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Impact of early food input on the Arctic benthos activities during the polar night

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Abstract In Arctic areas where benthic primary production does not occur or is not sufficient, the benthos depends on episodic events of food inputs from overlying waters, in particular spring ice algal and phytoplankton blooms. Climate change is expected to lead to earlier ice melts and subsequently to earlier spring blooms and food inputs to the benthos. The goal of the present study was to characterize benthic community structure and activities during the polar night in Rijpfjorden, a high Arctic fjord from Svalbard, and to assess experimentally how earlier climate-induced food inputs can impact these benthic activities. Two concentrations of freeze-dried phytoplankton were added to intact sediment cores, while additional control cores did not receive food addition. Sediment oxygen demand (SOD), nutrient fluxes, bioturbation coefficients (as indicator of benthic activities) and contents of organic matter and pigments in sediments were measured at the beginning of the experiment and 9 days after the addition. In the initial polar night conditions, SOD was $\sim$4.2 mmol O_2 m^{-2} d^{-1}, bioturbation coefficients were null for biodiffusion and 1.08 y^{-1} for bioadvection, and benthic biomass was 1.36 g 0.1 m^{-2}. In the cores with food addition, the phytoplankton added was quickly consumed, and after 9 days, SOD and bioturbation were higher in the food treatments compared with the control cores, both being higher with higher food concentration. This study documented a clear and quick response in benthic activities following the food input, suggesting that in winter/early spring, Arctic benthos may depend on early food inputs for its activities. Climate-induced changes in food supply to the seafloor could have drastic consequences for the benthic ecosystem functioning.

Keywords Svalbard · Pelagic–benthic coupling · Bioturbation · Biogeochemical fluxes · Feeding experiment · Ecosystem functioning

Introduction

Over the last decades, important changes in the thickness and extent of sea ice cover have been observed in the Arctic marine environment (Comiso 2003; Kwok and Rothrock 2009). Sea ice cover has decreased at an average rate of about 10 % per decade since the 1980s (Comiso et al. 2008; Polyakov et al. 2010). It is expected that within 20 years, the Arctic Ocean will become ice-free during the summer, leading to drastic changes in productivity regime and ecosystem structures, as already observed in some Arctic shelves (e.g., Arrigo and van Dijken 2011; Grebmeier 2012).

Today, Arctic marine ecosystems are strongly influenced by episodic events on various timescales (Wassmann et al. 1996). In ice-covered areas, it has been suggested that the mismatch between producers and grazers may result in strong vertical fluxes of undegraded particulate organic matter (OM) from the sea ice to the seafloor (Carroll and Carroll 2003). In Antarctica, it has been found that seasonal inputs of phytodetritus to the seafloor are stored in the sediment and used later by benthic organisms as a "food-bank" (Mincks et al. 2005). In the Arctic, however, benthic organisms seem to

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utilize quickly those inputs (Renaud et al. 2007b). When OM reaches the seafloor, a part of it can be used by benthic organisms (transformed into body biomass or used for physiologic activities) and the remaining portion can be buried in sediment and lost for the biological system. Interestingly, the benthic carbon remineralization rates on continental shelves are similar to those reported from lower latitudes (Glud et al. 1998; Rysgaard et al. 1998; Glud et al. 2000; Grant et al. 2002; Clough et al. 2005). Therefore, contrary to temperate areas, where temperature regulates most processes, in polar areas, benthic remineralization is regulated primarily by the availability of OM, light and hypoxia and not by temperature. Moreover, in many regions, high benthic abundance, biomass and production reflect the production patterns of the overlying water column (Grebmeier et al. 1988; Ambrose and Renaud 1995; Piepenburg et al. 1997). This significant transfer of OM and the efficient assimilation by the benthic community (Grebmeier et al. 1988; Grebmeier and Barry 1991; Ambrose and Renaud 1995; Klages et al. 2004) suggest a tight pelagic–benthic coupling in Arctic ecosystems. On an annual basis, nutrient fluxes, resulting from OM mineralization and authigenic processes, generally showed higher effluxes from the sediment with some more steady fluxes during the sea ice cover (Rysgaard et al. 1998; Kostka et al. 1999).

In some temperate areas, it has been suggested that benthic bacteria and protozoans may be the primary agents of benthic carbon remineralization to respond to pulsed inputs of OM to the seafloor (Rowe et al. 1991; Turley 2000; Gooday 2002). Compared to temperate areas, Arctic macrobenthos have been found to have an enhanced role in benthic carbon remineralization (Piepenburg et al. 1995; Rowe et al. 1997; Clough et al. 2005; Grebmeier et al. 2006b), in particular during ice algal blooms (Renaud et al. 2007b; Morata et al. 2011). Jorgensen et al. (2005) found that bioirrigating fauna in Svalbard fjords contributed more than 50 % to the total benthic respiration, not only caused by the worms' respiration but also by the burrows' extension inside anoxic sediment enhancing strong bacterial respiration. In temperate areas, laboratory experiments have shown that benthic infauna can react quickly to food input by increasing their bioturbation activities (Nogaro et al. 2008). In both subarctic and temperate areas, bioturbation has also been found to be impacted by subtle differences in temperature, sediment reworking activities being more pronounced during summertime (Ouelette et al. 2004; Duport et al. 2007; Maire et al. 2007). Biological sediment reworking rates are a perfect proxy for the benthic biological activities (i.e., burrowing behavior, feeding, excretion, mobility, etc.) (Mahaut and Graf 1987; François et al. 2002). Although bioturbation activities in Arctic sediments were rarely explored, the two studies highlighted strong nonlocal downward sediment transport in Arctic coastal sediments (down to a depth of 10 cm, Konovalov et al. 2010) versus low level of diffusive activities in deep Arctic Ocean sediments (down to 3 cm, Clough et al. 1997). Rysgaard et al. (2000) also showed that meiofauna in soft sediments at summertime could strongly contribute to bioturbation and to carbon mineralization. These few studies indicate the strong spatial variability in benthic bioturbatory activities in Arctic sediments. There are, however, no reports on temporal patterns. In particular, we do not know anything about the bioturbation (or any benthic activities) during the Arctic wintertime and the following ice-free period. Teal et al. (2008) reviewed the literature on biological mixing in soft sediments (based on surveys from the worldwide seas, but with almost no data from the Arctic) and reported (as Duport et al. 2007) significant effects of season on both bioturbation intensity and depth of mixed layer. On the other hand, McClintic et al. (2008) reported lack of seasonal effects in bioturbation intensity in Antarctic shelf sediments, and he explained it by a consistent year-round utilization of OM stored in Antarctic sediments ("food-bank" theory) rather than dependence on discrete pulses of food supply.

Different scenarios about the impact of climate change on the benthos have been suggested. Climate warming may extend the ice-free period in the Arctic, with an earlier ice melt during the spring and a later freeze-up (Wassmann 2011). This could lead to earlier ice disappearance and phytoplankton blooms (Perrette et al. 2011; Kahru et al. 2011) and potentially earlier food inputs to the benthos (scenario 1). It has also been suggested that a reduced ice cover may lead to an intensification of pelagic food webs, in particular to higher zooplankton grazing, and therefore a decrease in food inputs to the seafloor (scenario 2) (Carroll and Carroll 2003; Grebmeier et al. 2006a). Climate-warming-driven changes in organic carbon supply to seabed can modify the benthic community functioning, especially in food-limited parts of the seafloor, as was predicted, e.g., for bioturbation in sediments of abyssal plains (Vardaro et al. 2009). The goal of the present study was to characterize benthic community structure and functioning during the polar night and understand how earlier climate-induced food inputs can impact these communities' activities (respiration, nutrient fluxes and bioturbation) in high Arctic coastal sediments.

Methods

Study area

Rijpfjorden (80°N, 22°E) is located in the north of Nordaustlandet Island, in the Svalbard archipelago (Fig. 1). It is oriented south–north and opens to the north. It is very slightly influenced by warm Atlantic water masses transported along the west coast of Spitsbergen. The area is of particular interest because of its "true" Arctic character, as compared to most other Svalbard fjords, especially those

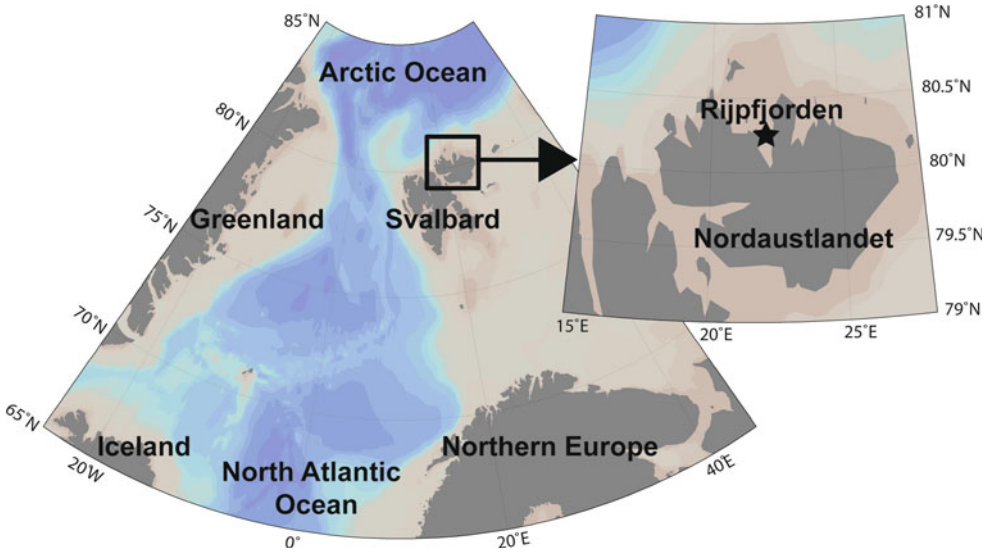

Fig. 1 Map of the study area, adapted from Ocean Data View (Schlitzer 2012). The sampling station in Rijpfjorden is indicated by a *star*

located off the west Spitsbergen, that are much more "Atlantic" in their hydrological settings. It is relatively shallow (200–250 m deep), with a broad shallow shelf of 100–200 m depth extending north to about 81°N (Leu et al. 2011). The bottom water temperatures are usually close to the freezing point most of the year, salinity >33, and the fjord has a heavy sea ice cover up to 1 m thick from October to June/July (Ambrose et al. 2006; Leu et al. 2011; Wang et al. 2013).

Sediment sampling and experimental design

Sediments were collected in Rijpfjorden on January 12, 2012, at 272 m (80°19′N, 22°15′E, Fig. 1), during the Polar Night Cruise on board the R/V Helmer Hanssen. Bottom water for incubation was collected at the same station, at 250 m.

Macrofauna was collected with the use of a 0.1 m^{-2} van Veen grab (three replicate grabs). Samples were sieved through 0.5-mm sieve and fixed with buffered formaldehyde. All individuals were identified to the lowest possible taxonomic level and enumerated. The animals were weighed to assess the wet biomass of species in samples. Mollusks were weighed with shells. All species were classified by their feeding mode and comparative mobility according to Fauchald and Jumars (1979), Feder and Matheke (1980) and unpublished observations. Fifteen functional groups representing combinations of five feeding types (carnivores, herbivores, suspension feeders, surface detritus feeders and subsurface detritus feeders—burrowers) and three mobility types (sessile, discretely mobile and mobile) were considered.

Sediment cores were collected using a box corer (45 cm × 45 cm) and deployed twice. In each box core, nine sediment cores (a total of 18 cores, 12 cm diameter, 20–25 cm deep) with intact surface layers were randomly subsampled. None of the sampled cores presented visual abnormal characteristics, such as different grain size, color or visible large organisms. Three cores were immediately sliced for characterization of initial T0 conditions in the sediment, whereas 15 cores were kept for the feeding experiment. The three cores, referred to as initial T0 cores, were sliced every 0.5 cm until 2 cm and every 1 cm until 10 cm. Slices were frozen for future measurements of porosity, pigments, OM and organic carbon (OC).

The fifteen incubation cores were kept in a cold room on board the ship, at controlled conditions (3 °C, dark). After sampling, they were directly filled with recently collected bottom water (about 1L) and aerated by bubbling to keep the overlying water saturated with oxygen. The cores were kept quiet for the first 24 h for sediment stabilization and for acclimatizing to the cold room conditions. Twenty-four hours after sediment sampling, after the overlying water was changed to remove the released metabolites, 5 g of fluorescent luminophores (red, 63–90 μm) was homogeneously and gently introduced in the overlying water in order to quantify the biological sediment reworking activity in the sediments (Mahaut and Graf 1987). Cores were randomly separated for the three treatments: no food (NF), five control cores—without food addition, representative of the natural polar night conditions; low food (LF), five cores with low food addition; high food (HF), five cores with high food addition. NF corresponds to climate change scenario 2, where vertical organic matter fluxes are slower/null, LF corresponds to the present-day scenario, with ice-associated spring bloom leading to a pulse of organic matter to the seafloor, and HF corresponds to scenario 1, where more intense blooms take place, bringing more material to the seafloor than presently.

The food added consisted of commercial freeze-dried mix of three phytoplankton species, *Arthrospira* sp.,

Hematococcus sp. and *Schizochytrium* sp. (PhytoPlan®, Two Little Fishies, Coconut Grove, FL) and had OC and total nitrogen contents of 45 and 5 %, respectively, OM content of 93 % and chl *a* concentration of 0.5 mg dw g^{-1}. Five LF cores received a single food pulse of 3 mg of this freeze-dried phytoplankton, and five HF cores received a single food pulse of 15 mg (Table 1). The amounts of freeze-dried phytoplankton added to the sediment cores have been determined to simulate spring inputs from the ice algal or phytoplankton bloom, during the 9 days of incubation, since algal blooms are often observed in sediment traps lasting for 1 or 2 weeks (i.e., Forest et al. 2010). Very high variability in vertical fluxes of OM has been observed in sediment traps (0–300 m) during ice algal and phytoplankton blooms in Arctic seas, where particulate OM (POC) flux has been found to vary from about 0.01 g m^{-2} d^{-1} to as high as about 3 g m^{-2} d^{-1} at 5 m (e.g., Bauerfeind et al. 1997; Noji et al. 1999; Forest et al. 2007; Juul-Pedersen et al. 2008; Reigstad et al. 2008; Zajączkowski et al. 2010). Values found in the literature are therefore extremely variable. Food concentrations in the present experiments were determined based on the values of POC fluxes observed in sediment traps deployed at depths from 130 to 200 m in the Barents Sea, Canadian Archipelago and Greenland Sea, during ice-associated bloom and ice breakup and during summer phytoplankton blooms (i.e., at depths and ice-associated ecosystems similar to those in the studied fjord, as no reference data from Rijpfjorden were available). POC fluxes from about 10–24 mgC m^{-2} d^{-1} (that makes a load of about 90–216 mgC m^{-2} in 9 days, corresponding to LF addition of = 119 mgC m^{-2}) have been reported during the spring (Noji et al. 1999; Forest et al. 2008; Juul-Pedersen et al. 2008). POC fluxes ranging from 40 to >200 mgC m^{-2} d^{-1} (so about 360 to >1,800 mgC m^{-2} in 9 days, corresponding to HF treatment with = 597 mgC m^{-2}) were measured during summer blooms (Forest et al. 2008; Reigstad et al. 2008).

Sediment core incubations

Twenty-four hours after sampling (T0) and after 9 days of experiment (T9), in order to measure nutrient fluxes and sediment oxygen demand (SOD), cores were sealed using tops that provided constant stirring of the overlying water (Renaud et al. 2007b). In addition, parallel to the sediment cores incubation, control cores without sediment but with similar volume of bottom water were incubated simultaneously to evaluate the effect of seawater microorganisms on oxygen and nutrient fluxes (Rysgaard et al. 2004; Renaud et al. 2007a). These values were used as blank and were withdrawn from the values obtained with sediment incubations. Oxygen concentrations were monitored every 2 h using microelectrode (Unisense A/S; Aarhus, Denmark) inserted into a small sampling port in the core top without introducing any air. Incubations were terminated after 24 h when 15–20 % of the oxygen had been consumed (Hall et al. 1996), and SOD was measured as the (negative) slope of the regression line between oxygen concentration and time, subtracting the mean control values (Renaud et al. 2007b). Oxygen consumption rates were converted into sediment carbon demand (SCD) by assuming a 1:1 stoichiometric relationship between oxygen and carbon consumption and then applying a respiratory coefficient of 0.85 (Smith 1978).

Sixty milliliters of overlying waters was sampled with a syringe at the beginning and at the end of the incubation for nutrient analyses. Nutrient fluxes were measured as a difference in nutrient concentration between the two times, withdrawing the mean control values (Rysgaard et al. 2004). After each water sampling, a reservoir was used to replace the water that was removed for flux measurements. Water samples for nitrate + nitrite (NO_3^-+NO_2^-), ammonium (NH_4^+) and phosphate (PO_4^{3-}) were frozen for future analyses, while samples for silicate ($Si(OH)_4^{3-}$) were kept cold in the fridge.

Cores were then reopened and kept with constant aeration by bubbling for 9 days. After this time, sediment cores were sealed again for the measurement of nutrients and oxygen fluxes as described previously. Once the incubations finished, sediment cores were sliced horizontally for the determination of the profiles of luminophores, OM and pigments. As for the initial T0 conditions, sediments from the top 2 cm were sliced every 0.5 cm and sediments from 2 to 10 cm were sliced every 1 cm. Sediment slices were gently homogeneously mixed and directly frozen (−20 °C). Samples were kept frozen until analyses.

Sediment and nutrient analyses

Sediment from the three initial T0 cores and the 15 experimental cores was analyzed for pigment contents, porosity, OM and OC, after the removal of visible macrofauna. Within 3 months, pigments were analyzed fluorometrically according to Holm-Hansen et al. (1965). About 1 g of sediment was sonicated and extracted in 10 ml of acetone during 24 h in the fridge and in the dark.

Table 1 Quantities of dry mass, organic matter, organic carbon and chlorophyll *a* (chl *a*) added to the experimental cores

	Dry mass (mg m^{-2})	Organic matter (mg m^{-2})	Organic carbon (mg m^{-2})	Chl *a* (mg m^{-2})
LF (3 mg)	265	246	119	130
HF (15 mg)	1,325	1,232	597	663

Sediment was then centrifuged (4,000 rpm for 10 min), and the supernatant was analyzed in a Turner Designs model 10-AU fluorimeter before and after acidification with 5 % HCl, in order to determine both chlorophyll *a* (chl *a*) and phaeopigments (phaeo) concentrations. The porosity was measured from density and water content in 10 ml of sediment after weighing the dry sediment (60 °C during 48 h) according to Manheim et al. (1974). OM content was measured as loss on ignition at temperature 450 °C for 4 h (Zaborska et al. 2006). In some samples (control cores—without food addition) in every two layers (out of the 10 cm) of sediment, OC contents were measured following the method of Kennedy et al. (2005) in order to determine the ratio between OC and total OM (OC/OM). About 10 mg of dried sediment was acidified with 50 µl of HCl 1 N three times. Analyses were run on a Thermo Quest Flash EA 1112 CHN analyser.

Nitrate + nitrite and silicate were analyzed by colorimetry on a Bruan and Luebbe Autoanalyzer 3 (Aminot and Kérouel 2007b, d), and phosphate and ammonium were determined by colorimetry and fluorimetry, respectively, on a Bruan and Luebbe Autoanalyzer 3HR (Strickland and Parsons 1978; Aminot and Kérouel 2007a, c). Analytical precisions for the nutrient analyses were 0.05 µM. All reagents and standards were prepared in acid-washed glassware, and standards were prepared with a nutrient-free artificial seawater matrix prepared at the laboratory. Fluxes were calculated from the slopes of the linear regressions of nutrient concentrations against time, withdrawing the values obtained for the control cores (without sediment).

Bioturbation

At the laboratory, sediments were freeze-dried (96 h) and gently crushed to powder and homogenized. Three replicates of 0.2 g of sediment per slice were placed in a Petri dish under a constant UV light source (350 ± 370 nm, Tube UV BLB G5T5 6 W). A digital camera (Nikon digital captor 2,342,016 pixels) was placed in a black box 12 cm from the sediment sample with identical image acquisition conditions for all images (aperture time 1 s; diaphragm aperture f/13, ISO 200), and the image resolution was 28 µm per pixel. Images were saved in red–green–blue (RGB) color in JPEG format. The images were analyzed using an image processing toolbox (@mathworks) in order to differentiate luminophores from the background sediment by using an appropriate set of RGB threshold levels (Michaud 2006). Finally, the particle size appropriate for each kind of luminophores was selected (3 pixels × 3 pixels for the smallest luminophores), and the pictures were corrected (cleaned) by removing the particle sizes smaller and larger than the actual size of the specific luminophore (63–90 µm).

The reaction–diffusion type model used in this paper to describe luminophore redistribution as a result of macrofaunal reworking is based on the model of François et al. (2002) which contains two transport terms, the apparent biodiffusion coefficient and the biotransport (bioadvection) coefficient (noncontinuous displacement of tracer). The biodiffusion coefficient (Db) takes into account the diffusion-like transport due to the activity of the organisms. The biotransport coefficient (*r*) represents a nonlocal mixing pattern associated with a biologically induced transfer of particles from one place to another in a discontinuous pattern. The model is not presented here in detail since it is well described in the recent literature (i.e., Duport et al. 2007). Depending on the mode of sediment mixing, the organisms are grouped in the bioturbation functional groups (biodiffusers, conveyors, gallery-diffusers) (François et al. 2002; Michaud et al. 2005; Gilbert et al. 2007), different from trophic or mobile functional groups (Fauchald and Jumars 1979; Pearson 2001).

Data analysis

Macrofauna was described in terms of density (ind. 0.1 m^{-2}), biomass (g ww 0.1 m^{-2}), species richness (number of species per sample), evenness (Pielou index) and species diversity (Shannon–Wiener index). The functional diversity based on feeding and motility groups was also analyzed.

The normality and homogeneity of variances among treatments were previously verified with the Bartlett test before application of parametric tests (Fisher–Snedecor tests applied through variance analysis ANOVA). A one-way ANOVA has been undertaken at the beginning of the experiment (T0) in order to make sure that initial oxygen and nutrient fluxes were similar in all treatments. One week later, the influences of time and treatment on benthic fluxes were tested using a two-way repeated analysis of variance with time as the repeated factor (T0 and T9) and treatment (NF, LF, HF) as main factor.

At the end of the experiment, after core slicing, OM concentrations and pigment contents were compared over depth among treatments using a two-way repeated ANOVA with depth as the repeated factor and treatment as main factor. The total chl *a*, OM content and bioturbation coefficients (Db and *r*) were compared among treatment using a one-way ANOVA.

Tukey's post hoc tests were carried out in each case of significant results on the main tests to determine which time and/or treatments and/or depths differed.

Results

Macrofauna composition

Macrofauna occurred at the sampling site with a mean density of 485.3 ind 0.1 m^{-2} ± 74.7 SD (Table 2). Mollusks made 47 % and polychaetes 46 % of all collected individuals. The biomass varied from 1.7 to 19.3 g 0.1 m^{-2}. This large variability was produced by the occurrence of few specimens of large echinoderms in two grabs—the ophiuroid *Ophiopleura borealis* and the asteroid *Ctenodiscus crispatus*. After exclusion of these large individuals, the average biomass was 1.36 g 0.1 m^{-2} ± 0.15 SD. Altogether, 70 taxa were identified (most of them to the species level). Mean species richness was 48.7 ± 5.7 SD, Pielou evenness 0.73 ± 0.03 SD and Shannon–Wiener index −2.83 ± 0.17. The fauna was dominated by bivalves *Yoldiella solidula* and *Montacuta* sp. (juvenile forms, mostly smaller than 1.5 mm) and polychaetes *Maldane sarsi, Myriochele oculata, Chaetozone* spp. and *Leitoscoloplos mammosus* in terms of the number of individuals. Polychaetes *Aglaophamus malmgrenii* and *M. sarsi* and unidentified nemerteans made the largest portion of the biomass (after the large echinoderms were excluded). Regarding the functional groups' composition in terms of feeding and motility modes, the fauna was dominated by mobile surface detritus feeders (35 % of all individuals), sedentary surface detritus feeders (19 %), followed by mobile subsurface detritus feeders (10 %) and sedentary subsurface detritus feeders (9 %).

Oxygen and nutrient fluxes

Solute concentrations in overlying water, at T0 (24 h after sampling), were 0.5 µmol O_2 L^{-1}, 4.6 µM (nitrate + nitrite), 2 µM (ammonium), 11.9 µM (silicate) and 0.6 µM (orthophosphate). Oxygen and nutrient fluxes at T0 were comparable in all cores (all treatments being included, ANOVA, $p > 0.05$) (Table 3). The initial biogeochemical conditions (T0) of the experiment, which represent the natural conditions during the polar night, were characterized by a low SOD (−4.25 ± 0.93 SD mmol O_2 m^{-2} d^{-1},

Table 3 Results of one-way analysis of variance to detect differences in fluxes among treatments (NF, LF, HF) as fixed factor at the beginning of the experiment (T0) at p level >0.05

Benthic fluxes	F	p
Oxygen	$F_{2,12} = 1.07$	0.37
Nitrate + nitrite	$F_{2,6} = 0.39$	0.69
Silicate	$F_{2,6} = 0.57$	0.58
Ammonium	$F_{2,6} = 1.32$	0.33
Phosphate	$F_{2,6} = 1.39$	0.32

Table 2 Dominant macrofaunal species at sampling station

Species	Feeding type	Mobility type	Average density (ind. 0.1 m^{-2})	Average biomass (g 0.1 m^{-2})
Yoldiella solidula (M)	sdep	mob	110.3 ± 16.5	0.14 ± 0.04
Montacuta sp. juv. (M)	u	u	89.3 ± 54.6	0.05 ± 0.06
Maldane sarsi (P)	bdep	sed	36.7 ± 10.7	0.28 ± 0.08
Myriochele oculata (P)	sus/sdep	dm	29.7 ± 4.9	0.01 ± 0.00
Chaetozone spp. (P)	sdep	mob	29.3 ± 10.1	0.02 ± 0.01
Leitoscoloplos mammosus (P)	bdep	mob	27.7 ± 5.5	0.02 ± 0.01
Lumbrineris mixochaeta (P)	car	mob	13.0 ± 3.6	0.02 ± 0.00
Heteromastus filiformis (P)	bdep	mob	10.7 ± 4.2	0.00 ± 0.00
Chaetoderma nitidulum (M)	car	mob	8.7 ± 2.1	0.03 ± 0.01
Diastylis sp. juv. (C)	sus/sdep	mob	8.3 ± 5.1	0.01 ± 0.00
Aphelochaeta spp. (P)	sdep	mob	7.3 ± 2.3	0.01 ± 0.00
Cossura longocirrata (P)	bdep	mob	7.3 ± 7.1	0.00 ± 0.00
Levinsenia gracilis (P)	sdep/her	mob	7.0 ± 6.0	0.00 ± 0.00
Scoletoma fragilis (P)	car	mob	6.7 ± 3.5	0.02 ± 0.01
Aglaophamus malmgrenii (P)	car	mob	5.7 ± 3.8	3.80 ± 0.17
Chone spp. (P)	sus	sed	5.7 ± 5.0	0.00 ± 0.00
Aphelochaeta marioni (P)	sdep	mob	5.3 ± 6.1	0.01 ± 0.01
Yoldiella lenticula (M)	sdep	mob	5.0 ± 4.4	0.07 ± 0.05
Nemertea indet	car	mob	4.7 ± 0.6	0.19 ± 0.16
Ctenodiscus crispatus (E)	sdep	mob	1.7 ± 0.6	3.25 ± 3.55
Diastylis goodsiri (C)	sus/sdep	mob	1.3 ± 1.5	0.08 ± 0.12
Ophiopleura borealis (E)	sdep/car	mob	0.3 ± 0.6	3.57 ± 6.19

Species that occurred with average density >5 ind. 0.1 m^{-2} and/or average biomass >0.05 g 0.1 m^{-2} are listed

Letters in parentheses indicate higher taxonomic group: *P* Polychaeta, *M* Mollusca, *C* Crustacea and *E* Echinodermata. Feeding and mobility types are indicated as: *sus* suspension feeder, *sdep* surface deposit feeder, *bdep* burrowing (subsurface)-deposit feeder, *car* predator/scavenger, *her* herbivore, *mob* mobile, *dm* discretely mobile, *sed* sedentary and *u* unknown (average ± SD, $n = 3$)

which corresponds to an SCD of 43 ± 9.5 SD, Fig. 2), nitrate, orthophosphate and ammonium release (averages 0.363 ± 0.133 SD mmol $NO_3^- + NO_2^-$ m^{-2} d^{-1}, 0.020 ± 0.016 mmol PO_4^{3-} m^{-2} d^{-1}, 0.069 ± 0.081 SD mmol NH_4^+ m^{-2} d^{-1}) and silicate consumption (average −0.029 ± 0.037 SD mmol $Si(OH)_4^{3-}$ m^{-2} d^{-1}) (Fig. 3).

At the end of the experiment (T9), the SOD increased significantly over time in all treatments and differed among treatments (significant effect of both treatment and time, ANOVA Table 4; Fig. 2). The combined effect of treatment and time had a tendency to affect SOD, although this effect was not statistically significant ($p = 0.07$, Table 5). SOD measured at T9 in NF was significantly different from fluxes measured at T0 (HSD Tukey's tests, $p < 0.0012$). All treatments with food addition tended to have higher SOD than NF treatment, at the end of the experiment (increase of 2.4 and 5.0 mmol O_2 m^{-2} d^{-1} for LF and HF, respectively, corresponding to an increase of 24 and 51 mgC m^{-2} d^{-1}, respectively), although only for HF a significant increase compared with NF was documented (HSD Tukey's test, $p < 0.0048$).

Nitrate, phosphate and silicate fluxes varied significantly over time, but not among treatments (ANOVA Table 4; Fig. 3). The treatment × time effect was not significantly interactive (ANOVA Table 4). Whereas nitrate was released into the water column in all the treatments at the beginning of the experiment, one week later, it was consumed toward the sediment. Phosphate and ammonia releases toward the water column decreased with time, and silicate consumption by the sediment increased with time (Fig. 3).

Sedimentary organic matter and pigments

In the initial (T0) and final (T9) conditions without food addition (NF), both sedimentary chl *a* (∼0.5 µg cm^{-3}) and OM (∼6 %) profiles showed homogeneous vertical distribution of concentrations across the 10-cm sediment core (Fig. 4a, e). The chl *a*/phaeo ratio showed significantly higher values in subsurface (∼0.11 at 2 and 6 cm) compared with surface sediment layers (0.05, Fig. 4a, b) (two-way ANOVA: $F_{9,120} = 8.22$, $p < 0.001$, HSD Tukey's test: $p < 0.005$). Porosity at the initial (T0) and final (T9) conditions at NF averaged 0.8 in surface sediments, whereas it decreased significantly below 2 cm depth (∼0.7, Fig. 4i, j) (two-way ANOVA depth effect: $F_{9,120} = 95.40$, $p < 0.001$, HSD Tukey's test $p < 0.003$).

At T9, in the LF and HF treatments, surface (0–2 cm) sediments showed significantly higher chl *a* content (∼1.5 µg.cm^{-3}) and chl *a*/phaeo ratio (ANOVA chl *a* treatment × depth effect: $F_{27,120} = 2.90$, $p < 0.001$, HSD Tukey's test $p < 0.001$; ANOVA chl *a*/phaeo treatment × depth effect: $F_{27,120} = 4.09$, $p < 0.001$, HSD Tukey's test $p = 0.02$) (Fig. 4b, c, d). A slight peak of OM (∼7–8 %) were detected around 1.5 cm in LF and HF cores (Fig. 4c, d, g, h), but they did not lead to significant difference between these two treatments and NF treatment. Porosity values in NF treatment were significantly different from those in LF treatment (ANOVA treatment effect: $F_{3,120} = 4.33$, $p = 0.006$, HSD Tukey's test $p < 0.003$) with higher values in surface layers (ANOVA depth effect: $F_{9,120} = 95.40$, $p < 0.001$, HSD Tukey's test $p < 0.003$).

The OC/OM ratio was measured in 11 samples and found to be 0.27 ± 0.03 SD. This ratio enabled us to

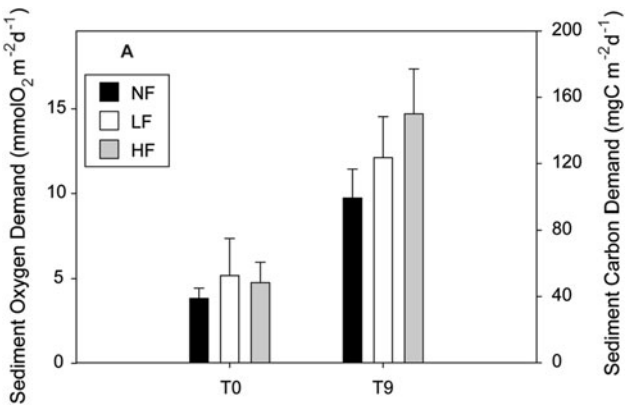

Fig. 2 Sediment oxygen and carbon demand for the initial conditions (T0) and after 9-day experiment (T9) for the three treatments: no food (NF), low food (LF) and high food (HF) (average ± SD, $n = 5$)

Table 4 Two-way ANOVA for sediment fluxes (oxygen, nitrate, silicate, ammonium and phosphate) using food treatments (NF, LF, HF) and time (T0 and T9) as factors

	Main effect				Interaction	
	Food treatment		Time			
	F	*p*	*F*	*p*	*F*	*p*
Oxygen	$F_{2,24} = 5.948$	***0.008***	$F_{1,24} = 115.212$	***<0.001***	$F_{2,24} = 2.938$	0.072
Nitrate + nitrite	$F_{2,12} = 0.895$	0.434	$F_{1,12} = 63.918$	***<0.001***	$F_{2,12} = 1.641$	0.234
Silicate	$F_{2,12} = 0.092$	0.913	$F_{1,12} = 36.833$	***<0.001***	$F_{2,12} = 1.932$	0.187
Ammonium	$F_{2,12} = 1.199$	0.335	$F_{1,12} = 0.490$	0.497	$F_{2,12} = 1.325$	0.302
Phosphate	$F_{2,12} = 0.491$	0.624	$F_{1,12} = 18.564$	***0.001***	$F_{2,12} = 1.790$	0.209

Significant levels ($p < 0.05$) are printed in italic/bold

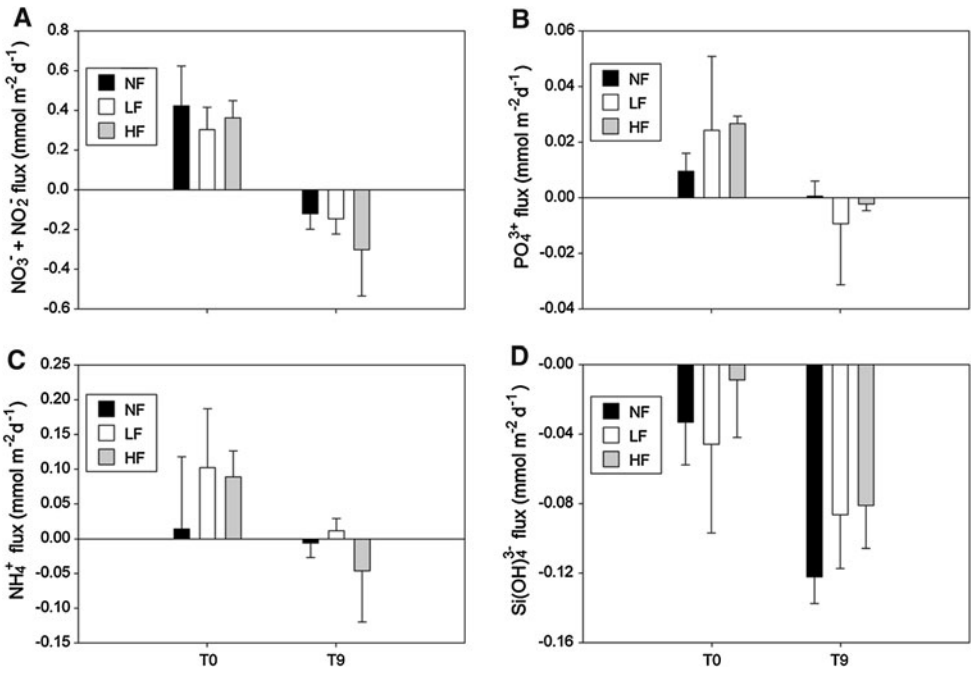

Fig. 3 Nutrient fluxes (nitrate and nitrite: $NO_3^- + NO_2^-$; phosphate: PO_4^{3-}; silicate: $Si(OH)_4^{3-}$; ammonium: NH_4^+) for the initial conditions (T0) and after 9-day experiment (T9) for the three treatments: no food (NF), low food (LF) and high food (HF) (average ± SD, $n = 3$)

Table 5 Sum of organic matter (OM), organic carbon (OC) and chlorophyll *a* (chl *a*) in the top 10 cm of sediment in the initial conditions (T0) and at the end of the experiment (T9) in the no-food (NF), low-food (LF) and high-food (HF) treatments

	OM (g m^{-2})	OC (g m^{-2})	Chl *a* (mg m^{-2})
T0	4,772.2 ± 213.2	1,307.1 ± 58.4	39.3 ± 5.0
T9-NF	4,407.0 ± 349.5	1,207.1 ± 95.7	38.6 ± 4.3
T9-LF	4,837.3 ± 522.6	1,324.9 ± 143.1	62.8 ± 14.8
T9-HF	4,918.9 ± 2,376.8	1,347.3 ± 651.0	49.5 ± 11.8

Note that organic carbon is estimated from organic matter values, using a OC/OM ratio of 0.27 ± 0.03 SD

calculate the total of OC present in the sediment cores from the OM contents. OM and OC did not differ between the various treatments and the initial T0 conditions (Table 5). Chl *a* biomass in the whole 10-cm core only was significantly higher in the LF treatment (~62 mg m^{-2}) compared with the NF (~38 mg m^{-2}) and HF treatments (~49 mg m^{-2}, Table 5) (ANOVA, $F_{3,12} = 4.56$, $p = 0.02$, HSD Tukey's test $p = 0.021$).

Bioturbation coefficients

After 9 days, almost all luminophores (~98 %) remained on surface in the NF treatment, whereas only ~90 and ~85 % were found in sediment surface of the LF and HF treatments, respectively. At 1, 1.5 and 3 cm, no luminophores (<0.1 %) were found anymore in the NF, LF and HF treatments, respectively (Fig. 5). The exponential decrease in the luminophore distribution over depth (Fig. 5) was, however, faster in the HF treatment since 13 % of the luminophores were found at 1 cm deep, versus 8 % of the luminophores at the same depth for the LF treatment.

Biodiffusion and nonlocal transport rates ranged from 0 to 0.25 cm^2 y^{-1} and from 0.3 to 11 y^{-1}, respectively (Fig. 6). Although biodiffusion coefficients tended to be slightly higher in food addition treatments, they were not significantly different compared with NF treatment (ANOVA, $F_{2,11} = 1.13, p = 0.36$). Advection rates were, however, significantly different between treatments (ANOVA, $F_{2,11} = 4.46$, $p = 0.038$). Only the HF treatment produced a significantly higher advective transport (5.23 ± 3 SD y^{-1}) compared with NF (1.08 ± 0.8 SD y^{-1}) (HSD Tukey's test, $p < 0.031$).

Discussion

Baseline and methodology

Polar night period

This is the first report on benthos in Rijpfjorden in wintertime and one of the very few benthic studies conducted hitherto in this fjord. Carroll and Ambrose (2012) visited a

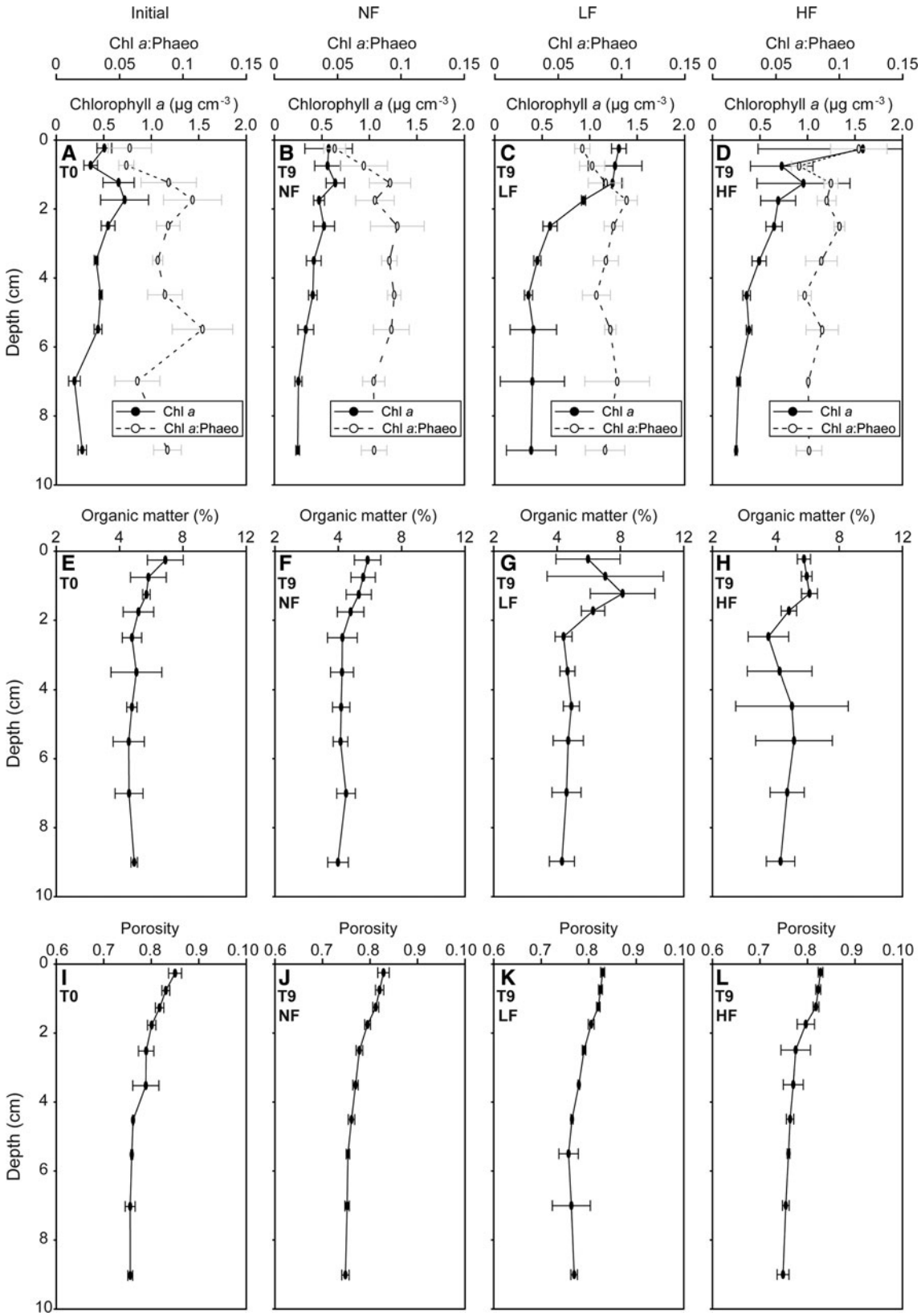

Fig. 4 Profiles of chlorophyll *a* and chlorophyll *a*-to-phaeopigment ratio (chl *a*/phaeo) (**a**, **b**, **c**, **d**), organic matter (**e**, **f**, **g**, **h**) and porosity (**i**, **j**, **k**, **l**) in the initial conditions (T0, **a**, **e**, **i**) and at the end of the experiment (T9) in the three treatments: no food (NF, **b**, **f**, **j**), low food (LF, **c**, **g**, **k**) and high food (HF, **d**, **h**, **l**) (average ± SD $n = 5$)

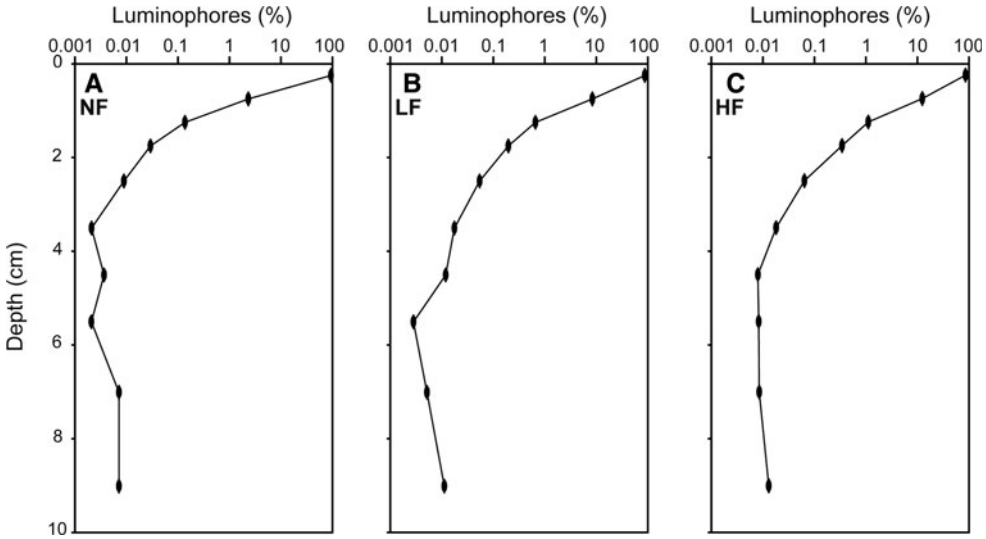

Fig. 5 Profiles of luminophores (% in log scale) for the three treatments: **a** no food (NF), **b** low food (LF) and **c** high food (HF) (average ± SD, $n = 5$)

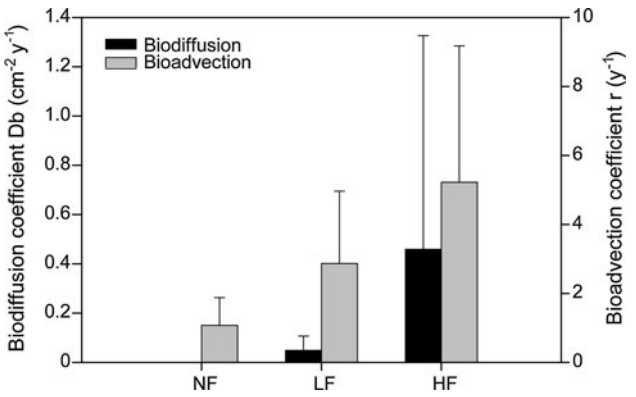

Fig. 6 Bioturbation coefficients, biodiffusion (cm^{-2} y^{-1}) and bioadvection (y^{-1}), in the three treatments: no food (NF), low food (LF) and high food (HF) (average ± SD, $n = 5$)

station located in inner fjord at 205 m and one located at 239 m on shelf off Rijpfjorden in August 2003. They reported comparable macrofauna densities (252–766 ind. 0.1 m^{-2}) and species richness (75–76 species per station) to values reported in the present study. Densities and dominant species reported from Rijpfjorden in winter and summer seasons are similar to those documented in other Svalbard fjords (e.g., Włodarska-Kowalczuk et al. 2005; Włodarska-Kowalczuk et al. 2012). The values of infaunal biomass reported in this study in winter are, however, much lower than those documented by Carroll and Ambrose (2012) in the same fjord in summer season (11.5–12.8 g 0.1 m^{-2}). The decline in infaunal biomass in Arctic fjords in winter was also observed by Pawłowska et al. (2011). In Adventfjorden (west Spitsbergen), biomass was six to seven times lower in winter (November, February) than in spring (May) and two to three times lower in winter than in summer (July). These changes in biomass followed the seasonal variability in particulate organic matter (and especially the chl *a*) sedimentation (Pawłowska et al. 2011).

Fluxes measured in the first T0 set represent the initial condition of the system. Since in winter, from January to March, primary production is at its lowest and vertical fluxes are at minimum (Juul-Pedersen et al. 2008; Zajączkowski et al. 2010), the measurements represent the baseline of the system, before any spring inputs reach the seafloor. Scarce winter studies in the Arctic mainly dealt with the pelagic domain (Søreide et al. 2008; Berge et al. 2008) or sympagic fauna (Werner and Auel 2005). Very few focussed on benthic activities and benthic food web structure during winter (Rysgaard et al. 1998; Grebmeier et al. 2006b; Renaud et al. 2007b; Link et al. 2011; Morata et al. 2011; Kedra et al. 2012). To our knowledge, only three studies measured sediment oxygen/carbon fluxes in winter at similar depths (Renaud et al. 2007b; Morata et al. 2011; Link et al. 2011), and two looked at benthic fluxes at shallower depths (Rysgaard et al. 1998; Grebmeier et al. 2006b). The SOD/SCD measured in the initial T0 set in the present study was about three times higher than those measured in the Beaufort Sea at similar depths and season (Renaud et al. 2007b), but in a similar range to values obtained in a Greenland fjord at same time but at shallower depths (Rysgaard et al. 1998). The SOD/SCD values measured in the present study are also within the range observed at similar depths in summer in other Svalbard fjords and areas (Pfannkuche and Thiel 1987; Hulth 1994; Glud et al. 1998; Jorgensen et al. 2005; Gihring et al. 2010), although not as high as those measured in the Barents Sea (Renaud et al. 2008). Similarly, at T0, total sedimentary chl *a* concentrations in the top 10 cm were also about four times higher than the amount observed in the Beaufort Sea (Morata et al. 2011), but in similar range to those observed in Svalbard area at similar depths

(Pfannkuche and Thiel 1987) and in Rijpfjorden in summer season (Carroll and Ambrose 2012), suggesting that the sediment in Rijpfjorden is still influenced by phytodetritus inputs persisting since the year before, sustaining active benthic communities throughout the winter.

In Young Sound sediment, Rysgaard et al. (1998) showed that aerobic pathways dominated in wintertime. The present study showed similar results, since benthic nutrient fluxes and particularly nitrate effluxes-to-stoichiometric fluxes ratio ($O_2/N \sim 6.66$; significant regression coefficient $R^2 = 0.63$, $p < 0.005$) strongly correspond to the steady-state Redfield average plankton compositions (6.6), also indicating aerobic mineralization (nitrification) at depth in sediments of Rijpfjorden at wintertime.

Experimental setup

Although at T9 the NF treatment should have presented similar results to the initial T0 conditions, the differences observed may be a result of changes in microbial activities. The aerobic remineralization processes observed at the initial T0 conditions were changed at the end of the experiment in NF treatment. SOD was not correlated with the other nutrient measured fluxes, suggesting that organic matter was not oxidized linearly by aerobic bacterial processes but rather by anaerobic dominant pathways. The OM input to the cores may favor anaerobic bacterial processes usually observed after spring blooms or in high-deposit systems. Reoxidation of metabolites in the experimental system may have occurred during the 9 days if metabolites' diffusion toward the sediment surface was accelerated by the boat motions (strong storms in January in North Atlantic). Although the cores were secured, the bad weather created a constant motion that may have agitated the sediment–water interface, creating a release of sediment metabolites to the overlying waters. Seawater was totally changed 24 h after the sampling, but it was only partially changed over the next days. Therefore, one of the suggestions to explain why the experimental conditions changed between initial T0 conditions and T9 NF treatment may be a consequence of this; the metabolites' accumulation in the oxygenated overlying water may have stimulated aerobic/anaerobic oscillation pathways and stimulated anaerobic mineralization (Aller 1994). Such modifications of stoichiometric ratios due to experimental setup were already observed by Michaud et al. (2009, 2010). Another explanation could be the slightly higher temperature in the cold room (3 °C) compared with the natural conditions (around 0–1 °C at the sampling time, J. Berge, Pers. Comm)—a difference that is known to induce changes in biogenic dissolution and oxygen solubility. However, this experimental artifact affected most likely all cores in the same way. So, although the oxygen and nutrient fluxes at T9 in NF were different than at the initial T0 conditions, the baseline must have changed and differed from the natural conditions in the same way in all treatments. Thus, although the absolute values must be taken with caution, the relative comparison between treatments at T9 remains therefore valid.

Impact of food inputs on sediment oxygen demand

The impact of food inputs on the benthic activities during the Arctic polar night had never been addressed experimentally. Only few studies have addressed natural changes of SOD and benthic nutrient fluxes during the winter/early spring to summer transition on Arctic shelves (Rysgaard et al. 1998; Grant et al. 2002; Lepore et al. 2007; Renaud et al. 2007b; Link et al. 2011). All the cited studies, except the one of Lepore et al. (2007), found an increase in SOD after the disappearance of ice cover and increase in organic matter vertical fluxes or pelagic algal biomass. The increase ranged from about 28 % in the Beaufort Sea (Link et al. 2011) to about 160–200 % in the Greenland Sea and North Water Polynya (Rysgaard et al. 1998; Grant et al. 2002) and a maximum change of 1,100 % in the Beaufort Sea (Renaud et al. 2007b). Conversely, in Antarctica shelf sediment, it has been found that OM reaching the seafloor during episodic events does not represent an important, immediate food source for the benthos, and it is rather preserved as a long-term "food-bank" (Mincks et al. 2005). Thus, the benthic activities are not strongly related to the seasonal variability in OM vertical fluxes (McClintic et al. 2008). In the present experimental study, the addition of freeze-dried phytoplankton led, after 9 days, to an SOD increase of about 24 and 51 % for LF and HF, respectively, invalidating the "food-bank" theory here. The higher food input led to a higher increase in SOD, although none of these values are comparable to the extreme values observed during an ice algal input to the bottom of the Beaufort Sea (Renaud et al. 2007b). During the time of the study in the Beaufort Sea, vertical fluxes of carbon were about 24 mg d^{-1} m^{-2} (Juul-Pedersen et al. 2008), which would represent an input of 216 mg m^{-2} for 9 days, a range between the LF and HF (Table 1). The response of the benthos is therefore not proportional to the absolute values of the food inputs. The results obtained in one area in the Arctic might not be always generalized to other Arctic shelves and fjords.

If the SOD rates were constant over the 9 days of the experiment, this would represent an increase in the C uptake of 220 and 458 mg m^{-2} in LF and HF, respectively, as compared with the C uptake in the NF treatment. The excess of carbon used by respiration in the food treatment matched the values added (Table 1). This suggests that all the material added to the experimental cores has been used

by the increased metabolism. Due to logistic constraints, it was impossible to continue the experiment after 9 days. It has been suggested that the Arctic benthos may respond quickly to inputs of fresh algal material (Graf 1992; McMahon et al. 2006; Sun et al. 2007), and the SOD observed after 9 days may be the maximum activity of the benthos. The amounts of OM, OC and chl *a* found in the LF and HF treatments (Table 5 LF and HF) at T9 are close to the initial values (recorded at T0) rather than values expected after experimental food addition. Since the benthos have already consumed the added algal material, if respiration keeps increasing or stays that high, the benthos will need to rely on additional alternative food sources to maintain its activities on a level higher than the baseline.

Interestingly, conversely, it has been suggested that some deposit feeders may primarily feed on the fraction of miscellaneous dead organic material and that therefore, there may be lack of time between the inputs of fresh material and its ingestion, which will start as the material starts to degrade (Hansen and Josefson 2004). In this case, the SOD rates observed in the present study may not be at their maximum and could keep increasing beyond 9 days. However, in a high Arctic fjord in Greenland, the spring bloom led to an increase in SOD, which lowered back to the baseline value about a month after the event (Rysgaard et al. 1998).

Reworking of organic matter and importance of macrofauna

Sediment carbon and nutrient fluxes gave information about the changes in activities of the overall benthic community including bacterial activities. Bioturbation coefficient provided, however, crucial information regarding the importance of macrofauna activities inside sediments (Fig. 6). The results from the NF treatment showed that although biodiffusion is null, bioadvection is non-negligible (1.08 y^{-1}) during the polar night and is similar to values observed within benthic communities in temperate areas during winter (Duport et al. 2007). The most abundant species (> 10 ind. 0.1 m^2) such as *Yoldiella solidula*, *Maldane sarsi*, *Chaetozone spp, Leitoscoloplos mammosus* and *Heteromastus filiformis* should explain the dominant conveyor behavior that we quantified in the NF sediments. Previous studies in other ecosystems or in experimental microcosms already showed that those species actively transfer sediment directly into deep layers from the surface or inversely into surface layers from deeper layers of the sediments (Bender and Davis 1984 for *Yoldia spp*, Smith and Schafer 1984 for *Maldane spp*, D'Andrea et al. 2004 for *Leitoscoloplos and Heteromastus spp*). Similar observation was made for *Ctenodiscus crispatus* (Shick 1976). This species, although with the highest biomass in the Rijpfjorden sediments, was not found in our cores, and so it cannot be used to explain the results of the experiment. Biodiffusers such as *Myriochele oculata* (Duchene and Rosenberg 2001) or *Aglaophamus malmgrenii* occurred with lower biomass (0.01 ind 0.1 m^{-2}) and probably had no detectable impact on the diffusive sediment mixing rates during the wintertime in Rijpfjorden. The conveyor transport mode of sediment was not very deep as observed in the profiles, but very subtle over the first millimeters of the sediments. The small bioturbation depth and the low bioadvection rates highlighted, however, that those biological activities are quite weak during the wintertime.

When food was added, both biodiffusion and bioadvection increased. Macro-organisms seem to have reacted to the input of "fresh" food. Indeed, although the amount of OM added (Table 1) was very low compared with the amount of OM already present in the sediment cores (addition of about 5 and 25 % for LF and HF, respectively, compared with the amount of OM already present in the cores, Tables 1 and 5), the amount of chl *a* added was much higher (addition of about 300 and 1,700 % for LF and HF, respectively, compared with the amount of chl *a* already present in the cores, Tables 1 and 5). Interestingly, after 9 days, the amount of chl *a* present in the cores with food addition did not reflect the input values, suggesting that almost all material added had been consumed. Although an important amount of OM was already present in the sediment (probably remaining from the last year productivity season), organisms seem to have selected the fresh input and increased their carbon demand according to the amount of fresh food added. These results confirm the results found in other Arctic seas, which suggested that the benthos respond not only to the quantity of food inputs, but also to their quality (Grant et al. 2002; Clough et al. 2005; Dunton et al. 2005; Morata and Renaud 2008; Morata et al. 2008; Morata et al. 2011).

In response to food input, bioadvection was more pronounced until 2–3 cm (Fig. 5), suggesting that the active sediment transport mode such as conveyors or gallery-diffusor behavior remained dominant in these conditions. The composition of macrobenthic community was described with the use of samples collected at the beginning of the experiment. Since temperature is known to increase bioturbation coefficients (Ouelette et al. 2004), it would be possible that the very small increase in temperature in the cold room during the cruise may have led to an increase in biological activities in all treatments. The small bioturbation coefficients measured in NF treatments (after 9 days of incubations) may therefore be an experimental artifact. But, although the absolute values must be taken with caution, the relative comparison between treatments at T9 remains valid.

If we are not able to precisely determine what species changed its bioturbation mode, we mainly propose two hypotheses: Hypothesis (1) presents species in the

sediments of conveyor group (*Yoldiella solidula*, *Maldane sarsi*, *Chaetozone spp, Leitoscoloplos mammosus* and *Heteromastus filiformis*) or biodiffuser group (*Myriochele oculata, Aglaophamus malmgrenii*) may change their behavior following food input to become biodiffusor, conveyor or gallery-diffusor. Such behavioral changes with variable food concentrations were already experimentally characterized with *Nereis diversicolor* and *Macoma balthica* in subarctic areas (de Goeij and Luttikhuizen 1998; Christensen et al. 2000). Stead and Thompson (2006) tested the hypothesis that the feeding behavior of a yoldiid bivalve *Yoldia hyperborea* changes with the pulses of nutrient-rich OM. After the addition of algae, there was an increase in activity; the bivalves switched from subsurface to surface deposit feeding and partial reemergence of animals from the sediment that lasted for 2–3 days. The animals then reburied back to their standard position (just below the sediment surface), which resulted in sediment mixing in upper sediment layers. As for Long Island Sound, the yoldiids seem to be important bioturbators, but their bioturbatory potential is not year-round constant; instead, these bivalves are most active during the spring bloom, as long as the fresh food in sediments is depleted. *Myriochele* spp. that live in tubes and are discretely mobile can also be both suspension and surface deposit feeders, similarly to *N. diversicolor* (Christensen et al. 2000). Hypothesis (2) states that there was no change in the mode of bioturbation, but species of the different groups became more active with food addition, increasing only the intensity of the bioturbation rates, as it has been already observed during the winter/summer transition in temperate areas (Duport et al. 2007).

Benthic fluxes were much higher when bioturbation is increased by food addition, although only SOD was significantly higher in HF treatment. If experimental conditions have changed dominant sedimentary mineralization pathways in our setup, increased bioturbation activities probably enhanced benthic fluxes. Burrows, for example, are known to increase the exchange surface area with the overlying water by introducing oxygen inside reduced sediments, promoting bacterial oxidation processes leading to higher respiration and nutrient release (Aller 1994; Gilbert et al. 2003; Jorgensen et al. 2005). Previous studies showed that benthic fluxes can be spatially dependent on the bioturbation functional group influence (Michaud et al. 2005, 2006; Michaud et al. 2009).

Conclusion

The present study is in agreement with previous Arctic studies, but contrasts with the results obtained in Antarctica, probably invalidating the food-bank theory in Rijpfjorden in winter. In our experiment from Arctic sediment, the benthos can use the bulk of OM remaining from the last productivity season, but events of fresh phytodetritus supply to the seafloor induce the clear signals in benthic activity, and the fresh material is quickly consumed, suggesting that the OM content, especially the quality of available food in the sediments in winter, remains a limiting factor for benthic communities.

It has been suggested that climate change may lead to either earlier and increased food inputs, or a weakening of today's highly episodic production, resulting in a continuous, but lower, food concentration (Wassmann and Reigstad 2011). While the LF treatment meant to reflect the present-day situation, with a spring bloom of a low intensity, the HF treatment simulated a climate change scenario where food inputs are higher, and NF treatment simulated a scenario with lower/no food inputs. Since benthic activities (respiration and bioturbation) were higher in HF, this would suggest that in this scenario, the benthos may increase its overall energy needs. If food supply remains high throughout the year, benthic communities may be sustained. However, if the inputs are only a short pulse, benthic communities may have higher needs (i.e., for physiology, reproduction) that may not be met, leading to a collapse of the community. In the case of lower/no food supply, despite the presence of organic matter and pigments in the sediment, activities were at their lowest. A minimum addition of fresh food is needed for triggering an increase in activities. If food supply is too low, this threshold may not be met and the benthos may not start its activities, such as reproduction. Our experiment suggests that the Arctic benthos may depend on spring inputs of fresh algal detritus from the overlying bloom: An increase or decrease in this supply may negatively affect the benthic communities, having repercussion on carbon and nutrient recycling.

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