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Glacier inputs influence organic matter composition and prokaryotic distribution in a high Arctic fjord (Kongsfjorden, Svalbard)

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ABSTRACT

With climate change, the strong seasonality and tight pelagic-benthic coupling in the Arctic is expected to change in the next few decades. It is currently unclear how the benthos will be affected by changes of environmental conditions such as supplies of organic matter (OM) from the water column. In the last decade, Kongsfjorden (79°N), a high Arctic fjord in Svalbard influenced by several glaciers and Atlantic water inflow, has been a site of great interest owing to its high sensitivity to climate change, evidenced by a reduction in ice cover and an increase in melting freshwater. To investigate how spatial and seasonal changes in vertical fluxes can impact the benthic compartment of Kongsfjorden, we studied the organic matter characteristics (in terms of quantity and quality) and prokaryotic distribution in sediments from 3 stations along a transect extending from the glacier into the outer fjord in 4 different seasons (spring, summer, autumn and winter) in 2012–2013. The biochemical parameters used to describe the sedimentary organic matter were organic carbon (OC), total nitrogen, bulk stable isotope ratios, pigments (chorophyll-*a* and phaeopigments) and biopolymeric carbon (BPC), which is the sum of the main macromolecules, i.e. lipids, proteins and carbohydrates. Prokaryotic abundance and distribution were estimated by 4′,6-diamidino-2-phenylindole (DAPI) staining. This study identifies a well-marked quantitative gradient of biogenic compounds throughout all seasons and also highlights a discrepancy between the quantity and quality of sedimentary organic matter within the fjord. The sediments near the glacier were organic-poor (<0.3%OC), however the high primary productivity in the water column displayed during spring was reflected in summer sediments, and exhibited higher freshness of material at the inner station compared to the outer basin (means C-chlorophyll-*a*/OC ~5 and 1.5%, respectively). However, sediments at the glacier front were depleted in BPC (~0.2–0.3 mg C g^{-1} DW) by 4.5 and 9 times compared to sediments from the inner and outer stations. $\delta^{13}C$ values in sedimentary organic matter of Kongsfjorden varied between −23.8 and −19.3‰ and reflected distinct sources of organic matter between basins. Bacterial total cell numbers in sediments of Kongsfjorden were $<2 \times 10^8$ cells ml^{-1} and the prokaryotic community structure was strongly influenced by the marked environmental biogenic gradients. Overall, the spatial variability prevailed over the seasonal variability in sediments of Kongsfjorden suggesting that glacier inputs prominently control the functioning of this benthic ecosystem and its communities.
Regional index terms: Norway, Svalbard, Kongsfjorden.

1. Introduction

The Arctic marine ecosystem displays strong seasonality, mainly related to changes in environmental and physical properties (light availability and sea ice cover), causing a pronounced seasonality in primary production (Moran et al., 2012; Ardyna et al., 2013) and subsequent vertical organic matter fluxes (Olli et al., 2002; Wassmann et al., 2006; Juul-Pedersen et al., 2008; Moran et al., 2012). The pelagic-benthic coupling is particularly tight in the Arctic Seas and the benthos relies upon the sedimentation of organic matter (OM) through the water column (Boetius and Damm, 1998; Grant et al., 2002; Clough et al., 2005; Grebmeier et al., 2006; Renaud et al., 2008). Consequently the pelagic seasonal changes are most often reflected in the benthic compartment, whether it is in terms of sediment characteristics (Cooper et al., 2002;

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Renaud et al., 2007b; Morata and Renaud, 2008; Morata et al., 2008), benthic activities through sediment oxygen demand (Rysgaard et al., 1998; Renaud et al., 2007b) or community structures (Korsun and Hald, 2000; Pawlowska et al., 2011). Despite the obvious seasonality in the organic compartment of the pelagic realm (Ardyna et al., 2014), very few benthic studies have explored seasonal changes relating to the organic matter characteristics in the corresponding sediments.

Settled OM derives mainly from the two main primary producers: the associated sea-ice algae and the pelagic phytoplankton. Secondary producers such as zooplankton (through faecal pellets and dead organisms) can also contribute significantly to the downward flux (Wexels Riser et al., 2008). Moreover, scattered arctic plant remains can also be carried by small glacial rivers, mainly in summer (Yoshitake et al., 2011). These different sources of organic matter have specific carbon stable isotope ratios. For instance, sea-ice particulate organic matter (POM) (i.e. ice algae) is enriched in ^{13}C, on average by 6–7‰, in comparison to pelagic-POM with ranges from −21.7 to −12.6‰ vs. −26.5 to −23.0‰, respectively (Søreide et al., 2006; Tamelander et al., 2006a; McMahon et al., 2006). Moreover, copepods are usually enriched in ^{13}C (−23.3 to −22.7‰; Søreide et al., 2006; Tamelander et al., 2006b) compared to pelagic-POM and terrestrial C3-plants (−35.2 to −25.5‰; Kuliński et al., 2014). Therefore, the use of bulk carbon stable isotopes can help us to differentiate the main biological inputs.

This blend of POM is composed of macromolecules mostly belonging to the three main classes: lipids, protids and carbohydrates. However, the majority of studies performed on the Arctic benthic compartment focused on pigments to determine the food supplied to the benthos. They used the amount of chlorophyll-*a* (chl-*a*) as a proxy of fresh inputs (Soltwedel and Vopel, 2001; Morata and Renaud, 2008), although pigments represent a very small OM fraction. The biopolymeric carbon (BPC) fraction, which is based on the three main classes of organic compounds, is a good indicator of the labile (i.e. more readily available) OM fraction (Fabiano et al., 1995; Tselepides et al., 2000) even if only a fraction is enzymatically digestible by benthic organisms (Dauwe et al., 1999; Pusceddu et al., 2003). Surprisingly, BPC has never been formalized in Arctic sediments, but some values of proteins, carbohydrates and lipids have been reported separately (Pfannkuche and Thiel, 1987; Boetius and Damm, 1998; Gaye et al., 2007; Lein et al., 2013).

With climate change, sources, as well as nutritional quality, of organic matter sinking downward are expected to change in the next few decades (Carroll and Carroll, 2003; Wassmann and Reigstad, 2011). The decrease of sea-ice thickness and the increase in duration of the open water (Comiso, 2006) induce profound changes in ice algae development and phytoplankton production. While sea-ice algae production is expected to decrease (Wassmann and Reigstad, 2011), pelagic primary production has already increased by about 15–25% in the Arctic in the last decade (Arrigo et al., 2008; Petrenko et al., 2013) and phytoplankton composition is shifting towards smaller size species (Li et al., 2009; Fujiwara et al., 2011). On the other hand, glacial retreat (Lefauconnier and Hagen, 1991) and permafrost thawing (Price et al., 2013) contribute to an increase in mass of terrestrial particles delivered into the marine environment. These changes in the biogenic fraction may have repercussions on the energy flow through benthic organisms, as well as on the benthic community structures and activities. Therefore, there is a growing need to study changes in OM inputs and its influence on benthic communities in order to understand the functioning of this sensitive ecosystem.

Kongsfjorden, a high Arctic fjord in the Svalbard archipelago, is influenced by several tidal glaciers and the Atlantic water inflow. Impacts on hydrology are, to a great extent, related to seasons with the largest freshwater runoff occurring in summer during the melting period. The glacial meltwater induces steep physical gradients of temperature and salinity as well as turbidity and sedimentation along the fjord system (Hop et al., 2002; Kotwicki et al., 2004), which affect the distribution of pelagic and benthic organisms (Włodarska-Kowalczuk and Pearson, 2004; Kotwicki et al., 2004; Piquet et al., 2014). In the last few decades, this fjord has received great interest owing to its high sensitivity to climate change (Hop et al., 2002). Both sea-ice and glaciers are strongly retreating with global warming (Lefauconnier and Hagen, 1991; Kohler et al., 2007; Payne, 2015). These changes induce modifications in the primary production patterns into the fjord in the pelagic (Hodal et al., 2012; Hegseth and Tverberg, 2013) and also benthic realm (Bartsch et al., 2016) and more broadly in the ecosystem functioning (Svendsen et al., 2002).

So far, benthic studies conducted in Kongsfjorden have mainly focused on the diversity, abundance, and food webs of benthos at different time scales (seasonal to decadal) (Renaud et al., 2011; Kędra et al., 2012; and references thereafter). Among these benthic communities, heterotrophic bacteria have a major role in carbon remineralization and the global respiration pattern. Indeed, microbial communities are highly important in the community oxygen consumption of the Arctic sediments (Piepenburg et al., 1995; Piepenburg et al., 1997). However, the benthic bacterial community structure has been poorly studied (Srinivas et al., 2009; Tian et al., 2009; Hatha et al., 2013) in comparison to the macrofaunal community (e.g., Włodarska-Kowalczuk et al., 1998; Legeżyńska et al., 2003; Laudien et al., 2004; Włodarska-Kowalczuk and Pearson, 2004; Kędra et al., 2010; Węsławski et al., 2011) and to a lesser extent meiofauna communities (Korsun and Hald, 2000; Kotwicki et al., 2004; Urban-Malinga and Moens, 2006; Veit-Köhler et al., 2008).

Investigations into the spatio-temporal variations of biochemical composition in sediments are critical for explaining benthic fluxes as well as benthic fauna (micro, meio and macrofauna) distribution and, therefore, for improving our understanding of the Arctic coastal ecosystems. However, very little information is available in Kongsfjorden. The characterization of sedimentary organic matter was limited to some values of organic matter, organic carbon and total nitrogen and bulk carbon stable isotope ratios (Zaborska et al., 2006; Urban-Malinga and Moens, 2006; Veit-Köhler et al., 2008; Gihring et al., 2010; Renaud et al., 2011; Kędra et al., 2012; Kuliński et al., 2014). To our knowledge, only one study has measured chlorophyll-*a* and phaeopigments in surface sediments during an in situ experiment of meiobenthic colonisation (Veit-Köhler et al., 2008) and no studies to date have considered the biopolymeric fraction.

The aim of this study was to biochemically characterize the sedimentary OM, to assess its main origin and nature, and to examine the microbial responses to shifts in quantity, quality and origin of this OM. We specifically addressed the following questions: how does the melting season (with high continental inputs), as well as the spring season (with phytoplankton bloom), affect the quality of sedimentary OM throughout the fjord? Which environmental factors influence the prokaryotic distribution in Kongsfjorden sediments? Is the seasonal variability observed in the water column mirrored in the sediments? In order to evaluate the importance of temporal and spatial variations, three stations distributed along a longitudinal transect (glacier-fjord mouth) were sampled during the four seasons in 2012–2013 within the framework of the Effect of Climate Change On The Arctic Benthos (ECOTAB) program.

2. Material and methods

2.1. Study site

Kongsfjorden (79°N and 12°E) is located on the Northwestern part of Spitsbergen Island in the Svalbard archipelago (Fig. 1). This Arctic fjord, oriented from south-east to north-west, is 27 km long and 10 km wide at its entrance. The fjord system is composed of 2 basins (Kotwicki et al., 2004): an inner basin well-marked with relatively shallow waters (depths of <100 m), and an outer, deeper basin with water depths around 300 m. Kongsfjorden receives warm and cold water inflows from the Atlantic and Arctic currents