

RESEARCH ARTICLE

10.1002/2016GB005378

Special Section:

The Arctic: An AGU Joint Special Collection

Key Points:

- The Pan-Arctic compilation of sediment oxygen demand exhibits spatial and seasonal variations
- Oxygen fluxes strongly depend on water depth and food supply, in line with global oceanic patterns
- The predicted SOD values (GAM model) show high respiration in the inflow and interior shelves

Supporting Information:

- Supporting Information S1

Correspondence to:

S. Bourgeois,
solveig.bourgeois@gmail.com

Citation:

Bourgeois, S., P. Archambault, and U. Witte (2017), Organic matter remineralization in marine sediments: A Pan-Arctic synthesis, *Global Biogeochem. Cycles*, 31, 190–213, doi:10.1002/2016GB005378.

Received 21 JAN 2016

Accepted 1 JAN 2017

Accepted article online 5 JAN 2017

Published online 28 JAN 2017

©2017. The Authors.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Organic matter remineralization in marine sediments: A Pan-Arctic synthesis

Solveig Bourgeois¹ , Philippe Archambault^{2,3,4} , and Ursula Witte¹ 

¹Oceanlab, School of Biological Sciences, University of Aberdeen, Newburgh, UK, ²Institut des Sciences de la Mer de Rimouski, Université du Québec à Rimouski, Rimouski, Quebec, Canada, ³Hopkins Marine Station, Stanford University, Pacific Grove, California, USA, ⁴Now at Québec-Ocean, Département de biologie, Université de Laval, Québec, Quebec, Canada

Abstract Climate change in the Arctic is ongoing and causes drastic modification on the ecosystem functioning. In soft-bottom environments, organic matter remineralization is considered an important ecosystem function. Here we provide a large-scale assessment of the current knowledge on the benthic organic matter remineralization and its potential response to climate change. Sediment oxygen demand (SOD) values ($n = 1154$), measured throughout the Arctic, were gathered from 30 publications and 16 databases, and nutrient flux values, available in a far lesser extent ($n < 80$), were also compiled. Generalized additive models were used to estimate the influence of explanatory variables on benthic oxygen fluxes and for interpolating SOD to the whole Arctic region. This first Pan-Arctic review of the distributions of SOD showed that oxygen fluxes strongly depended on water depth, i.e., followed the general trend observed for other regions, and also on the availability of labile organic matter. The continental shelves (representing ~50% of Arctic Ocean's total area) were characterized by the highest SOD values ($10.5 \pm 7.9 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$), and differences among shelves were observed; SOD values in inflow, interior, and outflow shelves were 11.8 ± 8.0 , 6.2 ± 5.6 , and $3.9 \pm 3.5 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$, respectively. Moreover, seasonal variation in SOD changed significantly among areas. The interpolation based on the best fitted model showed high respiration in the inflow and interior shelves. In the inflow shelves, characterized by productive waters, benthic activities replenish bottom water with nutrients which may augment primary productivity, whereas sediments from the interior shelves, e.g., under the direct influence of the Mackenzie River, consume nutrients.

1. Introduction

Ecosystem function, which encompasses compartments (e.g., stocks of materials) and process rates (e.g., remineralization of organic matter (OM), fluxes of energy, and matter among compartments), is strongly influenced by factors such as resource availability, disturbance regimes, biodiversity, and, more recently, climate change. Climate change is clearly and fundamentally altering marine ecosystems, and the most striking impacts can be seen in the Arctic Ocean [Hoegh-Guldberg and Bruno, 2010] where the drastic loss of sea ice caused by the significant warming experienced (National Snow and Ice Data Center data, November 2015, https://nsidc.org/cryosphere/sotc/sea_ice.html) is among the most noticeable signs of disruption. However, warming-related mechanisms also contribute to the reduction of sea ice such as the increase of heat fluxes into the Arctic Ocean, the increase in the amount of solar radiation absorbed by the Arctic, and the increase in cloudiness [Woodgate et al., 2006; Serreze et al., 2007; Stroeve et al., 2012; Bélanger et al., 2013]. Other signs of disruption are the rise in freshwater runoff [Haine et al., 2015] and the melting permafrost [Schuur et al., 2008]. In terms of ecosystem functioning, these rapid changes will likely affect the patterns of primary production [Carroll and Carroll, 2003; Wassmann and Reigstad, 2011] and, hence, the resource availability for pelagic and benthic communities, which in turn will affect rates and pathways of organic matter processing (e.g., flux to the seafloor and benthic OM remineralization).

In the Arctic, sea ice algae and phytoplankton are the two main primary producers at the basis of the food chain. Both are consumed by herbivorous zooplankton [Michel et al., 1996; Søreide et al., 2010; Leu et al., 2011] which are in turn consumed by higher trophic levels such as birds and fishes [Darnis et al., 2012], while simultaneously, heterotrophic bacteria and the rest of the microbial loop use and remineralize a nonnegligible part of the primary production [Kirchman et al., 2009a, 2009b]. Due to the strong seasonality in light and sea ice regimes, primary production (PP) in the Arctic occurs over a short period of time and widely varies at a regional scale depending on the physical property of the environment [Sakshaug, 2004; Pabi et al., 2008; Ardyna et al., 2013, 2014]. Export flux and pelagic-benthic coupling further depend on oceanographic conditions (e.g., mixing

and depth) as well as the primary (e.g., standing stocks and phytoplankton taxonomy) and secondary production regimes (e.g., grazing rates and fecal pellet production). For instance, a low zooplankton grazing capacity during the initial bloom can result in tight pelagic-benthic coupling [Gaillard *et al.*, 2015] due to the pulsed sedimentation of relatively fresh phytodetritus to the benthos [Renaud *et al.*, 2007b; Tamelander *et al.*, 2008]. Indeed, several studies show that benthic (bacterial and faunal) communities consume and actively degrade freshly deposited OM produced in top layers of the ocean [Piepenburg *et al.*, 1995; McMahon *et al.*, 2006; Sun *et al.*, 2009; Boetius *et al.*, 2013; Gaillard *et al.*, 2015].

The remineralization of OM in soft-bottom environments is considered an important ecosystem process [Jahnke, 1996], and organic matter flux to and remineralization at the seafloor, measured as O₂ consumption, have been studied on many occasions in the Arctic (see references in section 2), especially in the Canadian [Grant *et al.*, 2002; Renaud *et al.*, 2007b; Darnis *et al.*, 2012; Link, 2012] and the Amerasian Arctic [Grebmeier *et al.*, 2006b; Grebmeier, 2012; Mathis *et al.*, 2014]. In contrast, benthic nutrient fluxes (silicate, phosphate, nitrate, nitrite, and ammonium) have only been determined on few occasions [Devol *et al.*, 1997; Glud *et al.*, 2000; Kenchington *et al.*, 2011; Lein *et al.*, 2013; Link *et al.*, 2013a, 2013b; Mathis *et al.*, 2014] despite the fact that this process is important for the replenishment of nutrients in bottom waters and, ultimately, stimulation of surface water primary productivity. Sediment oxygen demand (SOD) has been shown to depend on resource availability [Boetius and Damm, 1998; Grant *et al.*, 2002; Clough *et al.*, 2005; Grebmeier *et al.*, 2006b; Renaud *et al.*, 2008; Link *et al.*, 2011, 2013a, 2013b; Roy *et al.*, 2014], which is often expressed as sediment organic carbon (OC) or pigment content as proxies for OC supply to the benthos [Grebmeier, 2012].

It is clear that climate change induces physical change and, subsequently, ecological shifts. Many models of phytoplankton PP in the Arctic Ocean estimated a 15–25% increase in PP over a decade (1998–2010), mainly as a result of an increase in the extent and duration of open water areas and melting ponds [Arrigo *et al.*, 2008; Pabi *et al.*, 2008; Arrigo and van Dijken, 2011; Bélanger *et al.*, 2013; Petrenko *et al.*, 2013]. Changes in the total amount of PP have also been accompanied by changes in the onset of spring blooms [Kahru *et al.*, 2011; Ji *et al.*, 2013], bloom phenology (i.e. occurrence of second bloom in fall [Ardyna *et al.*, 2014]), and shifts in species' size composition [Li *et al.*, 2009; Fujiwara *et al.*, 2011]. Moreover, the thinning of sea ice cover and the increased melt-pond cover could enhance under sea ice phytoplanktonic productivity [Arrigo *et al.*, 2012; Lowry *et al.*, 2014] and favor ice-algae export [Boetius *et al.*, 2013]. These changes will likely induce shifts in secondary production [Olli *et al.*, 2007] and export flux (whether it is in terms of quantity, quality, or timing) [Lalande *et al.*, 2009] which will directly affect the benthic ecosystem functions and ecosystem services such as the rates of organic carbon remineralization or sequestration [Findlay *et al.*, 2015].

In order to forecast and adapt to the consequences of both climate change and potentially increased human activities related to the exploitation of marine resources (e.g., extraction of oil and natural gas and fisheries), large-scale baselines for key processes such as benthic OM remineralization in polar latitudes are urgently needed. Nevertheless, despite the long history of benthic biogeochemical research in the Arctic, no publication has attempted to synthesize C remineralization data at a Pan-Arctic scale, and it is the objective of this paper to provide a review of the current knowledge of the benthic OM remineralization in the Arctic and their potential responses to climate change. Spatial and seasonal distributions of SOD as well as nutrient fluxes are analyzed. We hypothesize that (1) higher SOD is observed in shelf areas receiving an inflow of nutrient-rich water (Pacific and Atlantic) compared to that in outflow shelves, that (2) water depth and food supply to the benthos have a high influence on the SOD pattern, and that (3) seasonal variability in oxygen fluxes mirrors the processes occurring in the water column (e.g., timing of bloom and standing stocks). Different models are proposed in order to interpolate SOD to a Pan-Arctic scale and provide complete spatial coverage. An assessment of emerging spatial and temporal patterns, and comparison with other regions, is made. Finally, predictions for future regional trends in oxygen demand in response to ongoing climatic and ecological changes in the Arctic are proposed and discussed.

2. Methods

2.1. Sediment Oxygen Demand

Measurements of SOD ($\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) were gathered from 30 publications and 16 data archives (see references in Table 1) throughout the Arctic region, following the boundaries established by the

Arctic Monitoring and Assessment Program (www.amap.no). In total, the 1154 values could be compiled that spread over three decades (from 1980 to 2013). The Bering Sea (552 data points) is particularly well covered, and a reasonable amount of data could be sourced for the Greenland, Chukchi, and Beaufort Seas and central Arctic Ocean (86 to 170 data points; Figure 1a). In contrast, the Laptev, Kara, and East Siberian Seas have received little or no attention (0 to 20 data points). Because of difficulties in sampling during the winter, the available data mainly cover the period from March to September (Figure 1b).

Where required, SOD values were converted from benthic carbon remineralization values ($\text{mg C m}^{-2} \text{d}^{-1}$) by using the respiration coefficient (varies between 0.7 and 0.8) used in the respective publications. Most data stem from either in situ benthic flux chamber or ex situ shipboard sediment core incubation experiments by using Winkler titration, noninvasive probes, and polarographic electrodes to determine changes in oxygen concentrations in the overlying water column, and thus represent sediment total oxygen uptake (TOU). There are also a small number ($n = 81$) of diffusive oxygen uptake (DOU) measurements based on pore water oxygen microprofiles acquired by using microelectrodes [i.e., *Sauter et al.*, 2001a, 2001b ($n = 32$ values; Greenland Sea); *Wollenburg and Kuhnt*, 2000a, 2000b ($n = 28$ values; Laptev Sea); *Boetius and Damm*, 1998 ($n = 19$ values; Arctic Basin); *Boetius et al.*, 2013 ($n = 2$; Arctic Basin)]. The difference between TOU and DOU corresponds to the faunal respiration and irrigation, and the bias introduced by the use of both approaches was reviewed by *Glud* [2008], who showed that TOU is markedly higher than DOU when benthic community respiration is high, whereas values converge at low diagenetic activity and/or little fauna are present [Glud, 2008]. DOU data included in this study were acquired mainly in deep water and/or areas where the diagenetic activity was relatively low. Eighty percent of values fell below $1 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$, and the remainder did not exceed $3.51 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ [*Sauter et al.*, 2001a, 2001b; *Boetius and Damm*, 1998]; we therefore assume that the use of DOU instead of TOU will be of minor consequence for the following analysis (i.e., models).

2.2. Nutrient Fluxes

Benthic nutrient fluxes have been measured less frequently, and nitrate (NO_3^-) + nitrite (NO_2^-), ammonium (NH_4^+), phosphate (PO_4^{3-}), and silicate (SiO_2) flux data employed in this analysis were extracted from 11 publications [*Grebmeier and Cooper*, 1995; *Rysgaard et al.*, 1996, 1998, 2004; *Devol et al.*, 1997; *Glud et al.*, 1998, 2000; *Christensen*, 2006; *Link et al.*, 2013a, 2013b; *Morata et al.*, 2015]. In total, 72, 73, 49, and 61 values of nitrate (or nitrate + nitrite), ammonium, phosphate, and silicate fluxes, respectively, could be gathered for this review. All data points were generated based on the change in nutrient concentrations in the overlying seawater during sediment core incubations. For nitrate/nitrite fluxes, the majority of the publications have measured nitrate and nitrite ($\text{NO}_2^- + \text{NO}_3^-$) simultaneously, whereas a few studies measured them separately [*Devol et al.*, 1997; *Glud et al.*, 2000; *Link*, 2012; *Link et al.*, 2013a, 2013b]. *Link* [2012] and *Link et al.* [2013a, 2013b] showed that nitrite fluxes in Arctic sediments are extremely low compared to nitrate fluxes, and thus, it was assumed that the bias introduced by compiling the different results will be negligible. Phosphate fluxes were mostly measured as PO_4^{3-} [*Rysgaard et al.*, 1996, 1998; *Glud et al.*, 2000; *Morata et al.*, 2015], but *Link et al.* [2013a, 2013b] measured PO_4^{2-} fluxes.

2.3. Chlorophyll *a* at Sediment Interface

Concurrently to the benthic oxygen and nutrient flux data, a large number of chlorophyll *a* (chl *a*) data (mg m^{-2}) were assembled ($n = 1251$ values; Figure S1 in the supporting information and see references in Table 1). The majority of data in this data set refer to chl *a* concentrations in the top first centimeter of sediment, but some studies report integrated results for the top 2 cm ($n = 76$). For standardization purposes, it was assumed that 60% of chl *a* would have occurred in the top centimeter [*Soilwedel and Vopel*, 2001; *Morata et al.*, 2011]. Publications reporting bulk chl *a* concentrations for the top 5 or 10 cm were excluded from this analysis in order to avoid the insertion of large errors.

2.4. Data Presentation, Statistical Analysis, and Models

The maps of benthic oxygen and nutrient fluxes were created by using the free software Ocean Data View [*Schlitzer*, 2007]. All SOD as well as nutrient flux values were plotted together in order to provide a Pan-Arctic distribution pattern of the benthic remineralization function. In parallel, seasonal distribution patterns of SOD were also depicted, with boreal seasons being defined as follows: spring (1 March to 31 May), summer (1 June to 31 August), autumn (1 September to 30 November), and winter (1 December to 28 February).

Table 1. Summary of Surface Sediment Chlorophyll *a* (chl *a*, mg m⁻²) and Sediment Oxygen Demand (SOD, mmol O₂ m⁻² d⁻¹) in the Arctic Region

Region	Year	Season	Depth (m)	Sediment chl <i>a</i> (mg m ⁻²)	SOD (mmol O ₂ m ⁻² d ⁻¹)	References
Western Barents Sea	2003–2005	spring-summer	195–503	0.36–24.12	2.30–7.30	[<i>Renaud et al.</i> , 2008]
Barents (Svalbard) and Norwegian Seas (northern Norway)	1995	autumn	115–329		3.60–16.40	[<i>Glud et al.</i> , 1998]
Barents Sea (Svalbard)	1991	summer	170–2577		1.85–11.20	[<i>Hulth et al.</i> , 1994; <i>Piepenburg et al.</i> , 1995]
Barents Sea (NE Svalbard Shelf) and Arctic Ocean (Nansen Basin)	1980	summer	226–3920		1.71–12.00	[<i>Pfannkuche and Thiel</i> , 1987]
Northern Barents Sea (Svalbard)	2003–2004	spring-summer	17–2700	1.8–58.8		[<i>Søreide et al.</i> , 2013]
Barents Sea (Svalbard, Rijpfjorden)	2012	winter	272	8.80	4.25	[<i>Morata et al.</i> , 2015]
Laptev Sea, Arctic Ocean	1993	autumn	37–3237	0.00–45.6	0.07–2.34 ^a	[<i>Boetius and Damm</i> , 1998]
Laptev Sea, Arctic Ocean	1995	summer-autumn	51–3823	0.20–10.10	0.22–0.99 ^a	[<i>Wollenburg and Kuhnt</i> , 2000a, 2000b] ^b
Arctic Ocean	1994	summer	68–4190	0.00–0.41		[<i>Clough et al.</i> , 1997]
Central Arctic Ocean	1998	summer	1270–3170	0.06–0.36		[<i>Schewe</i> , 2001]
Arctic Ocean	2012	summer-autumn	3589–4808	0.98–3.36	0.34–0.41 ^a	[<i>Boetius et al.</i> , 2013]
Bering Sea	1990	summer	21–72		6.53–32.18	[<i>Grebmeier and Cooper</i> , 1995]
Northern Bering Sea	2006–2007	spring	27–119	2.55–46.53	0.36–27.79	[<i>Grebmeier and Cooper</i> , 2009, 2010, 2014a, 2014b] ^b
Northern Bering Sea	2008–2009	spring	33–80	0.65–17.44	1.71–11.34	[<i>Grebmeier</i> , 2010a, 2010b; <i>Grebmeier and Cooper</i> , 2014a, 2014b] ^b
Bering Sea	2007–2010	spring-summer	40–3941		1.24–24.50	[<i>Devol</i> , 2008] ^b
Chukchi and Beaufort Seas, Arctic Ocean	1994/1996/1998	summer	40–3648	0.00–27.80	0.29–20.68	[<i>Clough et al.</i> , 2005]
Northern Bering and Chukchi Seas	1984–1986	summer-autumn	19–54		0.65–45.62	[<i>Grebmeier and McRoy</i> , 1989; <i>Grebmeier and Cooper</i> , 2014a] ^b
Bering and Chukchi Seas	2004	summer	35–84	5.51–19.09	10.19–39.57	[<i>Pirtle-Levy et al.</i> , 2009; <i>Grebmeier and Cooper</i> , 2014a, 2014b] ^b
Bering, Chukchi and Beaufort Seas (Western Arctic shelf)	1992–1993	spring-autumn	11–48		5.13–18.00	[<i>Devol et al.</i> , 1997]
Chukchi and Beaufort Seas, Arctic Ocean	2002/2004	spring-summer	28–3274	1.00–37.47	0.33–47.81	[<i>Grebmeier and Cooper</i> , 2004a, 2004b, 2004c, 2004d, 2014a, 2014b] ^b
Amerasian Arctic	1988–2012	summer-autumn	12–2106	0.10–70.16	0.63–52.64	[<i>Grebmeier and Cooper</i> , 2014a, 2014b; <i>Grebmeier et al.</i> , 2015a] ^b
Beaufort Sea and Arctic Ocean	2004	summer	50–3894		0.22–7.68	[<i>Christensen</i> , 2006] ^b
Eastern Beaufort Sea	2003–2004	summer-autumn	44–420	0.08–9.79	0.00–9.41	[<i>Renaud et al.</i> , 2007a]
Beaufort Sea (Franklin Bay)	2004	winter-summer	250–251	0.49–1.30		[<i>Morata et al.</i> , 2011]
Beaufort Sea (Franklin Bay)	2004	winter-summer	231		1.77–20.22	[<i>Renaud et al.</i> , 2007b]
Southeastern Beaufort Sea	2009	summer	47–577	0.27–13.82	0.63–10.52	[<i>Link et al.</i> , 2013b]
Southeastern Beaufort Sea (Amundsen Gulf and Franklin Bay)	2008	spring-summer	100–595	0.70–11.00	1.21–4.63	[<i>Link et al.</i> , 2011]
Beaufort Sea and Canadian Arctic Archipelago	2008–2009	summer-autumn	45–810		0.52–19.82	[<i>Darnis et al.</i> , 2012; <i>Link</i> , 2012; <i>Link et al.</i> , 2013a]
Canadian High Arctic (Resolute)	1993	spring-winter	16–87		6.42–10.70	[<i>Welch et al.</i> , 1997]
Baffin Bay and Canadian Arctic Archipelago	2013	summer-autumn	456–794	2.48–12.88	2.41–4.03	(Makela, personal communication)
Baffin Bay and Canadian Arctic Archipelago	2013	summer	180–830	0.23–54.93		ArcticNet 2013 ^b

Table 1. (continued)

Region	Year	Season	Depth (m)	Sediment chl <i>a</i> (mg m ⁻²)	SOD (mmol O ₂ m ⁻² d ⁻¹)	References
Baffin Bay (North Water Polynya)	1998	spring-summer	252–680		1.61–5.45	[Grant et al., 2002]
Baffin Bay and Greenland Sea (East and West Greenland)	2001–2003	spring-autumn	36–85		3.43–8.27	[Rysgaard et al., 2004]
Western Greenland Sea (Young Sound)	1996	summer	20–163		3.09–20.12	[Glud et al., 2000]
Western Greenland Sea (Young Sound)	1996–1997	summer/winter	36		5.10–12.86	[Rysgaard et al., 1998]
Western Greenland Sea (Young Sound)	1994	summer	40		17.76	[Rysgaard et al., 1996]
Greenland Sea (Northeast Water Polynya)	1993	spring-summer	187–487		0.26–3.55	[Piepenburg et al., 1997]
Greenland and Norwegian Seas	1994–1997	spring-winter	189–3627		0.08–3.51 ^a	[Sauter et al., 2001a, 2001b] ^b
Greenland Sea	1992–1993	summer	145–490		0.72–9.12	[Rowe et al., 1997; Rowe, 2002] ^b
Greenland Sea	1994–1997	summer-autumn	344–3625		0.00–4.32	[Seiler, 1999] ^b
Greenland Sea (Northeast Water Polynya)	1993	spring-summer	330	0.00–1.65		[Ambrose and Renaud, 1997]
Greenland Sea (Northeast Water Polynya)	1992	summer	125–515	4.33–27.37		[Ambrose and Renaud, 1995]
Greenland Sea (Fram Strait)	1999	summer	744–3020	0.10–9.50		[Schewe and Soltwedel, 2003]
Greenland Sea, Arctic Ocean (Yermark plateau)	1997	summer	481–4268	0.10–24.80	/	[Soltwedel et al., 2000]

^aMeasurements of dissolved oxygen uptake.

^bValues from databases.

An analysis of covariance (ANCOVA) was carried out, in the statistical analysis environment R [R Core Team, 2015], to examine differences in SOD by using the water depth of sampled stations and the shelf type as variables. *P* values below 0.05 are considered statistically significant.

Generalized additive models (GAMs) [Hastie and Tibshirani, 1990] were used to determine the best descriptors of the distribution of SOD and predicted values for the entire Arctic. This analysis was favored in order to detect potential nonlinear relationships and to take into account the sampling density. In order to choose the best fitting GAM model for representation of benthic oxygen fluxes, a step-by-step approach was adopted, which consisted of (1) gradually log-transforming ($\log(x + 1)$) the response and then the descriptor variables and (2) the addition of new terms in the model (i.e., in the incremental complexity of the model) until the best fitting model was reached. Log transformation of the data set was performed in order to smooth the pattern, reduce the effect of outliers, and meet the validation criteria (normality and heterogeneity) of the model. The descriptor variable entering first in the model was the water depth (m). In order to consider the influence of labile food supply on the SOD, the chlorophyll *a* concentration in sediments was then added as a variable in the models.

The various GAM models were determined by means of R package “gam” (version 1.12 [Hastie, 2015]) at the statistical analysis environment R [R Core Team, 2015]. The models were compared by using the explained variance (r^2). The predicted values from the fitted models were obtained, either for the original values or for new values of the predictor variables, using the “predict” function. In order to interpolate SOD at a Pan-Arctic scale, an Arctic Ocean bathymetry, at a resolution of 1° ($n = 7916$ values), was used. When sediment chl *a* was included in the model as an explanatory variable, an intermediate step was performed in order to calculate the global chl *a* distribution in surface sediments. To achieve this, a GAM model was applied to the larger chl *a* data set ($n = 1251$; Figure S1) according to the water depth.

The discrepancy between the estimated (models) and observed (archives) values was highlighted by using the following equations:

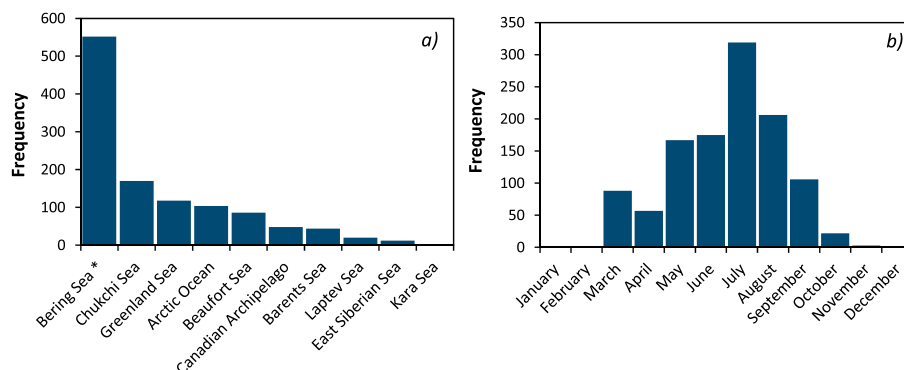


Figure 1. Frequency distributions of number of SOD measurements as a function of (a) Arctic seas and ocean and (b) months of the year. Asterisk, mainly in the Northern Bering Sea (445 over 552 stations).

$$\text{Relative anomaly}(\%) = \frac{(\text{SOD}_{\text{Predicted}} - \text{SOD}_{\text{Observed}}) \times 100}{\text{SOD}_{\text{Observed}}}$$

3. Results and Discussion

3.1. Sediment Oxygen Demand and Explanatory Variables

3.1.1. Water Depth

In the Arctic region, sediment oxygen uptake declined with increasing water column depth with a sharp decrease in the first 200 m. In addition, SOD was reduced by more than a third moving from shallow (0–200 m) to deeper (200–500 m) continental shelves (Figure 2a). The results from an ANCOVA (water depth as covariable) showed a significant difference in SOD between inflow (Bering/Chukchi and Barents Seas), interior (Beaufort, East Siberian, Laptev, and Kara Seas), and outflow (Canadian Archipelago and Greenland Sea) [Carmack and Wassmann, 2006] shelves (Figure 2b), with a higher activity on the inflow shelves ($11.8 \pm 8.0 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) than on the interior ($6.2 \pm 5.6 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) or outflow ($3.9 \pm 3.5 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) shelves. Furthermore, the variability is driven by the water depth of the stations sampled (medians of 64 m, 107 m, and 280 m, respectively). This relationship was significant (ANCOVA, variable water depth, $p < 0.0001$, $n = 961$). Overall, the continental shelves (wd. 0–500 m), which account for approximately half of the Arctic Ocean’s total area [Jakobsson, 2002], were characterized by high values of SOD ($10.46 \pm 7.94 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) in comparison to the slope/rise ($2.23 \pm 2.37 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) and the abyssal plain ($1.75 \pm 1.70 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) (Figure 2a). A similar pattern (i.e., SOD significantly greater at shallow (<500 m) than at deep sites) has previously been observed by Clough *et al.* [2005] at regional scale ($n = 27$ stations) during a study completed in the Western Arctic Ocean.

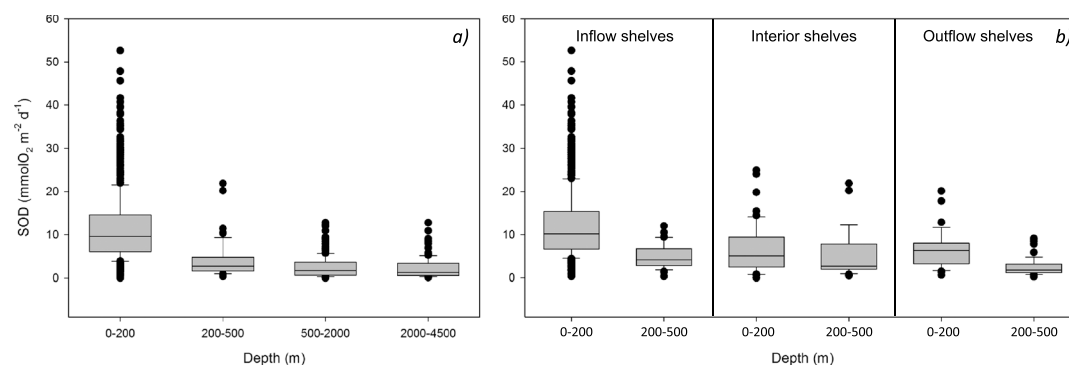


Figure 2. Sediment oxygen demand (SOD, $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) (a) in the whole Arctic and (b) in the shelves (inflow, interior, and outflow) as a function of ranges of water depth (m). The inflow shelves include the Bering and Chukchi Seas as well as western Spitsbergen and Barents Sea; the interior shelves include Kara, Laptev, East Siberian, and Beaufort Seas; and the outflow shelves include the Canadian Archipelago and Labrador and Greenland Seas [Carmack and Wassmann, 2006].

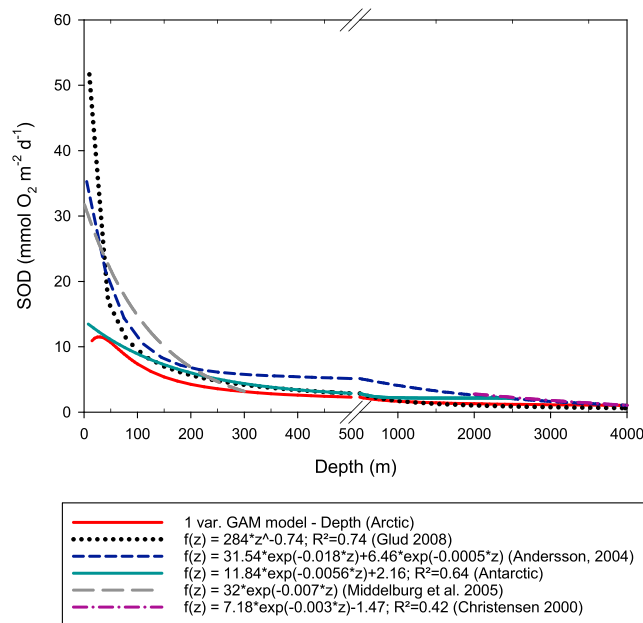


Figure 3. Benthic oxygen flux-depth relationship found in different marine environments: polar (Arctic and Antarctic), coastal [Middelburg *et al.*, 2005], deep sea [Christensen, 2000], and whole ocean/sea [Andersson *et al.*, 2004; Glud, 2008]. The curve fit on our data set comes from GAM. The SOD values in the Antarctica are extracted from five publications [Nedwell *et al.*, 1993; Hulth *et al.*, 1997; Baldwin and Smith, 2003; Hartnett *et al.*, 2008; Link and Piepenburg, 2013]. The other regression curves used in the publications are exponential decrease or power law.

benthic oxygen fluxes in the Arctic shelves than in the other continental shelves but also (2) that the decrease in rates with increasing water depth was less steep in the Arctic. Interestingly, both polar regions (Arctic and Antarctic) exhibit relatively similar pattern of benthic oxygen uptake (in terms of slope). Temperature dependence of oxygen consumption rates has previously been documented [Arnosti *et al.*, 1998; Thamdrup *et al.*, 1998], and oxygen uptake follows a linear regression with temperature, with the lowest oxygen uptakes measured in cold temperatures. But while the low temperatures experienced in the polar regions compared to the rest of the global ocean (temperate and tropical ecosystems) could explain some of the features, the SOD values from the Arctic shelves are dissimilar to other cold environments such as the deep sea, highlighting that additional factors, such as the food supply, are of relevance.

3.1.2. Resource Availability: Food Supply to the Benthos

Resource availability is an important biotic driver for the benthic ecosystem functions, and the quantity and quality of food supply (often expressed as organic carbon and pigments) to the benthos are generally related to the transformative processes occurring in the water column. It is well known that OM fluxes to the benthos decrease with increasing water depth [Suess, 1980; Buesseler *et al.*, 2007] due to the progressive degradation of the OM during the sinking phase. The residence time of the particles in the water column, which is mainly size- and density-dependent, will therefore have an influence on the supply of OM to the benthos and its functioning: large particles such as ice algal aggregates, fecal pellets, or marine snow (>200 μm in diameter) settle rapidly, whereas smaller particles reside in the water column for longer, become more degraded, and will have a less significant role in vertical mass fluxes [Suess, 1980]. The degradation processes are especially pronounced in the first hundred meters of water due to preferential mineralization of the more reactive compounds (such as chl *a* or lipids) [Andersson *et al.*, 2004]. As expected, chl *a* concentrations in Arctic sediments decrease with increasing water depth [Ambrose and Renaud, 1995; Renaud *et al.*, 2007a; Link *et al.*, 2011], as labile OM produced in the euphotic zone is progressively degraded.

Of course, the amount of OM reaching the seafloor and available to the benthos also depends on the quantities initially produced in the water column. In the Arctic, primary production varies widely regionally [Arrigo *et al.*, 2008; Pabi *et al.*, 2008] and is controlled by factors such as advection, water stratification, sea

The relationship between oxygen fluxes in marine sediments and water depth has been well documented for a wide range of environments [Christensen, 2000; Andersson *et al.*, 2004; Middelburg *et al.*, 2005; Glud, 2008], including the Arctic [Boetius and Damm, 1998; Clough *et al.*, 2005]. Typically, benthic oxygen consumption shows an exponential [see Andersson *et al.*, 2004] or a power law relationship with water depth (Figure 3), i.e., a rapid decrease of SOD, which is in agreement with our findings. Here GAM analysis showed that water depth explained up to 49% of the variation of benthic oxygen uptake in log-transformed data (Table 2). However, exceptions occur, and Piepenburg *et al.* [1995], for example, recorded a reverse relationship with higher benthic oxygen consumption in deep stations (>200 m) than in shallow ones (<200 m) in the northwestern Barents Sea. The comparison of SODs between various environments and the Arctic region (Figure 3) showed not only (1) lower

Table 2. Results of GAM Models (Deviance Explained and Smooth Terms) Relating Sediment Oxygen Demand (SOD) to Environmental Variables (Depth and Chlorophyll *a*)^a

Model Name	<i>n</i>	Deviance Explained	Variables-Smooth Terms	GAM Relationship
1 var GAM model –depth	1148 ^b	48.9%	$s(\log(\text{depth}))$; edf = 4.52 $F = 200.4$; $p < 0.0001$	
1 var GAM model –chl <i>a</i>	561	47%	$s(\log(\text{chl } a))$; edf = 5.86 $F = 74.29$; $p < 0.0001$	
2 var GAM model –depth and chl <i>a</i>	556	57.3%	$s(\log(\text{depth}))$; edf = 1.00 $F = 120.32$; $p < 0.0001$ $s(\log(\text{chl } a))$; edf = 6.01 $F = 15.57$; $p < 0.0001$	
2 var GAM model –depth and chl <i>a</i> with interaction	556	58.9%	$s(\log(\text{depth}))$; edf = 4.73 $F = 7.72$; $p < 0.0001$ $s(\log(\text{chl } a))$; edf = 5.35 $F = 5.40$; $p < 0.0001$ $s(\log(\text{depth}, \log(\text{chl } a)))$; edf = 3.78 $F = 2.53$; $p = 0.002$	

^aVar means variable, $\log(\text{depth})$ and $\log(\text{chl } a)$ mean $\log(\text{depth} + 1)$ and $\log(\text{chl } a + 1)$, respectively, and edf means effective degrees of freedom. This table is based on the study from Orlova *et al.* [2015] and contains our own data.

^bAmong the 1154 SOD values gathered, few ($n = 6$) were not associated to water depth (m) and thus cannot be used in the “1 var GAM model—depth.”

surface temperature, nutrients, and light (e.g., turbidity or ice cover) limitations. The Greenland and Barents Seas display the highest areal total annual primary productions (148 and 132 Tg C yr⁻¹ [Arrigo and van Dijken, 2011]) mainly due to the largest annual mean open water area [Pabi *et al.*, 2008]. Outflow and interior shelves are characterized by low PP rates per unit area (e.g., Canadian Archipelago

and Russian seas; $\sim 20\text{--}50\text{ g C m}^{-2}\text{ yr}^{-1}$ [Sakshaug, 2004]). PP on outflow shelves is mainly governed by the sea ice condition, the upper mixed layer depth, and nutrient limitations, primarily nitrate [Michel *et al.*, 2015]. In contrast, the inflow shelves receive nutrient-rich (Pacific or Atlantic) water inflows and the annual mean PP in the Barents and Chukchi Seas is higher and around $100\text{ g C m}^{-2}\text{ yr}^{-1}$ [Arrigo and van Dijken, 2011; Hunt *et al.*, 2013]. However, strong patchiness in PP and standing stocks can be observed in these regions. In the Southern Chukchi Sea, which is fed by the nutrient-rich Anadyr water, PP can locally reach up to $720\text{ g C m}^{-2}\text{ yr}^{-1}$ [Hunt *et al.*, 2013, and references therein].

SOD is strongly correlated to the availability of labile OM (chl *a*) [Boetius and Damm, 1998; Grant *et al.*, 2002; Clough *et al.*, 2005; Grebmeier *et al.*, 2006b; Renaud *et al.*, 2008; Link *et al.*, 2011, 2013a, 2013b] which underscores the strong pelagic-benthic coupling in the Arctic region. For instance, in the Canadian Arctic, food availability was significantly higher at sites with high SOD ("hot spot") than those with low SOD ("cold spot") [Link *et al.*, 2013a]. In this study, GAMs indicate that labile carbon supply (chl *a*) alone can explain up to 47% of the variation of SOD in the Arctic. The nutritive quality of the phytodetritus reaching the seabed is particularly close related to SOD [Morata and Renaud, 2008; Sun *et al.*, 2009], especially during sea ice-covered conditions when the primary production and export to the benthos are low [Link *et al.*, 2011; Morata *et al.*, 2015]. The large scatter in the compiled SOD values, especially in the inflow shelves (Figure 2), at similar water depths, may be driven by strong heterogeneity in the pelagic primary production among sites, as previously detailed in this section, and the efficiency of export to the seafloor.

3.1.3. Other Potential Explanatory Variables: Zooplankton and Benthic Communities' Structure and Activities

Other parameters, which are not taken into account in the models, are also likely explanatory variables for the SOD patterns, in particular the transformation of OM by zooplankton and benthic communities.

Zooplankton can be a nonnegligible supplier of OM to the benthos through production of fecal pellets (FPs) and sinking of dead organisms [see Sampei *et al.*, 2004]. Although copepod FPs are mostly retained within the upper 100 m of the water column when phytoplankton concentrations are low [Riser *et al.*, 2002], FP can represent up to 30–60% of total organic carbon (TOC) export flux in spring/summer [Riser *et al.*, 2002; Sampei *et al.*, 2004; Wexels Riser *et al.*, 2008]. When periods of high PP match with those of high zooplankton biomass, the zooplankton grazing activity also regulates the direct export of phytoplankton or ice algae to the benthos. Zooplankton graze on phytoplankton as well as on ice algae [Michel *et al.*, 1996; Søreide *et al.*, 2010; Leu *et al.*, 2011] and most of the particulate organic carbon (POC) export are mediated by herbivorous zooplankton. Zooplankton standing stocks and resulting grazing rates can vary widely between Arctic seas and shelves. For instance, the Barents Sea exhibits greater biomass of zooplankton than the Chukchi Sea, both defined as inflow shelves [Hunt *et al.*, 2013, and references therein]. This high biomass is supported by the advective input of zooplankton by the Atlantic and Arctic water masses. Greater depths and higher zooplankton grazing pressure likely result in a reduced OM flux to the seafloor compared to the Chukchi Sea [Hunt *et al.*, 2013].

Equally benthic communities exert great influence on benthic carbon remineralization [Piepenburg, 2005]. Macrobenthic community characteristics (in term of biomass, richness, and abundance) can explain an important part of the respiration pattern [Clough *et al.*, 2005; Grebmeier *et al.*, 2006a; Link *et al.*, 2011, 2013a], especially in the summer [Grant *et al.*, 2002; Link *et al.*, 2011], whereas meiobenthos and microbenthos dominate oxygen consumption in the spring [Grant *et al.*, 2002]. Macrofaunal biomass explained 74% of SOD in the Western Arctic Ocean [Clough *et al.*, 2005], and macrofauna dominate the sediment respiration in the shelf and upper slope in the Amerasian Arctic, whereas meiofauna and microfauna become more important in the deep slope and deep basin [Grebmeier *et al.*, 2006b, and references therein].

Macrofauna are also efficient particle mixers and thus the main actors in bioturbation, which in turn is considered a primary determinant in sediment oxygen concentrations [Solan *et al.*, 2004], as bioturbators enhance process rates (e.g., benthic carbon remineralization) through complex biogeochemical interactions [Lohrer *et al.*, 2004]. Arctic benthic macroinfauna responded rapidly to a pulse of fresh food (phytoplankton or ice algae) [Clough *et al.*, 2005; McMahan *et al.*, 2006; Sun *et al.*, 2007] which initiated bioturbation [Morata *et al.*, 2015], and SOD is directly affected by the presence of species classified as bioturbators [Michaud *et al.*, 2005]. Surprisingly, functional group richness had a low explanatory power in the SOD in the Canadian Arctic [Link *et al.*, 2013a]. Nonetheless, these authors highlighted that the abundance of gallery-burrowing *Polychaete* species, i.e., bioirrigators, was an explanatory variable for the variations in the fluxes.

Despite the apparent importance of these parameters on the benthic remineralization function, heterogeneity of the methods used (e.g., different units such as dry, wet, and C biomass for benthic biomass) and rarity of activity measurements such as bioturbation coefficients [Clough *et al.*, 1997; Jørgensen *et al.*, 2005; Morata *et al.*, 2015] prevented the integration of these parameters into the models.

3.2. Spatial and Seasonal Patterns in Sediment Oxygen Demands

SOD varied significantly between 0 and 52.6 mmol O₂ m⁻² d⁻¹ (Figure 2). The Pan-Arctic distribution of SOD (observation) is presented in Figure 4. The highest SOD was measured in shallow waters in the Amerasian Arctic, and particular “hot spots” of SOD were located in the Southern Chukchi Sea (40.7 mmol O₂ m⁻² d⁻¹), the Northern Bering Sea (45.6 mmol O₂ m⁻² d⁻¹), and head of Barrow Canyon (52.6 mmol O₂ m⁻² d⁻¹). These areas receive nutrient-rich Pacific water inflow over the shelf, and the Chukchi Sea is known for high PP [Hill and Cota, 2005; Arrigo *et al.*, 2008; Pabi *et al.*, 2008; for review see Harada, 2016]. Moreover, they are organic carbon depositional areas [Goñi *et al.*, 2013] largely due to bathymetric features (depressions and canyons) [Maslowski *et al.*, 2014; Mathis *et al.*, 2014]. In the last decade, this region has been the subject of extensive research with regard to benthic ecosystem functioning [Grebmeier *et al.*, 2006a, 2006b; Grebmeier, 2012]. The Northern Bering Sea experienced a major ecosystem shift with a decline of sediment oxygen uptake and benthic macrofaunal biomass from 1988 to 1998 followed by steady values until 2004 [Grebmeier *et al.*, 2006a]. In the Chukchi Sea, a decadal survey (1984–2010) revealed that the local hot spots of SOD, i.e., head of Barrow Canyon and Southern Chukchi Sea, are persistent over this time period [Grebmeier, 2012]. In this area, the low water temperatures limit the zooplankton communities in terms of abundance, size (dominated by smaller copepods and microzooplankton), and biological activities [Findlay *et al.*, 2015, and references therein], and the low grazing pressure in the water column allows a high carbon export to the sediments [Campbell *et al.*, 2009]. High SOD was also found in the Barents Sea (around Svalbard Archipelago) and at the Mackenzie Delta (Beaufort Sea) (Figure 4). Similar to the Bering and Chukchi Seas, the Barents Sea is a highly productive area [Sakshaug, 2004; Hunt *et al.*, 2013, and references therein], which receives large imports of nutrients from the Atlantic Ocean. In contrast to other Arctic seas, the Beaufort Sea is considered to be relatively oligotrophic with low PP [Carmack *et al.*, 2004; Sakshaug, 2004], while POC export flux is relatively important (1–12.9 g C m⁻² yr⁻¹ [Harada, 2016, and references therein]). The Mackenzie Delta and its adjacent shelf are strongly influenced by the Mackenzie River which is the fourth largest river in the Arctic in terms of annual water discharge (249–333 km³ yr⁻¹ [Dittmar and Kattner, 2003]). In coastal environments, rivers bring important quantities of dissolved and particulate OM (e.g., vascular plant debris, soils, and freshwater phytoplankton) as well as nutrients which stimulate several ecosystem functions such as the production, consumption, and remineralization of OM. Although terrestrial C inputs are usually considered as more refractory than marine C [Wakeham and Canuel, 2006], this source of OM can be actively degraded by microorganisms following priming with labile organic matter in deltaic/estuarine regions [Bianchi, 2011] and can also represent a directly used food resource for benthic infauna [Dunton *et al.*, 2012]. Furthermore, riverine nutrient inputs locally stimulate PP in the water column at the vicinity of the Mackenzie River mouth [Tremblay *et al.*, 2014], and marine algae-derived carbon can form up to 50% of the TOC in the Mackenzie adjacent shelf [Goñi *et al.*, 2000]. However, pelagic PP is often limited nearshore due to the light limitation caused by the high-suspended sediment loads from riverine discharge or shore erosion [Goñi *et al.*, 2000; Rachold *et al.*, 2000, 2004; Guo *et al.*, 2004]. This would also explain the decrease of SOD at very shallow depth (<30 m) (Figure 3). Despite the fact that the North Water Polynya (NOW) is considered a productive area (150–200 g C m⁻² yr⁻¹ [Klein *et al.*, 2002; Arrigo *et al.*, 2008; Ardyna *et al.*, 2011]), only moderate SOD values (~5 mmol O₂ m⁻² d⁻¹) have been measured in this region. Here only 1.4–2.6% of PPC reach the seafloor, amounting to a total POC at 50 m above bottom [Sampei *et al.*, 2002], probably because of the aforementioned combination of greater water depths and high zooplankton standing stock. Nonetheless, SOD in the central part of the NOW reached 8 mmol O₂ m⁻² d⁻¹, and therefore, it was identified as a “hot spot” [Link *et al.*, 2013a]. The lowest SOD was recorded in the Arctic Basin, the Laptev Sea, and in the deep Greenland Sea, all of which are characterized by relatively low POC export fluxes (from 0.1 to 1.6 g C m⁻² yr⁻¹ [Harada, 2016, and references therein]).

Studying seasonal variability in the Arctic is challenging due to logistical constraints posed by the darkness, extensive sea ice cover, and very low temperatures during the winter months. As a result, observations recorded during the polar night are scarce (Figures 1b and 5a). Conversely, late spring and early summer

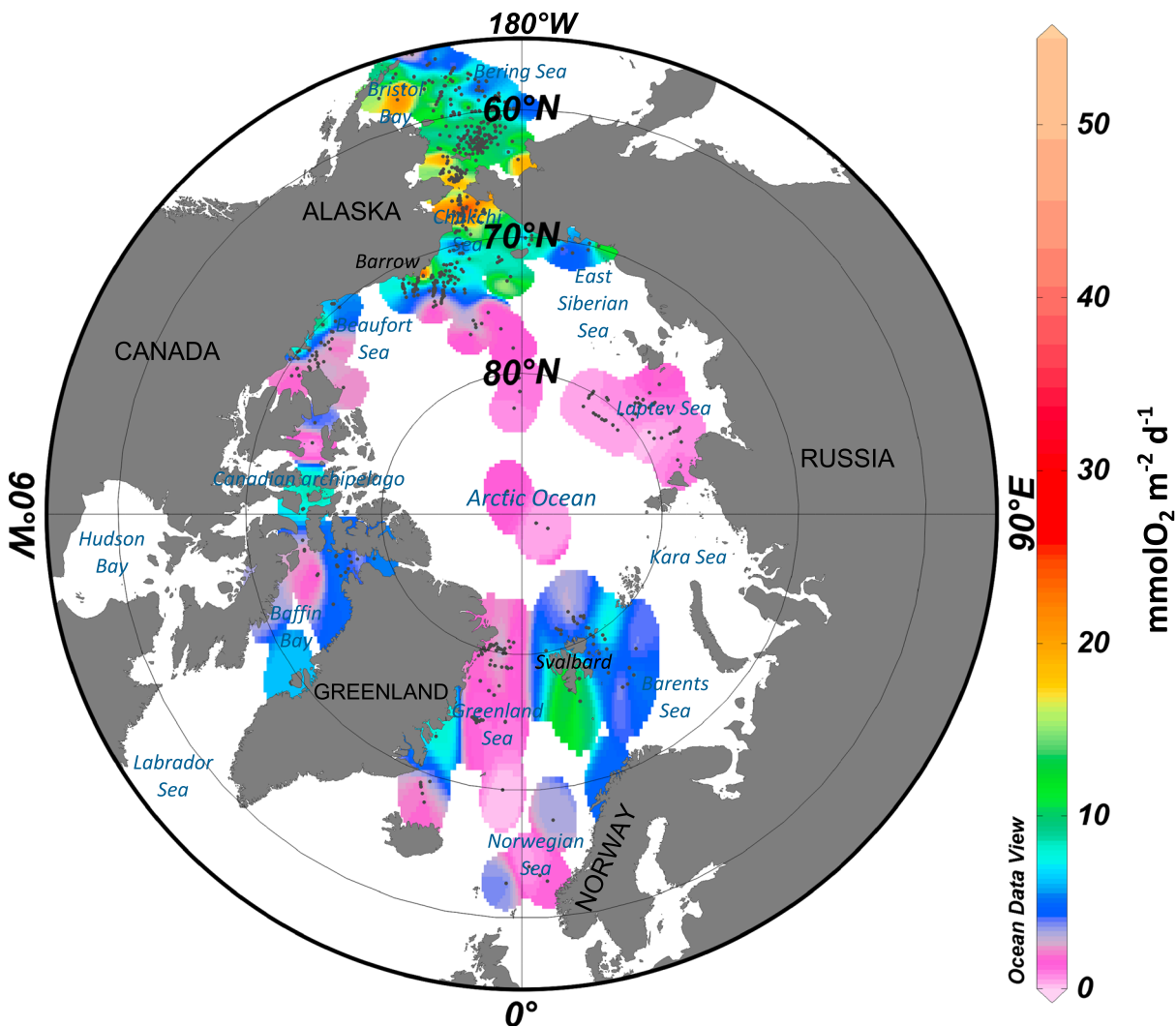


Figure 4. Pan-Arctic distribution of sediment oxygen demand ($\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$). The black crosses indicate the station locations. Observations are extracted from 30 publications and 16 databases for a total of 1154 values. Data are displayed as gridded field (method: weighted-average gridding).

months are specifically targeted by researchers trying to record the fingerprint of the spring bloom in sediments and its implication for benthic ecosystem functioning. Thus, the sampling effort directed toward the Arctic benthic fluxes is strongly skewed, constraining meaningful seasonal comparisons. Nonetheless, it is possible to observe some patterns. In the Barents and Eastern Beaufort Seas, the SOD exhibited lowest values in winter, a progressive rise in spring until reaching its peak in summer. The winter nutrient replenishment and the increase in light penetration in the upper water column trigger phytoplankton blooms at the end of May—early June in these subregions [Ardyna *et al.*, 2013]. In the Amerasian Arctic, strong seasonal and regional variabilities were observed (Figure 5). The Southeastern Bering Sea displayed higher SOD in spring than in summer, whereas the opposite pattern was observed in the Southern Chukchi Sea. The Eastern Bering Sea shelf is known for having a seasonal cycle with high rates of PP in the spring (May) and low rates in the summer [Rho and Whitledge, 2007; Moran *et al.*, 2012], and the spring bloom is relatively early compared to other regions [Ardyna *et al.*, 2013]. There is evidence for phytoplankton blooms under first-year ice in the Chukchi Sea [Lowry *et al.*, 2014], but as marginal ice zone blooms are more common in the southern Chukchi Sea where ice retreat begins in May [Lowry *et al.*, 2014], we can assume that the difference in timing of peak SOD between the Bering and Chukchi Seas is related to the timing of sea ice retreat. Thus, the seasonal pattern observed in the sediments mirrors water column processes and reinforces the concept of a strong pelagic-benthic coupling in the Arctic [Boetius and Damm, 1998; Grant *et al.*, 2002; Clough *et al.*, 2005; Grebmeier *et al.*, 2006b; Renaud *et al.*, 2008; Link *et al.*, 2011, 2013a, 2013b]. Interestingly, in the

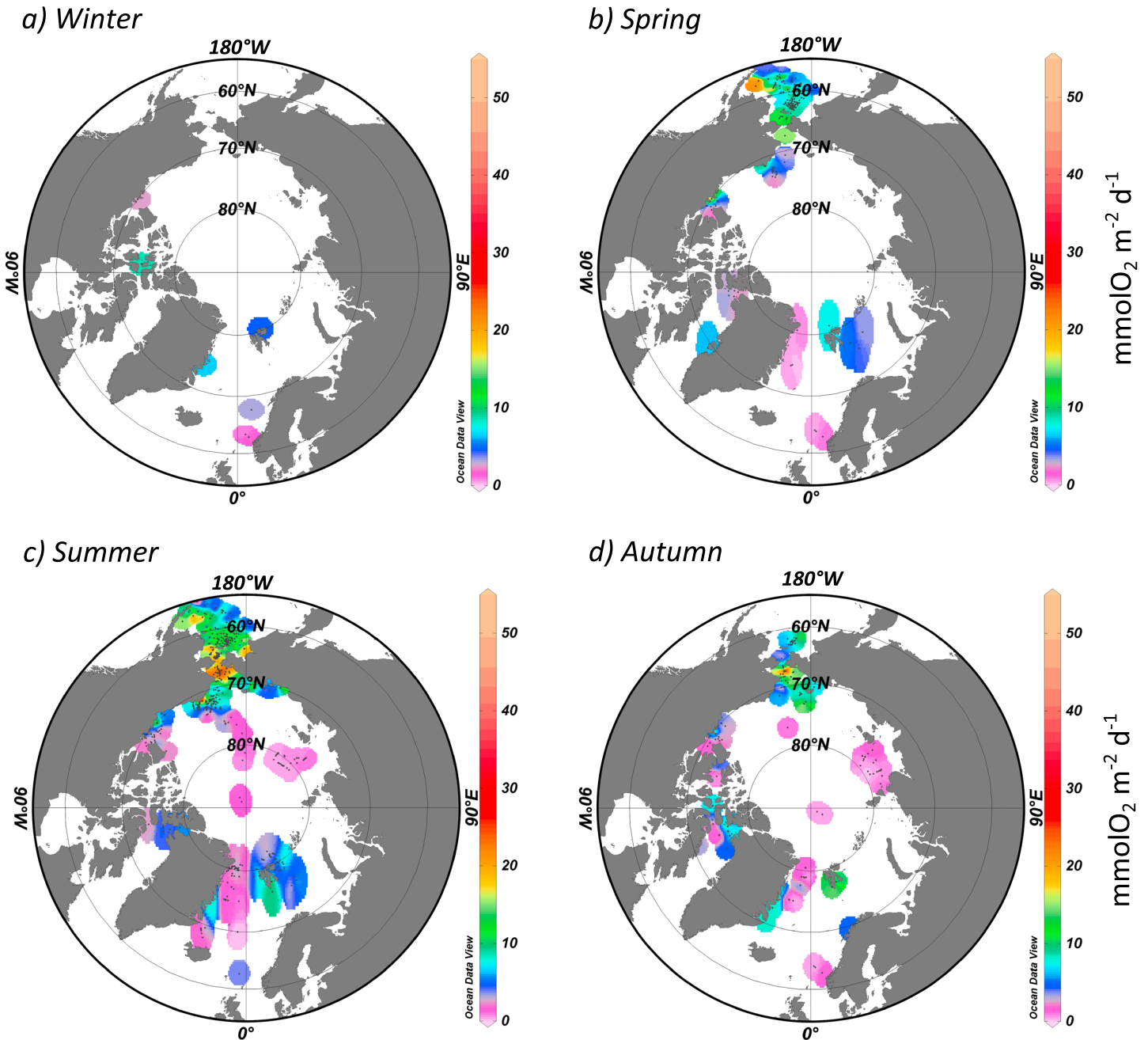


Figure 5. Distribution of sediment oxygen demand ($\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) in the whole Arctic region according the different seasons: (a) winter (1 December to 28 February, $n = 6$), (b) spring (1 March to 31 May, $n = 324$), (c) summer (1 June to 31 August, $n = 687$), and (d) autumn (1 September to 30 November, $n = 134$). Data are displayed as gridded field (method: weighted-average gridding).

Northern Greenland Sea and deep central Arctic the respiration patterns seem relatively constant throughout the seasons (Figure 5). This lack of seasonal signal could be due to the greater depths in combination with a low phytoplanktonic biomass (chl *a* concentrations: $1\text{--}2 \text{ mg m}^{-3}$ [Ardyna *et al.*, 2013]), as well as the relatively low sampling effort during winter (Figure S1). As a whole, the magnitude and timing of blooms have significant implications for the benthic remineralization function.

3.3. SOD Predictions, Disparities With Measured Values, and Interpolation to the Entire Arctic

The four generalized additive models proposed in this paper to predict the SOD at a Pan-Arctic scale are based on two explanatory variables, the water depth and/or food supply (chl *a*) (Table 2). The GAM analysis

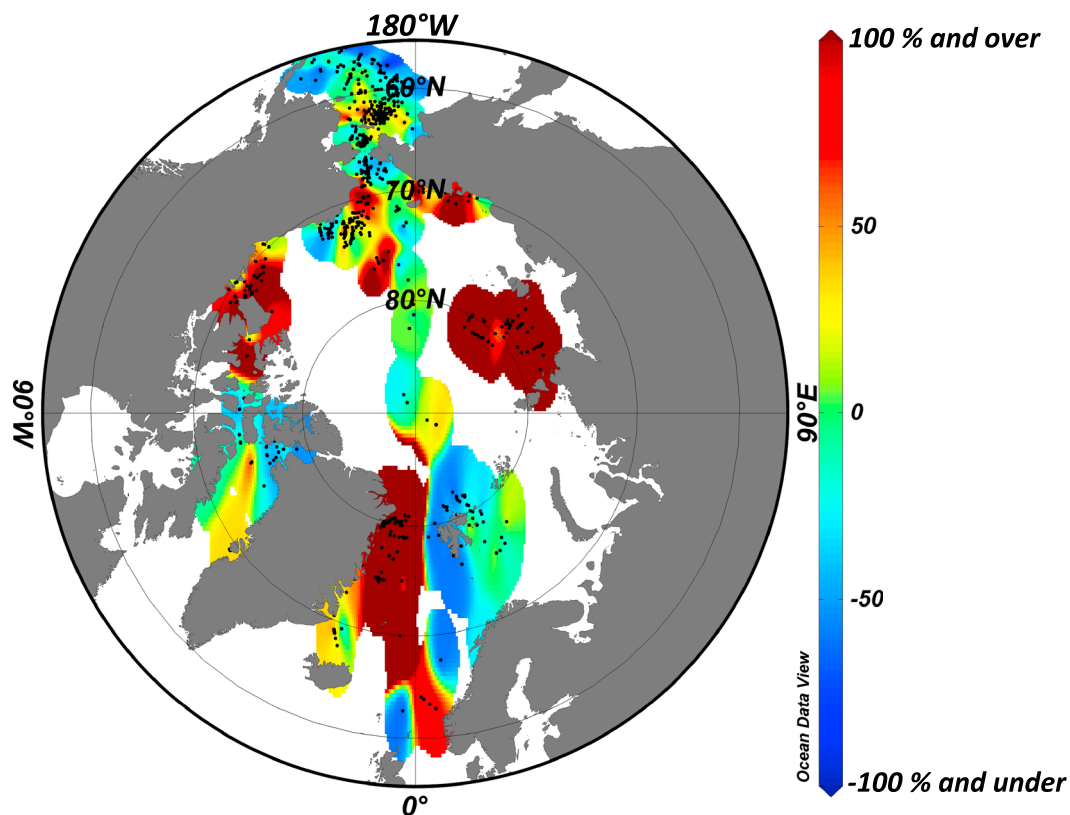


Figure 6. Relative anomalies of sediment oxygen demand between predicted and observed values ($(SOD_{pred} - SOD_{obs}) * 100 / SOD_{obs}$) for the “2 variables—depth and chl *a* (with interaction)” GAM model. Data are displayed as gridded field (method: weighted-average gridding). Positive values mean an overestimation of the predicted values.

revealed that (1) the water depth was the most important explanatory variable (49%, against 47% for chl *a*) in the SOD distribution and (2) the increment of chlorophyll *a* in GAM allowed a gain of up to 10% in the explained variance of sediment oxygen uptakes. Based on R^2 , the “two variables—depth and chl *a* (with interaction)” model is the best fit for describing the entire SOD data set (Table 2), explaining a total of 59% of variance. According to this model (see the last figure in Table 2), the effect of water depth is strongly reduced when the supply of labile food (chl *a*) is high, highlighting the prominent effect of food availability on SOD. The only drawback of this model is the overexpression of the “depth” variable, first through Pan-Arctic chl *a* estimates beforehand SOD prediction and then directly in SOD estimations.

The differences between the predicted values obtained through the model and the observations, which are represented in Figure 6, allow to identify strength and weaknesses of the model. Several seas or subregions were constantly overestimated or underestimated in all models (Figures 6 and S2). For instance, parts of the Bristol Bay (Bering Sea) and Southern Chukchi Sea exhibited very high SOD, but these were strongly underestimated throughout. The scarcity of these very high values clearly limits the capacity of the model to adequately predict them. In contrast, SOD in the East Siberian and Eastern Beaufort Seas was overestimated (>100%), which is probably due to the local relevance of other variables such as riverine OM input or macrofauna or zooplankton biomass. Interestingly, the deviation was particularly high for the Laptev and Greenland Seas which may be due to the fact that SOD was determined via oxygen microsensors, thus representing the dissolved oxygen uptake rather than total oxygen uptake. Thus, at first sight, we could suspect that the use of DOU (rather than TOU) leads to an underestimation of the observed values and, consequently, an overestimation in the predicted values. However, it is also very probable that the model overestimates the predicted values for these areas without influence of the measurement technique used. On average, inflow shelves exhibited lower relative anomalies than the other shelves or deep basin.

Implementation of the “two variables—depth and chl *a* (with interaction)” GAM model to the entire Arctic region (at a resolution of 1°) allowed the creation of a full Pan-Arctic distribution of SOD (Figure 7) to

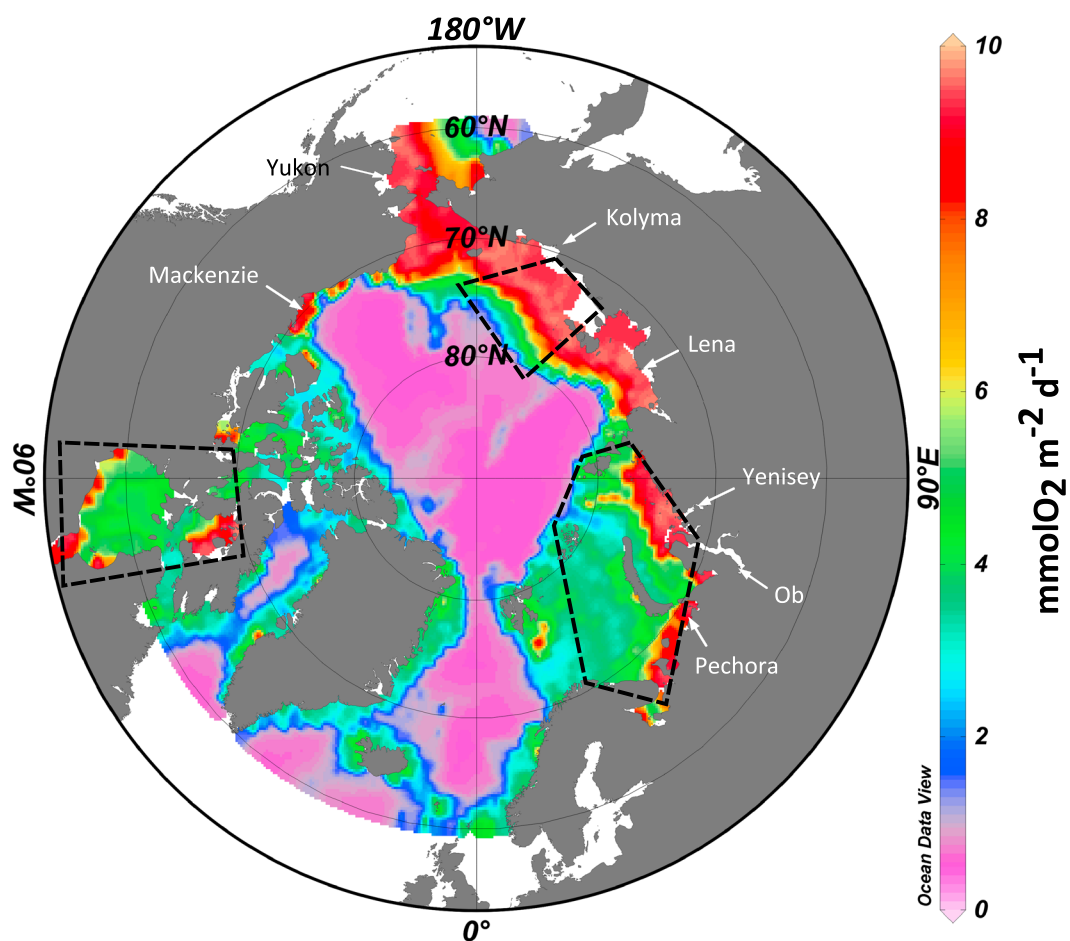


Figure 7. Interpolation of SOD ($\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) in the whole Arctic region using the “2 variables—depth and chl *a* (with interaction)” GAM model. Data are displayed as gridded field (method: weighted-average gridding). The locations of the main Arctic rivers are indicated on the figure. The dashed black polygons represent areas where no empirical data have been collected.

corroborate previous observations and provide predictions for data poor areas (see Figures 1 and 4). The model predicted SOD between 0.5 and $9.7 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ (Figure 7 and Table S1 in the supporting information). As noted previously, the central Arctic Basin as well as the offshore Greenland Sea exhibited low predicted SODs around 0.5 and up to $2 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$, and this pattern was also observed in the central Baffin Bay. In addition, the Amerasian Arctic shelf displayed once again strong SODs from the model. Again, the high patchiness in SOD (e.g., local hot spots) on this inflow shelf has not been captured well by our model, and this can be attributed to the lack of variables related to the benthic communities. Indeed, different studies showed the importance of the macrobenthos on the SOD in the Chukchi Sea [Clough *et al.*, 2005; Grebmeier *et al.*, 2015a, 2015b]. For instance, Grebmeier *et al.* [2015a, 2015b] attributed the high SOD in the Southern Chukchi Sea to the high bivalve biomass, as they are known to be large oxygen consumers in the sediments. The interpolation of SOD to the entire Arctic also highlighted high oxygen uptakes (up to $9.7 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) in the interior shelves along the coast of the East Siberian, Laptev, and Kara Seas, regions where data are scarce. These values are in agreement with a previous estimate of benthic carbon demand, based on an allometric relation between body size of benthos and respiration, for the coastal part of the Laptev Sea (3.3 – $10.4 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ after conversion [Schmid *et al.*, 2006]). The few in situ PP data available for the Russian seas indicate relatively low pelagic PP (around 25 and $50 \text{ g C m}^{-2} \text{ yr}^{-1}$) in these seas that are characterized by a stratified, nutrient-poor layer of Arctic water [Sakshaug, 2004; Harada, 2016], and ice-algae PP may not be sufficient in order to support the high oxygen demand predicted by the model. But the low number of PP measurements combined with potentially high patchiness, and an unknown riverine

influence, means that a high degree of uncertainty remains for these areas. The interior Arctic shelves receive freshwater inputs from four major world rivers, namely, the Yenisey, Lena, Ob, and Mackenzie (water discharge $> 310 \cdot 10^9 \text{ m}^3 \text{ yr}^{-1}$ [McKee et al., 2004]). Benthic regions of ocean margins impacted by major rivers are known to be very active zones of biogeochemical transformations [Aller, 1998]. Although riverine nutrient contributions to the Arctic Ocean PP are small in comparison to the Bering Strait inflow [Le Fouest et al., 2013], local effects (e.g., near river mouths [Tank et al., 2012]) can still be significant. For instance, Gaye et al. [2007] showed very high fluxes of fresh OM at the river mouths in the Kara Sea when river discharge is reduced. The combined marine and terrestrial OM input promotes high SOD in the vicinity of the river, as it was observed in the Mackenzie Delta [Link et al., 2013b]. On the contrary, in the Barents Sea, despite being considered as a very productive area [Chen et al., 2003; Arrigo et al., 2008; Pabi et al., 2008], the predicted SOD values were on average around or $< 5 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$, which is probably due to the greater depths of this sea. However, exceptions of elevated SODs ($\sim 9 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) were predicted along the Svalbard archipelago coast. Likewise, relatively moderate SOD ($< 5 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in average) was generated for the Eastern Canadian High Arctic (Canadian Archipelago and NOW) despite the fact that NOW is considered a productive area ($150\text{--}200 \text{ g C m}^{-2} \text{ yr}^{-1}$ [Klein et al., 2002; Arrigo et al., 2008; Ardyna et al., 2011]) see section 3.2 for explanation). Finally, high SODs ($4\text{--}9 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) were predicted in the south of the Hudson Bay and in the Foxe Basin (Eastern Canadian Arctic), and again, these values must be interpreted with some caution since no empirical data were available for ground-truthing.

3.4. Spatial Patterns in Nutrient Fluxes and Environmental Drivers

Nutrient fluxes are an integral part of the benthic remineralization function and are very important for understanding biogeochemical cycles and early diagenesis but unfortunately have been poorly studied in the Arctic. A dynamic diagenesis model for Arctic sediments showed that the processes of denitrification, iron, and sulfate reductions combined could account for up to 60% of the OM remineralization ($< 10\%$ for the denitrification, 25% for iron reduction, and 35% for sulfate reduction [Berg et al., 2003]), confirming the previous estimation of Rysgaard et al. [1998]. In Arctic sediments, the main nutrient fluxes measured are nitrate, ammonium, phosphate, and silicate, and their values ranged from -0.59 to 0.88 , -1.07 to 1.52 , -0.05 to 0.37 , and -0.03 to $6.2 \text{ mmol m}^{-2} \text{ d}^{-1}$, respectively. A recent study completed in the Pacific Arctic region showed that ammonium and silicate fluxes can reach up to 7 and $2.5 \text{ mmol m}^{-2} \text{ d}^{-1}$, respectively, at local hot spots [Mathis et al., 2014]. Nitrate and ammonium fluxes were highly heterogeneous (release and uptake) in sediments at water depth $< 200 \text{ m}$ (0.09 ± 0.24 and $0.18 \pm 0.39 \text{ mmol m}^{-2} \text{ d}^{-1}$, respectively) and closest to 0 at deepest stations (0.02 ± 0.14 and $-0.01 \pm 0.03 \text{ mmol m}^{-2} \text{ d}^{-1}$, respectively). Phosphate fluxes were higher in sediments at water depth $< 50 \text{ m}$ ($0.08 \pm 0.10 \text{ mmol m}^{-2} \text{ d}^{-1}$) than $> 50 \text{ m}$ ($0.01 \pm 0.02 \text{ mmol m}^{-2} \text{ d}^{-1}$). Silicate release by sediments was relatively high (mean: $0.6 \pm 1.3 \text{ mmol m}^{-2} \text{ d}^{-1}$) compared to other fluxes but did not exhibit a clear trend with water depth.

Overall, nutrient flux data exist for the Canadian Arctic, the Amerasian shelf, and isolated stations in the Greenland and Barents Seas (Figure 8). The Pan-Arctic distribution of denitrification processes exhibited relatively homogeneous values in the nitrate fluxes with the exception of those measured in the Barents Sea and in the vicinity of the Mackenzie River (Beaufort Sea), where a higher release and uptake by sediments were observed, respectively. Nitrate uptake is usually detected in sediments of continental shelves influenced by large river inputs and/or in sediments receiving high OM loads [Link et al., 2013b, and references therein]. Conversely, the high nitrate concentration (high release) in sediments of the Barents Sea (south of the Svalbard Archipelago) could be related to the degradation of high amounts of labile OM as proposed by Rysgaard et al. [1998] and Link et al. [2013b]. In this geographic area, high chl *a* concentrations (i.e., labile OM) were generally encountered in sediments [Morata and Renaud, 2008] due to high PP and subsequent chl *a* biomass in the water column [Engelsen et al., 2002; Chen et al., 2003; Hodal and Kristiansen, 2008; Ardyna et al., 2013] and to tight benthic-pelagic coupling [Morata and Renaud, 2008; Reigstad et al., 2008; Tamelander et al., 2008]. Like nitrate, phosphate was taken up by sediments not only in the vicinity of the Mackenzie River but also in the NOW, whereas the release to the pore water prevailed in other areas, as it is typically observed, since phosphate cannot be used as an electron acceptor during the diagenesis [Hensen et al., 2006]. Hence, the phosphate uptake could be explained by biological consumption for the formation of new biomass, the adsorption onto particle surface, authigenic formation of phosphorites, or bacterial phosphate accumulation [Hensen et al., 2006]. Link et al. [2013b] suggest that phosphate uptake

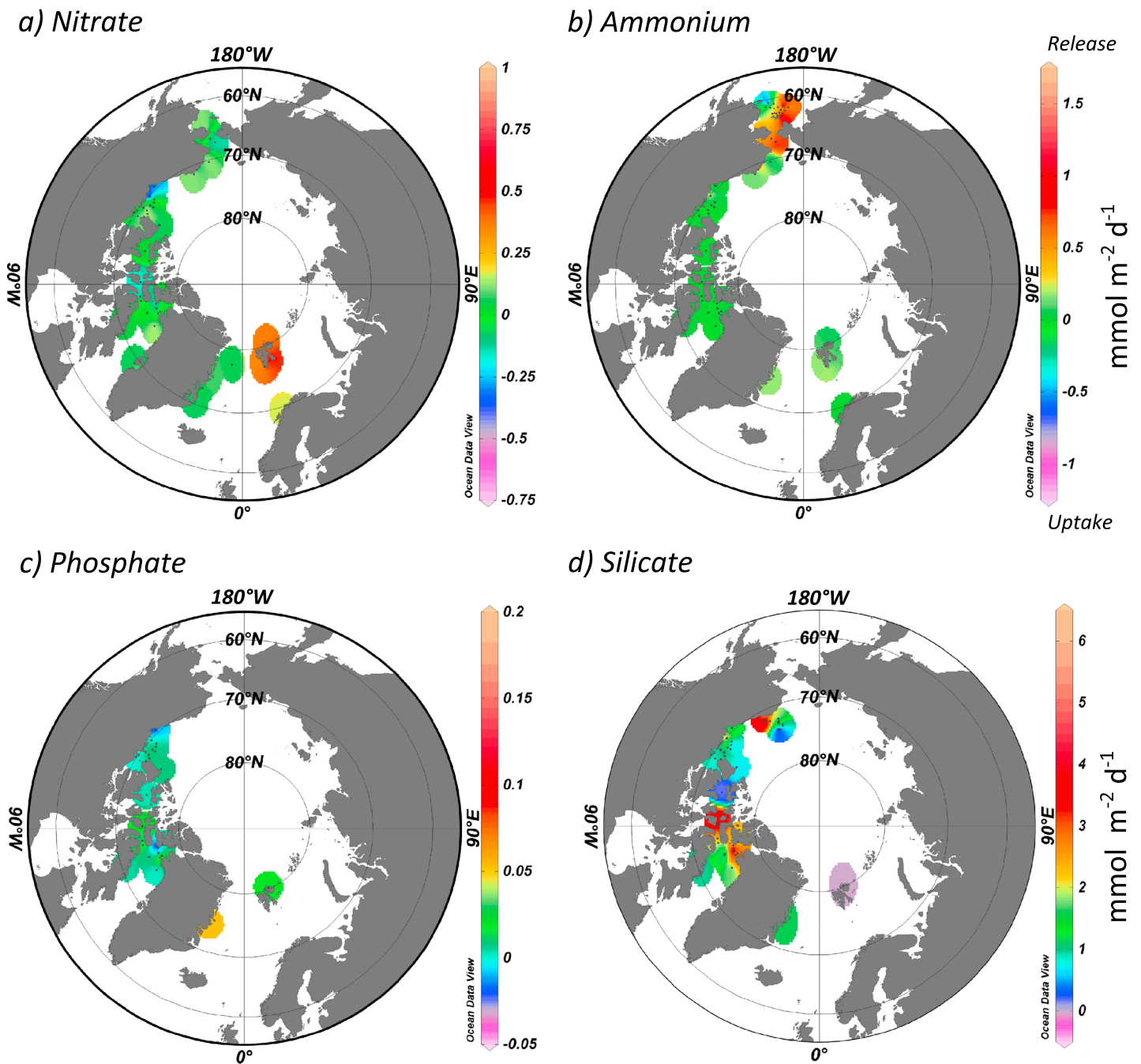


Figure 8. Distribution of nutrient fluxes ($\text{mmol m}^{-2} \text{d}^{-1}$) in the Arctic region: (a) nitrate ($n = 72$), (b) ammonium ($n = 73$), (c) phosphate ($n = 49$), and (d) silicate ($n = 61$). Positive flux means a release of the nutrient from sediment into the water column, while negative value indicates benthic uptake.

near the Mackenzie River mouth may be linked to a low oxygenation, to high OM input, and to the accumulation of compounds with high capacity to adsorb phosphate. Anoxic mineralization processes, which result in part in the release of ammonium, require high input of OM in surface sediments [Hensen *et al.*, 2006]. The ammonium flux map showed a high release of ammonium from sediments in the Chukchi and Bering Seas, as previously observed by Mathis *et al.* [2014]. In this inflow shelf, ammonium effluxes indicate high ammonium regeneration within sediments, probably originating from organic carbon contents and metabolic activities of benthic communities [Grebmeier and Cooper, 1995]. Indeed, these high ammonium releases occur in regions of high carbon export, which is reflected in high SOD [Mathis *et al.*, 2014]. Moreover,

ammonium fluxes were quite constant in the Canadian Arctic. In summary, on the very productive inflow shelves, benthic activity replenishes bottom waters with either nitrate, ammonium, or phosphate, whereas nitrate, phosphate, and ammonium are consumed by sediments in the interior shelves which are under the direct influence of Mackenzie River inputs (Beaufort Sea). Silicate fluxes were relatively high in the shallow waters of the Barrow Canyon, in the Canadian Archipelago (Lancaster Sound), and NOW Polynya (Baffin Bay). These silicate fluxes depend on the supply of biogenic opal (i.e., diatom frustules) and the specific dissolution rates [Zabel and Hensen, 2006]. The high biological remineralization at the seafloor could be related to the important contribution of diatoms in the PP in these areas [Michel *et al.*, 2002; Tremblay *et al.*, 2002; Hill *et al.*, 2005; Ardyna *et al.*, 2011]. As diatom frustules are often indigestible for herbivorous planktons [Juul-Pedersen *et al.*, 2008], a significant vertical export of biogenic silicate to the seabed is expected. Nonetheless, bacterial activity can strongly accelerate biogenic silica dissolution in the water column [Bidle and Azam, 1999].

Environmental and biological variables are important drivers of nutrient fluxes. Indeed, in the Canadian Arctic, nutrient fluxes are strongly related to short-term (chl *a* or pigment concentrations in sediment and vertical flux of POC) and, to a lesser extent, long-term environmental parameters (e.g., porosity, manganese, and iron) [Link *et al.*, 2013b]. In their dynamic model of early diagenesis and nutrient cycling, Berg *et al.* [2003] included variables not only adsorption processes and OM degradation pathways but also molecular diffusion, burial, bioturbation, and irrigation. Indeed, biotic factors, like bioirrigation, appear to have an important role in the nutrient fluxes at the sediment-water interface [Clough *et al.*, 1997; Michaud *et al.*, 2006; Na *et al.*, 2008; Davenport *et al.*, 2012; Stief, 2013; Mathis *et al.*, 2014], as is the case for SOD (see section 3.1.3). For instance, bioturbation activities enhance the release of ammonium and phosphate [Michaud *et al.*, 2006; Na *et al.*, 2008], especially the presence of gallery diffusers. In addition, different patterns could be observed among locations [Link *et al.*, 2013a] according to the life-history traits of species constituting the benthic community [Michaud *et al.*, 2006; Na *et al.*, 2008]. Biodiffusers living near the sediment surface tend to promote nitrate release, whereas biodiffusers living in the subsurface sediment cause nitrate uptake [Michaud *et al.*, 2006].

3.5. Predictions of Future Sediment Oxygen Demands

Based on the current knowledge on climate change-mediated changes in PP (see section 1), an increase in benthic activity (e.g., SOD) can be expected in areas where a switch from multiyear ice cover to seasonal ice cover results in an increased OM flux to the seafloor. On the other hand, areas that are going to become permanently ice free could experience a decline in benthic oxygen fluxes due to disappearance of sea ice algae and enhanced thermohaline stratification. In addition, regional factors such as freshwater discharge, riverine supply of refractory and labile OM, inflow of Pacific and Atlantic waters, and atmospheric inputs [Findlay *et al.*, 2015] as well as physical mechanisms (i.e., eddies [Harada, 2016]) can impact the sediment OM cycling.

In the Bering and Chukchi Seas, a strengthened Pacific inflow can supply additional nutrients which may augment PP [Findlay *et al.*, 2015, and reference therein]. However, the phytoplanktonic community has been shown to be sensitive to oceanic warming which can precipitate a change in size distribution [Fujiwara *et al.*, 2011]. A switch to smaller-sized phytoplankton with a hydrodynamic resistance to sinking [Li *et al.*, 2009] could in the future reduce the current high export of OM to the benthos [Findlay *et al.*, 2015]. Moreover, the rise in seawater temperature could change the zooplankton community (e.g., higher abundance, larger organisms, and increase of biological activities) and result in a longer pelagic food web which could weaken the current tight benthic-pelagic coupling. The other inflow shelf, the Barents Sea, is characterized by the presence of a large open water area throughout the year and is thought to be one of the areas in the Arctic most affected by the change in the extent and duration of sea ice cover [Arrigo and van Dijken, 2011]. Indeed, between 1998 and 2009, the total net PP in the Barents Sea significantly increased [Arrigo and van Dijken, 2011]. However, Wassmann and Reigstad [2011] predict a diminution of the PP in the Southern Barents Sea. Thus, a large part of the Atlantic-influenced shelves could likely be subject to a reduction in vertical export to the benthos in the future which could modify the dynamics of benthic oxygen uptake. In contrast, the decline in sea ice cover could result in increased PP and vertical export in the multiyear sea ice area of the Northern Barents Sea [Wassmann and Reigstad, 2011], which might stimulate SOD.

According to recent observations, the interior shelves have experienced a significant increase in PP, with the greatest increases found in Eurasian Arctic (i.e., Kara and East Siberian Seas) [Arrigo and van Dijken, 2011];

Bergeron and Tremblay, 2014], which coincided with a significant lengthening of the open water season [*Arrigo and van Dijken, 2011*]. Moreover, in the seas bordering the Russian coast, second blooms in the fall have become more widespread (+50% over the last decade) as the increased wind stress at the sea surface (when ice-free) enhances vertical mixing and nutrients are replenished from the deep waters [*Ardyna et al., 2014*]. Increasing food supply to the benthos could therefore significantly enhance benthic oxygen fluxes, particularly in relatively shallow shelves. However, riverine inputs in the vicinity river mouths could also limit PP through increased upper ocean stratification and turbidity, despite the discharge of large amounts of nutrients [*Findlay et al., 2015*]. For instance, even though the Mackenzie River runoff remained relatively unchanged for the last four decades [*Déry and Wood, 2005; McClelland et al., 2006; Yang et al., 2015*], the thawing permafrost [*Price et al., 2013*] resulted in a 50% increase in the mass terrestrial particles delivered to the Beaufort Sea in the last 10 years [*Doxaran et al., 2015*].

On the outflow shelves, the impact of climate change on benthic ecosystem functioning is likely to vary regionally. Similar to the Barents Sea, the Greenland Sea is characterized by the presence of a large area of open water throughout the year, but the total net PP has significantly decreased here between 1998 and 2009 [*Arrigo and van Dijken, 2011*]. In some ecologically significant regions, such as the well-mixed and highly productive North Water Polynya, a decline in PP has also been observed [*Bélanger et al., 2013*], suggesting that this area is becoming more oligotrophic [*Bergeron and Tremblay, 2014*]. The consequence would be a strong decrease in SODs in both areas. Conversely, we can expect an increase in the benthic activity in Northern Canadian Archipelago due to the reduced ice cover and likely increase of OM fluxes to the benthos.

Finally, the effect of climate change (e.g., reduction in sea ice cover and major changes in sea ice regime) on the dynamics of benthic oxygen uptake could initially be positive in the central Arctic basins due to the increase of algae standing stocks and vertical export to the seafloor. During the 2012 summer sea ice minimum extent, *Boetius et al.* [2013] observed the extensive deposition of fresh ice algae on the deep seafloor in the eastern-central Arctic Basin (Amundsen Basin). Indeed, such a pulse of fresh OM can lead to an immediate doubling of SOD [*Witte et al., 2003*]. Additionally, in the Canadian Basin (offshore Beaufort Sea), increased fresher of the upper ocean prompted a shift toward smaller plankton (i.e., picophytoplankton and bacterioplankton) in the summer [*Li et al., 2009*]. This change in the species' size will presumably lead to a reduction of vertical OM fluxes, and thus affect the benthic community respiration and sedimentary OM cycling. Moreover, the high stratification in the Canadian Basin [*Morison et al., 2012*] should further restrain sea ice algae blooms.

4. Summary and Perspectives

The benthic oxygen fluxes in the Arctic, compiled here for the first time, exhibit strong variation, with SOD maxima in the Southern Chukchi Sea, Northern Bering Sea, and at the head of Barrow Canyon and minima in the deepest part of the Arctic region. Clear differences among the Arctic shelves were discerned, with highest and lowest mean SODs found in the inflow and outflow shelves, respectively, which suggests that the shelves' environmental characteristics have a strong influence on the benthic ecosystem functioning. Moreover, the degree of seasonality in SOD was sea- and subregion-specific. Benthic OM remineralization pattern revealed positive and negative cross-boundary fluxes; nutrient (nitrate, ammonium, and phosphate) fluxes were positive in the inflow shelves, i.e., the very productive waters in the Amerasian shelf or over Svalbard continental shelf (Barents Sea), and negative in the interior shelves, i.e., the river-dominated ocean margin (e.g., Mackenzie shelf and Beaufort Sea).

In agreement with previous studies [*Boetius and Damm, 1998; Grant et al., 2002; Clough et al., 2005; Grebmeier et al., 2006b; Renaud et al., 2008; Link et al., 2011, 2013a, 2013b*], our GAM analyses showed that benthic oxygen demand strongly depends on water depth as well as the availability of labile OM which together explained up to 59% of the SOD variance. Overall, the proposed model provided good estimates for the large majority of SOD values and in particular captured well areas of high benthic activity in the Pacific inflow shelf and of low activity in the deep Arctic basins. Local hot spots of benthic carbon remineralization, often driven by factors such as zooplankton standing stocks or benthic community structure and activity, have not always been captured by the model.

In addition, this compilation of benthic remineralization data highlights the significant lack of measurements (or available data) of benthic oxygen fluxes in the Russian seas as well as nearshore and in the vicinity of the main Arctic rivers, as well as of nutrient fluxes across the Arctic Ocean. The lack of spatial coverage in these

particular regions limits the model, and the predicted values of SOD obtained for these data-poor regions must be interpreted with some caution. There is thus an urgent need for investigations in these areas in order (1) to provide a benchmark, (2) to confirm and sharpen the models, and (3) to determine the influence of the terrestrial inputs on the benthic ecosystem functioning in coastal and deltaic waters. Moreover, future research should also focus on studying the organic matter remineralization during the polar night in order to better evaluate the seasonality in SOD and nutrient fluxes. Another important goal of future research would be to improve our understanding of the relative importance of global change on benthic remineralization function.

Acknowledgments

This research was supported by NERC grant ArcDeep NE/J023094/1 awarded to U. Witte and by the ArcticNet "Hotspot Biodiversity Project" awarded to P. Archambault. We gratefully thank all the colleagues involved in the acquisition of the chlorophyll *a* and SOD data during the ArcticNet 2013 cruise. We are grateful to G. Pierce and L.J. Pérez Calderón for their advice regarding GAM analysis and to A. Makela for the language revision of an earlier version of the manuscript. We thank J.M. Grebmeier, L.W. Cooper, J.P. Christensen, and A.H. Devol for having made available the benthic oxygen fluxes and chlorophyll *a* data in the Shelf-Basin Interactions, Bering Sea Ecosystem Study, and Pacific Marine Arctic Regional Synthesis data archives, through EOL (Earth Observing Laboratory site, <http://data.eol.ucar.edu/>) and D. Seiler, E.J. Sauter and collaborators, J.E. Wollenburg, and W. Kuhn for access to the data through Pangaea. Data were provided by NCAR/EOL under sponsorship of the National Science Foundation. We are also grateful to the reviewers, J.M. Grebmeier and P. Renaud, for their constructive comments on this manuscript. Solveig Bourgeois was funded by NERC grant. The data produced in this manuscript, i.e., the predicted SOD values at a Pan-Arctic scale, will be made available on British Oceanography Data Centre and Polar data catalogue and can also be requested directly from the corresponding author.

References

- Aller, R. C. (1998), Mobile deltaic and continental shelf muds as suboxic, fluidized bed reactors, *Mar. Chem.*, *61*(3–4), 143–155, doi:10.1016/S0304-4203(98)00024-3.
- Ambrose, W. G., and P. E. Renaud (1995), Benthic response to water column productivity patterns: Evidence for benthic-pelagic coupling in the Northeast Water Polynya, *J. Geophys. Res.*, *100*(C3), 4411–4421, doi:10.1029/94JC01982.
- Ambrose, W. G., and P. E. Renaud (1997), Does a pulsed food supply to the benthos affect *Polychaete* recruitment patterns in the Northeast Water Polynya?, *J. Mar. Syst.*, *10*(1–4), 483–495, doi:10.1016/S0924-7963(96)00053-X.
- Andersson, J. H., J. W. M. Wijsman, P. M. J. Herman, J. J. Middelburg, K. Soetaert, and C. Heip (2004), Respiration patterns in the deep ocean, *Geophys. Res. Lett.*, *31*, L03304, doi:10.1029/2003GL018756.
- Ardyna, M., M. Gosselin, C. Michel, M. Poulin, and J.-É. Tremblay (2011), Environmental forcing of phytoplankton community structure and function in the Canadian High Arctic: Contrasting oligotrophic and eutrophic regions, *Mar. Ecol. Prog. Ser.*, *442*, 37–57, doi:10.3354/meps09378.
- Ardyna, M., M. Babin, M. Gosselin, E. Devred, S. Bélanger, A. Matsuoka, and J.-É. Tremblay (2013), Parameterization of vertical chlorophyll *a* in the Arctic Ocean: Impact of the subsurface chlorophyll maximum on regional, seasonal, and annual primary production estimates, *Biogeosciences*, *10*(6), 4383–4404, doi:10.5194/bg-10-4383-2013.
- Ardyna, M., M. Babin, M. Gosselin, E. Devred, L. Rainville, and J.-É. Tremblay (2014), Recent Arctic Ocean sea ice loss triggers novel fall phytoplankton blooms, *Geophys. Res. Lett.*, *41*, 6207–6212, doi:10.1002/2014GL061047.
- Arnosti, C., B. B. Jørgensen, J. Sagemann, and B. Thamdrup (1998), Temperature dependence of microbial degradation of organic matter in marine sediments: Polysaccharide hydrolysis, oxygen consumption, and sulfate reduction, *Mar. Ecol. Prog. Ser.*, *165*, 59–70, doi:10.3354/meps165059.
- Arrigo, K. R., and G. L. van Dijken (2011), Secular trends in Arctic Ocean net primary production, *J. Geophys. Res.*, *116*, C09011, doi:10.1029/2011JC007151.
- Arrigo, K. R., G. van Dijken, and S. Pabi (2008), Impact of a shrinking Arctic ice cover on marine primary production, *Geophys. Res. Lett.*, *35*, L19603, doi:10.1029/2008GL035028.
- Arrigo, K. R., et al. (2012), Massive phytoplankton blooms under Arctic sea ice, *Science*, *336*(6087), 1408–1408, doi:10.1126/science.1215065.
- Baldwin, R. J., and K. L. Smith Jr. (2003), Temporal dynamics of particulate matter fluxes and sediment community response in Port Foster, Deception Island, Antarctica, *Deep Sea Res., Part II*, *50*(10–11), 1707–1725, doi:10.1016/S0967-0645(03)00089-4.
- Bélanger, S., M. Babin, and J.-É. Tremblay (2013), Increasing cloudiness in Arctic dampens the increase in phytoplankton primary production due to sea ice receding, *Biogeosciences*, *10*(6), 4087–4101, doi:10.5194/bg-10-4087-2013.
- Berg, P., S. Rysgaard, and B. Thamdrup (2003), Dynamic modeling of early diagenesis and nutrient cycling. A case study in an arctic marine sediment, *Am. J. Sci.*, *303*(10), 905–955, doi:10.2475/ajs.303.10.905.
- Bergeron, M., and J.-É. Tremblay (2014), Shifts in biological productivity inferred from nutrient drawdown in the southern Beaufort Sea (2003–2011) and northern Baffin Bay (1997–2011), Canadian Arctic, *Geophys. Res. Lett.*, *41*, 3979–3987, doi:10.1002/2014GL059649.
- Bianchi, T. S. (2011), The role of terrestrially derived organic carbon in the coastal ocean: A changing paradigm and the priming effect, *Proc. Natl. Acad. Sci. U.S.A.*, *108*(49), 19,473–19,481, doi:10.1073/pnas.1017982108.
- Bidle, K. D., and F. Azam (1999), Accelerated dissolution of diatom silica by marine bacterial assemblages, *Nature*, *397*, 508–512, doi:10.1038/17351.
- Boetius, A., and E. Damm (1998), Benthic oxygen uptake, hydrolytic potentials and microbial biomass at the Arctic continental slope, *Deep Sea Res., Part I*, *45*(2–3), 239–275, doi:10.1016/S0967-0637(97)00052-6.
- Boetius, A., et al. (2013), Export of algal biomass from the melting Arctic sea ice, *Science*, *339*(6126), 1430–1432, doi:10.1126/science.1231346.
- Buesseler, K. O., et al. (2007), Revisiting carbon flux through the ocean's twilight zone, *Science*, *316*(5824), 567–570, doi:10.1126/science.1137959.
- Campbell, R. G., E. B. Sherr, C. J. Ashjian, S. Plourde, B. F. Sherr, V. Hill, and D. A. Stockwell (2009), Mesozooplankton prey preference and grazing impact in the western Arctic Ocean, *Deep Sea Res., Part II*, *56*(17), 1274–1289, doi:10.1016/j.dsr2.2008.10.027.
- Carmack, E. C., R. W. Macdonald, and S. Jasper (2004), Phytoplankton productivity on the Canadian Shelf of the Beaufort Sea, *Mar. Ecol. Prog. Ser.*, *277*, 37–50, doi:10.3354/meps277037.
- Carmack, E., and P. Wassmann (2006), Food webs and physical-biological coupling on Pan-Arctic shelves: Unifying concepts and comprehensive perspectives, *Prog. Oceanogr.*, *71*(2), 446–477.
- Carroll, M. L., and J. Carroll (2003), The Arctic seas, in *Biogeochemistry of Marine Systems*, edited by K. D. Black and G. B. Shimmield, pp. 127–156, Blackwell, Oxford.
- Chen, C.-T. A., K.-K. Liu, and R. Macdonald (2003), Continental margin exchanges, in *Ocean Biogeochemistry*, edited by M. J. R. Fasham, pp. 53–97, Springer, Berlin.
- Christensen, J. P. (2000), A relationship between deep-sea benthic oxygen demand and oceanic primary productivity, *Oceanol. Acta*, *23*(1), 65–82, doi:10.1016/S0399-1784(00)00101-8.
- Christensen, J. P. (2006), HLY-04-03 sedimentary water fluxes of O₂, TCO₂ and dissolved silica, Shelf Basin Interactions Project (SBI), Data Archive. [Available at <http://data.eol.ucar.edu/codiac/dss/id=62.258>]
- Clough, L. M., W. G. Ambrose Jr., J. Kirk Cochran, C. Barnes, P. E. Renaud, and R. C. Aller (1997), Infaunal density, biomass and bioturbation in the sediments of the Arctic Ocean, *Deep Sea Res., Part II*, *44*(8), 1683–1704, doi:10.1016/S0967-0645(97)00052-0.

- Clough, L. M., P. E. Renaud, and W. G. Ambrose Jr. (2005), Impacts of water depth, sediment pigment concentration, and benthic macrofaunal biomass on sediment oxygen demand in the western Arctic Ocean, *Can. J. Fish. Aquat. Sci.*, 62(8), 1756–1765, doi:10.1139/f05-102.
- Darnis, G., D. Robert, C. Pomerleau, H. Link, P. Archambault, R. J. Nelson, M. Geoffroy, J.-É. Tremblay, C. Lovejoy, and S. H. Ferguson (2012), Current state and trends in Canadian Arctic marine ecosystems: II. Heterotrophic food web, pelagic-benthic coupling, and biodiversity, *Clim. Change*, 115(1), 179–205, doi:10.1007/s10584-012-0483-8.
- Davenport, E. S., D. H. Shull, and A. H. Devol (2012), Roles of sorption and tube-dwelling benthos in the cycling of phosphorus in Bering Sea sediments, *Deep Sea Res., Part II*, 65–70, 163–172, doi:10.1016/j.dsr2.2012.02.004.
- Déry, S. J., and E. F. Wood (2005), Decreasing river discharge in northern Canada, *Geophys. Res. Lett.*, 32, L10401, doi:10.1029/2005GL022845.
- Devol, A. H. (2008), HLY-07-01 Pore Water Nutrient Data, Bering Sea Project (BEST), Data Archive. [Available at <http://data.eol.ucar.edu/codiac/dss/id=102.025>.]
- Devol, A. H., L. A. Codispoti, and J. P. Christensen (1997), Summer and winter denitrification rates in western Arctic shelf sediments, *Cont. Shelf Res.*, 17(9), 1029–1050, doi:10.1016/S0278-4343(97)00003-4.
- Dittmar, T., and G. Kattner (2003), The biogeochemistry of the river and shelf ecosystem of the Arctic Ocean: A review, *Mar. Chem.*, 83(3–4), 103–120, doi:10.1016/S0304-4203(03)00105-1.
- Doxaran, D., E. Devred, and M. Babin (2015), A 50% increase in the mass of terrestrial particles delivered by the Mackenzie River into the Beaufort Sea (Canadian Arctic Ocean) over the last 10 years, *Biogeosciences*, 12(11), 3551–3565, doi:10.5194/bg-12-3551-2015.
- Dunton, K. H., S. V. Schonberg, and L. W. Cooper (2012), Food web structure of the Alaskan Nearshore shelf and estuarine lagoons of the Beaufort Sea, *Estuaries Coasts*, 35(2), 416–435, doi:10.1007/s12237-012-9475-1.
- Engelsen, O., E. N. Hegseth, H. Hop, E. Hansen, and S. Falk-Petersen (2002), Spatial variability of chlorophyll-a in the marginal ice zone of the Barents Sea, with relations to sea ice and oceanographic conditions, *J. Mar. Syst.*, 35(1), 79–97, doi:10.1016/S0924-7963(02)00077-5.
- Findlay, H. S., et al. (2015), Responses in Arctic marine carbon cycle processes: Conceptual scenarios and implications for ecosystem function, *Pol. Res.*, 34, 24252, doi:10.3402/polar.v34.24252.
- Fujiwara, A., T. Hirawake, K. Suzuki, and S.-I. Saitoh (2011), Remote sensing of size structure of phytoplankton communities using optical properties of the Chukchi and Bering Sea shelf region, *Biogeosciences*, 8(12), 3567–3580, doi:10.5194/bg-8-3567-2011.
- Gaillard, B., T. Meziane, R. Tremblay, P. Archambault, K. K. Layton, A. L. Martel, and F. Olivier (2015), Dietary tracers in *Bathyrca glacialis* from contrasting trophic regions in the Canadian Arctic, *Mar. Ecol. Prog. Ser.*, 536, 175–186, doi:10.3354/meps11424.
- Gaye, B., K. Fahl, L. A. Kodina, N. Lahajnar, B. Nagel, D. Unger, and A. C. Gebhardt (2007), Particulate matter fluxes in the southern and central Kara Sea compared to sediments: Bulk fluxes, amino acids, stable carbon and nitrogen isotopes, sterols and fatty acids, *Cont. Shelf Res.*, 27, 2570–2594, doi:10.1016/j.csr.2007.07.003.
- Glud, R. N. (2008), Oxygen dynamics of marine sediments, *Mar. Biol. Res.*, 4(4), 243–289, doi:10.1080/17451000801888726.
- Glud, R. N., N. Risgaard-Petersen, B. Thamdrup, H. Fossing, and S. Rysgaard (2000), Benthic carbon mineralization in a high-Arctic sound (Young Sound, NE Greenland), *Mar. Ecol. Prog. Ser.*, 206, 59–71, doi:10.3354/meps206059.
- Glud, R., O. Holby, F. Hoffmann, and D. Canfield (1998), Benthic mineralization and exchange in Arctic sediments (Svalbard, Norway), *Mar. Ecol. Prog. Ser.*, 173, 237–251, doi:10.3354/meps173237.
- Goñi, M. A., M. B. Yunker, R. W. Macdonald, and T. I. Eglinton (2000), Distribution and sources of organic biomarkers in arctic sediments from the Mackenzie River and Beaufort Shelf, *Mar. Chem.*, 71(1–2), 23–51, doi:10.1016/S0304-4203(00)00037-2.
- Goñi, M. A., A. E. O'Connor, Z. Z. Kuzyk, M. B. Yunker, C. Gobeil, and R. W. Macdonald (2013), Distribution and sources of organic matter in surface marine sediments across the North American Arctic margin, *J. Geophys. Res. Oceans*, 118, 4017–4035, doi:10.1002/jgrc.20286.
- Grant, J., B. Hargrave, and P. MacPherson (2002), Sediment properties and benthic-pelagic coupling in the North Water, *Deep Sea Res., Part II*, 49(22–23), 5259–5275, doi:10.1016/S0967-0645(02)00189-3.
- Grebmeier, J. M. (2010a), HLY-08-01 Benthic Station Data, v1, Bering Sea Project (BEST), Data Archive. [Available at <http://data.eol.ucar.edu/codiac/dss/id=102.160>.]
- Grebmeier, J. M. (2010b), HLY-09-01 Benthic Station Data, v1, Bering Sea Project (BEST), Data Archive. [Available at <http://data.eol.ucar.edu/codiac/dss/id=102.161>.]
- Grebmeier, J. M. (2012), Shifting patterns of life in the Pacific Arctic and Sub-Arctic Seas, *Annu. Rev. Mar. Sci.*, 4(1), 63–78, doi:10.1146/annurev-marine-120710-100926.
- Grebmeier, J. M., and C. P. McRoy (1989), Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. III. Benthic food supply and carbon cycling, *Mar. Ecol. Prog. Ser.*, 53, 79–91.
- Grebmeier, J. M., and L. W. Cooper (1995), Influence of the St. Lawrence Island Polynya upon the Bering Sea benthos, *J. Geophys. Res.*, 100(C3), 4439–4460, doi:10.1029/94JC02198.
- Grebmeier, J. M., and L. W. Cooper (2004a), HLY-02-01 Benthic Station Data (benthic faunal data and sediment tracers), Shelf Basin Interactions Project (SBI), Data Archive. [Available at <http://data.eol.ucar.edu/codiac/dss/id=62.161>.]
- Grebmeier, J. M., and L. W. Cooper (2004b), HLY-02-03 Benthic Station Data (benthic faunal data and sediment tracers), Shelf Basin Interactions Project (SBI), Data Archive. [Available at <http://data.eol.ucar.edu/codiac/dss/id=62.1630>.]
- Grebmeier, J. M., and L. W. Cooper (2004c), HLY-04-02 Benthic Station Data (benthic faunal data and sediment tracers), Shelf Basin Interactions Project (SBI), Data Archive. [Available at <http://data.eol.ucar.edu/codiac/dss/id=62.2300>.]
- Grebmeier, J. M., and L. W. Cooper (2004d), HLY-04-03 Benthic Station Data (benthic faunal data and sediment tracers), Shelf Basin Interactions Project (SBI), Data Archive. [Available at <http://data.eol.ucar.edu/codiac/dss/id=62.2330>.]
- Grebmeier, J. M., and L. W. Cooper (2009), HLY0601 Master Station, Bering Sea Project (BEST), Data Archive. [Available at <http://data.eol.ucar.edu/codiac/dss/id=102.095>.]
- Grebmeier, J. M., and L. W. Cooper (2010), HLY0702 Master Station, Bering Sea Project (BEST), Data Archive. [Available at <http://data.eol.ucar.edu/codiac/dss/id=102.097>.]
- Grebmeier, J. M., and L. W. Cooper (2014a), PacMARS sediment chlorophyll-a, version 1.0, doi:10.5065/D6W9576K. [Available at the PacMARS EOL data archive site <<http://pacmars.eol.ucar.edu/>>.]
- Grebmeier, J. M., and L. W. Cooper (2014b), PacMARS sediment community oxygen uptake, version 1.0, doi:10.5065/D600004Q. [Available at the PacMARS EOL data archive site <<http://pacmars.eol.ucar.edu/>>.]
- Grebmeier, J. M., J. E. Overland, S. E. Moore, E. V. Farley, E. C. Carmack, L. W. Cooper, K. E. Frey, J. H. Helle, F. A. McLaughlin, and S. L. McNutt (2006a), A major ecosystem shift in the northern Bering Sea, *Science*, 311(5766), 1461–1464, doi:10.1126/science.1121365.
- Grebmeier, J. M., L. W. Cooper, H. M. Feder, and B. I. Sirenko (2006b), Ecosystem dynamics of the Pacific-influenced Northern Bering and Chukchi Seas in the Amerasian Arctic, *Prog. Oceanogr.*, 71(2–4), 331–361, doi:10.1016/j.pocean.2006.10.001.
- Grebmeier, J. M., et al. (2015a), Ecosystem characteristics and processes facilitating persistent macrobenthic biomass hotspots and associated benthivory in the Pacific Arctic, *Prog. Oceanogr.*, 136, 92–114, doi:10.1016/j.pocean.2015.05.006.

- Grebmeier, J. M., B. Bluhm, L. W. Cooper, S. G. Denisenko, K. Iken, M. Kedra, and C. Serratos (2015b), Time-series benthic community composition and biomass and associated environmental characteristics in the Chukchi Sea during the RUSALCA 2004–2012 Program, *Oceanography*, 28(3), 116–133, doi:10.5670/oceanog.2015.61.
- Guo, L., I. Semiletov, Ö. Gustafsson, J. Ingri, P. Andersson, O. Dudarev, and D. White (2004), Characterization of Siberian Arctic coastal sediments: Implications for terrestrial organic carbon export, *Global Biogeochem. Cycles*, 18, GB1036, doi:10.1029/2003GB002087.
- Haine, T. W. N., et al. (2015), Arctic freshwater export: Status, mechanisms, and prospects, *Global Planet. Change*, 125, 13–35, doi:10.1016/j.gloplacha.2014.11.013.
- Harada, N. (2016), Review: Potential catastrophic reduction of sea ice in the western Arctic Ocean: Its impact on biogeochemical cycles and marine ecosystems, *Global Planet. Change*, 136, 1–17, doi:10.1016/j.gloplacha.2015.11.005.
- Hartnett, H., S. Boehme, C. Thomas, D. DeMaster, and C. Smith (2008), Benthic oxygen fluxes and denitrification rates from high-resolution porewater profiles from the Western Antarctic Peninsula continental shelf, *Deep Sea Res., Part II*, 55(22), 2415–2424, doi:10.1016/j.dsr2.2008.06.002.
- Hastie, T. J. (2015), gam: Generalized additive models R package version 1.12.
- Hastie, T. J., and R. J. Tibshirani (1990), *Generalized Additive Models*, Chapman and Hall, London.
- Hensen, C., M. Zabel, and H. N. Schulz (2006), Benthic cycling of oxygen, nitrogen and phosphorus, in *Marine Geochemistry*, edited by P. D. H. D. Schulz and D. M. Zabel, pp. 207–240, Springer, Berlin.
- Hill, V., and G. Cota (2005), Spatial patterns of primary production on the shelf, slope and basin of the Western Arctic in 2002, *Deep Sea Res., Part II*, 52(24), 3344–3354, doi:10.1016/j.dsr2.2005.10.001.
- Hill, V., G. Cota, and D. Stockwell (2005), Spring and summer phytoplankton communities in the Chukchi and Eastern Beaufort Seas, *Deep Sea Res., Part II*, 52(24), 3369–3385, doi:10.1016/j.dsr2.2005.10.010.
- Hodal, H., and S. Kristiansen (2008), The importance of small-celled phytoplankton in spring blooms at the marginal ice zone in the northern Barents Sea, *Deep Sea Res., Part II*, 55(20), 2176–2185, doi:10.1016/j.dsr2.2008.05.012.
- Hoegh-Guldberg, O., and J. F. Bruno (2010), The impact of climate change on the world's marine ecosystems, *Science*, 328(5985), 1523–1528, doi:10.1126/science.1189930.
- Hulth, S., T. H. Blackburn, and P. O. J. Hall (1994), Arctic sediments (Svalbard): Consumption and microdistribution of oxygen, *Mar. Chem.*, 46(3), 293–316, doi:10.1016/0304-4203(94)90084-1.
- Hulth, S., A. Tengberg, A. Landén, and P. O. J. Hall (1997), Mineralization and burial of organic carbon in sediments of the southern Weddell Sea (Antarctica), *Deep Sea Res., Part I*, 44(6), 955–981, doi:10.1016/S0967-0637(96)00114-8.
- Hunt, G. L., et al. (2013), The Barents and Chukchi Seas: Comparison of two Arctic shelf ecosystems, *J. Mar. Syst.*, 109–110, 43–68, doi:10.1016/j.jmarsys.2012.08.003.
- Jahnke, R. A. (1996), The global ocean flux of particulate organic carbon: Areal distribution and magnitude, *Global Biogeochem. Cycles*, 10(1), 71–88, doi:10.1029/95GB03525.
- Jakobsson, M. (2002), Hypsometry and volume of the Arctic Ocean and its constituent seas, *Geochem. Geophys. Geosyst.*, 3(5), 1028, doi:10.1029/2001GC000302.
- Ji, R., M. Jin, and Ø. Varpe (2013), Sea ice phenology and timing of primary production pulses in the Arctic Ocean, *Global Change Biol.*, 19(3), 734–741, doi:10.1111/gcb.12074.
- Jørgensen, B. B., R. N. Glud, and O. Holby (2005), Oxygen distribution and bioirrigation in Arctic fjord sediments (Svalbard, Barents Sea), *Mar. Ecol. Prog. Ser.*, 292, 85–95, doi:10.3354/meps292085.
- Juul-Pedersen, T., C. Michel, M. Gosselin, and L. Seuthe (2008), Seasonal changes in the sinking export of particulate material under first-year sea ice on the Mackenzie Shelf (western Canadian Arctic), *Mar. Ecol. Prog. Ser.*, 353, 13–25, doi:10.3354/meps07165.
- Kahru, M., V. Brotas, M. Manzano-Sarabia, and B. G. Mitchell (2011), Are phytoplankton blooms occurring earlier in the Arctic?, *Global Change Biol.*, 17(4), 1733–1739, doi:10.1111/j.1365-2486.2010.02312.x.
- Kenchington, E., H. Link, V. Roy, P. Archambault, T. Siferd, M. Treble, and V. Wareham (2011), *Identification of Mega- and Macrobenthic Ecologically and Biologically Significant Areas (EBSAs) in the Hudson Bay Complex, the Western and Eastern Canadian Arctic*, DFO Can. Sci. Adv. Sec. Res. Doc.
- Kirchman, D. L., X. A. G. Morán, and H. Ducklow (2009a), Microbial growth in the polar oceans—Role of temperature and potential impact of climate change, *Nat. Rev. Microbiol.*, 7(6), 451–459, doi:10.1038/nrmicro2115.
- Kirchman, D. L., V. Hill, M. T. Cottrell, R. Gradinger, R. R. Malmstrom, and A. Parker (2009b), Standing stocks, production, and respiration of phytoplankton and heterotrophic bacteria in the western Arctic Ocean, *Deep Sea Res., Part II*, 56(17), 1237–1248, doi:10.1016/j.dsr2.2008.10.018.
- Klein, B., et al. (2002), Phytoplankton biomass, production and potential export in the North Water, *Deep Sea Res., Part II*, 49(22), 4983–5002, doi:10.1016/S0967-0645(02)00174-1.
- Lalande, C., S. Bélanger, and L. Fortier (2009), Impact of a decreasing sea ice cover on the vertical export of particulate organic carbon in the northern Laptev Sea, Siberian Arctic Ocean, *Geophys. Res. Lett.*, 36, L21604, doi:10.1029/2009GL040570.
- Le Fouest, V., M. Babin, and J.-É. Tremblay (2013), The fate of riverine nutrients on Arctic shelves, *Biogeosciences*, 10(6), 3661–3677, doi:10.5194/bg-10-3661-2013.
- Lein, A. Y., et al. (2013), Transformation of suspended particulate matter into sediment in the Kara Sea in September of 2011, *Oceanology*, 53(5), 570–606, doi:10.1134/S0001437013050081.
- Leu, E., J. E. Søreide, D. O. Hessen, S. Falk-Petersen, and J. Berge (2011), Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: Timing, quantity, and quality, *Prog. Oceanogr.*, 90(1–4), 18–32, doi:10.1016/j.poccean.2011.02.004.
- Li, W. K. W., F. A. McLaughlin, C. Lovejoy, and E. C. Carmack (2009), Smallest algae thrive as the Arctic Ocean freshens, *Science*, 326(5952), 539–539, doi:10.1126/science.1179798.
- Link, H. (2012), Studying the functioning of benthic hotspot and coldspot ecosystems in the Canadian Arctic PhD thesis, Univ. of Quebec at Rimouski - ISMER, Quebec, Canada.
- Link, H., and D. Piepenburg (2013), Dynamics of benthic ecosystem functioning in response to predicted environmental shifts The expedition of the research vessel “Polarstern” to the Antarctic in 2013 (ANT-XXIX/3), Reports on Polar and Marine Research.
- Link, H., P. Archambault, T. Tamelander, P. E. Renaud, and D. Piepenburg (2011), Spring-to-summer changes and regional variability of benthic processes in the western Canadian Arctic, *Polar Biol.*, 34(12), 2025–2038, doi:10.1007/s00300-011-1046-6.
- Link, H., D. Piepenburg, and P. Archambault (2013a), Are hotspots always hotspots? The relationship between diversity, resource and ecosystem functions in the Arctic, *PLoS One*, 8(9), e74077, doi:10.1371/journal.pone.0074077.
- Link, H., G. Chaillou, A. Forest, D. Piepenburg, and P. Archambault (2013b), Multivariate benthic ecosystem functioning in the Arctic-benthic fluxes explained by environmental parameters in the southeastern Beaufort Sea, *Biogeosciences*, 10(9), 5911–5929, doi:10.5194/bg-10-5911-2013.

- Lohrer, A. M., S. F. Thrush, and M. M. Gibbs (2004), Bioturbators enhance ecosystem function through complex biogeochemical interactions, *Nature*, 431(7012), 1092–1095, doi:10.1038/nature03042.
- Lowry, K. E., G. L. van Dijken, and K. R. Arrigo (2014), Evidence of under-ice phytoplankton blooms in the Chukchi Sea from 1998 to 2012, *Deep Sea Res., Part II*, 105, 105–117, doi:10.1016/j.dsr2.2014.03.013.
- Maslowski, W., J. C. Kinney, S. R. Okkonen, R. Osinski, A. F. Roberts, and W. J. Williams (2014), The large scale ocean circulation and physical processes controlling Pacific-Arctic interactions, in *The Pacific Arctic Region: Ecosystem Status and Trends in a Rapidly Changing Environment*, edited by J. M. Grebmeier and W. Maslowski, pp. 101–132, Springer, Dordrecht, Netherlands.
- Mathis, J. T., et al. (2014), Carbon biogeochemistry of the western Arctic: Primary production, carbon export and the controls on ocean acidification, in *The Pacific Arctic Region: Ecosystem Status and Trends in a Rapidly Changing Environment*, edited by J. M. Grebmeier and W. Maslowski, pp. 223–268, Springer, Dordrecht, Netherlands.
- McClelland, J. W., S. J. Déry, B. J. Peterson, R. M. Holmes, and E. F. Wood (2006), A Pan-Arctic evaluation of changes in river discharge during the latter half of the 20th century, *Geophys. Res. Lett.*, 33, L06715, doi:10.1029/2006GL025753.
- McKee, B. A., R. C. Aller, M. A. Allison, T. S. Bianchi, and G. C. Kineke (2004), Transport and transformation of dissolved and particulate materials on continental margins influenced by major rivers: Benthic boundary layer and seabed processes, *Cont. Shelf Res.*, 24(7–8), 899–926, doi:10.1016/j.csr.2004.02.009.
- McMahon, K., W. G. Ambrose Jr., B. Johnson, M. Sun, G. Lopez, L. Clough, and M. Carroll (2006), Benthic community response to ice algae and phytoplankton in Ny-Ålesund, Svalbard, *Mar. Ecol. Prog. Ser.*, 310, 1–14, doi:10.3354/meps310001.
- Michaud, E., G. Desrosiers, F. Mermillod-Blondin, B. Sundby, and G. Stora (2005), The functional group approach to bioturbation: The effects of biodiffusers and gallery-diffusers of the *Macoma balthica* community on sediment oxygen uptake, *J. Exp. Mar. Biol. Ecol.*, 326(1), 77–88, doi:10.1016/j.jembe.2005.05.016.
- Michaud, E., G. Desrosiers, F. Mermillod-Blondin, B. Sundby, and G. Stora (2006), The functional group approach to bioturbation: II. The effects of the *Macoma balthica* community on fluxes of nutrients and dissolved organic carbon across the sediment-water interface, *J. Exp. Mar. Biol. Ecol.*, 337(2), 178–189, doi:10.1016/j.jembe.2006.06.025.
- Michel, C., L. Legendre, R. G. Ingram, M. Gosselin, and M. Levasseur (1996), Carbon budget of sea-ice algae in spring: Evidence of a significant transfer to zooplankton grazers, *J. Geophys. Res.*, 101(C8), 18,345–18,360, doi:10.1029/96JC00045.
- Michel, C., M. Gosselin, and C. Nozais (2002), Preferential sinking export of biogenic silica during the spring and summer in the North Water Polynya (northern Baffin Bay): Temperature or biological control?, *J. Geophys. Res.*, 107(C7), 3064, doi:10.1029/2000JC000408.
- Michel, C., J. Hamilton, E. Hansen, D. Barber, M. Reigstad, J. Iacozza, L. Seuthe, and A. Niemi (2015), Arctic Ocean outflow shelves in the changing Arctic: A review and perspectives, *Prog. Oceanogr.*, 139, 66–88, doi:10.1016/j.pocean.2015.08.007.
- Middelburg, J. J., C. M. Duarte, and J.-P. Gattuso (2005), Respiration in coastal benthic communities, in *Respiration in Aquatic Ecosystems*, edited by P. del Giorgio and P. Williams, pp. 206–224, Oxford Univ. Press, Oxford.
- Moran, S. B., M. W. Lomas, R. P. Kelly, R. Gradinger, K. Iken, and J. T. Mathis (2012), Seasonal succession of net primary productivity, particulate organic carbon export, and autotrophic community composition in the eastern Bering Sea, *Deep Sea Res., Part II*, 65–70, 84–97, doi:10.1016/j.dsr2.2012.02.011.
- Morata, N., and P. E. Renaud (2008), Sedimentary pigments in the western Barents Sea: A reflection of pelagic-benthic coupling?, *Deep Sea Res., Part II*, 55(20–21), 2381–2389, doi:10.1016/j.dsr2.2008.05.004.
- Morata, N., M. Poulin, and P. E. Renaud (2011), A multiple biomarker approach to tracking the fate of an ice algal bloom to the sea floor, *Polar Biol.*, 34(1), 101–112, doi:10.1007/s00300-010-0863-3.
- Morata, N., E. Michaud, and M. Włodarska-Kowalczyk (2015), Impact of early food input on the Arctic benthos activities during the polar night, *Polar Biol.*, 38, 99–114, doi:10.1007/s00300-013-1414-5.
- Morison, J., R. Kwok, C. Peralta-Ferriz, M. Alkire, I. Rigor, R. Andersen, and M. Steele (2012), Changing Arctic Ocean freshwater pathways, *Nature*, 481(7379), 66–70, doi:10.1038/nature10705.
- Na, T., B. Gribsholt, O. S. Galaktionov, T. Lee, and F. J. R. Meysman (2008), Influence of advective bio-irrigation on carbon and nitrogen cycling in sandy sediments, *J. Mar. Res.*, 66(5), 691–722, doi:10.1357/002224008787536826.
- Nedwell, D. B., T. R. Walker, J. C. Ellis-Evans, and A. Clarke (1993), Measurements of seasonal rates and annual budgets of organic carbon fluxes in an Antarctic coastal environment at Signy Island, South Orkney Islands, suggest a broad balance between production and decomposition, *Appl. Environ. Microbiol.*, 59(12), 3989–3995.
- Olli, K., et al. (2007), The fate of production in the central Arctic Ocean-top-down regulation by zooplankton expatriates?, *Prog. Oceanogr.*, 72(1), 84–113, doi:10.1016/j.pocean.2006.08.002.
- Orlova, E. L., A. V. Dolgov, P. E. Renaud, M. Greenacre, C. Halsband, and V. A. Ivshin (2015), Climatic and ecological drivers of euphausiid community structure vary spatially in the Barents Sea: Relationships from a long time series (1952–2009), *Front. Mar. Sci.*, 1, 1–13, doi:10.3389/fmars.2014.00074.
- Pabi, S., G. L. van Dijken, and K. R. Arrigo (2008), Primary production in the Arctic Ocean, 1998–2006, *J. Geophys. Res.*, 113, C08005, doi:10.1029/2007JC004578.
- Petrenko, D., D. Pozdnyakov, J. Johannessen, F. Counillon, and V. Sychov (2013), Satellite-derived multi-year trend in primary production in the Arctic Ocean, *Int. J. Remote Sens.*, 34(11), 3903–3937, doi:10.1080/01431161.2012.762698.
- Pfannkuche, O., and H. Thiel (1987), Meiobenthic stocks and benthic activity on the NE-Svalbard shelf and in the Nansen Basin, *Polar Biol.*, 7(5), 253–266, doi:10.1007/BF00443943.
- Piepenburg, D. (2005), Recent research on Arctic benthos: Common notions need to be revised, *Polar Biol.*, 28(10), 733–755, doi:10.1007/s00300-005-0013-5.
- Piepenburg, D., T. H. Blackburn, C. F. von Dorrien, J. Gutt, P. O. J. Hall, S. Hulth, M. A. Kendall, K. W. Opalinski, E. Rachor, and M. K. Schmid (1995), Partitioning of benthic community respiration in the Arctic (northwestern Barents Sea), *Mar. Ecol. Prog. Ser.*, 118, 199–213, doi:10.3354/meps118199.
- Piepenburg, D., W. G. Ambrose Jr., A. Brandt, P. E. Renaud, M. J. Ahrens, and P. Jensen (1997), Benthic community patterns reflect water column processes in the Northeast Water Polynya (Greenland), *J. Mar. Syst.*, 10(1–4), 467–482, doi:10.1016/S0924-7963(96)00050-4.
- Pirtle-Levy, R., J. M. Grebmeier, L. W. Cooper, and I. L. Larsen (2009), Chlorophyll *a* in Arctic sediments implies long persistence of algal pigments, *Deep Sea Res., Part II*, 56(17), 1326–1338, doi:10.1016/j.dsr2.2008.10.022.
- Price, D. T., et al. (2013), Anticipating the consequences of climate change for Canada's boreal forest ecosystems, *Environ. Rev.*, 21(4), 322–365, doi:10.1139/er-2013-0042.
- R Core Team (2015), *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, Vienna, Austria.
- Rachold, V., M. N. Grigoriev, F. E. Are, S. Solomon, E. Reimnitz, H. Kassens, and M. Antonow (2000), Coastal erosion vs riverine sediment discharge in the Arctic Shelf seas, *Int. J. Earth Sci.*, 89(3), 450–460, doi:10.1007/s005310000113.

- Rachold, V., H. Eicken, V. V. Gordeev, M. N. Grigoriev, H.-W. Hubberten, A. P. Lisitzin, V. P. Shevchenko, and L. Schirmer (2004), Modern terrigenous organic carbon input to the Arctic Ocean, in *The Organic Carbon Cycle in the Arctic Ocean*, edited by P. D. R. Stein and D. R. W. MacDonald, pp. 33–55, Springer, Berlin.
- Reigstad, M., C. W. Riser, P. Wassmann, and T. Ratkova (2008), Vertical export of particulate organic carbon: Attenuation, composition and loss rates in the northern Barents Sea, *Deep Sea Res., Part II*, 55(20), 2308–2319, doi:10.1016/j.dsr2.2008.05.007.
- Renaud, P. E., N. Morata, W. G. Ambrose, J. J. Bowie, and A. Chiuchiolo (2007a), Carbon cycling by seafloor communities on the eastern Beaufort Sea shelf, *J. Exp. Mar. Biol. Ecol.*, 349(2), 248–260, doi:10.1016/j.jembe.2007.05.021.
- Renaud, P. E., A. Riedel, C. Michel, N. Morata, M. Gosselin, T. Juul-Pedersen, and A. Chiuchiolo (2007b), Seasonal variation in benthic community oxygen demand: A response to an ice algal bloom in the Beaufort Sea, Canadian Arctic?, *J. Mar. Syst.*, 67(1–2), 1–12, doi:10.1016/j.jmarsys.2006.07.006.
- Renaud, P. E., N. Morata, M. L. Carroll, S. G. Denisenko, and M. Reigstad (2008), Pelagic-benthic coupling in the western Barents Sea: Processes and time scales, *Deep Sea Res., Part II*, 55(20–21), 2372–2380, doi:10.1016/j.dsr2.2008.05.017.
- Rho, T., and T. E. Whitledge (2007), Characteristics of seasonal and spatial variations of primary production over the southeastern Bering Sea shelf, *Cont. Shelf Res.*, 27(20), 2556–2569, doi:10.1016/j.csr.2007.07.006.
- Riser, C. W., P. Wassmann, K. Olli, A. Pasternak, and E. Arashkevich (2002), Seasonal variation in production, retention and export of zooplankton faecal pellets in the marginal ice zone and central Barents Sea, *J. Mar. Syst.*, 38(1), 175–188, doi:10.1016/S0924-7963(02)00176-8.
- Rowe, G. T. (2002), Oxygen consumption at Polar_93_1, *Pangaea*, doi:10.1594/PANGAEA.78772.
- Rowe, G. T., G. S. Boland, E. G. Escobar Briones, M. E. Cruz-Kaegi, A. Newton, D. Piepenburg, I. Walsh, and J. Deming (1997), Sediment community biomass and respiration in the Northeast Water Polynya, Greenland: A numerical simulation of benthic lander and spade core data, *J. Mar. Syst.*, 10(1–4), 497–515, doi:10.1016/S0924-7963(96)00065-6.
- Roy, V., K. Iken, and P. Archambault (2014), Environmental drivers of the Canadian Arctic megabenthic communities, *PLoS One*, 9(7), e100900, doi:10.1371/journal.pone.0100900.
- Rysgaard, S., K. Finster, and H. Dahlgard (1996), Primary production, nutrient dynamics and mineralisation in a northeastern Greenland fjord during the summer thaw, *Polar Biol.*, 16(7), 497–506, doi:10.1007/BF02329069.
- Rysgaard, S., B. Thamdrup, N. Risgaard-Petersen, H. Fossing, P. Berg, P. B. Christensen, and T. Dalsgaard (1998), Seasonal carbon and nutrient mineralization in a high-Arctic coastal marine sediment, Young Sound, Northeast Greenland, *Mar. Ecol. Prog. Ser.*, 175, 261–276, doi:10.3354/meps175261.
- Rysgaard, S., R. N. Glud, N. Risgaard-Petersen, and T. Dalsgaard (2004), Denitrification and anammox activity in Arctic marine sediments, *Limnol. Oceanogr.*, 49(5), 1493–1502, doi:10.4319/lo.2004.49.5.1493.
- Sakshaug, E. (2004), Primary and secondary production in the Arctic seas, in *The Organic Carbon Cycle in the Arctic Ocean*, edited by P. D. R. Stein and D. R. W. MacDonald, pp. 57–81, Springer, Berlin.
- Sampei, M., H. Sasaki, H. Hattori, S. Kudoh, Y. Kashino, and M. Fukuchi (2002), Seasonal and spatial variability in the flux of biogenic particles in the North Water, 1997–1998, *Deep Sea Res., Part II*, 49(22), 5245–5257, doi:10.1016/S0967-0645(02)00188-1.
- Sampei, M., H. Sasaki, H. Hattori, M. Fukuchi, and B. T. Hargrave (2004), Fate of sinking particles, especially fecal pellets, within the epipelagic zone in the North Water (NOW) Polynya of northern Baffin Bay, *Mar. Ecol. Prog. Ser.*, 278, 17–25, doi:10.3354/meps278017.
- Sauter, E. J., M. Schlüter, and E. Suess (2001a), Organic carbon flux and remineralization in surface sediments, *Pangaea*, doi:10.1594/PANGAEA.738701.
- Sauter, E. J., M. Schlüter, and E. Suess (2001b), Organic carbon flux and remineralization in surface sediments from the northern North Atlantic derived from pore-water oxygen microprofiles, *Deep Sea Res., Part I*, 48(2), 529–553, doi:10.1016/S0967-0637(00)00061-3.
- Schewe, I. (2001), Small-sized benthic organisms of the Alpha Ridge, Central Arctic Ocean, *Int. Rev. Hydrobiol.*, 86(3), 317–335, doi:10.1002/1522-2632(200106)86:3 < 317::AID-IROH317 > 3.0.CO;2-V.
- Schewe, I., and T. Soltwedel (2003), Benthic response to ice-edge-induced particle flux in the Arctic Ocean, *Polar Biol.*, 26(9), 610–620, doi:10.1007/s00300-003-0526-8.
- Schlitzer, R. (2007), Ocean data view. [Available at <http://odv.awi.de>.]
- Schmid, M. K., D. Piepenburg, A. A. Golikov, K. von Juterzenka, V. V. Petryashov, and M. Spindler (2006), Trophic pathways and carbon flux patterns in the Laptev Sea, *Prog. Oceanogr.*, 71(2–4), 314–330, doi:10.1016/j.pocean.2006.09.002.
- Schuur, E. A., et al. (2008), Vulnerability of permafrost carbon to climate change: Implications for the global carbon cycle, *BioScience*, 58(8), 701–714, doi:10.1641/B580807.
- Seiler, D. (1999), Biogeochemical parameters from different sediment stations at the continental slope of Greenland, *Pangaea*, doi:10.1594/PANGAEA.55717.
- Serreze, M. C., M. M. Holland, and J. Stroeve (2007), Perspectives on the Arctic's shrinking sea-ice cover, *Science*, 315(5818), 1533–1536, doi:10.1126/science.1139426.
- Solan, M., B. J. Cardinale, A. L. Downing, K. A. M. Engelhardt, J. L. Ruesink, and D. S. Srivastava (2004), Extinction and ecosystem function in the marine benthos, *Science*, 306(5699), 1177–1180, doi:10.1126/science.1103960.
- Soltwedel, T., and K. Vopel (2001), Bacterial abundance and biomass in response to organism-generated habitat heterogeneity in deep-sea sediments, *Mar. Ecol. Prog. Ser.*, 219, 291–298, doi:10.3354/meps219291.
- Soltwedel, T., V. Mokievsky, and I. Schewe (2000), Benthic activity and biomass on the Yermak Plateau and in adjacent deep-sea regions northwest of Svålbard, *Deep Sea Res., Part I*, 47(9), 1761–1785, doi:10.1016/S0967-0637(00)00006-6.
- Søreide, J. E., E. Leu, J. Berge, M. Graeve, and S. Falk-Petersen (2010), Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic, *Global Change Biol.*, 16(11), 3154–3163, doi:10.1111/j.1365-2486.2010.02175.x.
- Søreide, J. E., M. L. Carroll, H. Hop, W. G. Ambrose, E. N. Hegseth, and S. Falk-Petersen (2013), Sympagic-pelagic-benthic coupling in Arctic and Atlantic waters around Svalbard revealed by stable isotopic and fatty acid tracers, *Mar. Biol. Res.*, 9(9), 831–850, doi:10.1080/17451000.2013.775457.
- Stief, P. (2013), Stimulation of microbial nitrogen cycling in aquatic ecosystems by benthic macrofauna: Mechanisms and environmental implications, *Biogeosciences*, 10(12), 7829–7846, doi:10.5194/bg-10-7829-2013.
- Stroeve, J. C., M. C. Serreze, M. M. Holland, J. E. Kay, J. Malanik, and A. P. Barrett (2012), The Arctic's rapidly shrinking sea ice cover: A research synthesis, *Clim. Change*, 110(3–4), 1005–1027, doi:10.1007/s10584-011-0101-1.
- Suess, E. (1980), Particulate organic carbon flux in the oceans—Surface productivity and oxygen utilization, *Nature*, 288, 260–263, doi:10.1038/288260a0.
- Sun, M.-Y., M. L. Carroll, W. G. Ambrose, L. M. Clough, L. Zou, and G. R. Lopez (2007), Rapid consumption of phytoplankton and ice algae by Arctic soft-sediment benthic communities: Evidence using natural and ¹³C-labeled food materials, *J. Mar. Res.*, 65(4), 561–588, doi:10.1357/002224007782689094.

- Sun, M.-Y., L. M. Clough, M. L. Carroll, J. Dai, W. G. Ambrose Jr., and G. R. Lopez (2009), Different responses of two common Arctic macro-benthic species (*Macoma balthica* and *Monoporeia affinis*) to phytoplankton and ice algae: Will climate change impacts be species specific?, *J. Exp. Mar. Biol. Ecol.*, *376*(2), 110–121, doi:10.1016/j.jembe.2009.06.018.
- Tamelander, T., M. Reigstad, H. Hop, M. L. Carroll, and P. Wassmann (2008), Pelagic and sympagic contribution of organic matter to zooplankton and vertical export in the Barents Sea marginal ice zone, *Deep Sea Res., Part II*, *55*(20), 2330–2339, doi:10.1016/j.dsr2.2008.05.019.
- Tank, S. E., M. Manizza, R. M. Holmes, J. W. McClelland, and B. J. Peterson (2012), The processing and impact of dissolved riverine nitrogen in the Arctic Ocean, *Estuaries Coasts*, *35*(2), 401–415, doi:10.1007/s12237-011-9417-3.
- Thamdrup, B., J. W. Hansen, and B. B. Jørgensen (1998), Temperature dependence of aerobic respiration in a coastal sediment, *FEMS Microbiol. Ecol.*, *25*, 189–200, doi:10.1111/j.1574-6941.1998.tb00472.x.
- Tremblay, J.-É., Y. Gratton, J. Fauchot, and N. M. Price (2002), Climatic and oceanic forcing of new, net, and diatom production in the North Water, *Deep Sea Res., Part II*, *49*(22–23), 4927–4946, doi:10.1016/S0967-0645(02)00171-6.
- Tremblay, J.-É., P. Raimbault, N. Garcia, B. Lansard, M. Babin, and J. Gagnon (2014), Impact of river discharge, upwelling and vertical mixing on the nutrient loading and productivity of the Canadian Beaufort Shelf, *Biogeosciences*, *11*(17), 4853–4868, doi:10.5194/bg-11-4853-2014.
- Wakeham, S. G., and E. A. Canuel (2006), Degradation and preservation of organic matter in marine sediments, in *The Handbook of Environmental Chemistry*, edited by J. K. Volkman, pp. 295–321, Springer, Berlin.
- Wassmann, P., and M. Reigstad (2011), Future Arctic Ocean seasonal ice zones and implications for pelagic-benthic coupling, *Oceanography*, *24*(3), 220–231, doi:10.5670/oceanog.2011.74.
- Welch, H. E., T. D. Siferd, and P. Bruecker (1997), Marine zooplanktonic and benthic community respiration rates at Resolute, Canadian High Arctic, *Can. J. Fish. Aquat. Sci.*, *54*(5), 995–1005, doi:10.1139/f97-006.
- Wexels Riser, C., P. Wassmann, M. Reigstad, and L. Seuthe (2008), Vertical flux regulation by zooplankton in the northern Barents Sea during Arctic spring, *Deep Sea Res., Part II*, *55*(20), 2320–2329, doi:10.1016/j.dsr2.2008.05.006.
- Witte, U., et al. (2003), In situ experimental evidence of the fate of a phytodetritus pulse at the abyssal sea floor, *Nature*, *424*(6950), 763–766, doi:10.1038/nature01799.
- Wollenburg, J. E., and W. Kuhnt (2000a), Benthic foraminifera in the Arctic Ocean, *Pangaea*, doi:10.1594/PANGAEA.728293.
- Wollenburg, J. E., and W. Kuhnt (2000b), The response of benthic foraminifera to carbon flux and primary production in the Arctic Ocean, *Mar. Paleontol.*, *40*(3), 189–231, doi:10.1016/S0377-8398(00)00039-6.
- Woodgate, R. A., K. Aagaard, and T. J. Weingartner (2006), Interannual changes in the Bering Strait fluxes of volume, heat and freshwater between 1991 and 2004, *Geophys. Res. Lett.*, *33* L15609, doi:10.1029/2006GL026931.
- Yang, D., X. Shi, and P. Marsh (2015), Variability and extreme of Mackenzie River daily discharge during 1973–2011, *Quat. Int.*, *380–381*, 159–168, doi:10.1016/j.quaint.2014.09.023.
- Zabel, M., and C. Hensen (2006), Quantification and regionalization of benthic reflux, in *Marine Geochemistry*, edited by P. D. H. D. Schulz and D. M. Zabel, pp. 429–456, Springer, Berlin.