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# Multivariate benthic ecosystem functioning in the Arctic – benthic fluxes explained by environmental parameters in the southeastern Beaufort Sea

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## Abstract

The effects of climate change on Arctic marine ecosystems and their biogeochemical cycles are difficult to predict given the complex physical, biological and chemical interactions among the ecosystem components. To predict the impact of future changes on benthic biogeochemical fluxes in the Arctic, it is important to understand the influence of short-term (seasonal to annual), long-term (annual to decadal) and other environmental variability on their spatial distribution. In summer 2009, we measured fluxes of dissolved oxygen, nitrate, nitrite, ammonia, soluble reactive phosphate and silicic acid at the sediment-water interface at eight sites in the southeastern Beaufort Sea at water depths from 45 to 580 m to address the following question and hypotheses using a statistical approach: (1) What is the spatial variation of benthic boundary fluxes (sink and source)? (2) The classical proxy of benthic activity, oxygen flux, does not determine overall spatial variation in fluxes. (3) A different combination of environmental conditions that vary either on a long-term (decadal) or short-term (seasonal to annual) scale determine each single flux. And (4) A combination of environmental conditions varying on the short and long-term scale drive the overall spatial variation in benthic boundary fluxes. The spatial pattern of the measured benthic boundary fluxes was heterogeneous. Multivariate analysis of flux data showed that no single or reduced combination of fluxes could explain the majority of spatial variation. We tested the influence of eight environmental parameters: sinking flux of particulate organic carbon above the bottom, sediment surface Chl *a* (both short-term), porosity, surface manganese and iron concentration, bottom water oxygen concentrations (all long-term), phaeopigments (intermediate-term influence) and  $\delta^{13}\text{C}_{\text{org}}$  (terrestrial influence) on benthic fluxes. Short-term environmental parameters were most important for explaining oxygen, ammonium and nitrate fluxes. Long-term parameters together with  $\delta^{13}\text{C}_{\text{org}}$  signature explained most of the spatial variation in phosphate, nitrate and nitrite fluxes. Sediment pigments and  $\delta^{13}\text{C}_{\text{org}}$  levels in surficial sediments were most important to explain fluxes of silicic acid. The overall spatial distribution of fluxes could be

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best explained (57 %) by the combination of sediment Chl *a*, phaeopigments,  $\delta^{13}\text{C}_{\text{org}}$ , surficial manganese and bottom water oxygen concentration. We conclude that it is necessary to consider long-term environmental variability in the prediction of the impact of ongoing short-term environmental changes on the flux of oxygen and nutrients in Arctic sediments. Our results contribute to improve ecological models predicting the impact if climate change on the functioning of marine ecosystems.

## 1 Introduction

Increased effort is put into estimating climate change effects in Arctic ecosystems (ACIA, 2004; Wassmann et al., 2011; Barber et al., 2012). Contrary to multilevel analyses of pelagic processes (Forest et al., 2011; Tremblay et al., 2011), few studies have tried to link environmental conditions to benthic ecosystem functioning in terms of multiple processes in the Arctic (Schmid et al., 2009). Marine sediments play a pivotal role in the remineralisation of the organic matter settling to the seafloor. They can be both a major source of nutrients and carbon to the overlying water column or/and a significant sink (Schulz, 2006). Typically, a significant fraction of exported organic matter undergoes biologically mediated degradation and oxidation through a complex web of redox reactions, while a small remaining fraction is permanently buried (Berner, 1980). Determining the spatial variation and partition between source fluxes from and sink fluxes to the sediments is important for improving our understanding of regional biogeochemical cycles (Ebenhöh, 1995; Zabel and Hensen, 2006), and only few data is available from the Arctic regions being particularly sensitive to climate change (Chang and Devol, 2009; Darnis et al., 2012; Davenport et al., 2012; Rysgaard et al., 1998).

Oxygen uptake is often used as a proxy of total benthic ecosystem functioning, more precisely of activity and remineralisation (Glud, 2008; Hensen et al., 2006; Holstein and Hensen, 2010; Wenzhöfer and Glud, 2002). But evidence is increasing, that benthic nutrient remineralisation is not directly correlated with oxygen uptake, particularly

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in coastal and shelf environments (Braeckman et al., 2010; Davenport et al., 2012; Holstein and Hensen, 2010; Michaud et al., 2009; Robert et al., 2012).

A wide range of environmental factors influence benthic processes. Determining their relative importance is difficult due to the number and complexity of biotic and abiotic interactions among the processes involved (Godbold and Solan, 2009). Organic carbon content in sediments has been proposed to be the principal driver of benthic remineralisation. Several different metabolic pathways contribute to the degradation of organic carbon, with oxygen, nitrate, manganese, iron and sulphate being most important agents of remineralisation (Canfield et al., 1993; Froelich et al., 1979). Their relative importance varies temporally and spatially due to changes in environmental conditions. Thus, organic carbon content of sediments seems less predictive of benthic remineralisation (Rysgaard et al., 1998) than the quantity of fresh organic matter deposited on the seafloor (Chang and Devol, 2009; Link et al., 2011). Also, historical input of organic matter, ambient water oxygen concentration and porosity modifies the oxygen penetration of sediments and therefore its reactivity (Gobeil et al., 2001). Finally, biologically mediated degradation in Arctic marine sediments seems to be enhanced if labile, marine derived matter is present (Sun et al., 2009). Thus, the quality of organic matter at the seafloor will influence the pattern of benthic nutrient remineralisation (Rysgaard et al., 1998).

The continental shelf off the Mackenzie Delta in the Beaufort Sea may be particularly sensitive to climate change: among Arctic rivers, the Mackenzie is the largest exporter of particulate organic matter and ranks third in total terrigenous organic carbon input (dissolved and particulate) to the Arctic seas (Rachold et al., 2004). Over the last two decades, this region has experienced a significant reduction in summertime ice cover (Galley et al., 2008), an increase in ultraviolet radiation (Bélanger et al., 2006), as well as an earlier onset of primary production in spring (Tremblay et al., 2011). These changes would result in a greater export of terrigenous carbon to the Arctic Ocean (Benner et al., 2004) and shifts in marine produced vertical carbon export (Forest et al., 2011). Direct and indirect effects of these changes on Arctic Ocean biogeochemical

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cycles are difficult to predict in quantitative terms given the complexity of physical, biological and chemical interactions among ecosystem components. It is clear, however, that the flux of organic matter to coastal and shelf Arctic sediments will be considerably altered, which in turn will severely affect benthic ecosystem functioning, including the processes of nutrient remineralisation. Reducing the current lack of knowledge on benthic boundary fluxes in Arctic regions, or on their link with environmental changes on different time scales, will help to evaluate biogeochemical budgets on larger time scales.

As part of the larger Malina program (<http://malina.obs-vlfr.fr/>), which aims to predict Arctic ecosystem reactions to changes in light penetration of the ocean and climate, we want to fill gaps in benthic ecosystem process knowledge. The objective of this study was to determine what drives spatial variation in benthic functioning measured as benthic boundary fluxes in the Beaufort Sea/Mackenzie Shelf. Emphasis is put on the ecological perspective and setting, and a hypothesis-driven approach, using multivariate statistics. Specifically, the following research question (1) and hypotheses (2–4) were addressed: (1) What is the spatial variation of benthic boundary fluxes (sink and source)? (2) The classical proxy of benthic activity, oxygen flux, does not determine overall spatial variation in fluxes. (3) A different combination of environmental conditions that vary either on a long-term (decadal) or short-term (seasonal to annual) scale determine each single flux. And finally (4) A combination of environmental conditions varying on the short and long-term scale drive the overall spatial variation in benthic boundary fluxes.

## 2 Material and methods

### 2.1 Study region

This study was conducted in the southeastern Beaufort Sea with emphasis on the shelf off the Mackenzie Delta (Fig. 1). The study area is dominated by coastal shelves

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and the maximum depth of our study was 580 m on the outer Mackenzie Shelf. Annual primary production ranges from 30 to 70 g C m<sup>-2</sup> yr<sup>-1</sup>, indicating generally oligotrophic conditions (Sakshaug, 2004). Rather low primary production daily rates (73 ± 37 mg C m<sup>-2</sup> d<sup>-1</sup>) were also found in summer or fall 2005–2007 in the eastern Beaufort Sea (Ardyna et al., 2011). In the Cape Bathurst Polynya at the eastern boundary of the study area, however, rates are apparently higher, reaching 90 to 175 g C m<sup>-2</sup> yr<sup>-1</sup> as based on satellite estimates (Arrigo and van Dijken, 2004). Ardyna et al. (2011) reported daily primary production rates of 159 ± 123 mg C m<sup>-2</sup> d<sup>-1</sup> in summer and fall, and intensive phytoplankton blooms related to ice-edge upwelling events were documented for coastal regions of the Mackenzie Shelf and Amundsen Gulf in 2008 (Mundy et al., 2009; Tremblay et al., 2011). An annual vertical POC flux of 1.6–1.8 g C m<sup>-2</sup> yr<sup>-1</sup> and 2.4 g C m<sup>-2</sup> yr<sup>-1</sup> was estimated at 200 m water depth for the Mackenzie Shelf and the Cape Bathurst Polynya, respectively (O'Brien et al, 2006; Forest et al., 2007; Lalande et al., 2009). Seafloor sediments are dominated by fine-grained material that is usually composed of more than 70 % silt and clay (Conlan et al., 2008). Sediment characteristics indicate that organic carbon at the seafloor is to a large part derived from either the Mackenzie River plume and erosion (O'Brien et al., 2006) or refractory marine material (Morata et al., 2008; Magen et al., 2010; Salton et al., 2011). The latter dominates the carbon flux in summer and on the eastern shelf (Naidu et al., 2000) whereas on the Mackenzie Shelf carbon of terrestrial origin is abundant in fall (Morata et al., 2008).

## 2.2 Field sampling

Samples were collected during the Malina program at eight sites ranging in water depth from 47 m to 577 m in July and August 2009 onboard the icebreaker CCGS Amundsen (Table 1). At each sampling event (“station”), an USNEL box corer (50 × 50 × 30 cm) was deployed for seafloor sediment collection. From each box core, three sub-cores of 10 cm diameter and approximately 20 cm sediment depth were taken for assessing benthic oxygen demand and nutrient remineralisation in microcosm incubations. Six

additional sub-cores of 2.4 cm diameter and 8 cm and 1 cm length were taken for determining sediment pigment concentration and water content and sediment solid phase composition, three sub-cores each, respectively (Table 1). Samples from the sediment surface (0 to 1 cm sediment depth) of additional sub-cores were stored in pre-weighed plastic vials and frozen immediately at  $-80^{\circ}\text{C}$  for later analysis. Near-bottom water temperature and salinity were determined by the shipboard CTD probe at each station 10 m above the seafloor. Salinity ranged from 32.2 PSU at the shallowest site (47 m) to 34.9 PSU at the deepest site (577 m). Temperature values varied between  $-1.6^{\circ}\text{C}$  and  $0.4^{\circ}\text{C}$  (Table 1).

### 2.3 Sediment pigment concentration

Chl *a* and phaeopigment concentrations were analysed fluorometrically following a modified protocol proposed by Riaux-Gobin and Klein (1993) as described in Link et al. (2011): two grams of wet substrate were extracted with 10 mL 90% Acetone (*v/v*) for 24 h at  $4^{\circ}\text{C}$ , 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. Quantities are expressed as microgram pigment per gram of dry sediment [ $\mu\text{g g}^{-1}$ ].

### 2.4 Surficial sediment composition and sinking particle fluxes

Porosity was determined by comparison of weight of wet and dried sediment. Porosity was calculated using a dry sediment density of  $2.65\text{ g cm}^{-2}$  (Bernier, 1980). The dried solid fraction was homogenised and the water content used to correct the analyses for the presence of sea salt.

For stable isotope composition analysis, grounded sediments were acidified twice for 48 h with a dilute HCl (1N) solution to dissolve solid carbonates. The acid supernatant was decanted and solids rinsed with nanopure water and dried. Samples were analysed for  $\delta^{13}\text{C}_{\text{ORG}}$  and  $\delta^{15}\text{N}$  with a CF-IRMS (continuous-flow Isotope Ratio Mass

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Spectrometry) coupled to a Costech 4010 elemental analyser. Here, we only report the stable isotope signature of  $\delta^{13}\text{C}_{\text{ORG}}$  of the surficial buried organic matter. Data are reported in standard notation in ‰ with respect to V-PDB for carbon. The analytical precision error was lower than 0.3 ‰ and three internal standards were measured during the isotopic analyses to continuously check the accuracy of the measurements.

Acid soluble Mn- and Fe-oxides were determined on homogenised dried sediments using 1N HCl solution. About 250 mg of dry sample was leached with a 12 mL solution during 24 h while shaking continuously at room temperature. The centrifuged and filtered solution was then diluted in 0.2 N HCl and analyzed with a flame atomic absorption spectrometer (5100PC Perkin-Elmer). The analytical precisions were better than  $\pm 3\%$  and  $\pm 7\%$  for Mn and Fe, respectively. Acid soluble Fe ( $\text{Fe}_{\text{HCl}}$ ) represents amorphous iron-oxides, FeS, some iron phyllosilicates and iron carbonates. Specific tests on particulate Mn extraction with 1N HCl ( $\text{Mn}_{\text{HCl}}$ ) have shown that  $\text{Mn}_{\text{HCl}}$  represents the whole fraction of Mn-oxides and Mn associated with carbonates (Anschutz et al., 2006).

Sinking fluxes of particulate organic carbon (POC) reaching the benthic boundary layer (approximately 20 m above bottom) were derived from a particle size distribution dataset obtained with an Underwater Vision Profiler 5 (UVP5, Picheral et al., 2010) deployed at every station (Table 1). Full methodology on the functioning of the UVP5 and on the estimation of sinking POC fluxes can be found in Forest et al. (2012). Briefly, particles in the range 0.08–4.2 mm (in equivalent spherical diameter) recorded with the UVP5 were transformed into sinking fluxes by applying a regional empirical algorithm linking sediment trap fluxes and the UVP5 dataset. The algorithm was calibrated using an optimization function following Guidi et al. (2008) and provided robust agreement between sediment trap POC fluxes and UVP5 POC fluxes ( $r^2 = 0.68$ ,  $n = 21$ ).

## 2.5 Benthic oxygen flux and nutrient remineralisation

Incubations of sediment microcosms were run in a dark, temperature-controlled room (2 to 4 °C) for 24 to 48 h. Prior to the onset of measurements, sediment cores were

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carefully topped with bottom water collected by the rosette at the same site, and then allowed to acclimate for six to eight hours while being saturated with oxygen to avoid suboxic conditions during incubations. 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 flux was determined as the change in oxygen concentrations in the water phase and was measured periodically (2 to 8 h intervals) with a non-invasive optical probe (Fibox 3 LCD, PreSens, Regensburg, Germany). During incubations, oxygen concentration never decreased by more than 25 % in order to avoid anoxic conditions and biogeochemical transformations. Hall et al. (1989) demonstrated the importance of maintaining the O<sub>2</sub> supply to obtain consistent and relevant data during core incubations.

To determine changes in nutrient concentration, samples of the overlying water phase were taken at three times during the incubation, including the onset and end. Water samples withdrawn for analysis were immediately replaced by an equivalent volume of bottom water of known nutrient composition. The total amount of water withdrawn and replaced during each sampling never exceeded 10 % of the total overlying water volume to prevent artefacts. Three additional incubation cores containing bottom water only acted as controls for assessing the oxygen consumption and nutrient changes due to processes within the water column or sample handling. Oxygen and nutrient fluxes were determined as the slope of the linear regression of the oxygen and nutrient concentration on incubation time and corrected for solute concentration in the replacement water. Median flux rates determined in the three control cores were subtracted from each sediment core measure. A positive flux means a release of the nutrient from sediment into the water column.

Samples were filtered through combusted GF/F filters and split into subsamples for nutrient analyses. For NH<sub>4</sub><sup>+</sup> measurements, 6 mL samples were immediately incubated with 3 mL orthophthaldialdehyde solution following an adaptation of the method proposed by Holmes et al. (1999). Samples were analysed using a Turner Design

fluorometer 5–6 h after the initiation of colorimetric reaction. Detection limit for ammonium was 0.1  $\mu\text{M}$ . For nitrate, nitrite, phosphate and silicic acid measurements, water samples were frozen at  $-80^\circ\text{C}$  and analysed within the following two weeks using an Autoanalyzer 3 (Bran and Luebbe) applying colorimetric methods adapted from Grasshoff et al. (1999). The precision of these methods was  $\pm 5\%$ .

## 2.6 Definition of short-term and long-term environmental factors

We used environmental parameters of different temporal variation to explain benthic boundary fluxes. As short-term scale we define seasonal to annual time scales and the parameters sediment surface Chl *a* concentration and vertical POC export. Results reported from different seasons and years in the Beaufort Sea have shown that sediment Chl *a* concentration and vertical POC export vary both over seasons and years (Link et al., 2011; Morata et al., 2008; Renaud et al., 2007a; Forest et al., 2007; Juul-Pedersen et al., 2010; Sallon et al., 2011) respectively. This is likely due to the seasonal and spatial dynamic of primary production and carbon fluxes in the region (Ortega-Retuerta et al., 2012; Tremblay et al., 2011; Forest et al., 2010).

As long-term we define temporal variations of decades and longer. Bottom water oxygen concentration of shelf waters changes on such time scales (Gilbert et al., 2010), as does iron oxide (Hensen et al., 2006) and manganese oxide concentration (Gobeil et al., 2001; Katsev et al., 2006) in sediments. In open ocean regions, changes in the ocean's dissolved oxygen are likely related to physical processes and thermohaline circulation. The major drivers of these changes are increased temperature, altered hydrological cycles and shifts in wind patterns that alter coastal currents and upwelling formation (Rabalais et al., 2009). The effect of interdecadal changes in deep-water characteristics have recently been proposed to explain a decline in dissolved oxygen saturation in deep waters of both coastal waters (Gilbert et al., 2005; Chan et al., 2008) and open basins (Fukasawa et al., 2004). At the sediment-water interface, the abundance of trace metals such as Mn and Fe-oxides allows to track the depositional redox conditions (Tribovillard et al., 2006). Sedimentary redox conditions reflect the balance

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between the O<sub>2</sub> diffusing from the bottom water and metabolic aerobic processes that mineralize the labile organic carbon at the sediment-water interface (Canfield et al., 1993; Froelich et al., 1979). Over a period of several decades, the upward migration of sedimentary redox boundary can generate surficial peak of metal-oxides as a result of generally increased water column productivity (Gobeil et al., 2001; Katsev et al., 2006) or progressive decline in the deep water oxygen saturation (Lefort et al., 2012). Changes in porosity of sediments depends on the sedimentation rate, which is generally about 1 mm yr<sup>-1</sup> in the study area (Richerol et al., 2008) and can therefore also be considered long-term.

Sediment phaeopigment concentration depends on vertical POC flux (short-term) but is also the accumulation of degraded material over several years (Morata et al., 2008). The signature of δ<sup>13</sup>C in surface sediments depends on the contribution of terrestrial versus marine produced carbon to the total carbon input and rather indicates input of sediments from the Mackenzie River (Goñi et al., 2005; Magen et al., 2010; Naidu et al., 2000). Therefore, sediment phaeopigment concentration and δ<sup>13</sup>C signature are considered “other” environmental factors.

## 2.7 Statistical analyses

We used best-subset multiple regression analyses to identify potential drivers of each single flux separately. Predicting variables allowed in the model were: Sediment surface Chl *a* concentration, sediment surface phaeopigment concentration, sediment surface porosity, sediment surface manganese-oxides concentration, sediment surface iron-oxides concentration, sediment surface δ<sup>13</sup>C, bottom water oxygen concentration and vertical flux of POC. Due to independent sampling of environmental and benthic flux data, the median value of each site of each of the predicting variables was attributed to the three flux replicates of each site. This allowed for keeping the high variability of benthic boundary fluxes in the model testing. Analysis of multicollinearity showed that sediment Chl *a* concentration and sinking POC in the lower water column were highly correlated (*R* = 0.92). Nevertheless, both predictors were retained in the initial

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5 full multiple regression model to determine which of the two would be predictors in the best solutions. Akaike's Information Criterion (AIC) was applied to choose the best linear model (Akaike, 1978; Quinn and Keough, 2002). In none of the best models, both predictors were retained. Normal distribution of the best model's residuals was verified with Shapiro-Wilk's test, and homogeneity of variance was tested using graphical methods (Quinn and Keough, 2002). If distribution of residuals was skewed, natural logarithm transformation was applied to the response variable and/or sediment surface Chl *a* and sinking POC data until assumptions were met by the best model. Normality could not be achieved for any  $\text{NO}_2^-$  model, thus only the graphical method was applied. 10 Outliers with severe influence on the model were identified using Cook's Distance (*D*) and removed if  $D > 1$ . One outlier in the silicic acid fluxes was found and removed from all further analyses (Table S1). We tested for collinearity of variables retained in the best-subset model using the variance inflation factor (VIF), with  $\text{VIF} > 10$  indicating critical collinearity (Quinn and Keough, 2002). This was not the case for any of the 15 best-subset models.

Principal Component Analysis (PCA) was used to determine the influence (eigenvector) of the six measured benthic boundary fluxes on the ordination of samples in a multidimensional space. Prior to PCA, homogeneity of each variable was assessed using a draftsman plot, and ammonium fluxes were transformed using natural logarithm. Moreover, flux data was standardized using the "normalise" routine in PRIMER-E (Clarke and Gorley, 2006). No pair of fluxes was correlated with  $R > 0.7$ , with the exception of nitrate and oxygen ( $R = 0.82$ ). 20

A stepwise distance-based linear model permutation test (DistLM, McArdle and Anderson, 2001) was performed to identify which set of environmental variables predict the multivariate variation of benthic boundary fluxes, thus taking into account possible interactions between different fluxes (in contrast to the multiple-regression approach described above). The resemblance matrix quantifying the between-samples similarities in terms of all six standardized fluxes was calculated based on Euclidean distances (Clarke and Gorley, 2006). Predicting environmental variables allowed to enter 25

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the model were sediment surface Chl *a* concentration, sediment surface phaeopigment concentration, sediment surface porosity, sediment surface manganese-oxide concentration, sediment surface iron-oxide concentration, sediment surface  $\delta^{13}\text{C}$  and bottom water oxygen concentration. To represent natural variation as much as possible in the analysis but to avoid arbitrary attribution, each environmental sample of a site was attributed to each replicate flux sample, thus triplicating the original data set. Sinking POC rates were excluded from this analysis due to a lack of replicates and due to its correlation with sediment Chl *a*. While the influence of multicollinearity on the model results can be tested for multiple regression (VIF, see above), this is not the case for the DistLM. After assessing normality and collinearity of the other predictor variables using a draftsman plot, sediment Chl *a* data was transformed using the natural logarithm to correct for skewness (Anderson et al., 2008). No pair of variables was correlated by  $R > 0.85$  and hence all variables were retained for possible inclusion in the model. The stepwise routine was run employing 9999 permutations and using the  $\text{AIC}_c$  (Akaike's Information Criterion corrected) selection criterion. The  $\text{AIC}_c$  was devised to handle situations where the number of samples ( $N$ ) is small relative to the number ( $\nu$ ) of predictor variables ( $N/\nu < 40$ ) (Anderson et al., 2008). Results were visualized with a distance-based redundancy analysis (dbRDA) (Anderson et al., 2008). All multivariate statistical analyses were performed using the PRIMER 6 statistical package with the PERMANOVA+ add-on (PRIMER-E, Plymouth Marine Laboratory, UK).

### 3 Results

#### 3.1 Spatial variability of benthic boundary fluxes

Sediment oxygen uptake varied between 0.5 and 11.5  $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$  with highest values in the shallower central Mackenzie Delta (390) and lowest values on the deeper eastern and central Mackenzie Slope (110, 235, and 345; Fig. 2, Table S1). This spatial pattern was generally also evident in the release of silicic acid from the sediments

(314.5–3494.7  $\mu\text{mol m}^{-2} \text{d}^{-1}$ , Table S1), although fluxes at sites at comparable water depths were higher in the eastern study area (Fig. 2). Phosphate was taken up by the sediments at the shallowest sites off the western and central Mackenzie Delta (690 and 390) and mostly released at all other sites (Fig. 2). Nitrate was mostly released from the sediments at eastern sites, while the shelf sites off the central and western Mackenzie Delta were characterized by high sediment uptake rates of nitrate (Fig. 2, Table S1). Uptake fluxes were found in most nitrite measurements, being highest off the shallow Mackenzie Shelf. Ammonium showed highest release rates recorded from station 390 on the shallower central Mackenzie Shelf and highest uptake rates found in the Cape Bathurst Polynya at station 140 (Fig. 2, Table S1). Within site, variability of phosphate and all three nitrogen-derived fluxes was higher than for silicic acid and oxygen fluxes (Fig. 2, Table S1).

### 3.2 Fluxes dominating the variation among sites

In the PCA plot, variation was high between the central (390) and western (690) Mackenzie Delta and all other samples, and low among deeper Mackenzie Shelf and Amundsen Gulf samples (235, 345, 110, 140) (Fig. 3). The first PCA axis (PC1) explained 46.2% of the total variance in the flux data, and the first three PCA axes (PC1, PC2, and PC3) together explained 88.3% (Table 2). Analysis of the eigenvectors showed that no single flux dominated the multivariate similarity pattern among samples (Fig. 3). Oxygen, phosphate and nitrate fluxes were most correlated with the first PCA axis, while silicic acid and ammonium fluxes showed a closer relationship to PC2 and PC3. Nitrite fluxes correlated almost equally with all PCA axes (Table 2, Fig. 3).

### 3.3 Environmental drivers of spatial flux variation

Results of environmental parameters used for statistical analyses are presented in Table S2. The best models explaining variation in each benthic boundary flux are shown in Table 3. Except for ammonium and nitrite fluxes, more than 68% of the variation

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in each flux could be explained by the environmental predictors (Table 3). Oxygen uptake strongly increased with vertical water-column POC flux, increased with sediment phaeopigment concentration and decreased with the porosity and concentration of iron oxide in surface sediments (adj.  $R^2 = 0.98$ ,  $p < 0.001$ ). Release of silicic acid decreased with phaeopigment concentrations but rose with sediment Chl *a* and bottom water oxygen concentrations (adj.  $R^2 = 0.92$ ,  $p < 0.001$ ). Phosphate fluxes strongly increased with  $\delta^{13}\text{C}$  signature and declined with sediment manganese oxide concentrations and with vertical POC flux (Adj.  $R^2 = 0.68$ ,  $p < 0.001$ ). Nitrate fluxes were best predicted by  $\delta^{13}\text{C}$  signature (positive), sediment manganese oxide and Chl *a* concentration (both negative, adj.  $R^2 = 0.81$ ,  $p < 0.001$ ). Nitrite fluxes increased with  $\delta^{13}\text{C}$  signature, bottom water oxygen levels and sediment porosities (adj.  $R^2 = 0.50$ ,  $p = 0.002$ ). Finally, ammonium release was found to strongly increase with Chl *a* and phaeopigment concentrations but to decrease with  $\delta^{13}\text{C}$  signature (adj.  $R^2 = 0.24$ ,  $p = 0.037$ ).

### 3.4 Influence of environmental parameters on the overall distribution of benthic boundary fluxes

The best distance-based linear model (DistLM), explaining 57 % of the overall variation in benthic boundary fluxes, is composed of sediment surface Chl *a*, phaeopigment and manganese oxide concentration,  $\delta^{13}\text{C}$  signature and bottom water oxygen concentration (Fig. 4, Table 4). The most important parameters contributing to the first axis of the dbRDA plot (explaining 70.5 % of fitted flux variation), which separates shallower and western sites from deeper and eastern sites, are sediment surface Chl *a* and manganese oxide concentration and bottom water oxygen concentration (Fig. 4). They explain more than 40 % of the total variation (Table 4). Sediment phaeopigment concentration and  $\delta^{13}\text{C}$  signature were most strongly correlated with the second dbRDA axis (explaining 20.8 % of fitted flux variation).

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## 4 Discussion

Benthic activity is most often derived from sediment oxygen demand (Graf, 1992; Wenzhöfer and Glud, 2002; Link et al., 2011) and assumed to decrease with increasing depth and distance from the continental source of particles and carbon. But the heterogeneous pattern of oxygen and nutrient fluxes at the sediment-water interface in the Beaufort Sea emphasizes that benthic remineralisation function is more complex than oxygen fluxes. Here we present for the first time a multiple dataset of benthic boundary fluxes, i.e. for oxygen, silicic acid, phosphate, nitrate, nitrite and ammonium, and their relation with environmental variables in the Canadian Arctic. We discuss their spatial pattern and influences of the environment at different time-scales with the aim to estimate dynamics of benthic ecosystem functioning related to variation in the quality and quantity of organic matter export.

### 4.1 What is the spatial variation of benthic boundary fluxes in the southeastern Beaufort Sea?

In 2009 the spatial pattern of oxygen fluxes was similar to those reported earlier from the region (2003–2004, 2008) (Darnis et al., 2012; Link et al., 2011; Renaud et al., 2007b). All those studies reported highest uptake off the Mackenzie Delta and the Cape Bathurst Polynya. Oxygen demand at shallowest sites (690 and 390) was twice the amount reported from 2004 (Renaud et al., 2007b) and half compared to the upwelling year 2008 (Tremblay et al., 2011). Values from other sites were similar for the three studied years. This indicates that (i) the influence of the Mackenzie Delta increases interannual variability of benthic oxygen uptake at its plume and (ii) that marine influence (such as primary production as in the Cape Bathurst Polynya) is more likely to contribute to the relative spatial distribution of benthic oxygen uptake.

The relatively higher release of silicic acid compared with oxygen uptake in the eastern part of the Beaufort Sea (140) can be explained by the different composition of organic matter exported to the seafloor. First, terrestrial input of organic material is

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high close to the Mackenzie Delta and along the Tuktoyaktuk Peninsula due to the strong influence of the Mackenzie River plume (Macdonald et al., 2004; Magen et al., 2010). This may increase the input of inorganic silicates (Juul-Pedersen et al., 2008), but these are unlikely to be biologically remineralised at the seafloor. Second, primary production in the Cape Bathurst Polynya area has a higher diatom contribution (Ardyna et al., 2011), which allows for an increased fresh silicic shell export (Simpson et al., 2008). Indeed, Sampei et al. (2011) identified the Cape Bathurst vicinity as a unique zone in biogenic silicate export out of the euphotic zone, with rates roughly one order of magnitude higher than elsewhere across the southeast Beaufort Sea.

Nitrate was replenished at the benthic boundary in deep waters of the slope and in the Cape Bathurst Polynya area (sites 235, 345, 110, 140), while sediments on the shallow Mackenzie Shelf (sites 390, 690, 680) act as sink. On the shallow Mackenzie Shelf, low oxygen penetration depth ( $> 1$  cm) and a steep gradient in nitrate concentration have been reported, indicating a redox horizon close to the sediment surface (Magen, 2009). Nitrate and nitrite uptake with denitrification processes at the top of the sedimentary column are typically encountered in sediments receiving excess organic matter such as shallow Arctic shelves and continental shelves affected by large river outflow (Hyacinthe et al., 2001; Chang and Devol, 2009; Hulth et al., 2005). Such an input of excess organic matter has also been found during the Malina study (Forest et al., 2012). Nitrate release in the other areas was also consistent with oxygen-saturated degradation. The highest nitrate release in the Cape Bathurst Polynya area (site 140) supports the findings of Simpson et al. (2008), who explained excess nutrient concentrations in the deep Amundsen Gulf water with degradation of more available fresh matter.

The generally low nitrite flux reflects its role as an intermediate product of nitrogen compound transformations. Highest uptake rates were linked to sites with high nitrate uptake or low nitrate release.

The pattern of ammonium effluxes, which are mainly originated from the anaerobic mineralization of organic N, is probably explained by the presence/absence of efficient

oxidative barriers at the top of the sedimentary column, such as oxygen and Mn-oxides (Luther et al., 1997; Anschutz et al., 2000, 2005). Highest ammonium effluxes were linked to sites where high organic matter input favours the shallowest oxygen penetration depth and thin Mn-oxides rich horizon, e.g., site 390 (Magen, 2009). The upward migration of ammonia to the bottom water probably promoted denitrification processes at the sediment interface at these sites. The within-site heterogeneous patterns of ammonium fluxes could be due to physiological responses of different macrofaunal species or densities in the cores (Braeckman et al., 2010), which are not available for our study.

Phosphate uptake from the two shallowest sites near the Mackenzie River delta may again be linked to the low oxygenation, a history of high organic matter input, and to the accumulation at the interface of newly formed reactive iron-oxides with high capacity to sorb phosphate (Hensen et al., 2006; Magen, 2009). Sediment phosphate release can be explained by either a loss of the sediment capacity to adsorb remobilised phosphate or a production of phosphate via aerobic organic matter mineralisation, or both. Desorption from particulate Fe-oxide when sediment Fe-oxide and associated phosphate are exposed to overlying water with lower dissolved P concentrations relative to pore water (Ruttenberg and Sulack, 2011) can also contribute to phosphate release at the sediment-water interface. The highest phosphate effluxes in the Cape Bathurst Polynya (site 140) probably reflected an increased oxic degradation of fresh matter, as Davenport et al. (2012) observed on the productive Bering Shelf.

Benthic boundary fluxes of silicic acid, oxygen and phosphate in 2009 were in the range of those reported for the region in 2008 (Darnis et al., 2012). It is noteworthy that phosphate was released from shallow Mackenzie Shelf sediments during the upwelling year 2008 and that notably less silicic acid was remineralised in the Cape Bathurst Polynya area in 2008. The increased remineralisation of silicic acid could be explained by the accumulation of excess biogenic silica following vertical export in the highly productive upwelling year of 2008. Phosphate on the other hand is more immediately

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remineralsed from organic matter and the release in 2008 could represent a more short-term reaction to organic matter input from the upwelling year.

Concentrations of nutrients at the onset of experiments were in the range described for deeper waters in the study region (Simpson et al., 2008). We therefore consider the described spatial pattern of fluxes a realistic estimate. Seasonal changes in nutrient fluxes have been shown in macrofauna nearshore experiments (Braeckman et al., 2010) and can be found in the Bering and Chukchi Sea (Chang and Devol, 2009; Davenport et al., 2012). Here we report nutrient fluxes and mechanisms for the late summer. Considering the seasonal effect in benthic polar systems (Lepore et al., 2007; Link et al., 2011), lower input of fresh organic matter in winter might therefore be accompanied by a different oxygen, ammonium and silicic acid fluxes.

When considering all fluxes synchronously, site 390 can be well separated from 690, these two are different from the lower Mackenzie Shelf (site 260 and 680), which finally can be separated from the Cape Bathurst Polynya site (110 and 140) and the deeper Beaufort slope sites (235 and 345) in their remineralisation functioning (see also Fig. 3). This spatial pattern has also been found using lipid biomarker analyses conducted on sediment samples collected at some of the sites we studied (Rontani et al., 2012; Tolosa et al., 2012). Particularly high concentrations of autochthonous fresh material derived from diatom production were found at site 390, with decreasing concentrations farther north from the Mackenzie Delta (Rontani et al., 2012; Tolosa et al., 2012).

We conclude that high oxygen demand, nitrate and phosphate uptake prevail in proximity to the Mackenzie outflow, with high ammonium and silicic acid release at the central Mackenzie Delta (site 390), while benthic activity replenishes bottom water with silicic acid, nitrate and phosphate in deeper waters and particularly in the productive Cape Bathurst Polynya area.

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## 4.2 The classical proxy of benthic activity, oxygen flux, does not determine overall spatial variation in fluxes

Although sediment oxygen consumption is widely used to describe benthic remineralisation function (Grebmeier et al., 2006b; Glud, 2008; Michaud et al., 2005; Holstein and Hensen, 2010), our results confirm this hypothesis and show that differences in benthic remineralisation including six major fluxes are not dominated by oxygen flux. In our study, the major differences between the shallow Mackenzie Shelf and all other sites are equally based on different oxygen, nitrate and phosphate fluxes while the eastern Mackenzie Shelf remineralisation differs greatly from the central shelf in silicic acid and ammonium release. Sampling sites in the Cape Bathurst Polynya and on the western Mackenzie slope were also distinct from all deeper sites with respect to silicic acid and ammonium release. Clearly, oxygen uptake alone cannot describe the spatial pattern of benthic ecosystem functioning in our region. While oxygen uptake is often related to organic matter degradation (e.g. Glud, 2008), further factors influence the quantity and quality of other nutrient remineralisation.

Recent experimental studies have shown that benthic fluxes other than oxygen, e.g. silicic acid or ammonium, respond to treatment of different organic matter input (Callier et al., 2008; Richard et al., 2007). Such effects have been related to particular species present in treatments, which influence microbial activity (Michaud et al., 2009; Robert et al., 2012). Although we can assume different benthic faunal composition on the Mackenzie Shelf, slope and Cape Bathurst area (Conlan et al., 2008), we do not know how each Beaufort Sea species influences each flux, and even less how they interact with the benthic microbial community. Hence, our results suggest that multiple fluxes need to be considered when the spatial variability of benthic ecosystem functioning in terms of nutrient replenishment is evaluated – whatever factors influence the spatial pattern of benthic nutrient remineralisation.

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### 4.3 A different combination of environmental conditions that vary either on a long-term (decadal) or short-term (seasonal to annual) scale determine each single flux

The heterogeneous spatial pattern of benthic boundary fluxes announces the complexity of different factor combinations determining each single flux. Our results of multiple regression analysis support our hypothesis. They show that different subsets of environmental factors can explain spatial variation of different single fluxes, to a surprisingly high part (up to 98 %).

While short-term environmental conditions do always explain part of the variation, a large sinking particle flux and an associated increased concentration of sediment Chl *a* most strongly increase oxygen uptake and ammonium release. Observational as well as experimental studies have already demonstrated rapid response of benthic communities to food input (Pfannkuche, 1993; Sun et al., 2007). Ammonium release has been linked to oxic degradation of high quality organic matter by bacterial or faunal communities in shallow and Arctic sediments (Rysgaard et al., 2004). The low explicative power of the best model for ammonium fluxes (24 %) indicates that other factors not identified here were playing a substantial role in driving its spatial variability. The faunal composition, which has important effects on ammonium release by sediment oxygenation and bioturbation, might be one of these lacking measurements (Braeckman et al., 2010; Laverock et al. 2011; Piot, 2012).

Environmental parameters of long-term variability (e.g.  $Mn_{HCl}$ , porosity, bottom water oxygen) are powerful predictors of phosphate, nitrate and nitrite fluxes, when the origin of organic matter (terrigenous vs. marine) is simultaneously considered. This combination may reflect the long-term influence of terrigenous matter sedimentation from the Mackenzie River (Macdonald et al., 2004). The long-term input of organic matter, porosity and surrounding bottom water oxygen concentration limit the depth of the sediment oxic layer. Also, the manganese oxide rich horizon with higher surficial  $Mn_{HCl}$  indicates a degradation of organic matter under suboxic conditions during the

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last decades, which is capable to produce upward dissolved Mn flux that precipitates at the sediment interface (Aller, 1988). These redox conditions also control denitrification and phosphate binding processes and seem to be more important for NO<sub>x</sub> and phosphate release than the input of fresh marine matter.

We would have assumed that silicic acid release was positively related to Chl *a* and phaeopigment concentration, since we considered sediment pigments a proxy of detrital input. Following dissolution kinetics, silicic acid release supposedly increases with silicate input (Tréguer et al., 1995), and we assumed that more detrital material sinking to the seafloor implies a high silicate input to sediments. However, phaeopigments at the seafloor reflect both silicic and non-silicic detrital material. Possibly, the input of terrigenous phaeopigment-loaded material from the Mackenzie is higher towards the western part of the Mackenzie plume (Sampei et al., 2011). Phaeopigment-enriched sediments could then represent diatom-poor organic matter input, and would therefore not lead to increased silicic acid release. Recently, Holstein and Hensen (2010) have also demonstrated the importance of bacterial silicate release in oxygenated sediments. Bacterial biomarker concentrations were more abundant in sediments with higher fresh labile matter (Chl *a*) compared to the total input of organic matter (Tolosa et al., 2012). These observations would further explain why an increase in silicic acid release was found in association with increasing Chl *a* and decreasing phaeopigments in our study.

In summary, while short-term factors such as fresh marine matter enhance the oxic degradation and nutrient replenishment, long-term factors reflecting decadal-scale input of organic matter dominates the remineralisation of NO<sub>x</sub> and phosphate on the southeastern Beaufort Shelf.

#### 4.4 A combination of environmental conditions varying on the short and long-term scale drive the overall spatial variation in benthic boundary fluxes

Despite the differences in environmental factors explaining each single flux (see above), the majority (57 %) of spatial variation in multiple benthic remineralisation

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function can be explained by a subset of the following five environmental factors: sediment surface Chl *a* (also a proxy for sinking particle fluxes), phaeopigment and manganese oxide concentration,  $\delta^{13}\text{C}$  signature and bottom water oxygen concentration. The similarity of the dbRDA plot and the PCA plot show, that the environmental variables explain benthic flux variation fairly well, with a little less congruence for the shallow Mackenzie sites (Anderson et al., 2008). The input of fresh organic matter (Chl *a*) alone can explain a third of the spatial variation, separating the deeper sites from the shelf and shallow sites, particularly site 390. This stresses the importance of short-term parameters for the estimation of nutrient release from Arctic sediments. The quality of organic matter has repeatedly been related to benthic oxygen demand (Renaud et al., 2007a; Link et al., 2011), infaunal diversity (Conlan et al., 2008) and bacterial activity (Rontani et al., 2012) in the southeastern Beaufort Sea. Assuming the importance of biological activity for phosphate (Davenport et al., 2012), nitrogen derivatives (Chang and Devol, 2009; Braeckman et al., 2010) and silicic acid (Holstein and Hensen 2010) release, high Chl *a* concentrations at the seafloor not only provides the fresh matter for bacterial degradation, but it also stimulates benthic ecosystem functioning in terms of biological activity of macrofauna, which additionally enhances nutrient release.

The greater marine fraction and phaeopigment content in organic matter input are the primary determinants of the different benthic boundary fluxes in the Cape Bathurst Polynya area when compared with fluxes close to the Mackenzie Delta. It is clear that locations influenced by the Mackenzie River plume, which feeds a high sedimentation flux of terrigenous particulate matter (Juul-Pedersen et al., 2010; Magen et al., 2010), will show a distinct benthic ecosystem functioning.

Finally, the influence of bottom water oxygenation and manganese oxides along the shelf-basin transect north of station 390 demonstrates how long-term environmental factors drive spatial variation in benthic boundary fluxes. Both these factors relate to mostly geochemical processes in the sediments (Gobeil et al., 2001), and may therefore describe a basic variation, on top of which short-term environmental factors further differentiate benthic fluxes.



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About 40 % of the total variation in benthic remineralisation function could not be explained by any of the environmental conditions included in the analysis. The most likely missing factor is faunal or bacterial abundance and composition in the analysed sediment cores. An increasing number of studies report the key role of benthic species for benthic boundary fluxes, particularly through their bioturbation or bioirrigation (Davenport et al., 2012; Kristensen et al., 2012). Benthic fauna thus can locally directly enhance nutrient remineralisation or indirectly by modifying bacterial abundance (Michaud et al., 2009; Piot, 2012).

It is noteworthy, that sediment porosity, a major parameter used to calculate diffusive fluxes across the sediment water interface (e.g. Hensen et al., 2006), does not play a significant role in our analysis. Again, this emphasizes the role of biological processes for spatial variation in benthic ecosystem functioning in the southeastern Beaufort Sea.

## 5 Conclusions

Can we use environmental factors to predict benthic ecosystem functioning on polar shelves? Although we could explain benthic boundary fluxes to a large part without chemistry-based models, we still cannot answer this question with an unambiguous “Yes”. But compared to the almost non-existent data of benthic fluxes in the Canadian Arctic, our results provide insights on the spatial gradients and driving factors of biogeochemical fluxes across the benthic boundary on Arctic shelves. In addition, the statistical relations found in the present study might help building more comprehensive ecosystem models that aim at predicting ecosystem functioning in Arctic shelf waters. We report that in summer, the sediments of the southeastern Beaufort Sea are usually a source of silicic acid, while the Mackenzie Delta is a region of nitrate and phosphate uptake and more marine influenced areas are areas of nitrate release. The dominating role of environmental factors varying on a short-term scale indicates that benthic remineralisation rates in terms of quantity will quite rapidly respond to climate changes. On a longer time scale, if terrigenous matter sedimentation from the Mackenzie River

and water temperatures increase with climate change, we can expect a decrease in oxygen concentration of coastal bottom waters and sediments, with the latter shifting from nutrient sources to sinks. The analysis of our results emphasizes the importance of biologically mediated degradation interacting with geochemical processes. Including more specific marker of fresh biologically degradable matter and faunal composition data in benthic boundary flux models should further enhance the predictive power of biological ecosystem models.

**Supplementary material related to this article is available online at:**  
<http://www.biogeosciences-discuss.net/9/16933/2012/bgd-9-16933-2012-supplement.zip>.

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**Table 1.** Station list. Labels, date of sampling, geographic position, bottom water temperatures and salinities, number of within-station replicate samples used to determine benthic boundary fluxes (BBF) and sediment surface properties (Chl *a*, phaeopigments, porosity, manganese and iron oxide). A = Amundsen Gulf, MD = Mackenzie Delta, MS = Mackenzie Shelf/Slope; C, E, N, W = central, east, north, west.

Station	Malina Station Label	Date	Depth [m]	Latitude [° N]	Longitude [° W]	Sal <sub>bot</sub>	T <sub>bot</sub> [°C]	BBF (n)	Sed Prop (n)
MD-C	390	31 July 09	47	70.178	133.569	32.24	−1.3	3	3
MD-W	690	1 August 09	55	69.486	137.942	32.49	−1.6	3	3
MD-E	260	4 August 09	60	71.269	130.613	32.32	−1.2	3	3
A-NW	110	6 August 09	400	71.696	126.477	34.77	0.3	3	3
A-CW	140	7 August 09	154	71.285	127.783	33.4	−1.4	1	1
			154	71.285	127.782			2	2
MS-W	680	10 August 09	125	69.611	138.235	32.31	−1.3	3	3
MS-C	345	16 August 09	577	71.382	132.652	34.86	0.2	3	3
MS-E	235	22 August 09	576	71.764	130.766	34.84	0.4	3	3

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## Multivariate benthic ecosystem functioning in the Arctic

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**Table 2.** Correlation-based Principal Component Analysis (PCA) of normalised benthic boundary fluxes determined in the southeastern Beaufort Sea in July/August 2009. Eigenvalues and % of variation explained by the first 5 ordination axes (PC1, PC2, PC3, PC4, and PC5) is given. Linear coefficients (eigenvector) of each PC are given for each flux.

	PC1	PC2	PC3	PC4	PC5
Eigenvalue	2.77	1.64	0.88	0.46	0.22
% variation	46.2	27.4	14.7	7.7	3.6
Eigenvector					
O <sub>2</sub>	-0.548	0.295	0.092	0.011	0.055
Si(OH) <sub>4</sub>	0.170	-0.612	-0.564	0.047	-0.287
PO <sub>4</sub> <sup>2-</sup>	-0.470	-0.306	-0.343	-0.269	0.670
NO <sub>3</sub> <sup>-</sup>	-0.543	0.065	-0.177	-0.314	-0.677
NO <sub>2</sub> <sup>-</sup>	-0.394	-0.376	0.252	0.779	-0.062
NH <sub>4</sub> <sup>+</sup> (ln)	-0.017	-0.546	0.679	-0.470	-0.062

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**Table 3.** Multiple regression analysis of benthic boundary fluxes against environmental factors in the southeastern Beaufort Sea in July/August 2009. Adjusted (Adj.)  $R^2$  and standardized regression coefficients of benthic parameters (Short-term variability proxies: Chl  $a$  – sediment chlorophyll  $a$  concentration, POC - sinking POC; medium-term variability proxies: Phaeo – sediment phaeopigment concentration,  $\delta^{13}\text{C}$  – isotopic carbon signature; long-term variability proxies: Mn – sediment surface manganese-oxides concentration, Fe – sediment surface iron-oxides concentration, Po - porosity,  $\text{O}_{2, \text{bot}}$  – bottom water oxygen concentration) predicting each benthic boundary flux. Whole model results are presented for the best-subset solution following Akaike’s criterion (Effects – number of parameters included in the model). Absence of standardized regression coefficients indicates that the parameter was not retained in the model.

Flux	Adj. $R^2$	$F$	$p$	Short term		Medium term		Long-term				AIC	Effects
				Chl $a$	POC	Phaeo	$\delta^{13}\text{C}$	Mn	Fe	Po	$\text{O}_{2, \text{bot}}$		
$\text{O}_2$	0.98	237.47	< 0.001	*	-1.13 (ln)	0.21			-0.15	-0.26		50.84	4
$\ln(\text{Si}(\text{OH})_4)$	0.92	89.61	< 0.001	0.34 (ln)	*	0.68					-0.15	-16.21	3
$\text{PO}_4^{2-}$	0.68	17.50	< 0.001	*	-0.62 (ln)		1.12	-1.43				206.14	3
$\text{NO}_3^-$	0.81	32.83	< 0.001	-0.77	*		1.00	-1.01				307.38	3
$\text{NO}_2^-$	0.50	6.69	0.002	0.43**	*		1.51			0.93	1.46	181.35	4
$\ln(\text{NH}_4^+)$	0.24	3.42	0.037	1.41 (ln)	*	-0.89	0.68					72.73	3

\* indicates that this short-term parameter was strongly correlated ( $R = 0.92$ ) to the (other) short-term parameter retained in the model.

\*\* indicates that the factor was retained but not significant in the model.

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**Table 4.** Distance-based linear model (DistLM) of benthic boundary fluxes against environmental drivers determined in the southeastern Beaufort Sea in July/August 2009. Proportion of variance in benthic boundary fluxes explained by environmental variables in stepwise sequential tests following AICc selection criterion Chl *a* = sediment chlorophyll *a* concentration, Phaeo = sediment phaeopigment concentration, dC13 = isotopic carbon signature, MnHCl = sediment surface manganese oxides concentration, O<sub>2,bot</sub> = bottom water oxygen concentration. Prop. is the proportion of variance explained by each single variable, Cumul. is the cumulative proportion of variance explained by multiple variables.

Sequential tests for stepwise model (Adj. $R^2 = 0.57$ )							
Variable	AICc	SS(trace)	Pseudo- $F$	$P$	Prop.	Cumul.	res.df
Chl <i>a</i>	88.69	122.14	36.72	< 0.01	0.344	0.344	70
Phaeo	78.39	37.04	13.05	< 0.01	0.104	0.448	69
O <sub>2,bot</sub>	74.18	16.79	6.38	< 0.01	0.048	0.496	68
dC13	66.44	23.33	10.04	< 0.01	0.065	0.561	67
MnHCl	61.47	15.11	7.09	< 0.01	0.043	0.604	66

### Percentage of multivariate flux variation explained by individual axes

Axis	% explained variation out of fitted model		% explained variation out of total variation	
	Individual	Cumulative	Individual	Cumulative
1	70.51	70.51	42.59	42.59
2	20.84	91.35	12.59	55.18
3	7.47	98.83	4.51	59.69
4	1.16	99.99	0.7	60.39
5	0.01	100	0.01	60.4

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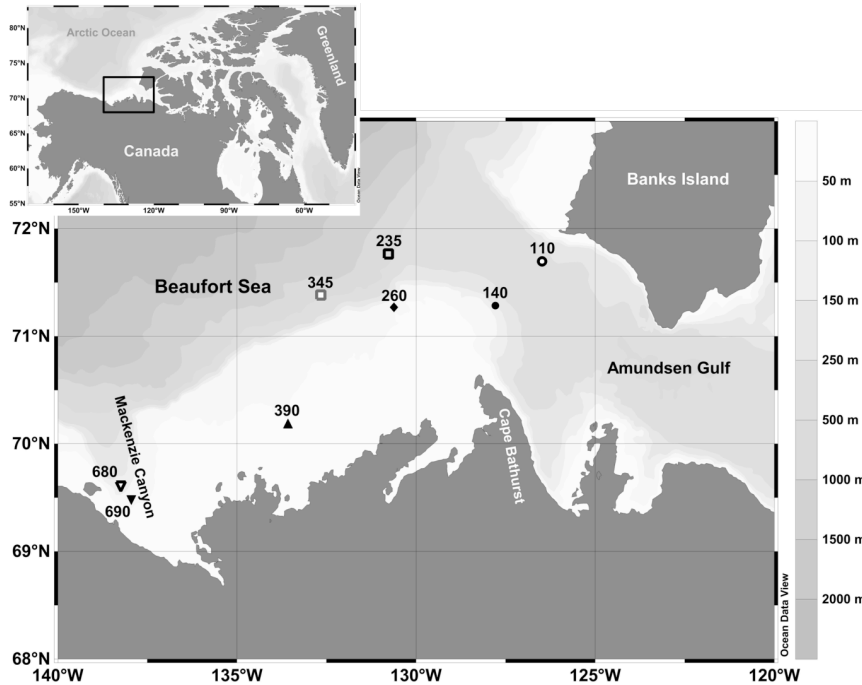
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**Fig. 1.** Locations of sites sampled for benthic boundary fluxes during the Malina expedition in the Beaufort Sea in summer 2009.

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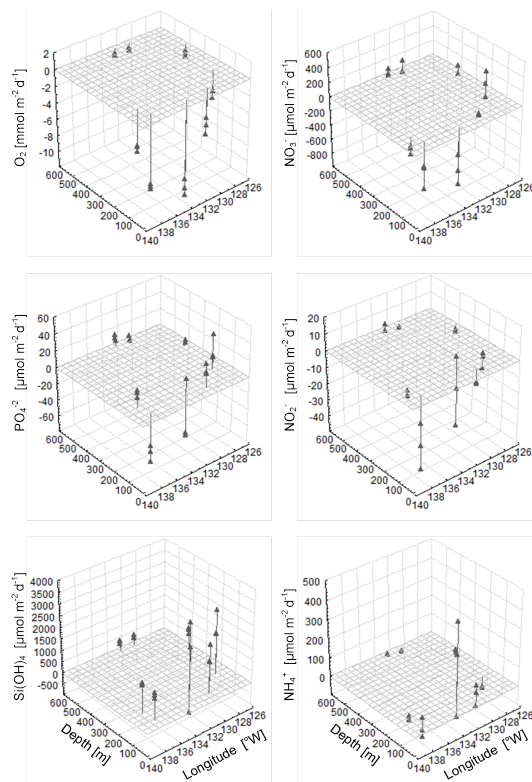
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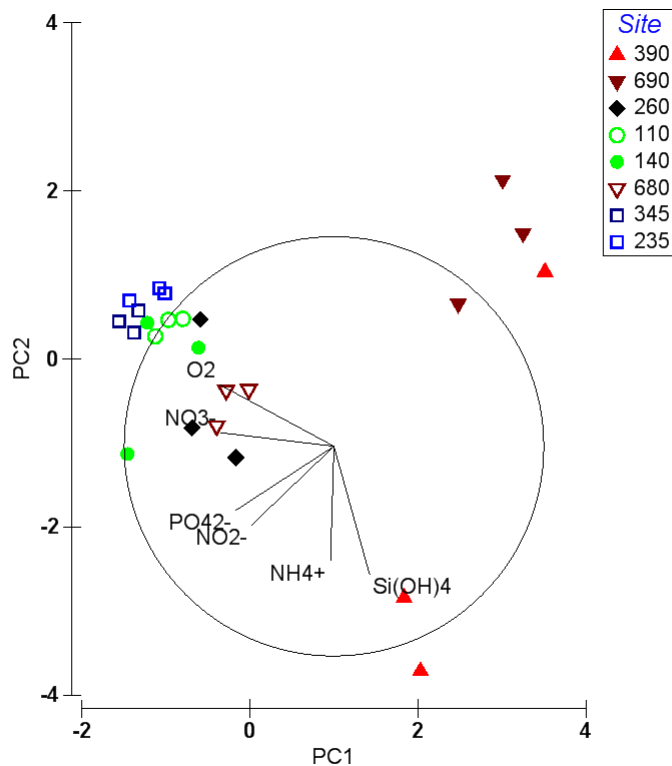
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**Fig. 2.** Spatial distribution of benthic boundary fluxes in the southeastern Beaufort Sea (z-axis; O<sub>2</sub> = oxygen, NO<sub>3</sub><sup>-</sup> = nitrate, PO<sub>4</sub><sup>2-</sup> = phosphate, NO<sub>2</sub><sup>-</sup> = nitrite, Si(OH)<sub>4</sub> = silicic acid, NH<sub>4</sub><sup>+</sup> = ammonium) across a longitudinal (x-axis) and water depth (y-axis) gradient. The values of three replicates from each site are shown in the x-y-z plots. Positive values indicate release from sediments, negative values uptake by sediments, the line is a reference to the zero-plane (values above the plane represent release, below the plane uptake).



**Fig. 3.** Principal Component Analysis (PCA) plot showing the non-metric multivariate similarity among replicate samples in terms of benthic boundary fluxes. Vectors indicate the direction and strength of each flux's contribution to the overall distribution (Table 2). Brown and red triangles: shallow Mackenzie Shelf and Delta; green circles: Cape Bathurst and Amundsen Gulf region (East); blue squares: deeper Mackenzie Slope.

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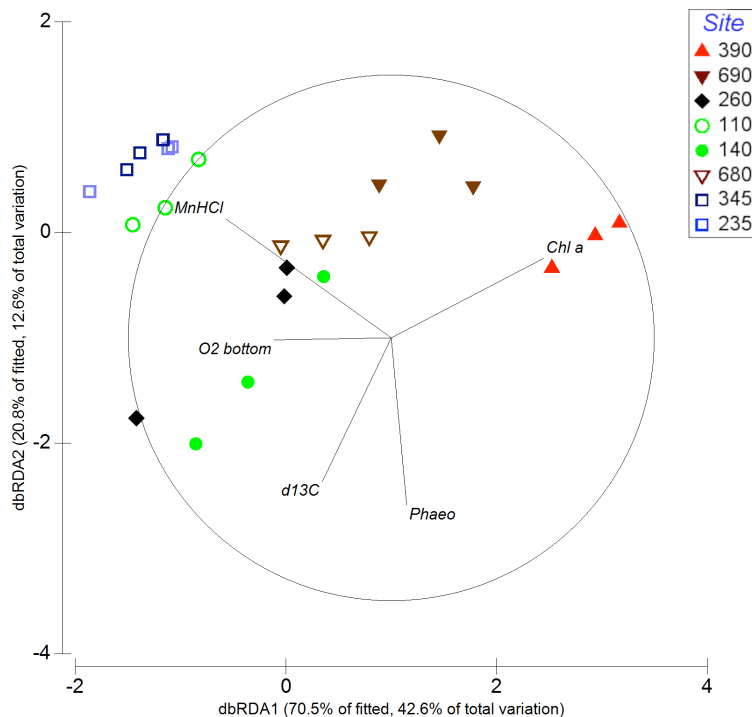
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**Fig. 4.** Distance-based Redundancy Analysis (dbRDA) plot of the distLM model based on the environmental parameters fitted to the variation in biogeochemical fluxes (Table 4). Vectors indicate direction of the parameter effect in the ordination plot. Chl *a* = natural logarithm of sediment Chl *a* concentration; dC13 =  $\delta^{13}\text{C}$  signature; Phaeo = sediment phaeopigment concentration; MnHCl = sediment surface manganese-oxides concentration; O2 bottom = bottom water oxygen concentration. Brown and red triangles: shallow Mackenzie Shelf and Delta; green circles: Cape Bathurst and Amundsen Gulf region (East); blue squares: deeper Mackenzie Slope.