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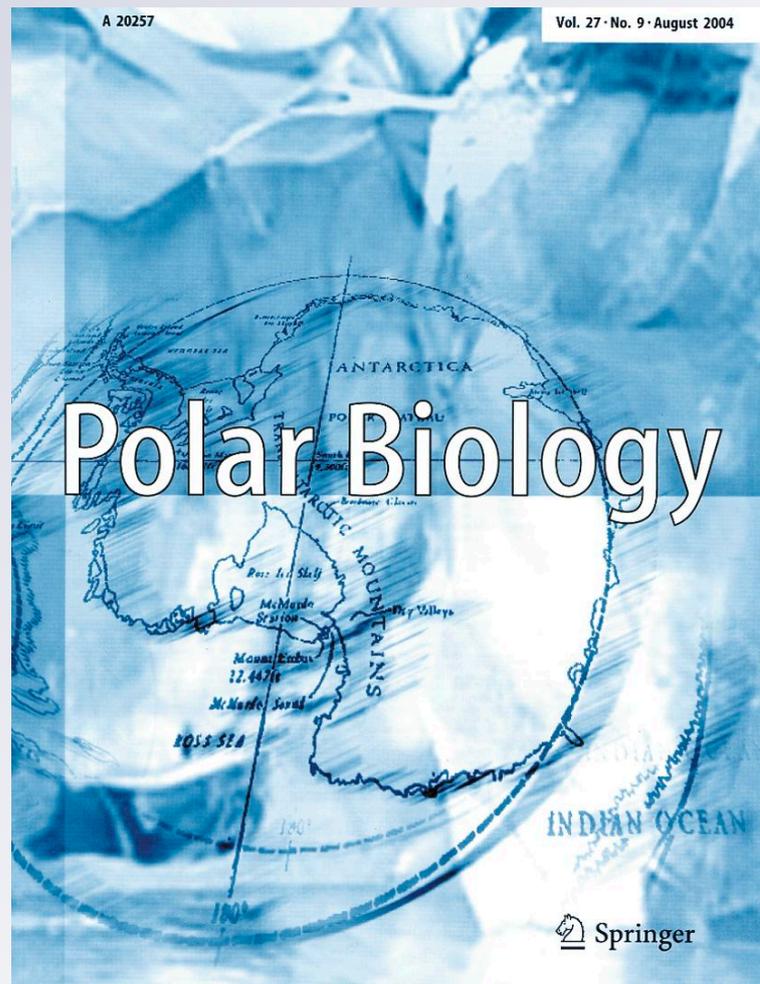
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Spring-to-summer changes and regional variability of benthic processes in the western Canadian Arctic

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Abstract Seasonal dynamics in the activity of Arctic shelf benthos have been the subject of few local studies, and the pronounced among-site variability characterizing their results makes it difficult to upscale and generalize their conclusions. In a regional study encompassing five sites at 100–595 m water depth in the southeastern Beaufort Sea, we found that total pigment concentrations in surficial sediments, used as proxies of general food supply to the benthos, rose significantly after the transition from ice-covered conditions in spring (March–June 2008) to open-water conditions in summer (June–August 2008), whereas sediment Chl *a* concentrations, typical markers of fresh food input, did not. Macrobenthic biomass (including agglutinated foraminifera >500 μm) varied significantly among sites (1.2–6.4 g C m^{-2} in spring, 1.1–12.6 g C m^{-2} in summer), whereas a general spring-to-summer increase

was not detected. Benthic carbon remineralisation also ranged significantly among sites (11.9–33.2 $\text{mg C m}^{-2} \text{day}^{-1}$ in spring, 11.6–44.4 $\text{mg C m}^{-2} \text{day}^{-1}$ in summer) and did in addition exhibit a general significant increase from spring-to-summer. Multiple regression analysis suggests that in both spring and summer, sediment Chl *a* concentration is the prime determinant of benthic carbon remineralisation, but other factors have a significant secondary influence, such as foraminiferan biomass (negative in both seasons), water depth (in spring) and infaunal biomass (in summer). Our findings indicate the importance of the combined and dynamic effects of food supply and benthic community patterns on the carbon remineralisation of the polar shelf benthos in seasonally ice-covered seas.

Keywords Arctic · Beaufort Sea · Pelagic-benthic coupling · Seasonality · Carbon remineralisation · Benthic biomass

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Introduction

Biological processes in the Arctic are known to exhibit a pronounced seasonality with ice cover being one of the major underlying mechanisms (Carmack and Wassmann 2006). Following the ice melt during the spring-to-summer transition, the mismatch between peak primary production and zooplankton grazing allows for an enhanced export of organic material to the seafloor (Wassmann et al. 2006). This provides an important food input to benthic communities, and several studies have described the significant increase in benthic activity in response to an organic matter pulse for the oceans in general (Graf 1992; Pfannkuche 1993) and for Arctic regions in particular (Rysgaard et al. 1998; Renaud et al. 2007b). The remineralisation of

organic matter at the seafloor is a source of nutrient release to the water column (Grebmeier et al. 2006a) and a significant pathway in the global carbon budget (Klages et al. 2004).

Strong pelagic-benthic coupling has been widely suggested as a general feature of Arctic shelves (Grebmeier and Barry 1991; Ambrose and Renaud 1995; Piepenburg et al. 1997; Wassmann et al. 2006), in terms of both quantity and quality of the organic matter exported from the water column and/or sea ice to the seabed (Morata et al. 2008). During the Shelf-Basin Interaction Study (SBI) in the Chukchi Sea, vertical export and benthic response were measured in spring and summer in 2002 and 2004 (Lepore et al. 2007). In 2002, the export of particulate organic carbon (POC) was much higher in summer than in spring and coincided with an, albeit less pronounced, increase in benthic respiration (Moran et al. 2005). In 2004, however, POC export and benthic carbon respiration were only slightly less under ice cover than in summer open-water conditions (Lalande et al. 2007; Lepore et al. 2007). The findings—elevated chlorophyll *a* (Chl *a*) concentrations under ice (Lalande et al. 2007), more than twice as high absolute export rates but only slightly higher benthic respiration—suggest that there was a distinct spring bloom but lateral advection of organic matter into the central Arctic Ocean, which resulted in a lack of a seasonal benthic activity boost (Lepore et al. 2007). Enhanced benthic respiration has been related to higher nutritive quality of the phytodetritus reaching the seabed (Morata and Renaud 2008; Sun et al. 2009). In the Barents Sea, a sharp increase in benthic activity was related to the supply of fresh food, as indicated by high Chl *a* export and high sediment pigment concentrations (Renaud et al. 2008). In the southeastern Beaufort Sea, spring-to-summer dynamics have been studied at one time-series site in Franklin Bay (Amundsen Gulf) during the Canadian Arctic Shelf Exchange Study (CASES) in 2004. A seasonal increase in benthic carbon remineralisation was recorded (Renaud et al. 2007b), whereas an increase in the availability of fresh food at the sea floor could only be confirmed after pigment analyses with a higher resolution (Morata et al. 2010). A considerable increase in benthic respiration from spring-to-summer has also been reported from the North Water Polynya (NOW), where carbon remineralisation was driven by micro- and meiobenthic communities in spring and by macrobenthic communities in summer (Grant et al. 2002). The composition of the benthic community also plays a major role in determining benthic carbon remineralisation in Arctic environments (Clough et al. 2005), as documented in experimental studies (McMahon et al. 2006). However, much less is known about seasonal changes of the structure and activity of benthic communities in relation to dynamics of food availability (Renaud et al. 2008; Witman et al. 2008).

The reduction in Arctic sea ice in response to climate change and ocean warming is well documented (Barber et al. 2009), but its effects on biological processes are hard to predict (ACIA 2004; Smetacek and Nicol 2005). Wassmann et al. (2011) highlighted that climate change has already resulted in clearly discernable changes in marine Arctic ecosystems, but the number of well-documented changes in planktonic and benthic systems was surprisingly low. Although total primary production in the Arctic Ocean will likely increase (Arrigo et al. 2008), its reduced seasonal variability and increased pelagic remineralisation might result in a general decrease in the vertical flux of fresh organic matter to the bottom (Piepenburg 2005; Forest et al. 2010; 2011). There is still controversy about the actual scope and direction of future changes in primary production and vertical flux patterns (Wassmann et al. 2008). Regardless, shifts in benthic community metabolism and composition are expected (ACIA 2004; Grebmeier et al. 2006b; Carroll et al. 2008; Sun et al. 2009; Archambault et al. 2010) and are likely to influence the ecosystem at higher trophic levels (Bluhm and Gradinger 2008). Our incomplete knowledge about spring-to-summer dynamics of benthic processes makes it difficult to reliably predict their response to climate-induced changes in the abiotic environment and to concurrent changes in the timing and magnitude of primary production, the quality of organic material deposited on the seafloor, and the composition of benthic communities. For this purpose, it is crucial to assess the relationships among seasonal dynamics in food supply, benthic standing stock and benthic carbon remineralisation on a regional scale.

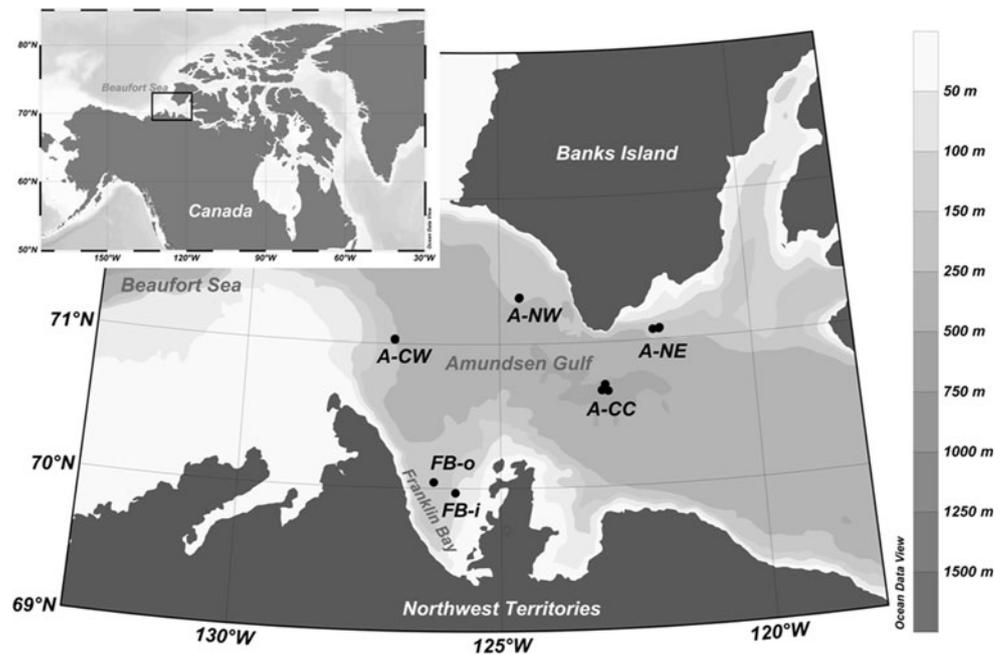
The objective of this study was to describe how seasonal changes in the availability of food influence benthic carbon remineralisation—the rate of carbon cycling—in the southeastern Beaufort Sea. Since ice cover is a major seasonal characteristic of polar regions, differences between the ice-covered period (spring) and subsequent open-water period (summer) were studied. Our hypotheses were that (1) the availability of food for benthic communities increases significantly following the ice melt, (2) benthic biomass increases after the ice melt, (3) benthic carbon remineralisation increases significantly following ice melt, and (4) spatial variability of benthic carbon remineralisation is determined by both food availability and benthic community patterns, here tested as biomass.

Materials and methods

Study region

This study was conducted in the southeastern Beaufort Sea with emphasis on the Amundsen Gulf, including

Fig. 1 Locations of sites sampled for benthic processes during ice-covered (spring) and open-water (summer) conditions in 2008. *A* Amundsen Gulf, *FB* Franklin Bay; *C, E, N, W* central, east, north, west; *i* ice-covered, *o* open water. Note that one point on the map can represent two sampling events when exact relocation in summer was achieved



Franklin Bay (Fig. 1). The area is usually covered by sea ice from November to June (Galley et al. 2008). In 2008, it was generally covered by sea ice until mid-May (Barber et al. 2010; NSIDC 2010). Primary production ranges from 30 to 70 g C m⁻² year⁻¹, indicating generally oligotrophic conditions (Sakshaug 2004). In the Cape Bathurst Polynya, rates are higher, reaching 90–175 g C m⁻² year⁻¹ (Arrigo and van Dijken 2004). Intensive blooms related to ice-edge upwelling events were documented for coastal regions of the Amundsen Gulf, including Franklin Bay, in June 2008 (Mundy et al. 2009; Tremblay pers. comm.). The study area is dominated by coastal shelves with maximum depths of 600 m in the centre of the Amundsen Gulf. Seafloor sediments are usually fine, composed of more than 70% silt and clay (Conlan et al. 2008). Sediment characteristics indicate that marine material dominated the flux in summer and is more degraded in the Amundsen Gulf, whereas on the Mackenzie Shelf material of terrestrial origin is abundant in fall (Magen et al. 2010; Morata et al. 2008). Sediment Chl *a* concentrations are reported to be low (0–2 mg m⁻² in the Amundsen Gulf and 3–4 mg m⁻² in Franklin Bay), with Chl *a*-to-phaeopigment ratios not exceeding 0.2 in summer and fall (Morata et al. 2008). In 2004, accessory sediment pigments consisted mostly of fucoxanthin in the western Amundsen Gulf and of Chl *b* in the eastern part (Morata et al. 2008). Sediment pigment concentrations in spring have only been reported for Franklin Bay, where concentrations were similar to those encountered in summer (Renaud et al. 2007a, b).

Environmental conditions

Near-bottom water temperature and salinity were determined by the shipboard CTD probe at each station 10 m above the seafloor. We used sea ice concentration maps available from the CERSAT Ifremer group (http://cersat.ifremer.fr/fr/data/discovery/by_parameter/sea_ice/psi_ssmi) based on the daily brightness temperature maps from the National Snow and Ice Data Centre (Maslanik and Stroeve 1990), which are acquired from the special sensor microwave imager (SSM/I) onboard the DMSP satellite to extract sea ice concentration data. Daily sea ice concentration data were extracted for each station between March and August 2008. The average of daily concentration for the 14 days preceding the sampling date was used to determine the ice cover for each station. Ice break-up in the region typically takes 1–2 weeks (Galley et al. 2008). We considered the period of 14 days long enough to assure that ice cover was not incidental (e.g. being due to a passing ice floe) and short enough to assure that it describes the ice condition that should be timely linked to benthic processes.

Field sampling

Samples were collected at five sites ranging in water depth from 100 to 595 m at least once in each season (ice-covered and open-water condition) between March and August 2008 onboard the icebreaker CCGS Amundsen (Table 1). Ice conditions for the Amundsen Gulf have been classified as ‘ice covered’ with ≥80% ice cover, ‘open’ with ≤20%

ice cover (Hammill 1987; Galley et al. 2008) and as ice 'break-up' with $\leq 80\%$ and $\geq 20\%$ ice cover (Galley et al. 2008). Adopting this approach, we considered a station to be 'ice-covered' if the 14-day average sea ice concentration was above 80% and 'open' if average sea ice concentration was below 20%. Fifty percent of ice cover represents the average ice concentration of 'break-up' condition and implies that a site was closer to 'ice-covered' than 'open' for at least 7 days before sampling. We verified ice concentration of all sites in break-up condition with weekly ice charts for the western Canadian Arctic published by the Canadian Ice Service (CIS) available on <http://www.ec.gc.ca/glaces-ice/>. Sites were located in the Amundsen Gulf (A-CC, A-CW, A-NE, A-NW) and Franklin Bay (FB) (Fig. 1). In Franklin Bay, sampling was conducted at two distinct sites within 2 days: FB-o was located where the ice edge had retreated for more than 10 days at 18 km distance from FB-i, which was located at the ice edge (Table 1). At each sampling event ('station'), an USNEL box corer was deployed for collecting seafloor sediments. From each box core, five sub-cores of 11 cm diameter and 20 cm sediment depth were taken for assessing benthic carbon remineralisation in microcosm incubations and three additional sub-cores of 5 cm diameter and 10 cm length were taken for determining sediment properties (Table 1).

Sediment pigment concentration

Samples from the sediment surface (0–1 cm) of additional sub-cores were frozen immediately at -20°C for later pigment analysis. Chl *a* and phaeopigment concentrations were analysed fluorometrically following a modified version of the protocol by Riaux-Gobin and Klein (1993). Two grams of wet substrate were incubated with 10 ml 90% Acetone (v/v) for 24 h at 4°C , and the supernatant was measured in a Turner Design 20 fluorometer before and after acidification. Chl *a* and total pigment concentration (Chl *a* + phaeopigments) were determined and used in statistical analyses. Quantities are expressed as microgram pigment per gram of dry sediment [$\mu\text{g g}^{-1}$].

Benthic carbon remineralisation

Incubations of sediment microcosms were run in a dark, temperature-controlled room ($2\text{--}4^{\circ}\text{C}$) for 24–48 h. Prior to the onset of measurements, sediment cores were carefully topped with bottom water collected by the rosette at the same site and then allowed to acclimate for 6–8 h while being saturated with oxygen to avoid suboxic conditions during the experiment. At the onset of measurements, the microcosms were hermetically closed and

bubbles were removed. During the incubation, the water overlying the sediment was constantly stirred without resuspending the sediment surface. Total sediment oxygen demand (SOD) was determined as the decrease in oxygen concentrations in the water phase and was measured periodically (4–8 h intervals) with a non-invasive optical probe (Fibox 3 LCD, PreSens, Regensburg, Germany), until it had declined by approximately 20%. Three additional incubation cores containing bottom water only acted as controls for assessing the oxygen uptake due to processes within the water column. SOD values were determined as the slope of the linear regression of oxygen concentration in sediment microcosms on incubation time. Average oxygen decrease rates determined in the three control cores were subtracted, and benthic carbon remineralisation values ($\text{mg C m}^{-2} \text{ day}^{-1}$) were calculated from SOD rates using a respiration coefficient of 0.8 (Brey 2001).

Macrobenthic biomass

Each sediment microcosm was sieved through a 0.5 mm mesh under running sea water at the end of incubations to determine biomass of macrofaunal communities. The sieve residue was preserved in a buffered 4% seawater-formaldehyde solution and analysed for species composition and abundance under a stereomicroscope in the lab. Metazoan infauna biomass was estimated by determining the formaldehyde wet weight (except at station A-CC-o2 see Table 1) and applying taxon-specific wet weight to carbon conversion factors (Brey et al. 2010). All macrofaunal foraminifera except for five individuals were agglutinated forms. For sorting, we used the method described by Moodley et al. (2002) based on the presence of cytoplasm and appearance of shells. Biomass of macrofaunal foraminifera was estimated from abundance figures using an average value of $5 \mu\text{g C individual}^{-1}$ (Altenbach 1985). Abundance of foraminifera at station A-CW-i could not be analysed, as the remains of this sample were discarded after macrofauna sorting. There is good evidence, however, that at this site the foraminiferan biomass was lower in spring than in summer, since no foraminifera were detected by visual inspection of the spring sieve residues, whereas in summer, tests were easily visible although abundances were lower than in all other samples. Total benthic biomass was computed by adding foraminiferan and infaunal biomass values, assuming 0 for the three stations where foraminiferan data were lacking. For statistical analysis, foraminifera data were assigned ranks in steps of 50 mg C m^{-2} . This interval allowed for capturing within-station variances and at the same time to assign the lowest rank to replicates at stations from which no data were available.

Table 1 Sampled stations, environmental conditions, temporal factor (season) and number of replicates used to determine sediment oxygen demand (SOD), chlorophyll *a* concentrations in the sediment (Chl *a*) and macrobenthic infauna biomass (Biomass)

| Station | CFL Station Label | Date | Water Depth [m] | Position | | Sea ice cover [%] | Sal _{bot} | T _{bot} [°C] | Season | SOD (n) | Chl <i>a</i> (n) | Biomass (n) |
|----------|-------------------|-----------|-----------------|----------|-----------|-------------------|--------------------|-----------------------|--------|---------|------------------|-------------|
| | | | | Latitude | Longitude | | | | | | | |
| A-NE-i | D 34 | 24/Mar/08 | 185 | 71.076 N | 121.811 W | 100 | 34.5 | −0.1 | Ice | 5 | 3 | 5 |
| A-NE-i-2 | D 35 | 02/Apr/08 | 215 | 71.069 N | 121.944 W | 98 | 34.5 | −0.1 | Ice | 5 | 3 | 5 |
| A-NE-o | D 34 | 13/Jul/08 | 185 | 71.070 N | 121.823 W | 0 | 34.3 | −0.6 | Open | 5 | 3 | 3 |
| A-NW-i | D 37 | 10/Apr/08 | 245 | 71.312 N | 124.603 W | 95 | 34.6 | −0.1 | Ice | 5 | 3 | 5 |
| A-NW-o | D 37 | 02/Aug/08 | 250 | 71.318 N | 124.595 W | 0 | 34.5 | −0.2 | Open | 5 | 3 | 5 |
| A-CW-i | 1020A | 06/May/08 | 255 | 71.029 N | 127.088 W | 90 | 33.1 | | Ice | 5 | 3 | 5 |
| A-CW-o | 1020A | 27/Jul/08 | 245 | 71.028 N | 127.088 W | 0 | n/a | −0.1 | Open | 5 | 3 | 5 |
| A-CC-i | 405 | 19/May/08 | 505 | 70.662 N | 122.887 W | 60 | 34.5 | | Ice | 4 | 3 | 5 |
| A-CC-o | 405B | 10/Jun/08 | 545 | 70.667 N | 123.010 W | 11 | 34.8 | 0.4 | Open | 5 | 3 | 5 |
| A-CC-o-2 | 405B | 21/Jul/08 | 595 | 70.707 N | 122.939 W | 0 | 34.8 | 0.4 | Open | 5 | 3 | n/d |
| FB-i | FB03 | 16/Jun/08 | 100 | 69.968 N | 125.862 W | 34* | 33.4 | −1.3 | Ice* | 5 | 3 | 5 |
| FB-o | 1,116 | 14/Jun/08 | 230 | 70.042 N | 126.277 W | 22 | 33.3 | −1.3 | Open | 5 | 3 | 5 |

Daily ice cover concentrations averaged over the 14 days preceding the date of sampling was used to determine sea ice cover [%]. A Amundsen Gulf, FB Franklin Bay, C, E, N, W central, east, north, west, CFL Circumpolar Flaw Lead System Study

* Station was located in fast ice, while general ice cover had retreated

Data analysis

One-way ANOVA was used to test seasonal differences in salinity and temperature (two levels: ice, open). Earlier studies have provided evidence that variance among sub-cores from the same box core is not significantly smaller than variance among different box cores taken at the same station (Renaud et al. 2007a). Sub-cores were, therefore, treated as true replicates in statistical analyses. An orthogonal two-way ANOVA was used to test the differences between ‘seasons’ (two levels: ice, open), ‘sites’ (five levels: A-CC, A-CW, A-NE, A-NW, FB) and their interactions in sediment Chl *a* concentration, total sediment pigment concentration, benthic biomass and carbon remineralisation. Tukey’s post-hoc tests were applied to identify differences when a source of variation was significant. Prior to ANOVA, normality was verified using Shapiro–Wilk’s test and homogeneity of variances was verified using Levene’s test and visual analysis of residuals. Data were transformed using natural logarithm if variances were not homogeneous. To identify the drivers of benthic carbon remineralisation in spring and summer (separately), Mallows’ C_p (MC_p) and adjusted R^2 were used to determine the best-subset linear multiple regression model. MC_p compares a given reduced model to the full model, and a smaller statistic indicates a better model (Quinn and Keough 2002). Water depth, sediment Chl *a* concentration, total sediment pigment concentration,

infaunal biomass and ranked foraminiferan biomass were predicting variables of the full model. We tested for collinearity of variables retained in the best-subset model using the variance inflation factor (VIF). When VIF is >10 , collinearity is assumed critical (Quinn and Keough 2002). This was not the case for either of the best-subset models.

Results

Temporal dynamics from spring-to-summer

Environmental conditions

Near-bottom water temperature at the study sites varied between -1.3 and 0.4°C , and near-bottom salinity ranged between 33.1 and 34.8, as determined by the shipboard CTD probe 10 m above the seafloor (Table 1). The greatest difference was a decrease in temperature of 0.5°C (from -0.1 to -0.6°C) at site A-NE from March to July (Table 1). However, neither temperatures nor salinities differed significantly between spring and summer (one-way ANOVA, salinity $F_{1, 7} = 0.23$, $P = 0.64$; temperature $F_{1, 7} = 0.44$, $P = 0.53$). Average sea ice cover during the 14 days before sampling at a given site varied from 100 to 60% between March and May and from 34 to 0% between June and August (Table 1). The higher ice cover in June

Table 2 Carbon remineralisation, sediment parameters and macrobenthic biomass at each location (A = Amundsen Gulf, FB = Franklin Bay; C, E, N, W = central, east, north, west) and season

| Location | Season | Chl <i>a</i> [$\mu\text{g g}^{-1}$] | Phaeo [$\mu\text{g g}^{-1}$] | Infauna [mg C m^{-2}] | Foram [mg C m^{-2}] | Carbon remineralisation [$\text{mg C m}^{-2} \text{d}^{-1}$] |
|----------|--------|---------------------------------------|--------------------------------|----------------------------------|--------------------------------|--|
| A-NE | Ice | 0.72 ± 0.18 | 6.80 ± 0.54 | $2,526 \pm 881$ | 237 ± 32 | 16.7 ± 2.9 |
| | Ice | 0.55 ± 0.08 | 8.53 ± 0.37 | $1,138 \pm 186$ | n/d | 13.0 ± 2.6 |
| | Open | 0.74 ± 0.32 | 10.83 ± 3.97 | $8,382 \pm 2,366$ | 662 ± 140 | 16.9 ± 1.9 |
| A-NW | Ice | 0.54 ± 0.06 | 9.02 ± 0.51 | $1,102 \pm 246$ | 128 ± 36 | 12.7 ± 0.6 |
| | Open | 0.53 ± 0.02 | 10.39 ± 0.51 | $12,566 \pm 9,012$ | 83 ± 11 | 23.4 ± 4.5 |
| A-CW | Ice | 0.31 ± 0.15 | 9.93 ± 1.09 | $2,919 \pm 1,712$ | n/d | 20.8 ± 2.0 |
| | Open | 0.80 ± 0.15 | 13.45 ± 0.73 | $3,912 \pm 1,320$ | 36 ± 6 | 24.2 ± 1.5 |
| A-CC | Ice | 0.24 ± 0.05 | 5.05 ± 0.35 | 916 ± 168 | 592 ± 22 | 11.9 ± 2.2 |
| | Open | 0.16 ± 0.02 | 6.23 ± 0.66 | 900 ± 723 | 155 ± 7 | 11.6 ± 3.1 |
| | Open | 0.15 ± 0.04 | 7.08 ± 0.28 | n/d | n/d | 11.9 ± 1.8 |
| FB | Ice | 1.36 ± 0.12 | 9.14 ± 1.00 | $6,166 \pm 3,513$ | 232 ± 23 | 33.2 ± 2.4 |
| | Open | 2.39 ± 0.79 | 14.61 ± 1.40 | $3,600 \pm 719$ | 5 ± 2 | 44.4 ± 4.0 |

Within-station averages \pm SE. *Chl a* chlorophyll *a* concentration, *Phaeo* phaeopigment concentration, *Foram* foraminifera $>500 \mu\text{m}$, n/d not determined

(34 and 22%) was measured in Franklin Bay, where sampling was conducted at a distance of 18 km (FB-o) and <0.5 km (FB-i) to a visible ice edge. CIS ice charts showed that sites A-CC and FB were completely ice-covered at least seven of 14 days prior to sampling on May 19th and June 16th, respectively. Based on these results, stations were grouped into ice-covered (or spring) stations when ice cover was $\geq 34\%$ and into open-water (or summer) stations when ice cover was $\leq 22\%$.

Sediment pigment concentration

Chl *a* concentrations in the surficial seafloor sediments varied between 0.24 and $1.36 \mu\text{g g}^{-1}$ under ice cover and between 0.15 and $2.39 \mu\text{g g}^{-1}$ in open-water conditions (Table 2). There was a significant interaction between site and season ($F_{4, 26} = 3.09$, $P = 0.03$; Fig. 2a, b). Phaeopigment concentrations ranged from 5.05 to $9.93 \mu\text{g g}^{-1}$ and from 6.23 to $14.61 \mu\text{g g}^{-1}$, respectively. They increased at all sites from spring-to-summer (Table 2). Total sediment pigment concentrations varied from 5.29 to $10.51 \mu\text{g g}^{-1}$ under ice cover and from 6.39 to $17.00 \mu\text{g g}^{-1}$ in open water. The values were significantly different between seasons ($F_{1, 26} = 13.19$, $P < 0.01$) and among sites ($F_{4, 26} = 13.57$, $P < 0.001$; Fig. 2c, d). No interaction between season and site was observed ($F_{4, 26} = 0.52$, $P = 0.72$). Four site groups were identified using Tukey's post-hoc test with A-CC having a significantly lower sediment pigment concentration than all other sites. Highest pigment concentrations were found at FB.

Benthic biomass

Macrofauna in the sediment samples was mostly composed of infaunal polychaetes contributing between 33 and 84% of total biomass at the different stations (unpub. data). Macrobenthic infauna biomass varied from 916 to $6,166 \text{ mg C m}^{-2}$ under ice cover and from 900 to $12,566 \text{ mg C m}^{-2}$ in open water (Table 2). At some sites, large agglutinated foraminifera (test sizes $>500 \mu\text{m}$) were particularly abundant, with biomass values ranging from undetermined to 592 mg C m^{-2} under ice cover conditions and undetermined to 662 mg C m^{-2} in open water. They accounted for between $\ll 1$ and $>10\%$ of the total macrobenthic biomass (Table 2). Total macrobenthic biomass (infauna and foraminifera) reached values from $1,230$ to $6,398 \text{ mg C m}^{-2}$ under ice cover and from $1,055$ to $12,649 \text{ mg C m}^{-2}$ in open-water conditions. There was a significant interaction between site and season ($F_{4, 43} = 3.17$, $P = 0.02$; Fig. 2e, f), and three groups were identified following Tukey's post-hoc test.

Benthic carbon remineralisation

Carbon remineralisation by the sediment community ranged from $11.9 \text{ mg C m}^{-2} \text{ day}^{-1}$ to $33.2 \text{ mg C m}^{-2} \text{ day}^{-1}$ in spring under ice cover and from $11.6 \text{ mg C m}^{-2} \text{ day}^{-1}$ to $44.4 \text{ mg C m}^{-2} \text{ day}^{-1}$ under open water in summer (Table 2). The values varied significantly between seasons ($F_{1, 49} = 11.34$, $P < 0.00$) and among sites ($F_{4, 49} = 33.37$, $P < 0.00$) (Fig. 2g, h). Following Tukey's Post-hoc test, four groups were identified with only FB showing higher

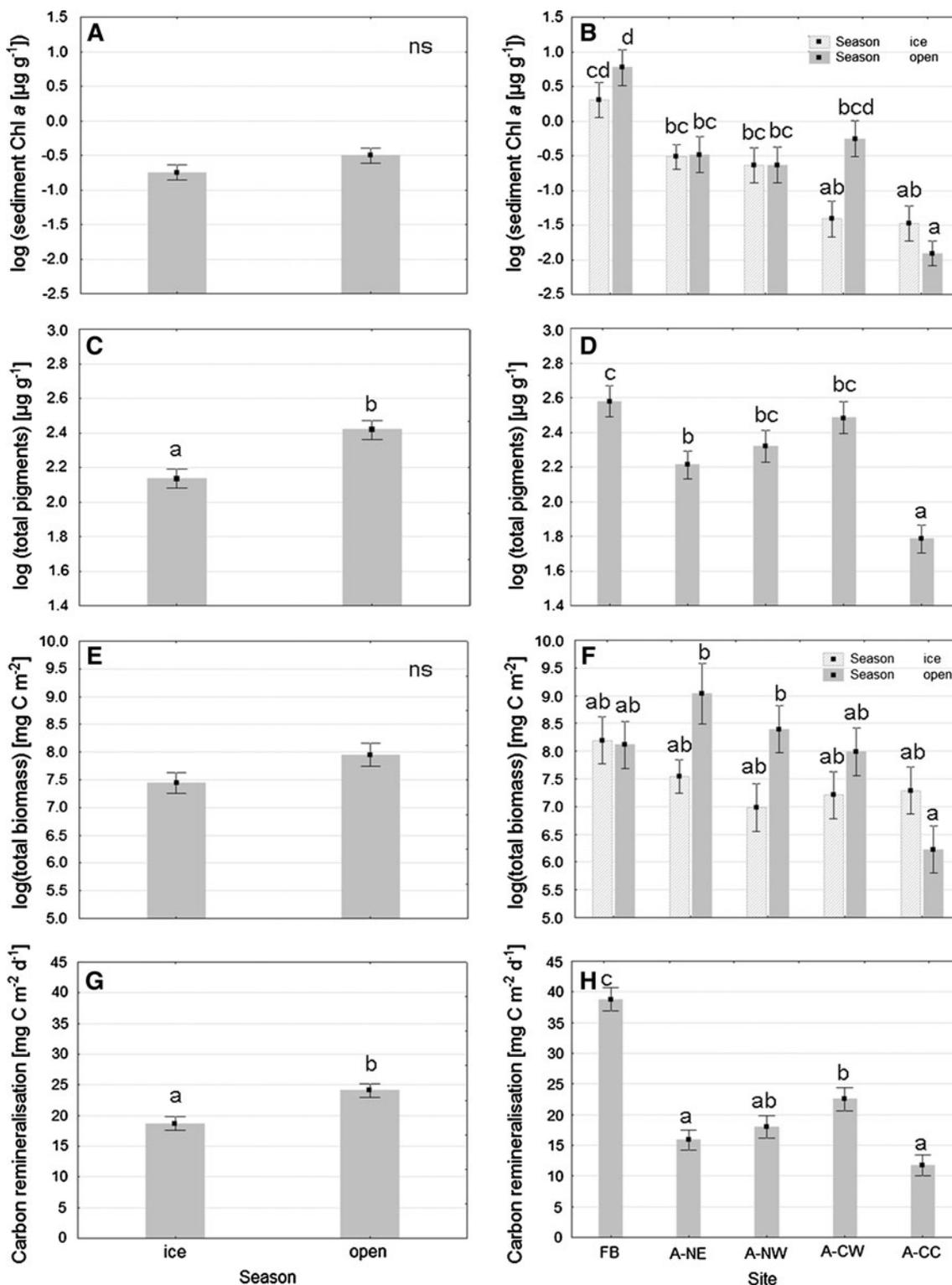


Fig. 2 Seasonal and spatial patterns in benthic processes in the southeastern Beaufort Sea in 2008. Differences in season (**a, c, e, g**), Site (**d, h**) and significant interactions between season and site (**b, f**) in sediment Chl *a* concentration (**a, b**), sediment pigment concentration (**c, d**), benthic biomass (**e, f**), and benthic carbon

remineralisation (**g, h**) following univariate orthogonal two-way ANOVA are presented. Means \pm SE. Lower case letters indicate significantly different groups identified using Tukey's post-hoc testing, *ns* not significant, A Amundsen Gulf, FB Franklin Bay, C, E, N, W central, east, north, west; *i* ice-covered, *o* open water

Table 3 Adjusted R^2 and standardized regression coefficients of benthic parameters

| Season | Adjusted R^2 | F | P | Depth | Infauna | Chl a | Pigments | Foram | MCp | Effects |
|--------|----------------|--------------|------------------|-------------|---------|-------------|----------|--------------|-------------|----------|
| Ice | 0.57 | 13.42 | <0.001 | 0.35 | | 1.02 | | -0.43 | 4.88 | 3 |
| | 0.58 | | | 0.34 | 0.18 | 0.94 | -0.40 | 5.15 | 4 | |
| | 0.55 | | | | | 0.74 | -0.31 | 5.19 | 2 | |
| | 0.56 | | | | 0.18 | 0.66 | -0.28 | 5.39 | 3 | |
| | 0.59 | | | 0.52 | 0.20 | 0.94 | 0.27 | -0.29 | 6.00 | 5 |
| Open | 0.74 | 22.07 | <0.001 | | | 0.25 | | -0.23 | 2.89 | 3 |
| | 0.71 | | | | 0.21 | 0.77 | | 3.97 | 2 | |
| | 0.74 | | | | 0.33 | 0.81 | -0.27 | -0.30 | 4.12 | 4 |
| | 0.73 | | | 0.11 | 0.32 | 0.67 | | -0.23 | 4.54 | 4 |
| | 0.68 | | | | | 0.84 | | 5.19 | 1 | |

Bold values are statistically significant at $P < 0.001$

Depth water depth, *Infauna* biomass of infaunal macrobenthos, *Foram* biomass of foraminifera $>500 \mu\text{m}$, *Chl a* sediment chlorophyll a concentration, *Pigments* total sediment pigment concentration, predicting benthic carbon remineralisation in the two different seasons (ice-covered spring, open-water summer). Whole model results are presented for the best-subset solution following MCp criteria (Effects—number of parameters included in the model). Absence of standardized regression coefficients indicate the parameters were not retained in the model

carbon remineralisation than all other sites (Fig. 2h). Remineralisation was lowest at A-CC. No interaction between season and site was observed ($F_{4, 49} = 2.12$, $P = 0.09$).

Drivers of spatial variability of benthic carbon remineralisation in spring and summer

MCp criteria and adjusted R^2 identified the best-subset regression model for ice-covered conditions in spring with depth, Chl a concentration and foraminiferan biomass retained as predictive variables (Table 3). Benthic carbon remineralisation was positively related to depth and Chl a concentration (standardized regression coefficient 0.35 and 1.02, respectively) and negatively related to foraminiferan biomass (standardized regression coefficient -0.43). The model explained 57% (adjusted R^2) of the variance in our data. Foraminiferan biomass and Chl a concentration were also retained in the following three subset models with either depth and infaunal biomass, none, or infaunal biomass as additional predictor variable.

The best open-water model, explaining 74% (adjusted R^2) of the total variance, did also encompass three predictive variables (Table 3). Again, Chl a concentration exhibited the highest relation to benthic carbon remineralisation (standardized regression coefficient 0.63) and foraminiferan biomass was negatively related (-0.23), but this time, infaunal biomass was the third significant variable contributing to the best-subset model (0.25). These three variables were retained in the four best models, with total sediment pigment concentration and/or water depth as additional predictors in the subsequent models, that were disqualified following MCp (Table 3).

Discussion

Hypothesis 1: food availability for the benthos increases after the ice melt

Site and season had effects of similar importance on the distribution of total sediment pigment concentration, but their influence on Chl a distribution cannot be separated. Water depth seemed to affect both parameters: The lowest concentrations were found at the deepest site in the central Amundsen Gulf and the highest concentration at the shallowest site in Franklin Bay. These results correspond with the general finding that the vertical flux of organic matter decreases with depth (Christensen 2000; Carmack and Wassmann 2006).

The significant effect of season on total sediment pigment concentration, i.e., its general increase from ice to open-water season, supports our hypothesis that food supply to benthic communities in the southeastern Beaufort Sea rises after the ice melt characterizing the spring-to-summer transition. The lack of an interaction between site and season indicates that this temporal trend was independent of the significant concentration differences among the sites. A similar conclusion has been reported for vertical flux patterns in the southeastern Beaufort Sea (Juil-Pedersen et al. 2010): sedimentation rates were significantly higher in summer than in fall, but also showed a higher variability among the different sites in summer than in fall. The importance of seasonal food pulses for the benthos has been recognized since some time (Pfannkuche 1993), and the pronounced seasonality of the production period and, hence, the vertical flux of organic matter is one

of the major factors explaining the tight pelagic-benthic coupling observed in Arctic shelf regions (Grebmeier and Barry 1991; Klages et al. 2004).

Sediment Chl *a* concentration in the study area, as determined by fluorometry, was slightly higher in 2008 (0.7–3.5 mg Chl *a* m⁻²) than in 2004 (0 to 2 mg Chl *a* m⁻²) (Morata et al. 2008). In Franklin Bay, they were even up to four times higher (7–11 vs 3–4 mg Chl *a* m⁻²). An upwelling event in late 2007 and early 2008, the year of our study, led to enhanced primary production and vertical export particularly in Franklin Bay and close to the Mackenzie river delta (Tremblay pers. comm.; Williams and Carmack 2008), where a higher input of food to the seabed may thus have allowed preserving the seasonal signal. However, the other sites of this study were not affected by this event (vertical flux 38–68 mg POC m⁻² day⁻¹, Sallon et al. 2011) and were located in an area generally expected to receive less input from the water column than other Arctic regions (Lalande et al. 2009). Moreover, analysis of carbon flux in the central Amundsen Gulf has shown that high pelagic turnover did not allow for intensive organic matter export despite an increased primary production in this area (Forest et al. 2011; Sallon et al. 2011). Despite the interannual difference, the generally low quantity of recently exported ‘fresh’ material may have prevented a measurable seasonal increase in Chl *a* concentration at the seafloor here.

The detection of a seasonal signal in total sediment pigment concentration but not in Chl *a*, the indicator of fresh material, is not in contradiction. Morata et al. (2010) have demonstrated that a combination of analytical methods were necessary to verify the arrival of a food pulse that had not been detectable using fluorometric analysis of sediment pigments in the course of a spring-to-summer transition. The response of benthic communities to algal input can be rapid but of limited duration (Sun et al. 2007), and we may have sampled some sites after the onset of such a rapid consumption. This would imply a processing of fresh (Chl *a*) to more decomposed (phaeopigments) algal material. Indeed, we report a tendency of increasing Chl *a* concentration combined with the significant increase in total pigment concentration from spring-to-summer. Considering a possibly insufficient resolution for the transient signal of sedimentary Chl *a* concentration, our results support the hypothesis of enhanced high-quality food supply to the benthos after the ice break-up that may be rapidly processed by benthic communities.

Our findings also highlight that there is a spatial variability in the importance of the processes driving the food supply to the benthos. The general spatial pattern of sediment pigment concentration reflects differences in primary production and depth at the different sites. Lowest concentrations of sediment pigments were found in the central

Amundsen Gulf, where the depth reduces organic matter export (Carmack and Wassmann 2006). Highest concentrations were found in Franklin Bay and A-CW sites that were situated in or at the margin of the upwelling zone reported for 2008 (Tremblay pers. comm.), but similar values were reported for most sites at ca. 200 m depth. Whereas Lepore et al. (2007) suggested a lack of spring-to-summer signal for years of enhanced primary production and export in Chukchi Sea, here, the seasonal increase in both Chl *a* and total sediment pigment concentration was highest at sites A-CW and FB (Table 2). We would have expected a more evident increase for A-NW in this context, but the late summer sampling date (August) may have allowed for a more complete degradation of algal material, since the spring bloom at this site.

Hypothesis 2: benthic biomass increases after the ice melt

Total benthic biomass did not change significantly after the ice break-up, but did show a tendency to increase. This may reflect a lag between food input and faunal production and reproduction. Metabolic responses and, therefore, carbon remineralisation react more quickly to food inputs than does biomass (Brey et al. 2010). At one site (A-NE), we did observe a seasonal transition from juvenile to adult individuals in polychaete species between the two sampling events, but a quantification of such growth processes is difficult due to the small size of the encountered infauna. The influence of predation has neither been investigated in our study area nor suggested to limit the increase in biomass in other polar regions (Ambrose and Renaud 1997, Bluhm and Gradinger 2008). Moreover, faunal composition also responds to environmental changes on time scales greater than 1 year (Cusson et al. 2007; Piepenburg et al. 2010) and does, therefore, integrate the effects of past processes that have not been covered during our sampling. It is noteworthy that spatial patterns of biomass did not match those of sediment pigment concentration or carbon remineralisation as can often be expected in polar regions (e.g. Carroll et al. 2008; Witman et al. 2008). Values at FB were not higher than at other sites, and at sites A-NE, A-NW and A-CW biomass increased strongly from spring-to-summer. Total benthic biomass is only one of the several benthic community factors reacting to food supply patterns, as metabolic rates differ widely among species (Michaud et al. 2009). The southeastern Beaufort Sea is one of the most diverse Arctic shelf regions (Piepenburg et al. 2010). Local community composition can be quite variable (Cusson et al. 2007), which involves changes in trophic positions and, therefore, in carbon cycling efficiency (Tamelander et al. 2006; Sun et al. 2009). A better proxy than mere biomass would be achieved if functional

composition of benthic communities were considered in the analysis (Bolam et al. 2002; Michaud et al. 2005), and hence, we coarsely separated biomass into infauna and foraminifera for analysis of driving factors.

We did not determine the biomass of microbes and meiofauna, which have higher reproduction and growth rates and are thus more likely to show a detectable short-term biomass increase in response to organic matter input (Soltwedel 2000; Rex et al. 2006). We did not find an increase in foraminifera biomass over the seasonal transition as it has been reported from other investigations (Altenbach 1992; Moodley et al. 2002). Our restriction to individuals of macrofaunal size may explain the deviation from processes described for foraminifera communities elsewhere, since total communities in those studies were dominated by meiofaunal species of smaller size and presumably faster metabolic reactions. These differences in community composition likely influence the timing and amplitude of the benthic response to seasonal food input (Renaud et al. 2007a).

Hypothesis 3: benthic carbon remineralisation increases after the ice melt

In our 2008 data, the spatial and temporal distribution of benthic carbon remineralisation largely reflected that of sediment pigment concentration: there were significant effects of both season and site, with the latter being even more pronounced than the former. There was no interaction between the two effects, indicating that the carbon cycling generally increased from spring-to-summer, independent from spatial differences in the extent of this rise. Our results, therefore, support the hypothesis that benthic carbon remineralisation in our study area increases after the ice break-up.

Microcosm incubations are a widespread and robust method for benthic community metabolic measures (e.g. Tengberg et al. 2004) and produce reliable estimates for benthic carbon remineralisation (Renaud et al. 2007a). During our measurements, the temperature of the experiments was slightly higher (max. 4°C) than in situ bottom water temperature as measured 10 m above ground during CTD casts. Even though this might influence the accuracy of our absolute carbon cycling estimates (max. 30% overestimation following Q_{10}), it is common practice in Arctic studies to run shipboard incubations between 0 and 4°C (e.g. Grant et al. 2002; Renaud et al. 2007a). Moreover, temperatures were generally constant for incubations during this study and, hence, did not affect the comparability of the data gained in the course of our study.

Benthic carbon remineralisation rates were lower in summer 2008 (11.6 to 44.4 mg C m⁻² day⁻¹) than those observed by Renaud et al. (2007a) in the same region in

summer 2004 (18.0 to 58.8 mg C m⁻² day⁻¹). At first glance, this seems to be in contradiction to the primary production reported to be higher in 2008 than 2004 (Forest et al. 2011). However, carbon turnover in the water column has also been reported to be particularly high in 2008 leading to vertical fluxes similar to those in 2004 and a weaker pelagic-benthic coupling (Sallon et al. 2011). Our data suggest that food availability at the seafloor was comparable or even higher than in 2004 (0.7–3.5 in 2008 vs. 0–2 mg Chl *a* m⁻² in 2004). The lower benthic activity observed in 2008 may be explained by two other factors. First, experimental studies have emphasized the fast but also rather short-term response of sediment community respiration to organic matter input (Graf 1992; Sun et al. 2007). The signal may already be lost after two weeks. It is possible that most of our summer data were obtained in a later, more declined or beginning phase of benthic activity, and that data from 2004 were rather obtained during the peak response shortly after the sedimentation pulse. This may also explain the important differences of organic matter degradation between sites compared to seasons. Nevertheless, we are confident that our sampling design was appropriate to detect the benthic response to food supply. The general increase in sediment pigment concentration during the open-water period covered by our study indicates that the effects of enhanced food supply during and/or shortly after the ice melt were still measurable. Organic matter export to the seafloor occurs over several days to weeks, and it is likely that the Arctic benthic communities maintain the shift from ‘winter to summer mode’ for more than 2 weeks, particularly if high-quality food (Chl *a*) is still available. Second, the difference in benthic activity patterns between 2004 and 2008 may also be caused by differences in faunal composition. The results of Michaud et al. (2005) show that sediment oxygen uptake is strongly influenced by the functional groups of species present. Renaud et al. (2007a) have reported very high densities of amphipods at some sites in 2004, which were never observed in 2008. However, more data on faunal composition are needed to test this hypothesis.

The significant differences between sites highlight the amount of spatial variability in parameters influencing the benthic activity such as vertical export, depth and other biotic as well as abiotic factors. Tanelander et al. (2006) have demonstrated important spatial variability in pelagic-benthic coupling on the northwestern Barents Sea, ultimately influencing the benthic food web. The spatial pattern of benthic carbon remineralisation in our study is generally congruent with that in sediment pigment concentration, and highest values were observed in Franklin Bay, the shallowest site (FB), and lowest values at the deepest site in the central Amundsen Gulf (A-CC). Carbon cycling increase from spring-to-summer was significantly

greater at FB than at all other sites, indicating that not only water depth but also other parameters are involved. Primary production and vertical export was higher at FB than in other regions of the southeastern Beaufort Sea (Tremblay pers. comm.), and we may have been sampling closer to bloom conditions than at other sites. This may lead to a generally higher benthic activity. The interplay of food quantity, quality and benthic community composition needs to be considered for the explanation of spatial patterns in benthic carbon remineralisation.

Hypothesis 4: spatial variability of benthic carbon remineralisation is determined by both food availability and benthic biomass

In our data, the importance of the factors driving benthic carbon remineralisation slightly changed in the course of the transition from ice-covered conditions in spring to open-water conditions in summer: In both spring and summer, sediment Chl *a* concentration was the most important predictor. In summer, macrobenthic infauna biomass was a secondary significant predictor and foraminiferan biomass retained in the model; in spring foraminiferan biomass was identified as second significant and depth as additional third factor affecting carbon cycling.

A number of studies have described the significant impact of water depth and benthic food availability on carbon remineralisation (Graf 1992; Bessiere et al. 2007; Renaud et al. 2007a, 2008). In a study ranging down to 3,650 m depth, besides these two factors, benthic biomass was found to be correlated to benthic carbon remineralisation (Clough et al. 2005). Our results partly corroborate these, but also suggest that depth does not directly predict spatial patterns of benthic carbon cycling on the southeastern Beaufort Sea shelf. The general relationship between water depth and sediment pigment concentration (Ambrose and Renaud 1995; Renaud et al. 2007a) and between water depth and benthic biomass (Conlan et al. 2008) on Arctic shelves has been reported. It is likely that depth had an indirect influence on benthic carbon remineralisation via other parameters during our study, and its inclusion in the best spring model only indicates the dominating influence of other parameters on spatial variability and the aforementioned effects of local processes (e.g. in Franklin Bay) in summer. Areas of enhanced primary production and pelagic-benthic coupling can create 'hotspots' of benthic processes, irrespective of water depth (Witman et al. 2008; Grebmeier et al. 2009). In the low-production ice-covered season, when food input to the benthos is generally low and limits benthic activity at all sites, the quantity of high-quality food is the most important driver. After the ice melt, sufficient fresh detritus is reaching even greater depths and the level of benthic

activity generally rises (Renaud et al. 2008). The metabolic rate is still primarily determined by the actual availability of high-quality food rather than by total sediment pigment concentration (Sun et al. 2009). The significance of infaunal biomass in summer only could be explained by a dormant stage of organisms during starvation periods. The consistent negative effect of foraminiferan biomass on benthic carbon remineralisation in both spring and summer raises questions on the metabolic mechanisms in this group. Recently, Piña-Ochoa et al. (2010) have described use of denitrification processes by many foraminiferan species. This could imply the respiration of nitrate rather than oxygen from the water phase, but it is still unclear, whether foraminiferan denitrification is restricted to anaerobic conditions (Høgslund et al. 2008; Piña-Ochoa et al. 2010). Depending on the oxygen penetration of sediments, which is generally deeper in greater water depths, foraminifera can be abundant down to more than 5 cm sediment depth (Fontanier et al. 2005). Also, the importance of smaller organisms as compared to macrofauna increases with water depth, most likely caused by the limited supply of food in terms of quantity and quality (Piepenburg et al. 1995; Clough et al. 2005; Rex et al. 2006). As their abundance is higher at deeper sites, benthic carbon remineralisation seems to decrease with foraminiferan biomass. Foraminifera are often neglected in studies on benthic macrofauna, due to the high effort for sorting specimens (Soltwedel 2000; Wollenburg and Kuhnt 2000). Clough et al. (1997) conducted one of the few studies recording foraminifera and macrofauna in conjunction with benthic processes in the Arctic. However, foraminiferan contribution to the variability in benthic processes was not statistically analysed, and their contribution to benthic carbon remineralisation was not measured in their study. As demonstrated by Gooday et al. (2009) for the deep sea, the size and abundance of macrofaunal foraminifera in Arctic environments imply the need to consider this parameter in the examination of benthic processes.

Conclusions

We hypothesized that an increase in food availability is the prime cause for the general rise in benthic carbon remineralisation after the ice melt in open-water conditions. This hypothesis is not only supported by the concurrent spring-to-summer increase in sediment pigment concentrations and benthic carbon remineralisation but also by the great importance of Chl *a* in predicting benthic carbon cycling. Our results of the two regression models also support our hypothesis that both food supply to the benthos and benthic biomass are the most important determinants for benthic carbon remineralisation, and their different spatiotemporal

patterns during this study imply that they are not directly correlated. Overall, these findings indicate the importance of biotic parameters rather than an abiotic factor such as depth in determining the spatial variability of benthic carbon remineralisation, particularly on a regional scale like in our study. The general relationship between food supply and benthic metabolism in seasonally ice-covered polar shelf seas may be regionally modified by the composition of the benthic community. If we assume that a decrease in ice cover accompanied with enhanced pelagic recycling will lead to rather degraded organic matter exported to the benthos over a longer season, we can expect an increase in competition for quality food among benthic communities. Thus, climate changes may favour a shift in community composition towards boreal species on Arctic shelves.

To better understand the effects of the underlying factors driving the spatial and seasonal variability of benthic processes, analyses of the relationship between spatial patterns and annual to decadal changes in seasonal dynamics are necessary. The faunal composition of benthic communities represents a long-term integration of environmental conditions and the significant role of infauna for spatial variability in our study emphasizes that difference in benthic community composition influence carbon cycling at the seafloor. Our findings strongly suggest that it is important to consider the interplay of seasonal dynamics and spatial patterns, involving fast-changing factors such as food supply and slow-changing variables such as benthic community composition over different years, when evaluating shifts of benthic ecosystem processes in relation to the rapid decline of sea ice in the Arctic.

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