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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

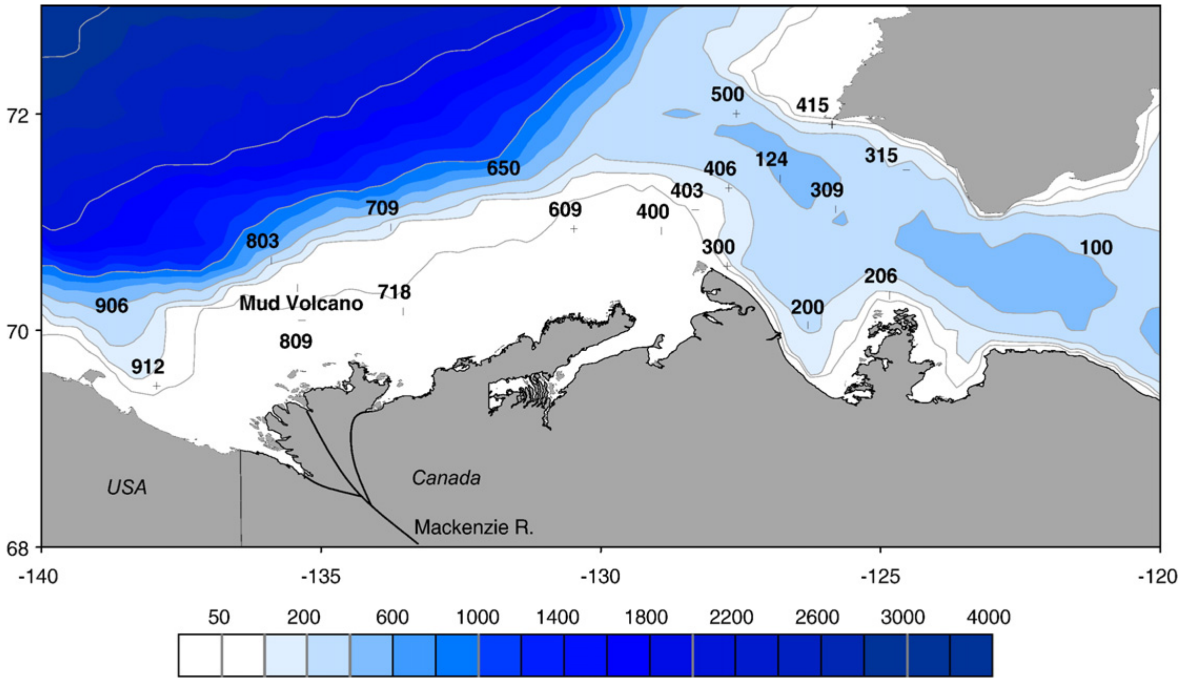

Fig. 1. Map of the eastern Beaufort Sea with station locations and numbers (or names) indicated. Shading indicates water depth. Latitude is in °N and longitude is negative (°W).

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).

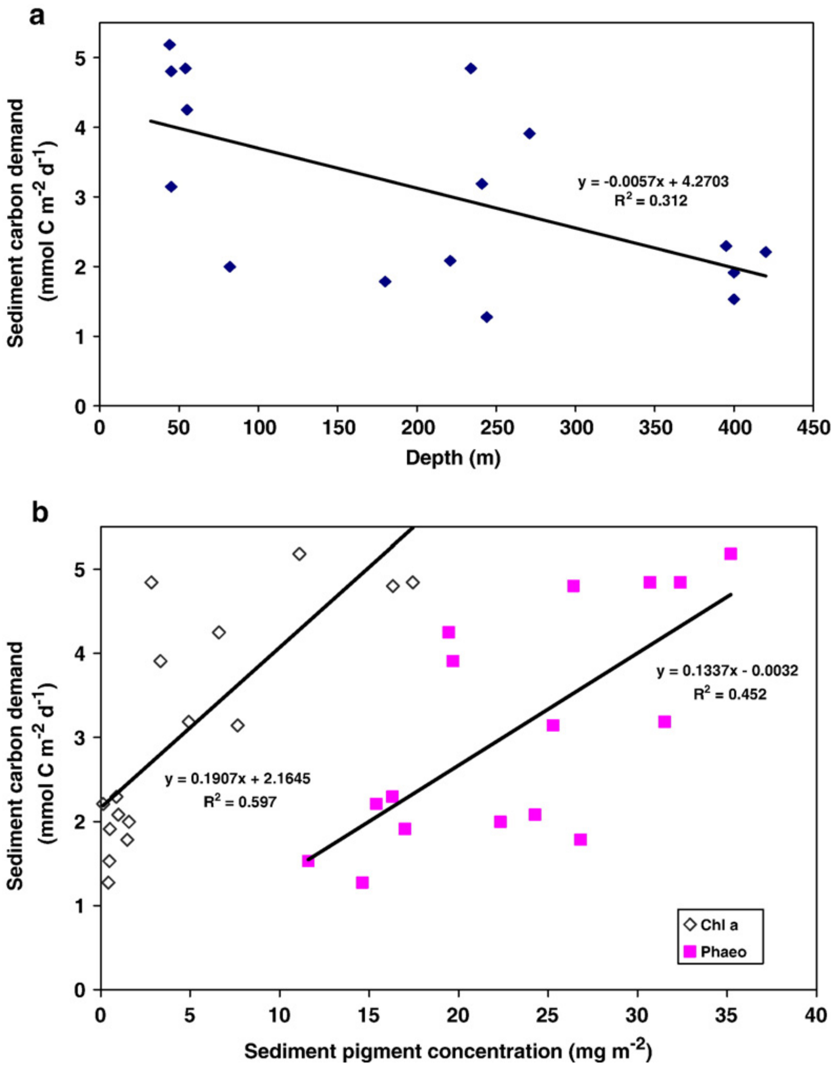

Fig. 2. Carbon demand (mmol C m^{-2} d^{-1}) from sediment core incubations plotted against (a) depth (m) and (b) sediment pigment concentration (chlorophyll *a* and phaeopigments) from the top 2 cm (mg m^{-2}). Regression lines are significant at $p<0.05$ and adjusted r^2 values are given.

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

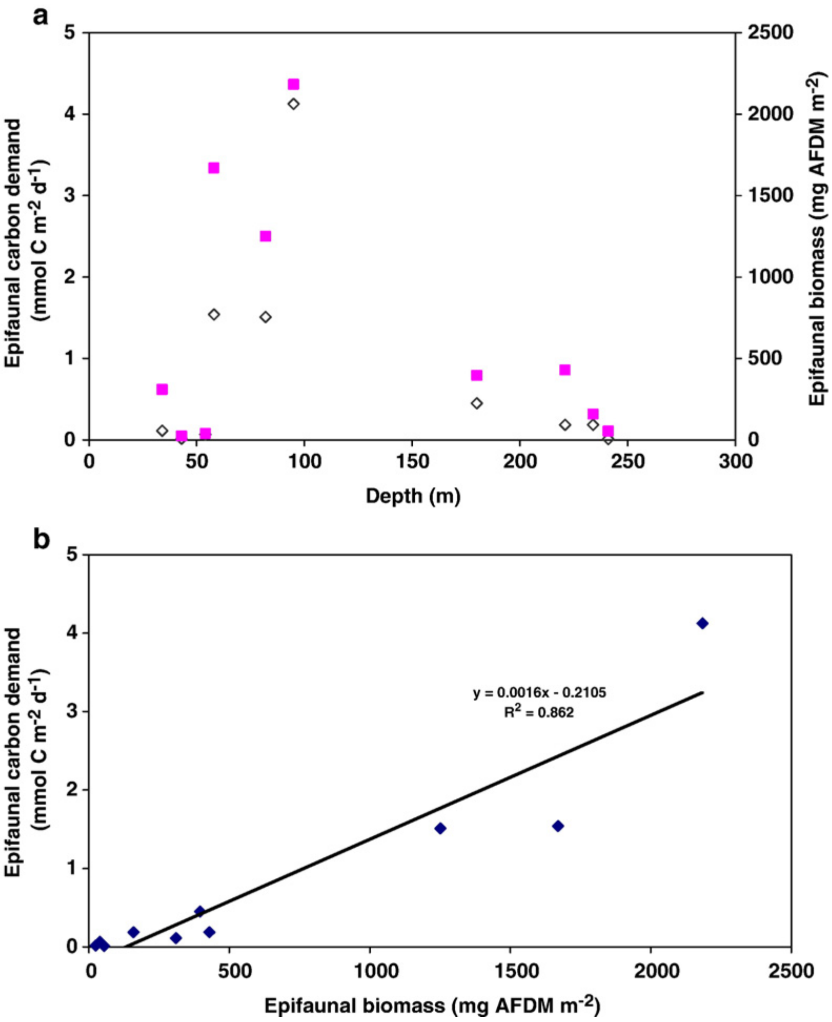

Fig. 3. (a) Scatter plots of epifaunal carbon demand (open diamonds, mmol C m^{-2} d^{-1}; left axis) and biomass (filled squares, mg AFDM m^{-2}; right axis) against depth (m). Station numbers for each point can be determined from Table 2. (b) Plot of epifaunal carbon demand (mmol C m^{-2} d^{-1}) against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

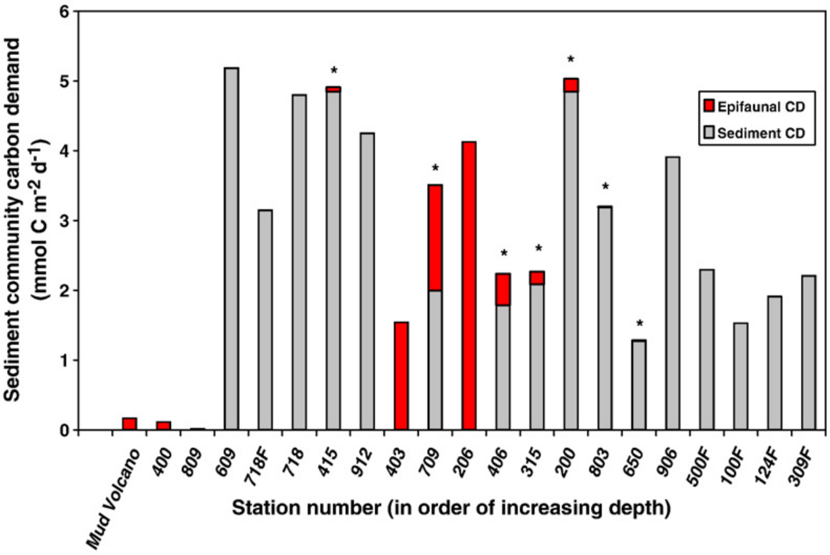

Fig. 4. Partitioning of carbon demand (CD; mmol C m^{-2} d^{-1}) between sediment (pale bars) and epifaunal (dark bars) components of the benthic community by station. Asterisks indicate stations where both measurements were made. Station information can be obtained in Table 1.

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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References

Aller, R.C., Aller, J.Y., 1998. The effect of biogenic irrigation intensity and solute exchange on diagenetic reaction rates in marine sediments. J. Mar. Res. 56, 905–936.

Ambrose Jr., W.G., 1993. Effects of predation and disturbance by ophiuroids on soft-bottom community structure in Oslofjord: results of a mesocosm study. Mar. Ecol. Prog. Ser. 97, 225–236.

Ambrose, W.G., Renaud, P.E., 1995. Benthic response to water column productivity patterns: evidence for benthic–pelagic coupling in the Northeast Water Polynya. J. Geophys. Res. 100, 4411–4421.

Ambrose, W.G., Clough, L.M., Tilney, P.R., Beer, L., 2001. Role of echinoderms in benthic remineralization in the Chukchi Sea. Mar. Biol. 139, 937–949.

Arctic Climate Impact Assessment, 2004. Impacts of a Warming Arctic. Cambridge University Press, Cambridge.

Bluhm, B.A., Piepenburg, D., von Juterzenka, K., 1998. Distribution, standing stock, growth, mortality and production of *Strongylocentrotus pallidus* (Echinodermata: Echinoidea) in the northern Barents Sea. Polar Biol. 20, 325–334.

Brockington, S., Clarke, A., 2001. The relative influence of temperature and food on the metabolism of a marine invertebrate. J. Exp. Mar. Biol. Ecol. 258, 87–99.

Calbet, A., Landry, M.R., 2004. Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. Limnol. Oceanogr. 49, 51–57.

Clough, L.M., Renaud, P.E., Ambrose, W.G., 2005. Impacts of water depth, sediment pigment concentration, and benthic macrofaunal biomass on sediment oxygen demand in the western Arctic Ocean. Can. J. Fish. Aquat. Sci. 62, 1756–1765.

Dauwe, B., Middleburg, J.J., Herman, P.M.J., 2001. Effect of oxygen on the degradability of organic matter in subtidal and intertidal sediments of the North Sea area. Mar. Ecol. Prog. Ser. 215, 13–22.

Deming, J., Baross, J., 1993. The early diagenesis of organic matter: bacterial activity. In: Engel, M., Macko, S.A. (Eds.), Organic Geochemistry. Plenum, New York.

Dunton, K.H., Goodall, J.L., Schonberg, S.V., Grebmeier, J.M., Maidment, D.R., 2005. Multi-decadal synthesis of benthic–pelagic coupling in the western arctic: role of cross-shelf advective processes. Deep-Sea Res., Part 2, Top. Stud. Oceanogr. 52, 3462–3477.

Forest, A., Sampei, M., Hattori, H., Makabe, R., Sasaki, H., Fukuchi, M., Wassmann, P., Fortier, L., 2006. Particulate organic carbon fluxes on the slope of the Mackenzie Shelf (Beaufort Sea): physical and biological forcing of shelf-basin exchanges. J. Mar. Syst. doi:10.1016/j.marsys.2006.10.008.

Goñi, M.A., Yunker, M.B., Macdonald, R.W., Eglinton, T.I., 2005. The supply and preservation of ancient and modern components of organic carbon in the Canadian Beaufort Shelf of the Arctic Ocean. Mar. Chem. 93, 53–73.

Grant, J., Emerson, C.W., Hargrave, B., Shortle, J.L., 1991. Benthic oxygen demand on continental shelves off Eastern Canada. Cont. Shelf Res. 11, 1083–1097.

Grant, J., Hargrave, B., MacPherson, P., 2002. Sediment properties and benthic–pelagic coupling in the North Water. Deep-Sea Res., Part. 2, Top. Stud. Oceanogr. 49, 5259–5275.

Grebmeier, J.M., McRoy, C.P., 1989. Benthic–pelagic coupling on the shelf of the northern Bering and Chukchi Seas. III. Benthic food supply and carbon cycling. Mar. Ecol. Prog. Ser. 53, 79–91.

Grebmeier, J.M., Barry, J.P., 1991. The influence of oceanographic processes on pelagic–benthic coupling in polar regions: a benthic perspective. J. Mar. Syst. 2, 495–518.

Grebmeier, J.M., Cooper, L.W., Feder, H.M., Sirenko, B.I., 2006. Ecosystem dynamics of the Pacific-influenced Northern Bering and Chukchi Seas in the Amerasian Arctic. Prog. Oceanogr. 71, 331–361.

Heip, C.H.R., Duineveld, G., Flach, E., Graf, G., Helder, W., Herman, P.M.J., Lavaleye, M., Middleberg, J.J., Pfannkuche, O., Soetaert, K., Soltwedel, T., de Stiger, H., Thomsen, L., Vanaverbeke, J., de Wilde, P., 2001. The role of the benthic biota in sedimentary metabolism and sediment-water exchange processes in the Goban Spur area (NE Atlantic). Deep-Sea Res., Part 2, Top. Stud. Oceanogr. 48, 3223–3243.

Highsmith, R.C., Coyle, K.O., 1990. High productivity of northern Bering Sea amphipods. Nature 344, 862–863.

Holm-Hansen, O., Lorenzen, C.J., Holms, R.W., Strickland, J.D., 1965. Fluorometric determination of chlorophyll. J. Cons.-Cons. Int. Explor. Mer. 30, 3–15.

Intergovernmental Panel on Climate Change, 2001.Climate change 2001: the scientific basis. In: Houghton, J.T., Ding, Y., Griggs, D.J., Nogeur, M., van der Linden, P.J., Xiaosu, D. (Eds.), Contributions of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

Intergovernmental Panel on Climate Change, 2007.Climate change 2007: the physical science basis. Summary for Policymakers. 1-21. IPCC Secretariat, Geneva.

Macdonald, R.W., Carmack, E.C., McLaughlin, F.A., Iseki, K., Macdonald, D.M., O'Brien, M.C., 1987. The distribution of nutrients in the southeastern Beaufort Sea: implications for water circulation and primary production. J. Geophys. Res. 92, 2939–2952.

Macdonald, R.W., Solomon, S.M., Cranston, R.E., Welch, H.E., Yunker, M.B., Gobeil, C., 1998. A sediment and organic carbon budget for the Canadian Beaufort Shelf. Mar. Geol. 144, 255–273.

Mahaut, M.-L., Sibuet, M., Shirayama, Y., 1995. Weight-dependent respiration rates in deep-sea organisms. Deep-Sea Res., Part 1, Oceanogr. Res. Pap. 42, 1575–1582.

McMahon, K.W., Ambrose, W.G., Johnson, B.J., Sun, M.Y., Lopez, G.R., Clough, L.M., Carroll, M.L., 2006. Benthic community response to ice algae and phytoplankton in Ny Ålesund, Svalbard. Mar. Ecol. Prog. Ser. 310, 1–14.

Moore, P.G., 1977. Inorganic particulate suspensions in the sea and their effects on marine animals. Oceanogr. Mar. Biol. Ann. Rev. 15, 225–363.

Moran, S.B., Kelly, R.P., Hagstrom, K., Smith, J.N., Grebmeier, J.M., Cooper, L.W., Cota, G.F., Walsh, J.J., Bates, N.R., Hansell, D.A., Maslowski, W., Nelson, R.P., Mulsow, S., 2005. Seasonal changes in POC export flux in the Chukchi Sea and implications for water column-benthic coupling in Arctic shelves. Deep-Sea Res., Part 2, Top. Stud. Oceanogr. 52, 3427–3451.

Morata, N., Renaud, P.E., in press. Sedimentary pigments in the western Barents Sea: reflecting the benthic-pelagic coupling? Deep-Sea Res., Part 2, Top. Stud. Oceanogr.

Peterson, G.H., Curtis, M.A., 1980. Differences in energy flow through major components of subarctic, temperate and tropical marine shelf communities. Dana 1, 53–64.

Piepenburg, D., 2000. Arctic brittle stars (Echinodermata: Ophiuroidea). Oceanogr. Mar. Biol. Ann. Rev. 38, 189–256.

Piepenburg, D., 2005. Recent research on Arctic benthos: common notions need to be revised. Polar Biol. 28, 733–755.

Piepenburg, D., Schmid, M.K., 1996a. Brittle star fauna (Echinodermata: Ophiuroidea) of the Arctic northwestern Barents Sea: composition, abundance, biomass and spatial distribution. Polar Biol. 16, 383–392.

Piepenburg, D., Schmid, M.K., 1996b. Distribution, abundance, biomass, and mineralization potential of the epibenthic megafauna of the Northeast Greenland shelf. Mar. Biol. 125, 321–332.

Piepenburg, D., Schmid, M.K., 1997. A photographic survey of the epibenthic megafauna of the Arctic Laptev Sea shelf: distribution, abundance, and estimates of biomass and organic carbon demand. Mar. Ecol. Prog. Ser. 147, 63–75.

Piepenburg, D., Blackburn, T.H., von Dorrien, C.F., Gutt, J., Hall, P.O.J., Hulth, S., Kendall, M.A., Opalinski, K.W., Rachor, E., Schmid, M.K., 1995. Partitioning of benthic community respiration in the Arctic (Northwestern Barents Sea). Mar. Ecol. Prog. Ser. 118, 119–213.

Piepenburg, D., Ambrose, W.G., Brandt, A., Renaud, P.E., Ahrens, M.J., Jensen, P., 1997. Benthic community patterns reflect water column processes in the Northeast Water Polynya (Greenland). J. Mar. Sys. 10, 467–482.

Renaud, P.E., Riedel, A., Michel, C., Morata, N., Gosselin, M., Juul-Pedersen, T., Chiuchiolo, A., in press-a. Seasonal variation in benthic community oxygen demand: a response to an ice algal bloom in the Beaufort Sea, Canadian Arctic? J. Mar. Syst. doi:10.1016/j.marsys.2006.07.006.

Renaud, P.E., Carroll, M.L., Ambrose Jr., W.G., in press-b. Effects of global warming on Arctic sea-floor communities and its consequences for higher trophic levels. In: Duarte, C.M., Agustí, S. (Eds.) Impacts of Global Warming on Polar Ecosystems. Fundacíon BBVA, Bilbao.

Renaud, P.E., Morata, N., Carroll, M.L., Denisenko, S.G., Reigstad, M., in press-c. Pelagic–benthic coupling in the western Barents Sea: processes and time scales. Deep-Sea Res., Part 2, Top. Stud. Oceanogr.

Rowe, G.T., Boland, G.S., Briones, E.G.E., Cruz-Kaegi, M.E., Newton, A., Piepenburg, D., Walsh, I., Deming, J., 1997. Sediment community biomass and respiration in the Northeast Water Polynya, Greenland: a numerical simulation of benthic lander and spade core data. J. Mar. Syst. 10, 497–515.

Rysgaard, S., Nielsen, T.G., 2006. Carbon cycling in a high-arctic marine ecosystem — Young Sound, NE Greenland. Prog. Oceanogr. 71, 426–445.

Rysgaard, S., Thamdrup, B., Risgaard-Petersen, N., Fossing, H., Berg, P., Christensen, P.B., Dalsgaard, T., 1998. Seasonal carbon and nutrient mineralization in a high-Arctic coastal marine sediment, Young Sound, Northeast Greenland. Mar. Ecol. Prog. Ser. 175, 261–276.

Sherr, E.B., Sherr, B.F., Fessenden, L., 1997. Heterotrophic protists in the Central Arctic Ocean. Deep-Sea Res., Part 2, Top. Stud. Oceanogr. 44, 1665–1682.

Smallwood, B.J., Wolff, G.A., 1999. Megafauna can control the quality of organic matter in marine sediments. Naturwissenschaften 86, 320–324.

Smith Jr., K.L., 1978. Benthic community respiration in the N.W. Atlantic Ocean: *in situ* measurements from 40 to 5200 m. Mar. Biol. 47, 337–347.

Smith, C.R., 1986. Nekton fall, low-intensity disturbance and community structure of infaunal benthos in the deep sea. J. Mar. Res. 44, 567–600.

Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M., Ruesink, J.L., Srivastava, D.S., 2004. Extinction and ecosystem function in the marine benthos. Science 306, 1177–1180.

Stein, R., Macdonald, R.W. (Eds.), 2004. The Organic Carbon Cycle in the Arctic Ocean. Springer-Verlag, Berlin.

Stirling, I., 1980. The biological importance of polynyas in the Canadian Arctic. Arctic 33, 303–315.

Vopel, K., Thistle, D., Rosenberg, R., 2003. Effect of the brittle star *Amphiura filiformis* (Amphiuridae, Echinodermata) on oxygen flux into the sediment. Limnol. Oceanogr. 48, 2034–2045.

Wassmann, P., Reigstad, M., Haug, T., Rudels, B., Carroll, M.L., Hop, H., Gabrielsen, G.W., Falk-Petersen, S., Denisenko, S.G., Arashkevich, E., Slagstad, D., Pavlova, O., 2006. Food webs and carbon flux in the Barents Sea. Progr. Oceanogr. 71, 232–287.

Wexels Riser, C., Wassmann, P., Reigstad, M., Seuthe, L., in press Vertical flux regulation by zooplankton in the northern Barents Sea during Arctic spring. Deep-Sea Res., Part 2, Top. Stud. Oceanogr.

Wlodarska-Kowalczuk, M., Weslawski, J.M., 2001. Impact of climate warming on Arctic benthic biodiversity: a case study of two Arctic glacial bays. Clim. Res. 18, 127–132.