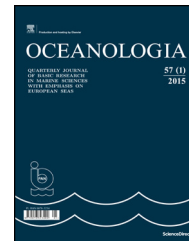




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ORIGINAL RESEARCH ARTICLE

# Total benthic oxygen uptake in two Arctic fjords (Spitsbergen) with different hydrological regimes

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Received 8 July 2016; accepted 27 November 2017

Available online 6 December 2017

## KEYWORDS

Sediment oxygen uptake;  
Respiration partitioning;  
Carbon demand;  
Svalbard fjord;  
Arctic

**Summary** Benthic total oxygen uptake (TOU) was measured in two Arctic fjords (NW Spitsbergen shelf) with different hydrological regimes: Hornsund with “cold” coastal Arctic waters and Kongsfjorden with “warm” Atlantic shelf waters. TOU rates in Kongsfjorden were more than 50% higher than in Hornsund. This is presumably related to the relatively higher biomass of bacterial and faunal (meiobenthos and macrofauna) communities in Kongsfjorden as compared to Hornsund caused by the source of organic matter: Kongsfjorden is dominated by marine, Hornsund by terrigenous organic matter. We conclude that the quality of organic matter supplied to marine sediments influences the biomass of benthic organisms and the rate of oxygen consumption. Therefore the Kongsfjorden sea bed has much higher oxygen uptake and hence a greater carbon demand than Hornsund.

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Peer review under the responsibility of Institute of Oceanology of the Polish Academy of Sciences.



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## 1. Introduction

In deeper waters, where primary production does not occur, benthic parameters like oxygen or carbon demand depend on the food supply from external sources. Therefore, they are considered 'recipients' of biological processes occurring in the water column, from which valuable amounts of nutrients are received (Pusceddu et al., 2007). Present-day rises in air and ocean temperatures are well documented, especially in the

<https://doi.org/10.1016/j.oceano.2017.11.005>

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Arctic areas. It should be assumed that such changes will intensify in the coming years (Johannessen et al., 2004). Increasing temperatures, ice cover melt and fluvial run-off growth will affect all trophic levels in ecosystems (Piepenburg, 2005). But it is unclear how these changes will impact the fjord ecosystems in the Svalbard archipelago. For this purpose, two comparable stations in two fjords in the west of Spitsbergen, differently exposed to the present-day hydrological regime, were investigated.

The measurement of oxygen consumption, i.e. total oxygen uptake (TOU), is still the standard method of estimating the flow of energy and carbon demand of organisms within marine sediments (Rowe et al., 2008). At shallow depths it is generally assumed that TOU is a direct estimate of the coupling between benthic and pelagic processes (Graf, 1992). In the Arctic region, a number of TOU measurement campaigns have been run, e.g. in the Chukchi and north Bering Seas (Grebmeier and McRoy, 1989), in Greenland fjords (Glud et al., 2000; Rysgaard et al., 1996, 1998, 2004) and in the Svalbard area (Glud et al., 1998; Hulth et al., 1994; Kostka et al., 1999; Piepenburg et al., 1995; Thamdrup and Fleischer, 1998).

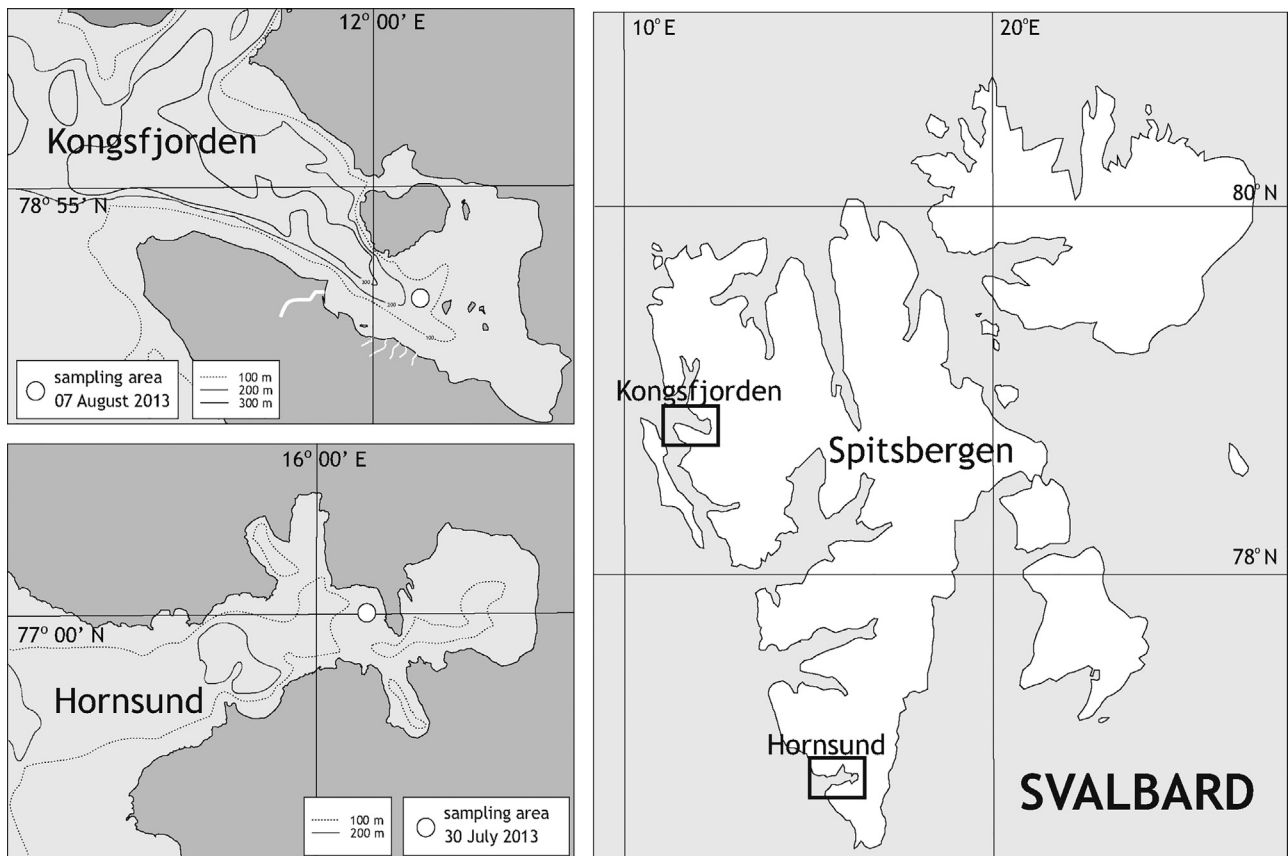
The present investigation was designed to address the following questions: What is the oxygen consumption by sediments in environmentally different fjords? How is oxygen uptake related to the meio- and macrofaunal communities?

## 2. Material and methods

### 2.1. Study area

The area of west Svalbard is strongly influenced by the relatively warm and nutrient-rich water arriving from the Atlantic Ocean, whereas cold Arctic water determines the environmental conditions to the east and north of Svalbard (Jones and Anderson, 1990). Kongsfjorden and Hornsund are located at 79°N and 77°N, respectively. The Atlantic water carried by the West Spitsbergen Current (WSC) directly influences the temperature of Kongsfjorden. On the other hand, cold water masses from the Barents Sea driven by the South Cape Current (SCC) affect Hornsund farther south. Kongsfjorden and Hornsund are two glacial fjords without sills at their entrances. They are of comparable size: Hornsund is 30 km long and up to 15 km wide and has an average depth of 90 m, while Kongsfjorden is 26 km long, up to 16 km wide but is significantly deeper, over 300 m at the entrance (Fig. 1). Two sampling areas were situated in the inner part of each fjord at about 100 m depth. The sediments of the fjords consist of poorly-sorted, medium-grained silt.

The sampling stations were located in the central/inner parts of both fjords on a flat bottom where the sediment is soft. The geographical positions, bottom water temperature and oxygen content are listed in Table 1.



**Figure 1** Localization of the investigated fjords at Svalbard archipelago (right panel) and the sampling areas in Kongsfjorden (left top panel) and Hornsund (left bottom panel).

## 2.2. Sediment core incubation

Total benthic oxygen uptake (TOU) was measured using incubations of surficial sediments and bottom water within chambers. Undisturbed sediment cores with ambient bottom water were collected with a box corer on 30 July 2013 at the stations in Hornsund and on 7 August 2013 in Kongsfjorden. Six cores, 11.4 cm in diameter and containing approximately 15 cm of overlying water, were collected from each cast by inserting Plexiglas tubes into the sediments. The tubes with sediment cores were placed in a container and filled with well oxygenated bottom water if necessary. The area of sediment covered approximately 100 cm<sup>2</sup> and the seawater volume above the interface varied from 0.85 to 1.8 dm<sup>3</sup>. Plexiglas lids with a rubber O-ring were equipped with an electric steering motor, and Teflon-coated magnetic bars were gently placed on the core tubes without trapping any air. The incubation temperature in the container was adjusted when necessary to correspond to in-situ bottom water temperatures (2.8/3.5°C respectively). The chambers were maintained in the dark and at the in-situ temperature, during which oxygen concentration was measured over periods of about 50 h. Six replicate incubations were made in each area. Direct measurements of dissolved oxygen were carried out using a microsensor (oxygen electrode) (Unisense Denmark), an IntelliCAL LDO101 probe and an appropriate HACH multimeter.

The oxygen uptake rates [mmol m<sup>-2</sup> d<sup>-1</sup>] were calculated as a function of the incubation time on the basis of the oxygen concentration in the overlying water column. They were defined as Total Oxygen Uptake TOU, which includes diffusion and biologically mediated transport of oxygen into sediment. At the same time a “control” tube filled with seawater was incubated without sediments.

Additionally, oxygen profiles in the sediment were measured immediately after sampling with a high-performance microsensor (Unisense Denmark) for non-destructive measurements of oxygen. The response time of the oxygen microsensor is less than 0.3 s and it has insignificant oxygen consumption, giving fast and accurate oxygen measurements.

## 2.3. Laboratory analysis and calculations

Meio- and macrofauna were extracted from the sediment after incubation from each core, identified to the highest taxonomic level, counted and weighed. For this purpose a

Plexiglas tube with an inner diameter of 3.6 cm was pushed into the sediment. Meiofaunal material was fixed with a 4% formaldehyde–seawater solution. LUDOX silica density gradient centrifugation (density 1.18 g cm<sup>-3</sup>) was used to extract meiofaunal organisms from the sediment (Heip et al., 1985). After centrifugation, the supernatant was passed through 500 μm and 32 μm sieves. Samples retained on the 32 μm sieve were stained with Rose Bengal dye (Sigma–Aldrich). Subsequently, the meiofauna organisms were identified to the highest taxonomic level (phylum, class or order), and the abundance of particular taxa was expressed per 10 cm<sup>2</sup>. For biomass calculation nematodes were measured individually using an image analyser (AxioCam Zeiss). The body length (*L*) was measured from head to tail (excluding filiform tails). The width of the nematodes (*W*) was measured at the thickest part of the body. Individual nematode biomass was calculated using an adjusted version of Andrassy's formula (1956): wet weight [μg] = *L* [μm] × *W*<sup>2</sup> [μm]/1,600,000. Macrobenthic organisms from each core were sorted, identified to the highest taxonomic level and weighed. Meiofaunal respiration was estimated using the function of Grant and Schwinghamer (1987)  $R = 2.90 V^{0.80}$ , where *V* is the total meiofaunal biovolume. For estimating macrofaunal respiration we used the biomass of the major taxa and the mass-specific metabolic rates given by Piepenburg et al. (1995). Oxygen consumption rates were converted into carbon demand by assuming a 1:1 stoichiometric relationship between oxygen and carbon consumption. Hargrave (1973) assumed that sediment oxygen uptake could be converted to carbon release by applying a respiratory coefficient RQ value of 0.85.

## 2.4. Statistical analysis

To determine whether there are statistically significant differences between the two basins, the Kruskal–Wallis *H* test, a rank-based nonparametric test, was used to compare independent variables of oxygen consumption and faunal communities.

## 3. Results

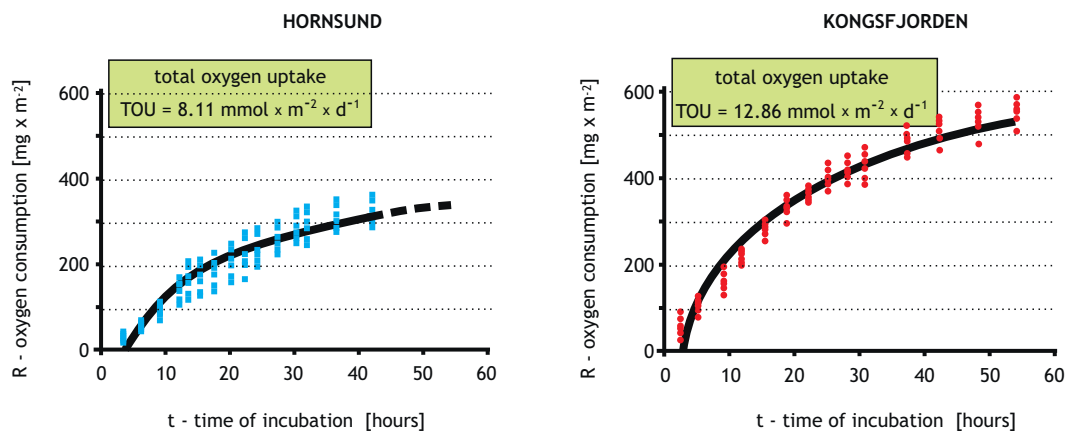
### 3.1. What is the oxygen consumption by sediments in environmentally different fjords?

Mean total oxygen uptake TOU was 8.11 (±0.87) in Hornsund and 12.86 (±0.69) mmol m<sup>-2</sup> d<sup>-1</sup> in Kongsfjorden (Fig. 2). The Kruskal–Wallis test showed that these results differed significantly (*p* = 0.0039) between the fjords (Fig. 3). The variability in the measurements at both sites was low, with a relative standard deviation of 5%, reflecting the necessary precision of the method and the homogeneous variation of the benthic community on the sea floor. Finally, during the respiration experiment, 27% and 25% of the initial oxygen content were consumed in the incubation chambers.

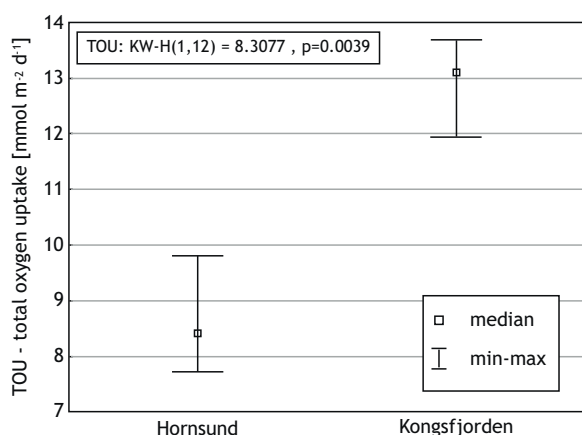
The oxygen concentration profiles in sediment for the Hornsund and Kongsfjorden stations are illustrated in Fig. 4. The Kongsfjorden site had a higher initial value, likely reflecting a higher oxygen concentration in the water column.

**Table 1** The sampling stations in Hornsund and Kongsfjorden – geographical position, bottom water temperature and oxygen content.

Site	Geographical position	Depth [m]	Bottom water temperature [°C]	Bottom oxygen content [%]
Hornsund	77°00.02'N 16°05.44'E	98	2.8	77.6
Kongsfjorden	78°55.85'N 12°08.37'E	105	3.5	88.4

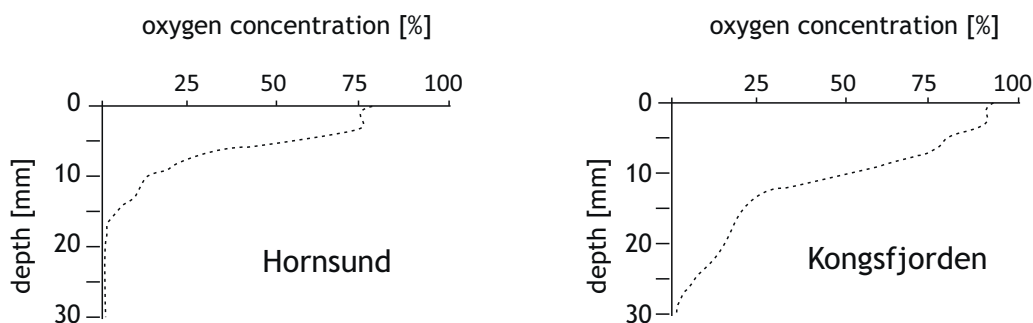


**Figure 2** Total sediment oxygen consumption [ $\text{mg m}^{-2}$ ] over incubation time in Hornsund (left panel) and in Kongsfjorden (right panel) for the ambient temperature in both areas; calculated total oxygen uptake (TOU) within the rectangles.



**Figure 3** Total oxygen uptake in Hornsund and Kongsfjorden – Kruskal–Wallis test result.

The oxygen concentration gradients in the sediment were rather steep in both areas, despite the high bottom water  $\text{O}_2$  concentrations: 77.6% in Hornsund and 88.4% in Kongsfjorden. In Hornsund the suboxic zone was reached at a depth of 1–2 cm, and in Kongsfjorden the thickness of the oxic sediment layer was greater, up to 2–3 cm, where oxygen was almost depleted.



**Figure 4** Oxygen concentration profiles in the 30 mm thick sediment surface layer in Hornsund (left panel) and in Kongsfjorden (right panel).

### 3.2. How is oxygen uptake related to the meio- and macrofaunal communities?

The biomass of the macrofauna was highly variable within both areas but the meiofaunal biomass was in the same range and there was no difference with respect to nematode dominance (Table 2).

The total biomass of macrofauna (extracted from the incubated sediment cores) in Kongsfjorden was a dozen times larger than in Hornsund, which resulted in proportionate levels of oxygen consumption, i.e. 7.8% and 0.7% of the total benthic oxygen uptake, respectively. The meiofauna contributed roughly 5% of the total sediment oxygen uptake in both fjords.

## 4. Discussion

Hornsund and Kongsfjorden are among the best studied areas in the Svalbard archipelago (e.g. Svendsen et al., 2002). Incubation of sediment cores and monitoring dissolved oxygen concentration in the ambient water allows the energy flow through benthic communities to be estimated. The oxygen uptake of the sediment is still a widely used method for measuring total benthic mineralization, which is a proxy of total benthic ecosystem functioning, i.e. activity and benthic remineralisation (Glud, 2008; Holstein and Hensen, 2010). By benthic remineralisation we mean the degradation

**Table 2** Average biomass [ $\text{g m}^{-2}$ ] of meiofauna and macrofauna (particular taxa) extracted from incubated cores and calculated respective oxygen consumption rates [ $\text{mmol m}^{-2} \text{d}^{-1}$ ].

Area	Biomass wet weight [ $\text{g m}^{-2}$ ]				Oxygen consumption rates [ $\text{mmol m}^{-2} \text{d}^{-1}$ ]		
	Macrofauna		Meiofauna		Macrofauna		Meiofauna
Hornsund	Crustacea	—	Nematoda	$0.53 \pm 0.10$	Crustacea	—	
	Polychaeta	$3.1 \pm 0.6$	Polychaeta	$0.01 \pm 0.01$	Polychaeta	0.045	
	Mollusca	$2.1 \pm 4.8$	Harpacticoida	$0.01 \pm 0.01$	Mollusca	0.008	0.45
	Others	$0.1 \pm 0.2$	Others	$0.02 \pm 0.01$	Others	0.003	
	Total	$5.4 \pm 5.3$	Total	$0.57 \pm 0.21$	Total	0.056	
Kongsfjorden	Crustacea	$3.6 \pm 3.1$	Nematoda	$0.40 \pm 0.14$	Crustacea	0.263	
	Polychaeta	$32.6 \pm 9.7$	Polychaeta	$0.01 \pm 0.01$	Polychaeta	0.469	
	Mollusca	$25.7 \pm 19.9$	Harpacticoida	$0.01 \pm 0.01$	Mollusca	0.088	0.50
	Others	$3.7 \pm 4.9$	Others	$0.01 \pm 0.01$	Others	0.093	
	Total	$65.7 \pm 27.1$	Total	$0.42 \pm 0.16$	Total	0.913	

of organic matter (OM), whereby carbon dioxide and inorganic nutrients flow from the sediments back into the water column (Link et al., 2013). Benthic communities use organic matter to grow and maintain their populations. Part of the organic matter that reaches the bottom is recycled and reused, e.g. for secondary production, while the remainder becomes buried in the sediment (Clough et al., 1997). The quantity and quality of organic matter falling to the seafloor serves as food and influences all biotic assemblages, including microbial production (Meyer et al., 2013). The total oxygen uptake of the sediments investigated in this study is close to that in other studies of Svalbard fjords at comparable depths measured by core incubation (Table 3).

These values are also similar to oxygen uptake rates in shelf sediments of temperate latitudes. The benthic respiration rate in Arctic is thus of the same magnitude as in warmer areas, indicating that the benthic Arctic system is no less productive (Glud et al., 1998).

Diverse bottom communities play a crucial role in the remineralization of the organic matter settling on the sea bed. Benthic communities consist of mega- (>4 mm), macro- (500  $\mu\text{m}$ –4 mm), meio- (32  $\mu\text{m}$ –500  $\mu\text{m}$ ) and microfauna (<32  $\mu\text{m}$ ) (Bluhm et al., 2011). Generally, in Arctic shelf sediments in the Barents Sea, oxygen uptake is dominated by the microbenthos (57%), followed by the macrobenthos (21%), megabenthos (15%) and meiobenthos (7%) (Piepenburg et al., 1995). In Hornsund and Kongsfjorden, there are distinct differences in both density and biomass in the standing

stock of all benthic assemblages, which are reflected by different oxygen uptake rates and carbon demands. Also the total bacteria number was relatively higher in Kongsfjorden than in Hornsund,  $4.27$  and  $3.39 \times 10^9$  cell  $\text{cm}^{-2}$ , respectively, same as bacterial biomass  $2.16$  and  $1.56$   $\text{gC m}^{-2}$ , respectively (Jankowska, unpublished data). The measured sediment oxygen uptakes may be equivalent to total benthic carbon demands of  $52$  and  $86$   $\text{gC m}^{-2} \text{y}^{-1}$  in Hornsund and Kongsfjorden, respectively (Table 4).

It is commonly assumed that the organic carbon which is not channelled through the pelagic food chain governs both the biomass and the production of the benthos (e.g. Danovaro et al., 1999). The amount of organic carbon reaching the benthos depends principally on the intensity of primary production in the water column (Ambrose and Renaud, 1995; Graf, 1989). On the other hand, the density, composition and activity of benthic communities, including bacteria, micro-, meio- and macrofauna, reflect processes such as pelagic-benthic coupling, mineral and organic sedimentation, freshwater input and advection of labile organic material from outside the local area (e.g. Grebmeier and Barry, 1991; Kotwicki et al., 2004). Advection seems to be an important mechanism providing food to benthic communities, especially in Kongsfjorden, where the carbon demand is relatively higher. Carbon accumulation and burial is relatively higher in Hornsund, whereas carbon mineralization is disproportionately greater in Kongsfjorden (Table 4). It appears that pelagic-benthic coupling is regulated not only

**Table 3** Summary of the reports on previous total benthic oxygen uptake rates from the fjords of Svalbard archipelago.

Region	Water depth [m]	Method	Oxygen uptake rate [ $\text{mmol m}^{-2} \text{d}^{-1}$ ]	Source
Eastern Svalbard	200–300	Core incubation	3.2–11.9	Pfannkuche and Thiel (1987)
Around Svalbard	170–257	Core incubation	1.85–11.2	Hulth et al. (1994)
Kongsfjorden	326	Core incubation	9.33	Hulth et al. (1994)
Hornsund, Bellsund	115–155	Sediment incubation	11.1–24.2	Kostka et al. (1999)
Hornsund	155	In situ measurement	16.4	Jørgensen et al. (2005)
Van Mijenfjord	115	In situ measurement	13.1	Jørgensen et al. (2005)
Storfjorden	175	In situ measurement	9.0	Jørgensen et al. (2005)
Hornsund	98	Core incubation	7.7–9.8	This study
Kongsfjorden	105	Core incubation	11.9–13.7	This study

**Table 4** Carbon accumulation and burial values [ $\text{g C m}^{-2} \text{y}^{-1}$ ] and estimated carbon demand [ $\text{g C m}^{-2} \text{y}^{-1}$ ] by benthic fauna of Hornsund and Kongsfjorden.

	Hornsund	Kongsfjorden	Reference
Carbon accumulation rate	38–42	29–35	Zaborska et al., 2018
Carbon burial	35–39	15–16	Zaborska et al., 2018
Meiofauna carbon demand	1.68	1.86	This study
Macrofauna carbon demand	0.44	7.13	This study
Total benthic carbon demand	51.62	86.49	This study

by the availability of organic matter but also by its quality (Clough et al., 1997; Morata et al., 2015). The main difference between these two fjords is the source of carbon for the benthic assemblages. In Kongsfjorden most organic carbon comes from fresh, marine sources, in contrast to Hornsund where most organic carbon is of terrestrial origin (Grzelak et al., 2016; Kozirowska et al., 2016). Terrigenous organic matter is weakly mineralized in the sediments: this is reflected in the relatively low benthic density, biomass and diversity. It can be concluded that the lower sediment oxygen uptake in Hornsund reflects the quality of organic carbon delivered to marine sediments.

Benthic remineralisation is also influenced by sediment reworking and the irrigation activities of macro- and meiofauna (Bonaglia et al., 2014; Braeckman et al., 2010). Therefore, infauna is responsible for transport processes (bioturbation), including particle reworking and burrow ventilation or solute transfer (bio-irrigation), which makes them important for the oxygen and nutrient cycling process (Kristensen et al., 2012). For example, they introduce oxygen into reduced sediments, thereby promoting bacterial oxidation processes, which lead to higher respiration rates. This infaunal activity therefore contributes extensively to ecosystem functioning (Bonaglia et al., 2014; Braeckman et al., 2010; Morata et al., 2015).

In summary, the significantly higher total oxygen uptake rates in Kongsfjorden are directly related to the relatively higher biomass of the bacterial community and the greater biomass of fauna (meiobenthos and macrofauna), both resulting in the faster carbon accumulation rate in relation to Hornsund (Zaborska et al., 2018). This may be indirectly affected by organic matter in Kongsfjorden, acquired predominantly from marine sources (Grzelak et al., 2016; Kozirowska et al., 2016). We conclude that it is the quality, not the quantity of organic matter supplied to marine sediments that influences the rate of oxygen consumption in sediments of the fjord.

## Acknowledgements

This study was financially supported by NCN project number 2012/04/A/NZ8/00661 (GAME project) and project number 2012/05/B/ST10/01908. Current position of dr Katarzyna Grzelak is supported by National Science Centre postdoctoral fellowship FUGA (grant number 2016/20/S/NZ8/00432). Our thanks go to Marta Głuchowska, Kajetan Deja and Mikołaj Mazurkiewicz for their assistance in the field. We also thank the crew of r/v “Oceania” for their technical support.

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