; Renaud et al., in press-a,c; Morata and Renaud, in press). Both chlorophyll *a* and phaeopigment concentrations in surface sediment explain significant percentages of the variation in sediment carbon demand, and likely provide an indication of newly deposited organic material. Renaud et al. (in press-c) have noted that sediment pigment concentration in the Barents Sea was highly correlated with flux in sediment traps 100–400 m above the bottom, suggesting rapid deposition, and subsequent rapid utilization of this material. Half of the stations cluster near the *y*-axis in Fig. 2b, likely indicating locations where phytodetritus has not been deposited or has been largely processed. Epibenthic megafauna were most abundant, and had highest biomass and carbon demand, at the three stations (403, 709, 206) situated along steep depth contours. These areas also have very high infaunal abundance (over 15,000 ind. m^{-2}) due in part to local physical processes (K. Conlan, Canadian Museum of Nature, pers. com.). These findings suggest, again, that pelagic–benthic coupling in the Beaufort Sea is strong, just as has been observed in more productive areas of the Arctic.

4.2. Epifaunal communities and carbon demand

Epifaunal communities in the study area were highly variable in composition, abundance, and biomass. Ophiuroids were by far the largest component of epibenthic megafauna identified from bottom photographs, although sea urchins and large isopod crustaceans were locally important. Photographic surveys allow a larger area to be sampled, an effective tool when assessing importance of organisms that may exhibit aggregative behaviors or are large enough not to be sampled effectively by other methods. Despite this, the method has inherent biases associated with organism mobility and scales of patchiness, so not all epifaunal organisms were sampled well. Since ophiuroids are among the most abundant megafauna on Arctic continental shelves (reviewed in Piepenburg, 2000), we feel our results represent a good first-order estimate, albeit an underestimate, of community structure and function of large epifauna.

Our data are consistent with other studies from around the Arctic noting high abundances of ophiuroids in shallow shelf areas with significant potential for carbon mineralization. Studies from the Laptev, Barents, and Chukchi Seas, and from northeast Greenland indicate maximum densities between 158 and 430 ind. m^{-2} corresponding to carbon demands of 0.8–4.2 mmol C m^{-2} d^{-1} (Piepenburg et al., 1995; Piepenburg and Schmid, 1996a,b, 1997; Ambrose et al., 2001), while our maximum values are 243 ind. m^{-2} and 4.1 mmol C m^{-2} d^{-1} (Table 2). These rates and biomass values reflect only a few of the predominant large epifaunal species in the area. Carbon demand by sea urchins with mean abundances reaching 15 ind. m^{-2} was not determined, but conversion factors for a smaller Antarctic species suggest a minimum value in the range of 0.12–0.49 mmol C m^{-2} d^{-1} (Brockington and Clarke, 2001). This conservative estimate increases epifaunal carbon demand by more than a factor of 6 at this station (415).

Epifaunal abundance and biomass exhibited distinct peaks in the depth range 60–90 m, with sharp declines in both shallower and deeper areas (Fig. 3a). These patterns in community structure were reflected in function as shown by the strong relationship between epifaunal carbon demand and biomass (Fig. 3b). Epifaunal abundance is generally thought to be related to large-scale water column processes determining food availability (Piepenburg, 2000; Ambrose et al., 2001). It is possible that high sediment loads of riverine discharge, resuspension, and physical disturbances due to grounded ice limit epifaunal abundances in shallow areas of the Beaufort shelf. Additionally, high turbidity likely reduces primary production in the Mackenzie plume as light penetration during summer may be less than 1 m (P.E. Renaud, pers. obs.). In waters deeper than 100 m, food supply may be lower than in shallower depths and limit large epifauna, but we have limited data with which to evaluate this hypothesis. The negative relationship between sediment carbon demand and depth (Fig. 2a) provides only indirect support for this possibility. Carbon demand by epifauna is high only within a limited depth range, but may have ecosystem significance for both carbon cycling and for nutrient regeneration. Processes that impact the physical and biological conditions in this narrow depth range may, then, have important consequences for carbon cycling on Arctic shelves.

4.3. Partitioning of carbon flow

The role of the benthos in the function of marine ecosystems is primarily defined by the partitioning of carbon flow through the different community components. Understanding the strength of alternate carbon cycling pathways, and which environmental factors determine that strength, is critical for evaluating the fate of organic carbon (burial, remineralization, availability to higher trophic levels) and how the system may respond to environmental variability. Surprisingly few studies have investigated the partitioning of carbon flow in benthic communities, and these few studies have suggested that Arctic shelf benthos may operate differently from analogous systems in temperate and tropical regions (e.g. Piepenburg et al., 1995). More autochthonous production may reach the seafloor on Arctic shelves than in temperate and tropical latitudes, resulting in more efficient transfer to higher trophic levels (Peterson and Curtis, 1980). Further, empirical and modeling studies suggest an enhanced role of macrofauna relative to microbes and meiofauna on Arctic shelves (Grant et al., 1991, 2002; Piepenburg et al., 1995; Rowe et al., 1997; Clough et al., 2005; Grebmeier et al., 2006; Renaud et al., in press-a; Table 3). If more energy is channeled through macrofauna, then more carbon may be available for higher trophic levels.

Our studies of partitioning within the sediment column suggest that the microfaunal component is more important than the macrofaunal portion at nearly all stations where the two were compared, despite a similar range in the percentage of sediment carbon demand accounted for by each group (microfauna: 31–75%; macrofauna: 25–69%; Table 2). There were, however, three stations where microfaunal carbon demand was greater than that for the entire sediment community (and those stations are not included in the percentages listed above). While these results suggest, and probably rightly so, increased importance of microfauna at these stations (note that both summer and autumn sampling at station 718, located in the Mackenzie plume, showed this result), it also reflects methodological issues with our determination of microfaunal carbon demand. Minivial incubations involve both scaling issues (i.e. the cores used for minivial and whole sediment incubations are of different cross-sectional areas) and the likely overestimation of bacterial activity due to a slurry effect. Homogenization of the top 2 cm of sediment and exposing the entire sediment section to highly oxygenated water breaks up microgradients of nutrients and redox conditions, possibly enhancing bacterial carbon demand (Aller and Aller, 1998; Dauwe et al., 2001; Grant et al., 2002). This suggests that our already-substantial estimates of the role of macrofauna, may be conservative.

Recent efforts to assess the role of epibenthic megafauna in Arctic carbon cycling have been inspired largely by the widespread occurrence of dense assemblages of

Table 3
Summary of Arctic and temperate studies of carbon demand partitioning between macroinfauna and epifauna

Location	Depth	% Macrofauna	% Epifauna	Reference
Chukchi Sea	29–213 m		0–26	Ambrose et al. (2001)
North Water Polynya	250–570 m	0–70 (spring) 70–80 (summer)		Grant et al. (2002)
Chukchi Sea	30–280 m	Up to 61		Grebmeier and McRoy (1989)
Goban Spur	208–4470 m	15–57	0–0.1	Heip et al. (2001)
Bay of Biscay	2100 m	13	2	Mahaut et al. (1995)
Barents Sea	<200 m	14–75 (avg 17)	20–94 (avg 21)	Piepenburg et al. (1995)
	>200 m	5–75 (avg 21)	2–4 (avg 3)	
Young Sound, Greenland	<40 m		17.5	Rysgaard and Nielsen (2006)
	>40 m		26	
Beaufort Sea	38–440 m	33–69	0.1–41	Present study

Empty cells represent areas for which there are no data.

brittle stars across all Arctic shelves (see review by Piepenburg, 2000). In areas of dense ophiuroid beds, epifaunal carbon demand can be comparable to or greater than sediment carbon demand (Piepenburg, 2000, 2005). In our study, as in studies in the Barents (Piepenburg et al., 1995) and Chukchi (Ambrose et al., 2001) Seas, epibenthic megafauna are primarily important in shallow waters, accounting for up to 41% of the total sediment community carbon demand (Table 3, Fig. 4). Our results are from areas sampled during summer and autumn, largely outside the period of maximum phytodetrital deposition (as suggested by low sedimentary chlorophyll *a*: Fig. 2b), and demand may be higher during periods of high primary production. The success of many Arctic ophiuroid species is a consequence of their flexibility in feeding style, as some of the most abundant species are capable of both suspension feeding during periods of high flux, and deposit feeding at other times (Piepenburg, 2000). Coupled with their considerable mobility, epifauna, and especially ophiuroids, can respond rapidly to episodic pulses in food inputs to the seafloor (e.g. Smith, 1986).

Not only do ophiuroids actively process carbon at the sediment surface, their feeding and burrowing activities can also have important consequences for carbon cycling by sedimentary microbes and fauna (Ambrose, 1993; Smallwood and Wolff, 1999; Vopel et al., 2003; Solan et al., 2004). The ecosystem function of even small densities of epifauna may, therefore, be far more significant than their carbon demand would suggest, especially in shallow water systems dependent on nutrient regeneration by sedimentary communities to fuel primary production. Our study focused on only several large epifaunal taxa. One component of the benthos not quantified is the epi-/hyperbenthic amphipods. At several stations (300, 400) they (*Anonyx* spp., *Ampelisca* spp.) were found to occur in large numbers in box core samples (thousands per m^2), and their high carbon demand is hinted at by our incubations for station 300 (Table 2). Unfortunately, these organisms were not sampled effectively and their function in the ecosystem is left for future studies to elucidate (but see Highsmith and Coyle, 1990).

4.4. Ecosystem role of the benthos and possible impacts of climate change

Although our station distribution may not be representative of the entire shelf region, carbon demand ranges are fairly well constrained regardless of depth. Assuming a winter (basal) community carbon demand of 1.5 mmol C m^{-2} d^{-1} (Table 2, Renaud et al., in press-a) for 183 days, and a demand of 4 mmol C m^{-2} d^{-1} during the rest of the year (Table 2, Fig. 4), we can estimate an annual carbon demand for shelf benthos of approximately 1.01 mol C, or 12.1 g C m^{-2} for the entire year. Macdonald et al. (1987) have estimated the annual export production of the eastern Beaufort Sea shelf to be around 20 g C m^{-2} a^{-1}. Our estimate of annual carbon demand by the benthic community, therefore, represents more than 60% of the new production in the region. Subsidies from off-shelf or riverine input are not likely to change this percentage much. Annual vertical flux at the shelf break is estimated to be only 1 g C m^{-2} (Forest et al., in press). On the Beaufort shelf, riverine discharge accounts for approximately 40% of the total organic carbon input to the system (Goñi et al., 2005). But this riverine material is largely refractory, and only 20% of this carbon is remineralized (either in the water column or on the seafloor), while 60% is buried in delta and shelf sediments and the rest is exported off-shelf (Macdonald et al., 1998). By remineralizing well over half of the production on the shelf, the benthos clearly plays a large role in carbon cycling in the Beaufort Sea.

How will this role change due to climate changes being experienced in the Arctic now, and those predicted for the coming decades? We have few models to consult that can answer this question, but many of the predicted environmental changes could have significant impacts on Arctic shelf benthos (see Renaud et al., in press-b for a more detailed review of these issues). At this time, coastal erosion contributes only modestly to total organic supply, but accelerated melting of permafrost and predictions of more powerful storms in the region are expected to enhance both inorganic and organic sediment inputs (Arctic Climate Impact Assessment, 2004). This will increase the proportion of more refractory, lower quality organic matter available to shelf fauna. Already we see reduced abundances of large epifauna at depths shallower than 50 m. It is unclear to what extent this is a consequence of salinity, turbidity, physical disturbance, or food supply. Increased water turbidity, primarily during the season when both river discharge and photosynthesis are generally at their peaks, may decrease the quantity and quality of food supply for benthic communities generally thought to be food limited (Grebmeier and McRoy, 1989; Rysgaard et al., 1998; Piepenburg, 2005). High sediment loads may also clog filtering apparatus of both epifauna and infauna (Moore, 1977), leading to their retreat or disappearance from the shallow areas where both faunal groups play such important roles. This has been suggested to be one impact of climate change in fjords and bays as glaciers retreat and sediment loads increase (Wlodarska-Kowalczuk and Weslawski, 2001). Northward expansion of boreal invertebrates and fish has also been predicted under climate change scenarios (Renaud et al., in press-b).

It has been hypothesized that the presence of dense ophiuroid assemblages is due to low fish predation levels in Arctic waters (Piepenburg, 2000). Expansion of predatory fish from boreal regions may, therefore, profoundly impact epifaunal communities in the Arctic. This, along with potential change in community structure, will have unknown effects on carbon cycling by Arctic benthos.

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Seasonal variation in benthic community oxygen demand: A response to an ice algal bloom in the Beaufort Sea, Canadian Arctic?

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Abstract

Understanding pathways of carbon cycling on Arctic shelves is critical if we are to evaluate the potential effects of climate change on these systems. We investigated the relationship between ice algal standing stock and benthic respiration between January and July 2004 at a time series station in the southeastern Beaufort Sea. Both ice algal chlorophyll *a* and benthic sediment oxygen demand showed >10-fold increases from between March and April. While some of the increase in oxygen demand can be attributed to bacteria and meio-fauna, most was due to the activities of macroinfauna. We also observed a trend toward lower sediment pigment content during the pulse in benthic carbon remineralization. While chl *a* sedimentation also increased by a factor of 7 during this period, fluxes were not sufficient to provide for the increased carbon demand. We suggest that sedimenting ice algae provided a cue for increased benthic activity, and that direct consumption of ice algae and increased oxygen availability in the sediment due to bioturbation by epifaunal organisms led to the enhancement in respiration rates. Seasonal patterns in primary productivity and the activity of resident epifaunal and infaunal communities are, thus, important factors in determining carbon cycling patterns on Arctic shelves.

Keywords: Beaufort Sea; Carbon cycling; Ice algae; Benthic–pelagic coupling; Respiration; Benthos; Sedimentation

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1. Introduction

The Arctic is experiencing drastic climate change. Recent studies have documented significant air and ocean temperature increases, and reductions in ice cover, and it is predicted that these changes will accelerate over the next 50–100 years (Vinnikov et al., 1999; Intergovernmental Panel on Climate Change, 2001; Moritz et al., 2002; ACIA, 2004; Johannessen et al., 2004). It is unclear how these changes will impact ecosystems on the expansive continental shelves of the Arctic's marginal seas, but qualitative and quantitative shifts of many components and pathways of the carbon cycle are likely to occur (Walsh et al., 2004; Wassmann, 2004).

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Understanding current pathways may help to identify where impacts of climate change are most likely to be observed.

The Arctic Ocean and its marginal seas overlie 25% of the world's continental shelves. These shelf systems exhibit pronounced seasonality as ice cover and the polar winter limits the period of algal production. Strong seasonal pulses of phytodetritus to the benthos (Wefer, 1989; Honjo, 1990) fuel some of the richest benthic communities and fisheries in the world, indicating tight linkages between benthic and pelagic processes (e.g. Peterson and Curtis, 1980; Carey, 1991; Grebmeier and Barry, 1991; Ambrose and Renaud, 1995; Piepenburg et al., 1997; Wollenburg and Kuhnt, 2000). Additionally, a larger fraction of sedimenting carbon is buried in the Arctic Ocean than in many other areas of the world's oceans (Stein and MacDonald, 2004). Clearly, the benthos plays an important role in the carbon cycle of Arctic shelves.

Logistical difficulties due to ice cover have limited most studies of the sources and fate of carbon on Arctic shelves to the period from late spring to early fall. There has been some suggestion, however, that early season production by algae growing within and beneath the sea ice may represent a significant fraction of carbon flux to the benthos in these regions (Ambrose and Renaud, 1997; Bauerfeind et al., 1997; Hargrave et al., 2002). Ice algae communities are notoriously patchy (e.g. Gosselin et al., 1997; Rysgaard et al., 2001), but they have been suggested to account for a significant proportion of the total primary production in the Arctic (Horner and Schrader, 1982; Legendre et al., 1992; Gosselin et al., 1997). Since ice algae are known to sink rapidly upon release from the sea ice (Michel et al., 1997a,b) and can be processed by benthic fauna (Ambrose et al., 2001), it has been suggested that they are of particular importance to benthic communities (Ambrose and Renaud, 1995, 1997; Ritzrau, 1997; Ritzrau and Thomsen, 1997; Hargrave et al., 2002; Carroll and Carroll, 2003). Evidence for such importance, however, is largely circumstantial.

This study represents the first effort to quantify the response of a benthic community to an ice algal bloom. Taking advantage of the infrastructure provided by the Canadian Arctic Shelf Exchange Study (CASES), we were able to monitor the ice algal community and its export from the sea ice, sediment carbon and phytopigment content, and benthic community respiration from mid-winter to ice break-up. In this study, we ask: (1) What are the seasonal dynamics of the ice algal community? (2) How are these dynamics reflected in sediment biochemical parameters? and (3) What is the impact of ice algal seasonality on benthic community respiration?

2. Materials and methods

2.1. Study site

From December 2003 to June 2004, the Canadian Coast Guard icebreaker *Amundsen* was frozen into the annual shore-fast ice in western Franklin Bay, southeastern Beaufort Sea (70°02′N, 126°18′W; Fig. 1). Water depth at our sampling station was 231 m. The timing and magnitude primary productivity in this region vary considerably (Arrigo and van Dijken, 2004), and are linked to ice dynamics. Ice sampling was conducted in an undisturbed area approximately 1.5 km NE of 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, and then decreased to 1.55 m on the last sampling day on 20 June. Near-bottom temperature, salinity, and transmissivity data were obtained from twice-daily CTD casts from the ship.

2.2. Ice algal measurements

Multiple ice cores were collected with a manual corer (Mark II coring system, 9 cm internal diameter; Kovacs Enterprise) at two sites representative of low (3.4 ± 2.5 cm) and high (16.2 ± 3.5 cm) snow conditions for analysis of ice algal communities. Ice thickness was recorded at the time of sampling. The bottom 4 cm of cores from each snow depth were cut and pooled together, and slowly melted in 0.2 μm filtered surface seawater to minimize osmotic stress (Garrison and Buck, 1986). Estimates of chlorophyll a biomass (chl *a*) on 10 cm sections over the total length of ice cores were performed on three occasions (25 March, 24 April and 4 May), showing that 94.6% ± 2.5% of the total integrated chl *a* biomass in ice cores was found in the bottom <10 cm section. Concentrations of chl *a* were determined fluorometrically (Turner Designs Model 10-AU) on duplicate subsamples filtered on Whatman GF/F filters after 24 h extraction in 90% acetone at 4 °C. The concentration of chlorophyll *a* was calculated according to Holm-Hansen et al. (1965).

2.3. Under-ice sedimentation and water column sampling

Vertical pigment fluxes were measured from February 23 to June 20, using sequential deployments ($n = 16$) of particle interceptor traps. The traps, which were PVC cylinders with a height/diameter ratio of 7 (10 cm diameter), were attached to a tripod on the sea ice and deployed at 1, 15, and 25 m from the undersurface of the

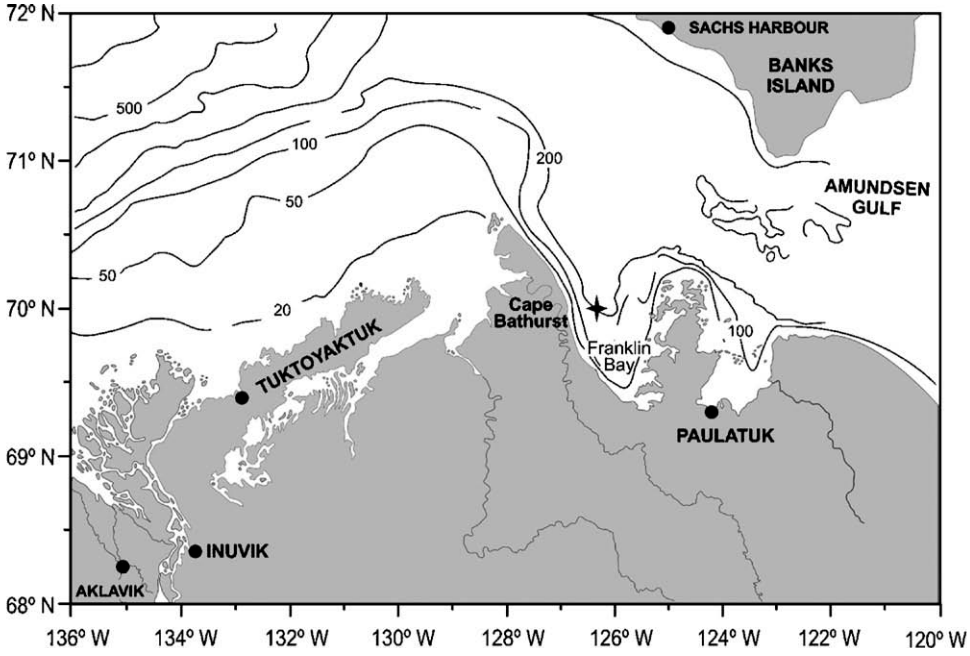

Fig. 1. Map of the southeastern Beaufort Sea. The study site for the time-series in Franklin Bay is identified by the cross. Depth is expressed in meters.

ice. Prior to deployment, the traps were filled with 0.22 μm filtered seawater collected well below the deployment depth to ensure higher water density in the traps compared to ambient water. The particle interceptor traps were deployed for 7.8 ± 0.8 days ($n = 6$) from March to mid-May, while the deployment time was reduced to 6.2 ± 0.4 days ($n = 8$) from mid-May to end of June, in response to higher sinking fluxes. Upon recovery, material from the traps was prefiltered through a 425 μm mesh prior to subsequent analysis in order to remove large swimmers. Samples were gently mixed to achieve homogenous subsampling. Water at the ice–water interface was collected using a hand pump with Tygon tubing attached to an adjustable arm that was held parallel to the undersurface of the ice. The tubing and pump were thoroughly rinsed with the sampled water prior to sample collection in sterile containers. Duplicate 100–500 mL subsamples from particle interceptor traps and interfacial water were analyzed for chlorophyll *a* and total pigments. These subsamples were filtered onto Whatman GF/F filters, and analysed as described above.

2.4. Sediment sampling and benthic respiration

Sediment was sampled on 5 dates between 14 January and 7 May 2004, and then again on 4 July 2004. On 6 April, sampling was performed 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. On this date we used multiple deployments of a small corer; but on all other occasions a spade corer (45 cm × 45 cm) was deployed through a hole cut in the sea ice near the ship. During winter and spring, only a single core was collected, due to the difficult and time-consuming logistics involved in cutting the sampling hole in ice that was up to 3 m thick near the ship. In July, when the area was ice-free, the box corer was deployed three times. Only cores with intact surface layers, indicated by surface 'fluff' or delicate epifauna, were used.

Replicate sub-cores (10 cm diameter × 20–25 cm deep with as much overlying water preserved as possible) were taken for estimating the respiration of the entire infaunal sediment community. While sub-coring may be viewed as pseudoreplication, our analyses indicated that variance in respiration rates among sub-cores from the same box core deployment was not different than the variance from different deployments at the same station (unpub. data). Incubation cores (3–4 per sampling date) were topped off with bottom water collected using the ship's rosette and bubbled to saturate the overlying water with oxygen. Control cores were filled with bottom water and bubbled. Cores were always kept in the cold room at 0–2 °C. All cores were sealed using tops that provided constant stirring. Oxygen concentrations were monitored during the incubations using a microelectrode (Unisense A/S; Aarhus, Denmark) inserted into a small sampling port in the core top. Incubations were terminated when 15–30% of the oxygen had been consumed (usually 30–48 h).

To estimate how much of the whole-core respiration was due to micro- and meio-fauna, we performed additional incubations ("minivials") following the methodology of Grant et al. (2002). Approximately 24 subcores (1.4 cm diameter × 2 cm deep) were taken on the 6 sampling dates. Macrofauna was removed as the sediment was transferred into pre-cleaned 24 mL glass scintillation vials. Vials were filled with Whatman GF/F-filtered near-bottom water to overflowing and sealed using caps with conical inserts to prevent air bubbles. All vials were shaken and the oxygen concentration in half the vials was determined after 0.5–1 h using a microelectrode. This time allowed for settlement of sediment, as well as chemical oxidation of reduced mineral species present in the top 2 cm of sediment. The remaining vials were incubated for 48–56 h, after which the oxygen concentrations were measured. The difference between time zero (t_0) and time final (t_f) is an estimate of oxygen consumption by the meio-fauna, protozoa, and bacteria in the sediment. After eliminating vials where macrofauna was found after the incubation, sample sizes ranged from 4 to 14 vials. The entire procedure was performed in a cold room (0–2 °C) under very low light.

2.5. Sediment analysis

Triplicate sub-cores for sediment pigments (5 cm diameter × 10 cm deep) and organic carbon and nitrogen (1.9 cm diameter × 2 cm deep) were taken during the winter; one of each type of sub-core was taken from each of the three replicate deployments in July. Pigments were analyzed fluorometrically according to Holm-Hansen et al. (1965). Each sub-core was extruded and sliced at 1 cm intervals. Half of each slice was frozen in 60 mL centrifuge tubes, which were then wrapped in foil. Within 3 weeks, this sediment was thawed and 20 mL of 100% acetone was added. Pigments were extracted in the freezer in the dark, during which tubes were shaken periodically. After 48 h, sediment was centrifuged (4000 rpm for 10 min at 0 °C) and the supernatant was analyzed in a Turner Designs model 10-AU fluorometer before and after acidification with 20% HCl.

Samples for organic carbon and total nitrogen content were stored at − 20 °C until analysis. Sediment was dried at 60 °C for 24–48 h and ground until homogeneous. A subsample (1 g) was acidified three times with 2 mL of 1 N HCl (drying and grinding between each acid treatment) to dissolve carbonates. Homogenized sediment was then run on a Fisons model 1108 CHN Analyzer with acetanilide as a standard.

2.6. Data analysis

Respiration, sediment pigment, carbon, and nitrogen data were analyzed by one-way analyses of variance (ANOVA) or Kruskal–Wallis (KW) tests (unequal variances), with sampling date as the discriminating factor, using the JMP-IN (SAS Institute) software package. Where ANOVA tests were significant, the Tukey HSD post-hoc test was performed to elucidate the differences. Bonferroni contrasts were performed following significant KW tests. Before performing the ANOVA tests, homogeneity of variances was tested using Bartlett's test (Sokal and Rohlf, 1995).

3. Results

3.1. Near-bottom hydrographic measurements

Values obtained from the CTD indicated a range in near-bottom (within 10 m) temperature from +0.2 to − 0.7 °C, and in salinity between 33.8 and 34.7 over the 6 month period of the study. It is interesting to note that temperature was relatively constant between +0.2 and +0.05 °C for the first 6 sampling dates and decreased to − 0.7 °C between May and July. Near-bottom transmissivity was variable, yet exhibited a noticeable decline in the period of 10 March to 20 April, when most readings (with one exception) were below the lowest measurements recorded outside this time interval (Fig. 4).

3.2. Surface and ice biomass and sinking export

There was a clear seasonal trend in the ice algae biomass in the bottom ice, as evidenced by monthly averaged chl *a* concentrations for high and low snow covers combined (Fig. 2a). Average bottom ice chl *a* concentrations were <0.3 mg chl *a* m^{-2} during the months of February–March. These concentrations increased by more 10-fold in April (avg = 5.6 mg chl *a* m^{-2}), and reached ca. 15 mg chl *a* m^{-2} in May. A strong decrease in bottom ice chl *a* was observed during the month of June, with average values of 2.5 mg chl *a* m^{-2}. KW tests on means showed statistically significant differences ($p < 0.001$) in ice algae concentrations among months, with post-hoc Bonferroni contrasts (at alpha = 0.05) indicating that May concentrations were higher than during any other time period. When the alpha-value was raised to 0.10, April values were also significantly higher than the average value for February–March. There were no phaeopigments observed in the bottom ice (values of 0 throughout the season).

While ice coring can potentially underestimate ice algal biomass (Ambrose et al., 2005), comparative

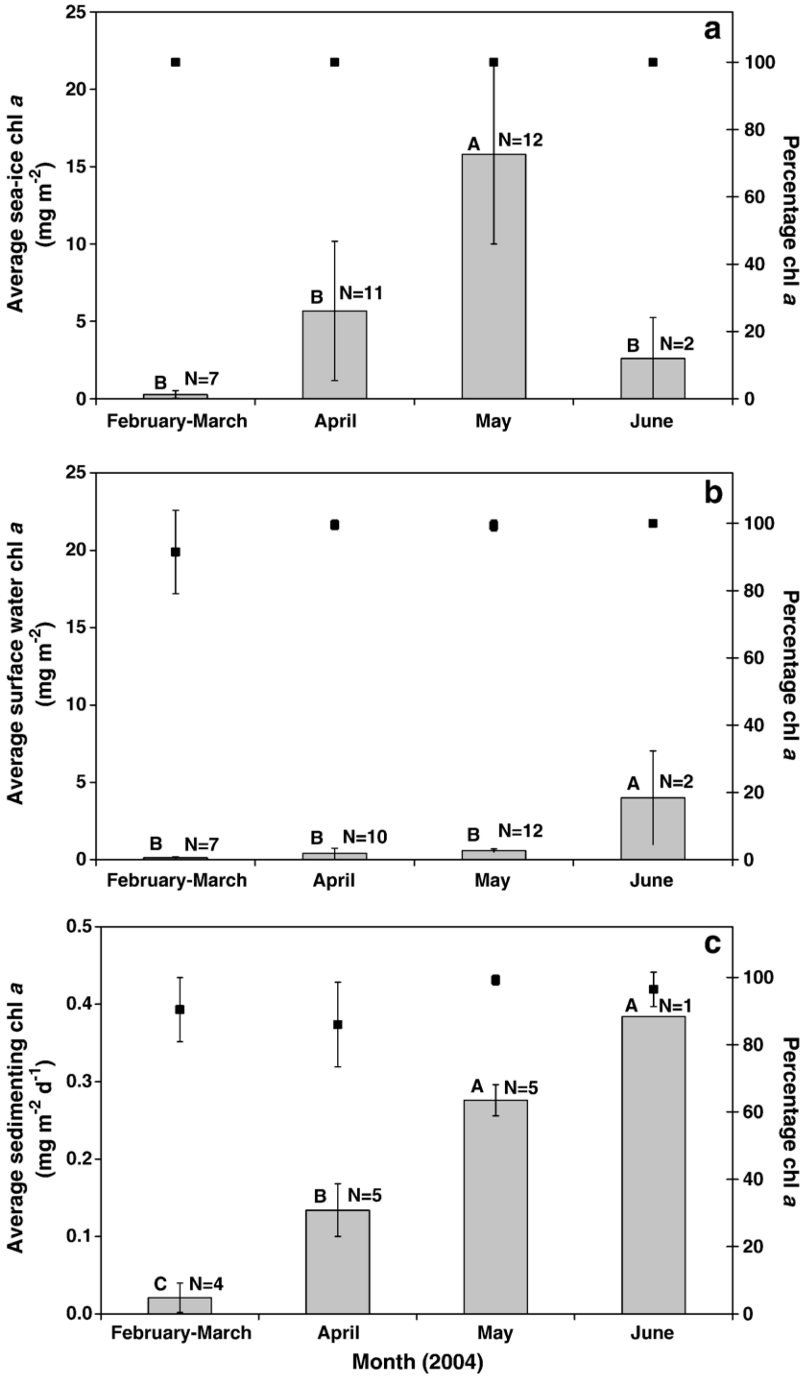

Fig. 2. Seasonal trends in average chlorophyll *a* concentration from (a) the bottom of the sea ice, (b) the top 1 m of seawater directly under the ice, and (c) particle interceptor traps deployed 1 m below the ice at a station in the southeastern Beaufort Sea. Data are averages of 1 or 2 months of samples in 2004. N= number of samples represented by the means. All error bars represent ± 1 standard deviation. Black squares represent the average percentage of total pigments from each sampling period that was chlorophyll *a* (right axis). Date was determined to have a significant effect on chlorophyll *a* concentrations in all material ($p < 0.001$; Kruskal–Wallis test); bars with the same upper case letter are not significantly different from each other (Bonferroni test at alpha = 0.05). Percent chlorophyll *a* was not significantly different among time periods in any of the material sampled ($p \gg 0.05$).

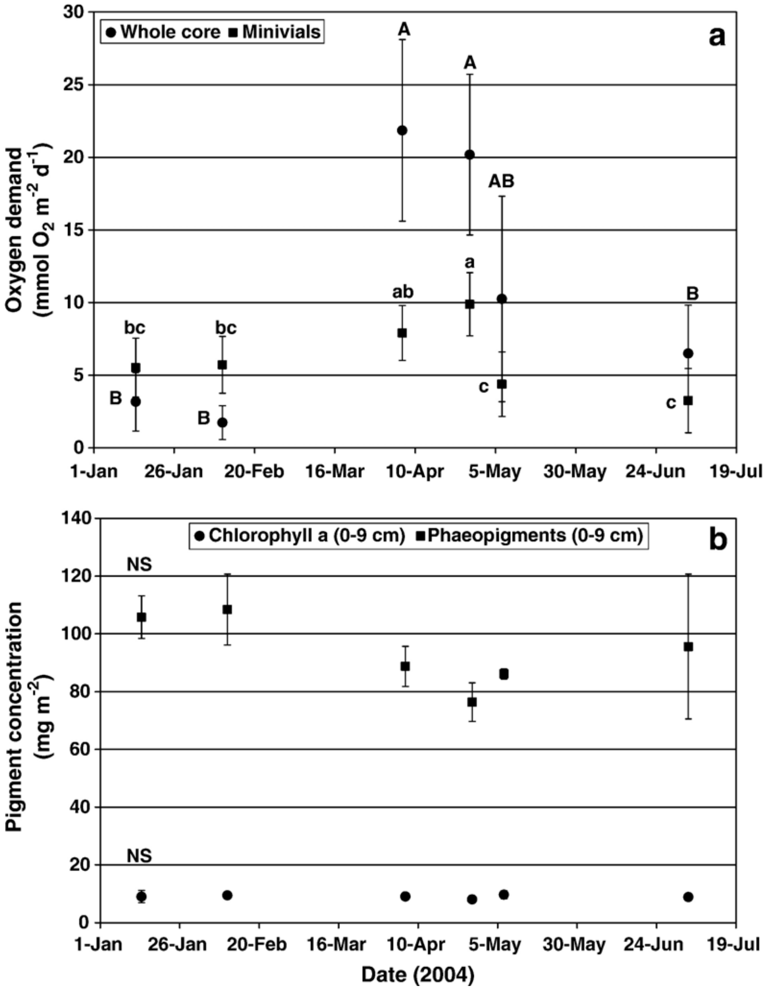

Fig. 3. Time-series measurements of (a) sediment oxygen demand from whole-core (circles) and minivial (squares) incubations, and (b) concentration of sediment chlorophyll *a* (circles) and phaeopigments (squares). When analysis of variance indicated significant date effects ($p<0.05$), letters appear beside or above symbols. Symbols marked with the same letter are not significantly different by Tukey's HSD test. NS indicates that the measurements did not vary significantly among dates. In (a), upper case letters refer to results of statistical tests for whole-core incubations; lower case letters reflect results from minivial incubations. All error bars represent ± 1 standard deviation.

results from SIPRE cores and cores obtained by divers in Arctic first-year ice have shown that this underestimation primarily occurs at the time of ice melt, with the loosening of the ice algae community. During the period of ice growth, SIPRE and divers cores provide comparative results (Welch et al., 1988). During our study, ice growth was taking place from February to the end of May. Hence, we are confident that the ice algae biomass estimates for February to May are reasonable. For the month of June, when melt was taking place, there was a potential underestimation of the ice algal biomass, although it cannot be quantified. This possibility, however, does not change the seasonal trends presented here.

Surface water (top 1 m under the ice) chl *a* was consistently low (<0.60 mg chl *a* m^{-2}) until June, when average values increased to 4.0 mg chl *a* m^{-2} (Fig. 2b). Biomass values were significantly higher in June than during the previous periods ($p<0.001$; KW). Chl *a* made up more than 90% of the total pigments in surface waters for the entire February to June period.

Seasonal trends for sinking fluxes of chl *a* at 1 m under the ice were similar to those for ice algae (Fig. 2c). Very low sinking fluxes of chl *a* were observed during February–March (average = 0.02 mg d^{-1}). These fluxes increased 7-fold in April (average = 0.13 mg chl *a* m^{-2} d^{-1}), and continued to increase during May and June, at a time when maximum sinking fluxes were observed (0.38 mg chl *a* m^{-2} d^{-1}). Means from all months were significantly different, except for May and June deployments when results were indistinguishable ($p< 0.001$;

ANOVA). Seasonal trends in the sinking fluxes of chl *a* at 15 and 25 m (not shown) closely followed those observed at 1 m beneath the sea ice. Sinking fluxes of pigments at 25 m made up, on average, 69% of pigment sinking fluxes observed at 1 m (% var=27% for the whole sampling season). The percent chl *a* in total pigments (chl *a*+ phaeopigments) in the 1 m traps varied between 86 to 99% during the season, with no significant differences among sampling months ($p>0.11$; Fig. 2c).

3.3. Benthic respiration

Sediment-community oxygen demand varied by more than one order of magnitude (1.75 to 21.0 mmol O_2 m^{-2} d^{-1} between 10 February and 6 April) over the sampling period (Fig. 3a). Respiration rates measured on 6 April and 27 April were significantly higher than rates measured on 14 January, 10 February or 4 July ($p<0.0001$; ANOVA). Variances were not significantly different among sampling dates ($p>0.05$; Bartlett's test), supporting the use of ANOVA tests.

The range in oxygen demand by micro- and meiofauna in the minivial incubations was less than that for the entire community, only varying by a factor of two (Fig. 3a). The mean respiration rate on 27 April was significantly higher than rates measured in January, February, May, and July; the rate on 6 April was also significantly higher than on the last two sampling dates ($p<0.0001$; ANOVA). Bartlett's test again indicated an equality of variances ($p>0.05$).

3.4. Sediment parameters

Phytopigment (chlorophyll *a* and phaeopigments) concentrations in the top 9 cm of sediment at the overwintering station showed an opposite trend to that in the ice algae and respiration data. Phaeopigment concentration was highest from mid-January to mid-February. It decreased between February and early April, where it remained fairly stable until mid-May; it was slightly higher again during the July sampling (Fig. 3b). ANOVA failed to detect significant differences among sampling dates, but a *p*-value of 0.053, suggests a trend toward lower values during April and May. Chlorophyll *a* values in the top 9 cm showed no significant differences among sampling dates ($p>0.05$; ANOVA; Fig. 3b). Trends and results of statistical analyses of data from only the top 2 cm of sediment were virtually identical to that of the top 9 cm (data not shown). Bartlett's test indicated equality of variances for both analyses ($p>0.05$).

Organic carbon and total nitrogen content in the top 2 cm of the sediments did not vary among sampling dates. Organic carbon values ranged from 1.28% (SD=0.07) to 1.41% (0.14), and total nitrogen values varied between 0.13% (0.0005) and 0.16% (0.03). *P*-values for both ANOVAs were higher than 0.50.

4. Discussion

A sharp increase in benthic oxygen demand coincided with the onset of an ice algal bloom at our time series station in the southeastern Beaufort Sea (Figs. 2a and 3a). At the same time, there was a strong increase in the sinking flux of chl *a*, as measured from short-term particle interceptor traps deployed immediately underneath the ice (Fig. 2b). With interfacial water chl *a* concentrations more than one order of magnitude lower than those in the bottom ice during the months of April and May (Fig. 2a and b), it is most likely that the increase in chl *a* sinking flux observed at that time was from ice algae released from the bottom ice. The release of ice algae in early April cannot be explained by ice melt, since this was a period of ice growth. Phaeopigments were absent from the bottom ice and were found in very low concentrations in particle interceptor traps (Fig. 2a and c), indicating very little or no grazing under the ice. It is possible that ice algae were released from the bottom ice as a result of brine drainage (Melnikov, 1998). It is also possible that turbulence under the ice may have dislodged ice algae.

Increased chl *a* sedimentation and benthic oxygen demand were not accompanied by an increase in sediment pigments, organic carbon, or total nitrogen content (Fig. 3b and Section 3.1). In fact, there was a strong trend toward a significant decrease in sediment pigments during the short pulse in benthic respiratory activity (Fig. 3). These results suggest that, while the onset of ice algal growth and sedimentation coincided with the observed increased in sediment community oxygen demand, it is unlikely that the input of ice algae alone is sufficient to explain the ten-fold increase in respiration rates that we observed from early April to mid-May. While there is a growing body of evidence supporting the value of ice algae as an early-season food source for benthic macrofauna (see below), it is more likely that our results reflect a combination of direct consumption and indirect responses to ice algal sedimentation.

4.1. Direct response to ice algal deposition

There is something of a paradox to be addressed when discussing the coupling between the pelagic and benthic environments. It seems straightforward that processes in the two realms should be linked as benthic communities rely on production from the euphotic zone as their source of energy; and there are several extensive reviews documenting this linkage (Grebmeier and Barry, 1991; Carey, 1991; Graf, 1992). Alternately, textbook values for "typical" sinking rates and horizontal velocity fields suggest that, even on relatively shallow continental shelves, material reaching the benthos must come from tens of kilometers away. Indeed, there are studies that document the importance of advective processes (e.g. Tanaka, 2003). There is overwhelming support, however, to suggest that surface waters directly above a benthic sampling location have a tight link with community structure and/or sediment biogeochemical processes on Arctic shelves (Atkinson and Wacasey, 1987; Grebmeier et al., 1989; Grebmeier and McRoy, 1989; Ambrose and Renaud, 1995, 1997; Hobson et al., 1995, 2002; Piepenburg et al., 1997; Grant et al., 2002). Aggregation can result in sinking rates of greater than 200 m d^{-1} (Asper and Smith, 2003). While we do not claim that ice algae directly over our benthic sampling site led to benthic respiration patterns, we use the timing and magnitude of the ice algal bloom at this location as a proxy for regional patterns of ice algal production that are potentially responsible for our observations of benthic processes.

Ice algae have been proposed to be an important high quality food source for benthic communities, especially early in the season before pelagic production increases (Ambrose and Renaud, 1997; Hargrave et al., 2002; Carroll and Carroll, 2003). This is the first study, however, to simultaneously track ice algal community development and its sinking from the ice, and benthic processes. Recently, ice algae have been shown to be readily consumed and assimilated by benthic fauna as evidenced from addition experiments where pigments, fatty acids, and stable isotopes were monitored (McMahon et al., 2006). In that study, sediment chlorophyll and essential fatty acid content was increased by over 80% due to food additions, but decreased to background levels within 19 days. The rates of consumption and assimilation of ice algae were comparable to those in phytoplankton addition treatments. Clearly, ice algae are a potentially valuable early-season food source for at least some components of the benthic community, and elicit a rapid response upon arrival at the sediment surface.

Rysgaard et al. (1998), studying a fjord system in east Greenland, attributed much of the increase in benthic oxygen consumption he observed to microbial activity. Our data strongly suggest, however, that the enhanced community respiration we measured was due primarily to macroinfauna. Minivial incubations did indicate a doubling of micro- and meio-faunal respiration rates between February and late April, but this increase was modest compared with the 10-fold increase in rates for the entire community (Fig. 2b). Clough et al. (2005) found that the role of macrofauna was far greater than that of meio-fauna at depths shallower than 500 m in the Chukchi Sea in the summer. They also noted that benthic macrofaunal biomass explained 75% of the variability in benthic respiration rates. Grant et al. (2002) found a similar pattern in the North Water polynya (northern Baffin Bay).

Using a 1:1 stoichiometric relationship between oxygen and carbon utilization, and a respiration coefficient of 0.85 (Smith, 1978), we estimate the benthic carbon demand during the period of highest sediment oxygen demand at around 210 mg m^{-2} d^{-1}. Carbon fluxes

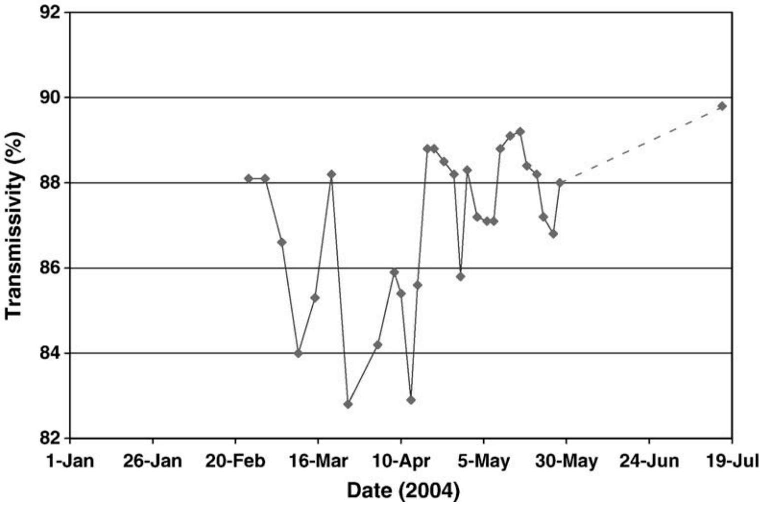

Fig. 4. Near-bottom transmissivity data from CTD casts at the time-series station.

measured in under-ice traps did not approach this value until June, and were between 20 and 28 mg m^{-2} d^{-1} from February to May (T. Juul-Pedersen et al., unpub. data). While some benthic fauna may derive a significant portion of their early-season food from sedimenting ice algae, it is unlikely that the pigment sedimentation rates we measured were sufficient to account for such a significant increase in benthic community respiration. It is possible, however, that the arrival of fresh phytodetritus at the sea floor served as a cue to benthic fauna to increase their activity. It follows directly then that we would not see an increase in sediment pigment concentrations at periods of peak respiration, but instead a trend toward a net loss in sediment pigments (Fig. 2b and c). Infauna stimulated directly by sedimenting ice algae may have consumed all the new ice algal material that was deposited plus pigmented matter from the sediment inventory.

4.2. Indirect response to ice algal deposition

Epifaunal invertebrates, primarily echinoderms (e.g. sea stars, brittle stars, sea cucumbers, sand dollars), are abundant and important components of Arctic shelf communities (Welch et al., 1992; Piepenburg and von Juterzenka, 1994; Piepenburg et al., 1995; Bluhm et al., 1998; Ambrose et al., 2001). With densities up to 700 individuals m^{-2}, ophiuroids alone can account for up to 80% of the total benthic-community metabolism (Piepenburg et al., 1995). Bottom photographs from our sampling station in the Beaufort Sea indicate that ophiuroid densities reach at least 60 individuals m^{-2} at this site (P. Renaud, pers. obs.). Furthermore, non-quantitative traps deployed at this station suggest that large epi-/hyper-benthic amphipods (e.g *Anonyx* spp.) are quite abundant, but are not effectively enumerated from bottom photography. Evidence from laboratory assays (Ambrose et al., 2001) and stable-isotope studies (Hobson et al., 1995, 2002) suggest that some of the most abundant ophiuroids and amphipods consume ice algae. Through their feeding activities, epibenthic organisms bioturbate the surface sediment, altering its biological (Ambrose, 1993) and geochemical (Lohrer et al., 2004; Solan et al., 2004; Wenzhöfer and Glud, 2004) structure. Klages et al. (2004) suggested that availability of dissolved oxygen may limit metabolic activity in Arctic sediments. Infaunal bioturbators enhance oxygen exchange in sediments by a factor of 1.5–3 (Glud et al., 2000), and it is likely that the large densities of epifauna at our study site would have a similar effect. As epifauna were excluded from our incubation cores, their direct contribution to benthic oxygen demand is not reflected in the data presented, but indirect effects of bioturbation would have been reflected in our measurements since the sediment would presumably have been exposed to bioturbation before collection. We propose, therefore, that any direct enhancement of sediment-community oxygen demand due to deposition of ice algae could have been augmented by the increased feeding and burrowing activities by epifauna, at least in part by ophiuroids, scavenging for the newly deposited phytodetritus.

In addition to cuing feeding and burrowing activities, arrival of fresh phytodetritus on the sea floor may stimulate reproduction-related events that could result in enhanced respiration. This has been observed for many benthic taxa that exhibit seasonal reproduction (e.g. Rokop, 1974; Tyler et al., 1982, 1992; Uitto and Sarvala, 1991; Blake, 1993). As food supply to the benthos is highly seasonal in the Arctic, the synchrony of reproductive events with phytodetrital input to insure adequate food for developing larvae or new recruits may be particularly important (Gage and Tyler, 1991, Ólafsson et al., 1994, Ambrose and Renaud, 1997).

4.3. Other potential factors

Our sediment-community respiration rates for January, February, May, and July are similar to rates measured on shelves throughout the Arctic (reviewed in Glud et al., 1998; Clough et al., 2005). These values are also similar to those from many temperate shelf areas, indicating that benthic systems in the Arctic are not significantly less productive than elsewhere. Although we observed order of magnitude increases in *both* ice algal standing stocks and benthic oxygen demand (Figs. 2a and 3a), it is possible that the respiration results in this study were due to factors unrelated to the onset of the ice algal bloom. Some of these factors may include deposition of phytoplankton, increased bottom temperatures, resuspension of bottom sediments, and advection of potential food from outside the local area.

The dramatic, order-of-magnitude increase in sediment-community oxygen demand in April (Fig. 3a) was unexpected, but not completely without precedent. For example, infauna are capable of respiration rates that vary by a factor of 7 over a diel cycle (Wenzhöfer and Glud, 2004). Additionally, Rysgaard et al. (1998) observed an increase in benthic respiration of a lesser magnitude in a shallow Greenland fjord, but that was much later in the season and attributed to a phytoplankton bloom initiated by ice break-up. It is highly unlikely that the increase in respiration we observe in this study was due to phytoplankton. Empirical studies from the southeastern Beaufort Sea indicate very low phytoplankton production during April, with spring blooms of highly variable magnitude taking place much later in the year (May/June, or as late as July; Arrigo and van Dijken, 2004; Carmack et al., 2004). Under-ice suspended chl *a* concentrations during our study period were very low from February through May (Fig. 2b). Additionally, the high proportion of chl *a* in the sedimenting pigmented material indicates that the sinking material was from a fresh algal source. Food, and not water temperature, has been proposed to be the most important limiting factor for benthic organisms on Arctic shelves (Rysgaard et al., 1998). This assertion has considerable support from two decades of research indicating strong linkages between sediment pigment content and community structure and function (Christensen and Kanneworff, 1985; Carey, 1991; Grebmeier and Barry, 1991; Ambrose and Renaud, 1995; Clough et al., 1997; Piepenburg et al., 1997; Grant et al., 2002). Indeed, over the first 5 sampling dates, including the period where we saw the large increase in benthic respiration rates, near-bottom temperatures only varied by approximately 0.1 °C.

The modest decrease in transmissivity observed in this study coincided with the onset of ice algal growth and the marked increase in benthic respiration (Figs. 2a, 3a, 4). It is possible that the transmissivity signal reflected a pulse of newly deposited ice algae and/or fecal pellets to the sediment surface. Alternatively, it may be evidence of a resuspension or near-bottom advection event. Advection of labile material from outside the local area may be an important mechanism providing food for benthic organisms (Dayton and Oliver, 1977; Rosenburg, 1995), and one that would confound the coupling of pelagic and benthic processes expected for this location.

The impacts of climate change on carbon cycling in Arctic marine communities are difficult to predict (Wassmann, 2004). This study suggests, however, that factors changing the patterns of ice algal production on Arctic shelves may have significant consequences for carbon processing and storage in benthic sediments. It is increasingly clear that the structure and seasonal activity of benthic faunal communities interact with the primary productivity regime to determine carbon preservation and regeneration patterns on Arctic shelves.

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Paper VI

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

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In preparation

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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

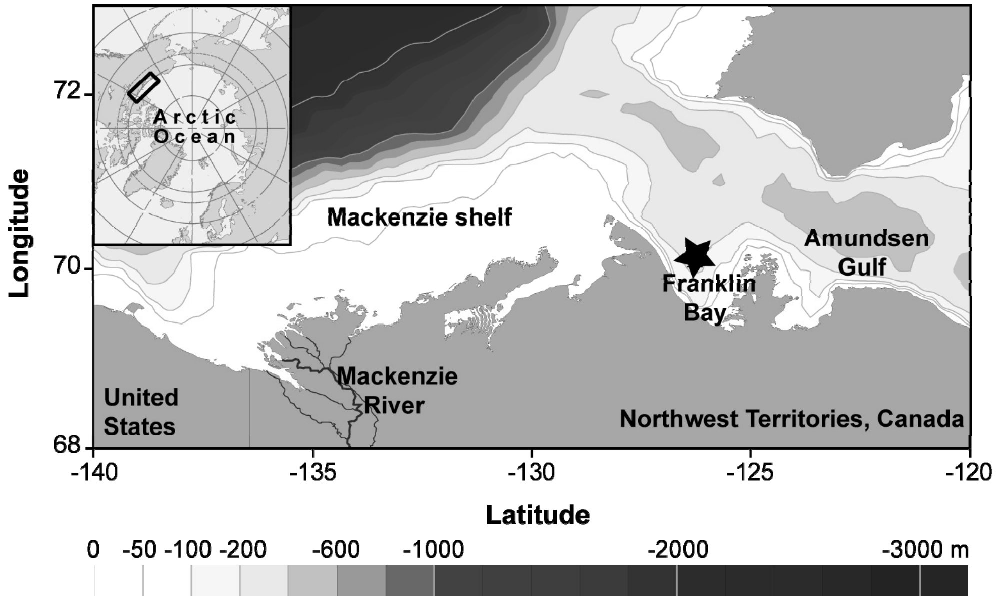

Figure 1. Study area. Overwintering station is indicated by a star in the Franklin Bay.

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 δ^{13}C determination, and undecalcified samples 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, 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.

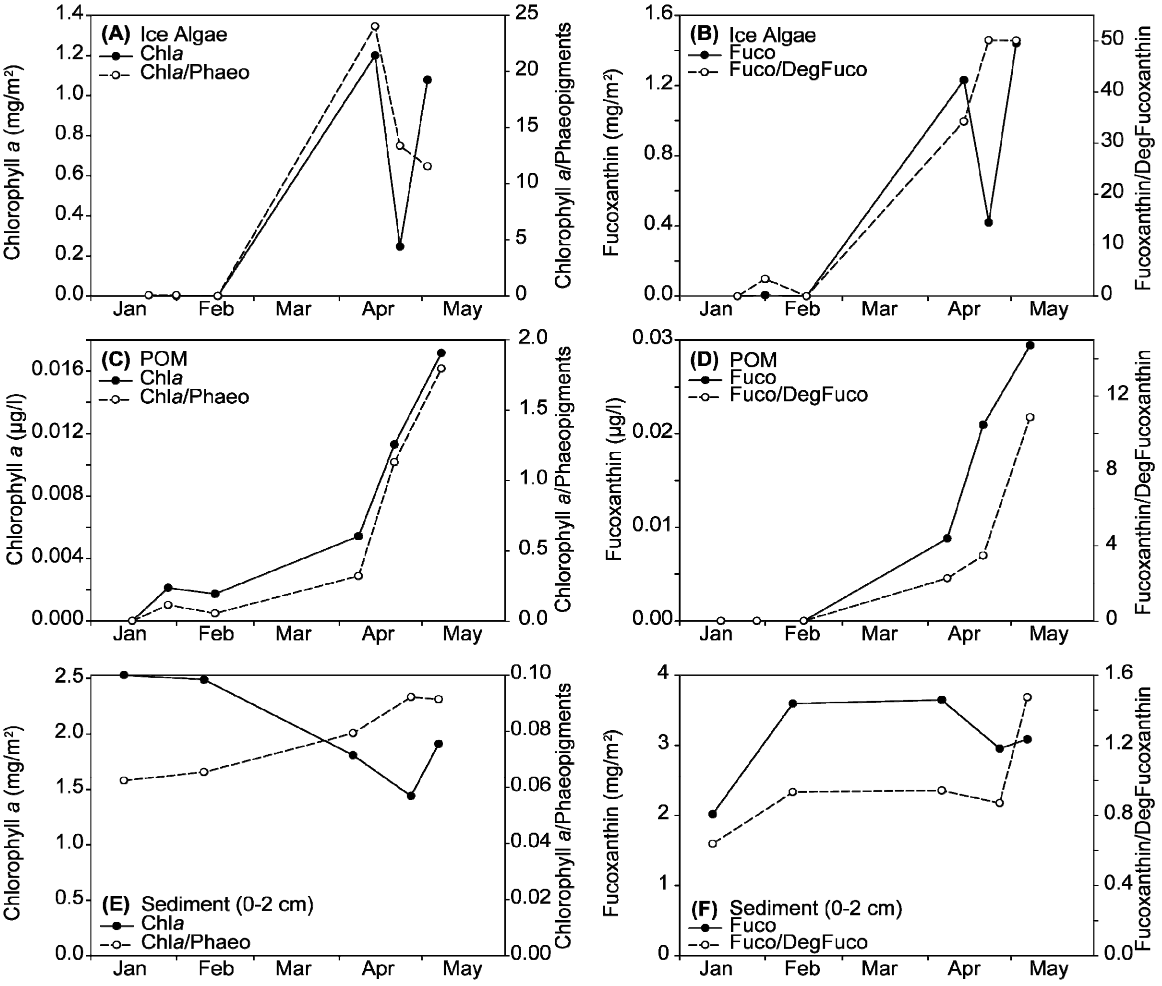

Figure 2. Temporal variations of the concentrations of chlorophyll *a* and accessory pigments in (a,b) ice , (c,d) particulate organic matter, and (e,f) sediment.

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.

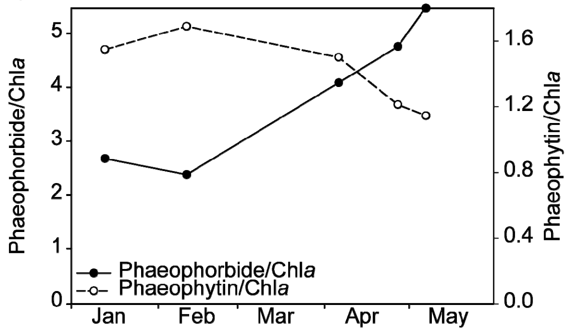

Figure 3. Variations of the ratios phaeophorbide/chl *a* and phaeophytin/chl *a*.

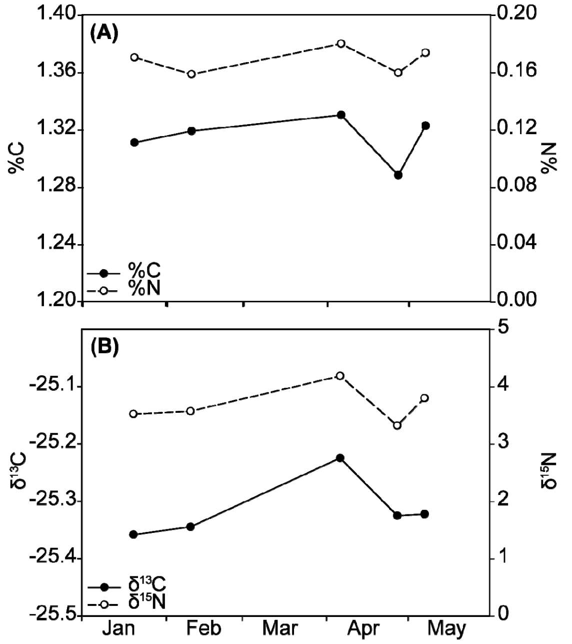

Figure 4. (a) Percentage of organic carbon (%C) and nitrogen (%N) in the sediment. (b) Sedimentary stables isotopes δ^{13}C and δ^{15}N composition.

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

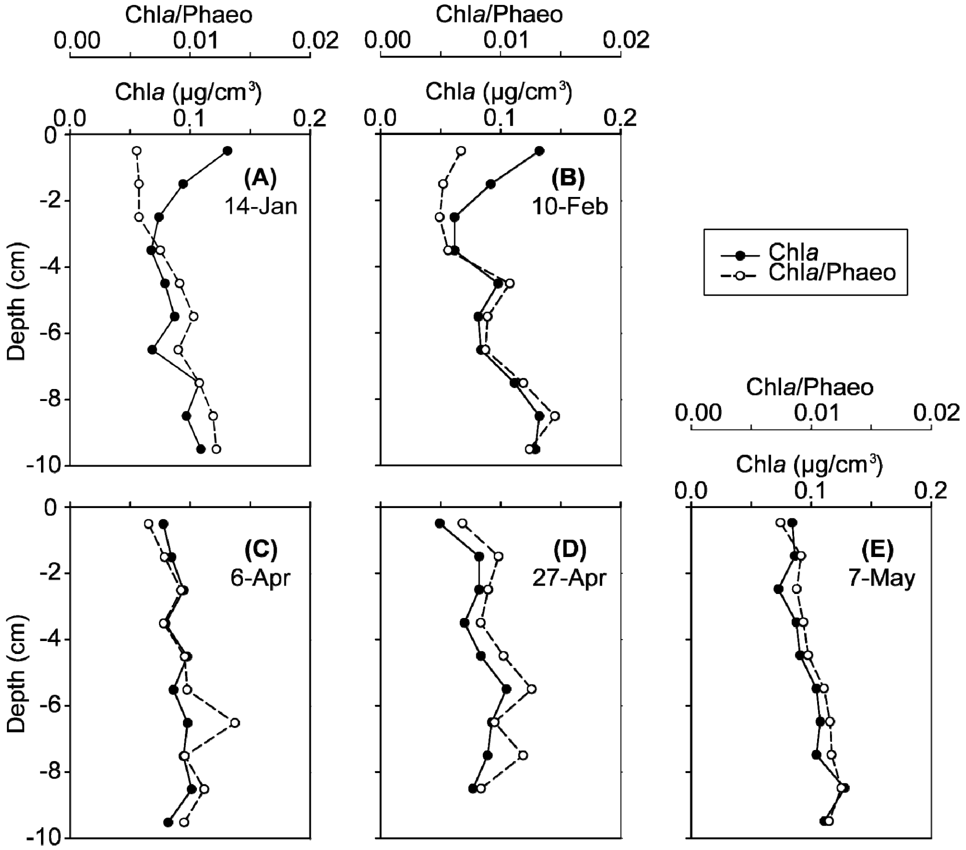

Figure 5. Profiles of sedimentary chlorophyll *a* (chl *a*) and ratio of chlorophyll *a* to phaeopigments (chl *a*/phaeo) over the first 10 cm, from January to May.

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,

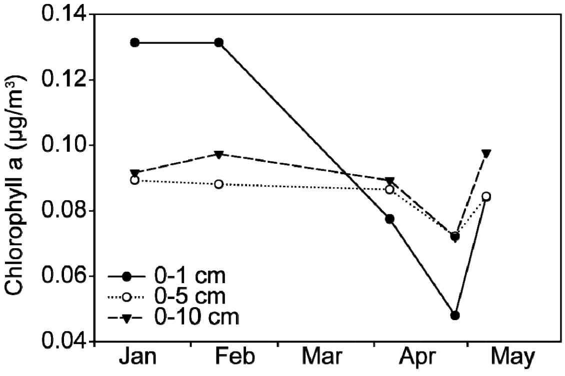

Figure 6. Chlorophyll *a* concentration in the first cm of sediment, and average chlorophyll *a* concentration in the first 5 and 10 cm of sediment from January to May.

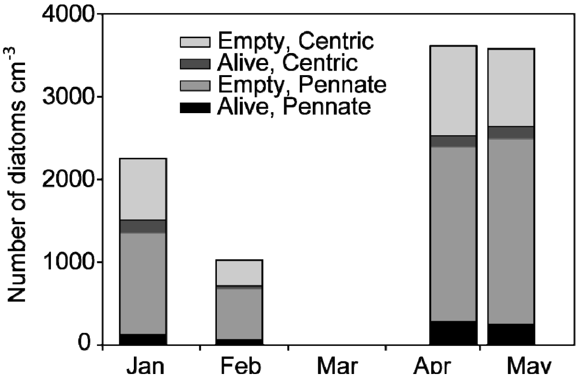

Figure 7. Relative percentage of empty, full (viable), pennate and centric diatoms in the sediment.

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.

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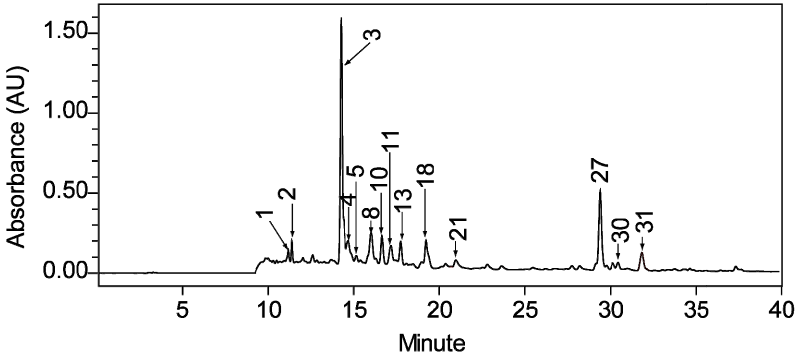
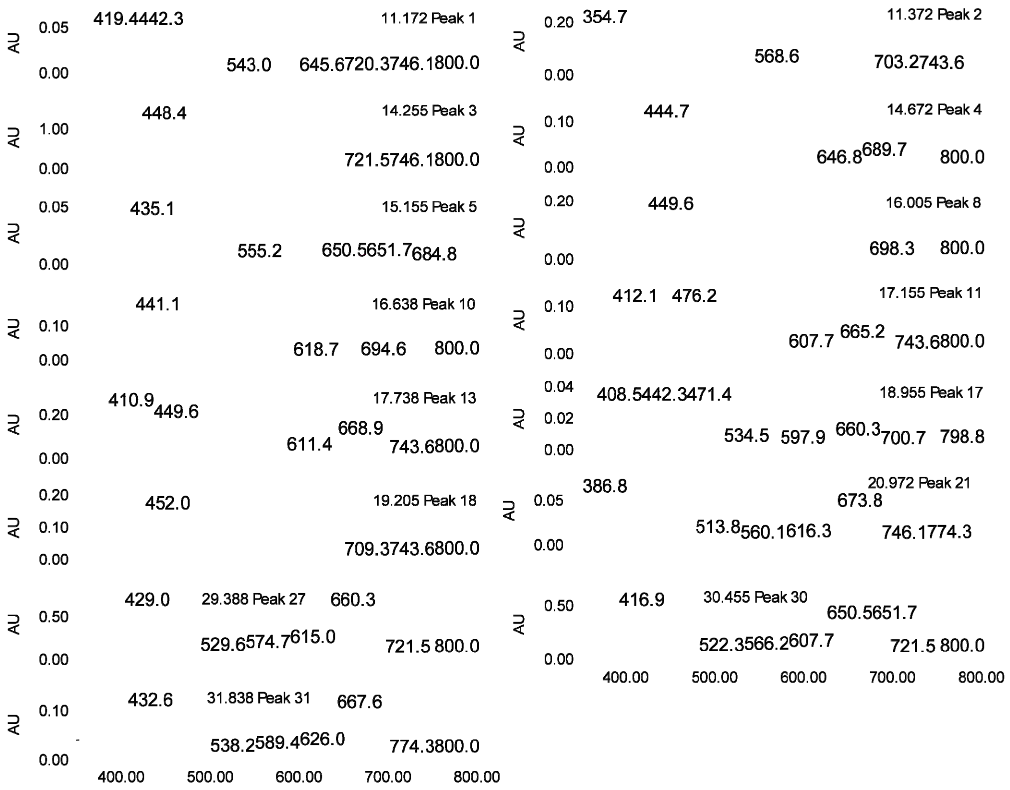
Appendices 7-9

Appendix 7a: Chromatogram and PDA absorbance: CASES summer 2004, station 718, sediment depth 1-2 cm.

Note that peaks of area >1% are identified in the PDA chromatogram by numbers. Their PDA spectrums at 438 nm are presented below the chromatogram, and their identification and area is presented in the table on the right of the chromatogram.

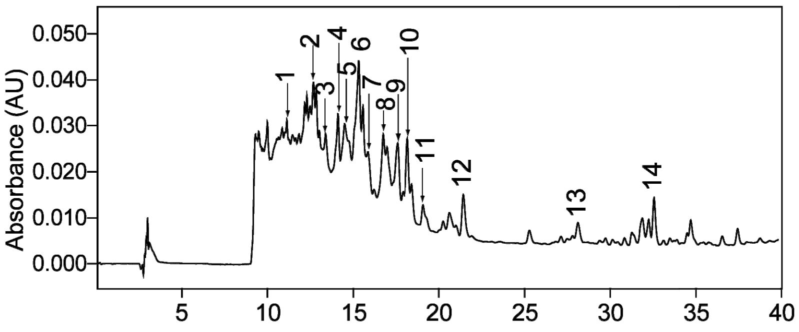


Peak #	Name	Retention Time	Area	% Area
1	Unknown	11.17	445463.8	1.04
2	UV absorbing compound	11.38	643695.4	1.51
3	Fucoxanthin	14.25	14232980	33.28
4	Fucoxanthin	14.67	2495301	5.84
5	Phaeophorbide *b*	15.15	625372.3	1.46
8	Degraded fucoxanthin (?)	16.01	3137368	7.34
10	Degraded fucoxanthin (?)	16.64	1966160	4.60
11	Unidentifiable	17.16	2064516	4.83
13	Phaeophorbide *a*	17.73	1688568	3.95
17	Unknown	18.96	440843.2	1.03
18	Diatoxanthin (?)	19.21	2391912	5.59
21	Chlorophyll degradation product	20.96	659468.1	1.54
27	Chlorophyll *a*	29.39	5791186	13.54
30	Chlorophyll degradation product	30.45	447584.4	1.05
31	Chlorophyll degradation product	31.84	1626327	3.80

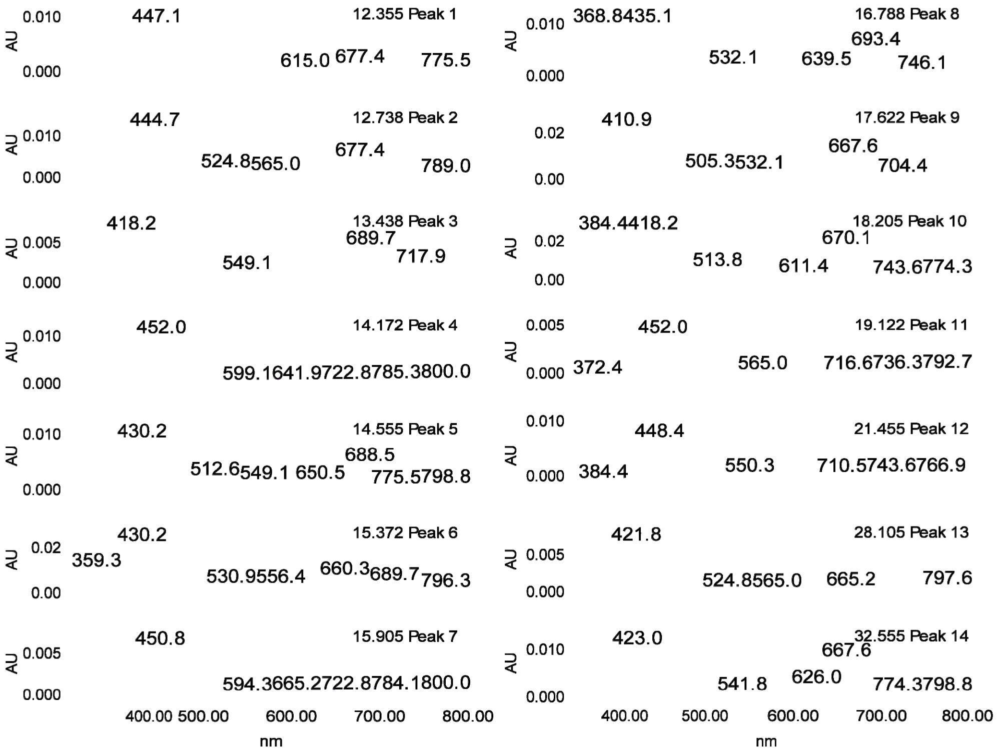


Appendix 7b: Chromatogram and PDA absorbance: CASES fall 2003, station 100, sediment depth 0-1 cm.

Peaks are identified in the PDA chromatogram by numbers. Their PDA spectrums at 438 nm are presented below the chromatogram, and their identification and area is presented in the table on the right of the chromatogram.

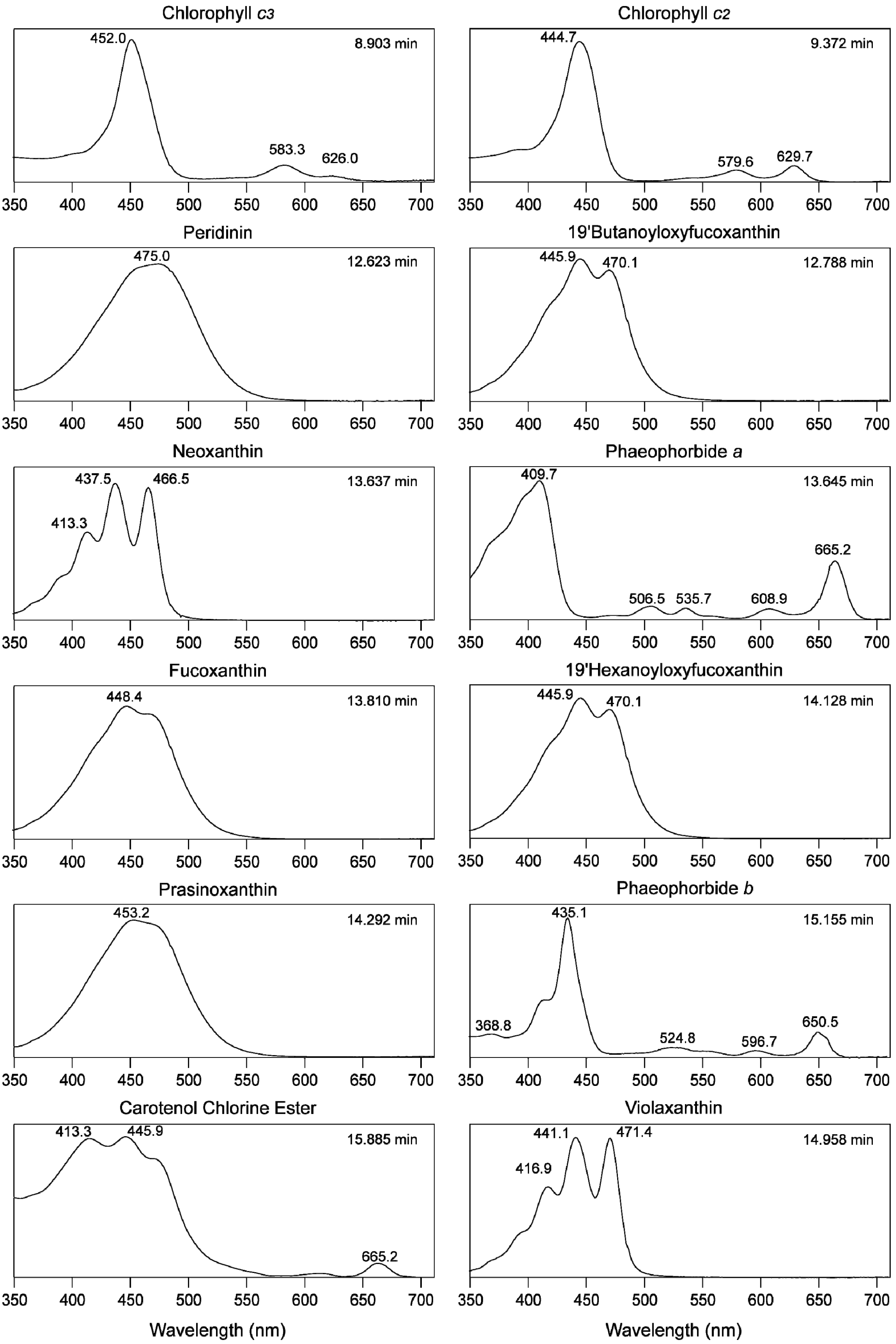


Peak #	Name	Retention Time	Area	% Area
1	Unknown	12.36	140358.1	4.50
2	Unknown (c2?)	12.73	323384.9	10.36
3	Unknown	13.44	114872.6	3.68
4	Prasinoxanthin	14.16	138417.7	4.44
5	Chlorophyll degradation product	14.55	280173.5	8.98
6	Chlorophyll degradation product	15.36	637110.3	20.42
7	Unk. (Prasinoxanthin allomere?)	15.90	90965.91	2.92
8	Chlorophyll degradation product	16.79	354977.8	11.38
9	Phaeophorbide *a*	17.62	227539.5	7.29
10	Unknown	18.20	329047.7	10.54
11	Unk. carotenoid (Diatoxanthin?)	19.12	72104.43	2.31
12	Unk. carotenoid	21.46	115001.8	3.69
13	Chlorophyll degradation product	28.11	41763.67	1.34
14	Chlorophyll degradation product	32.55	254716.5	8.16



Appendix 8: Absorption spectrum of pigments studied.

Spectrums identified on the PDA (438 nm) from single runs of standards (DHI, Denmark), with the exception of phaeophytin *b* (standard prepared in the lab by acidification of chlorophyll *b*) and phaeophorbide *b* and CCE (only identified in samples, and quantified with RF of similar pigment).



Chlorophyll *c3*

Chlorophyll *c2*

Peridinin

19'Butanoyloxyfucoxanthin

Neoxanthin

Phaeophorbide *a*

Fucoxanthin

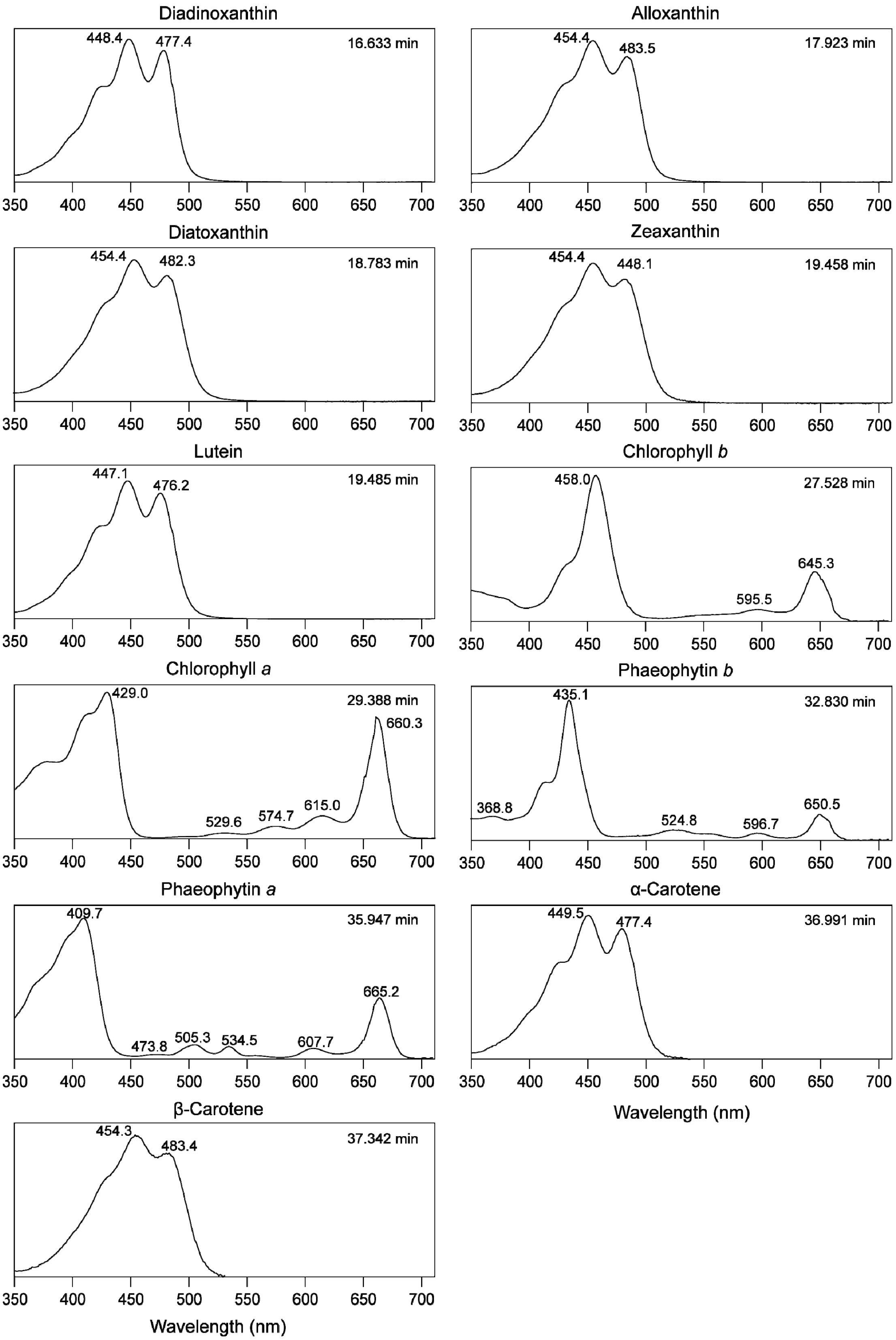
19'Hexanoyloxyfucoxanthin

Prasinoxanthin

Phaeophorbide *b*

Carotenol Chlorine Ester

Violaxanthin


Diadinoxanthin
448.4
477.4
16.633 min
Alloxanthin
454.4
483.5
17.923 min
Diatoxanthin
454.4
482.3
18.783 min
Zeaxanthin
454.4
448.1
19.458 min
Lutein
447.1
476.2
19.485 min
Chlorophyll *b*
458.0
595.5
645.3
27.528 min
Chlorophyll *a*
429.0
529.6
574.7
615.0
660.3
29.388 min
Phaeophytin *b*
435.1
368.8
524.8
596.7
650.5
32.830 min
Phaeophytin *a*
409.7
473.8
505.3
534.5
607.7
665.2
35.947 min
α-Carotene
449.5
477.4
36.991 min
β-Carotene
454.3
483.4
37.342 min
350
400
450
500
550
600
650
700
Wavelength (nm)

Appendix 9: Comparison of absorption spectrum between standard and sample for selected pigments