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Food and disturbance effects on Arctic benthic biomass and production size spectra

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ABSTRACT

Body size is a fundamental biological unit that is closely coupled to key ecological properties and processes. At the community level, changes in size distributions may influence energy transfer pathways in benthic food webs and ecosystem carbon cycling; nevertheless they remain poorly explored in benthic systems, particularly in the polar regions. Here, we present the first assessment of the patterns of benthic biomass size spectra in Arctic coastal sediments and explore the effects of glacial disturbance and food availability on the partitioning of biomass and secondary productivity among size-defined components of benthic communities.

The samples were collected in two Arctic fjords off west Spitsbergen (76 and 79°N), at 6 stations that represent three regimes of varying food availability (indicated by chlorophyll *a* concentration in the sediments) and glacial sedimentation disturbance intensity (indicated by sediment accumulation rates). The organisms were measured using image analysis to assess the biovolume, biomass and the annual production of each individual. The shape of benthic biomass size spectra at most stations was bimodal, with the location of a trough and peaks similar to those previously reported in lower latitudes. In undisturbed sediments macrofauna comprised 89% of the total benthic biomass and 56% of the total production. The lower availability of food resources seemed to suppress the biomass and secondary production across the whole size spectra (a 6-fold decrease in biomass and a 4-fold decrease in production in total) rather than reshape the spectrum. At locations where poor nutritional conditions were coupled with disturbance, the biomass was strongly reduced in selected macrofaunal size classes (class 10 and 11), while meiofaunal biomass and production were much higher, most likely due to a release from macrofaunal predation and competition pressure. As a result, the partitioning of benthic biomass and production shifted towards meiofauna (39% of biomass and 83% of production), which took over the benthic metazoan key-player role in terms of processing organic matter in sediments. Macrofaunal nematodes composed a considerable portion of the benthic community in terms of biomass (up to 9%) and production (up to 12%), but only in undisturbed sediments with high organic matter content. Our study indicates that food availability and disturbance controls the total bulk and partitioning of biomass and production among the size classes in Arctic benthic communities.

1. Introduction

Body size may be used as a unifying tool in the description of the structure of food webs in both terrestrial and aquatic ecosystems. Most biological processes are scaled to the size of organisms, which is why this easily measurable feature of an animal is a powerful tool for ecological comparisons of the different assemblages (Peters, 1983). All individuals belonging to the same size class, independent of their taxonomical identity, share basic characteristics in terms of bioenergetics. Organisms are aggregated into size-based communities, which at the global level, are even more sensitive to environmental changes than taxon-based communities (Saiz-Salinas and Ramos, 1999). It is predicted that the third universal ecological response for climate-induced changes is the reduction of body size, which can have tremendous effects on ecosystem functioning (Daufresne et al., 2009).

In terrestrial and aquatic pelagic systems, the biomass size spectra of communities have been widely explored and shown to be an efficient descriptor of functioning, particularly in terms of productivity and energy flow. Benthic biomass size spectra (BBSS) in marine systems have received much less attention due to the time-consuming and troublesome laboratory analysis required to

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construct the spectrum. Recently, Basset et al. (2012) recommended the size-based approach as an objective taxonomic-free method to assess the ecological status, trophic state and perturbation of benthic communities and called for the intensification of studies in this field. The BBSS of the whole infaunal community (both meio- and macrofauna) has been reported in a few temperate marine localities (e.g., Duplisea, 2000; Hua et al., 2013; Schwinghamer, 1983; Warwick, 1984). Arctic studies of benthic size spectra were limited to one taxonomic group, Nematoda, and the sedimentary habitats of deep-sea basins (Soltwedel et al., 1996; Tseitlin et al., 2001).

Benthic community size spectra may be useful in the predictions of production and respiration of an entire community (Bourassa and Morin, 1995; Edgar, 1990), as well as other aspects of ecosystem functioning such as the remineralization of organic matter (Donadi et al., 2015). Environmental factors (e.g., temperature, turbidity, and disturbance) can have an influence on the partitioning of benthic biomass and production among the different size components, which has important implications on carbon cycling (Schwinghamer, 1981). This basic knowledge is essential if we are to predict changes in organism size following climate related environmental shifts. However, both the basic patterns and factors affecting the spatial variability of the partitioning of biomass and production in benthic communities among size classes remain largely undescribed for benthic systems (Albertelli et al., 1999). This knowledge gap is especially significant in the Arctic, where the effects of global climate change are predicted to occur earlier and stronger than at lower latitudes (ACIA, 2006).

Disturbance and food availability have been recognized as primary factors that shape the community structure and dynamics of biological structures from individual to ecosystem levels (e.g., Peterson et al., 2011 and the literature therein). The classical Dynamic Equilibrium Model explains the effects of varying disturbance and productivity regimes and the interplay between these factors on the diversity of biological communities (Huston, 1994). It predicts that strong disturbance coupled with low food availability results in biological diversity impoverishment, which has been demonstrated in a number of models and experimental studies (e.g., Svensson et al., 2007). In marine benthic communities, however, Austen and Widdicombe (2006) showed that various compartments of the community, particularly macro- and meiofauna (groups defined primarily by the size criterion), can respond differently to environmental variability and disturbance.

Arctic glacial fjords are regarded as favorable systems for *in situ* studies on the influence of environmental variability on marine biota because they offer relatively pristine conditions and steep gradients of primary production (Piwosz et al., 2009), as well as hydrological and geochemical settings in water columns and sediments (e.g., temperature, salinity, turbidity in water, stability, grain size and water content in sediments; Svendsen et al., 1996). The structure and functioning of fjordic ecosystems is shaped by the interplay of two processes: the terrigenous inflows of glacial meltwaters and transported sediments and the advection of water masses transporting larvae and organic carbon produced in open shelf waters. In the Arctic, terrigenous inflows are generated by tidewater glaciers; melt water sources are usually located in the inner parts of fjords and they transport large amounts of fresh water and mineral material. High turbidity, an elevated rate of mineral material sedimentation, and instabilities in bottom sediments are all perceived as agents of natural chronic physical disturbance to benthic fauna (e.g., Kendall et al., 2003; Włodarska-Kowalczuk et al., 2005). The clear patterns of benthic response in terms of species composition, distribution, diversity and spatial heterogeneity have been thoroughly described as gradients of 'glacial disturbance' observed in West Spitsbergen fjords (e.g., Włodarska-Kowalczuk and Węsławski, 2008; Włodarska-Kowalczuk et al., 2012).

The aim of our study is to determine the response in the structure (biomass size spectra) and function (secondary production) of benthic communities to different levels of food availability and disturbance. The study is performed in west Spitsbergen fjords, dynamic coastal environments at the interface of marine and terrestrial systems that are currently exposed to climate warming related changes. An increase of Atlantic water inflow into the Arctic (in particular, the west Spitsbergen area) and the increase of water temperature in summer on the west Spitsbergen shelf have already been reported (Walczowski and Piechura, 2007). This has caused shifts in phenology and composition of the Arctic biota, which changed the pathways of energy flow through the size-defined pelagic components of the marine food webs (Węsławski et al., 2009). To our knowledge, our study is the first to present the patterns and environmental controls of benthic biomass and production size spectra in Arctic coastal sediments that includes the whole metazoan infaunal community (both meio- and macrofauna). The only Arctic based studies of benthic size spectra are limited to one taxonomic group - Nematoda in deep-sea basins (Schewe, 2001; Soltwedel et al., 2000; Tseitlin et al., 2001) - or were based on the weight of only one (the biggest) individual of each macrofaunal species (and referred to as species size spectra, Kendall et al., 1997).

2. Materials and methods

2.1. Study area

The Spitsbergen Island is located in the Svalbard archipelago (between 74° and 81°N and between 10° and 35°E). The study was performed in two glacial, open fjords off west Spitsbergen: Kongsfjorden and Hornsund (Fig. 1). The fjords' hydrography is shaped by the interplay of the three main water masses: cold Arctic water transported by the East Spitsbergen Current, relatively warmer Atlantic water transported by the West Spitsbergen Current and the Local Brackish Waters. The inner part of the Kongsfjorden contains the most active glacier in the Svalbard archipelago, Kongsbreen. The input of mineral material into the fjord with the glacial meltwaters is estimated to be 2.6×10^5 m^3 tonnes per year (Elverhøi et al., 1980). The glacial inputs of freshwater and mineral suspensions produce steep environmental gradients in the fjord system. The sediment accumulation rate in the Kongsfjorden glacial bay was estimated to exceed 6–9 cm y^{-1} within 0.5 km from the glacier front (Trusel et al., 2010), and 5 km from the glacier front Zaborska et al. (2006) documented it to be 2.50 cm y^{-1}. In the middle part of the fjord, sediment accumulation was reported to be 0.24 cm y^{-1} (Kuliński et al., 2014), and in the outer part of the fjord it was 0.14 cm y^{-1} (Kuliński et al., 2014). The decreasing sedimentation rate trend from inner to outer parts of Kongsfjorden was also reported by Zajączkowski (2000), who observed a sharp decrease in the sedimentation rate from over 800 g m^{-2} d^{-1} in the glacial bay to 25 g m^{-2} d^{-1} in the outer part of fjord. In Hornsund thirteen tidewater glaciers are located in the inner part of the fjord (Brepolen), but the glacial effects on marine systems are much less pronounced than in Kongsfjorden. The sediment accumulation rates in Hornsund vary between 0.18 cm y^{-1} in the outer part of fjord (Zaborska et al. unpublished data), 0.22 cm y^{-1} in the middle part (Zaborska et al., 2016) and 0.69 cm y^{-1} in the inner part (Zaborska et al. unpublished data). Similarly, Drewnik et al. (2016) reported that in Hornsund, the sedimentation rate varied between 10 to 160 g m^{-2} d^{-1}, with a slightly decreasing trend from the fjord head to the entrance.

Both fjords seabed are covered with mud (App. Table A1), but in the inner part of Kongsfjorden, the sediment is poorly consolidated and unstable with a relatively high water content (Włodarska-