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Partitioning the contributions of mega-, macro- and meiofauna to benthic metabolism on the upper continental slope of New Zealand: Potential links with environmental factors and trawling intensity

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Understanding and predicting change in deep-sea benthic ecosystem function remains a major challenge. Here, we conducted analyses combining data on the abundance and biomass of benthic fauna and sediment community oxygen consumption (SCOC) on New Zealand's continental margin to estimate and compare the contributions of meio-, macro-, and megafauna to total benthic metabolism and identify potential links with environmental factors and trawling intensity. We focussed on two regions in close proximity-the high surface primary productivity Chatham Rise and low surface productivity Challenger Plateau. Mean megafauna biomass was twenty times greater on Chatham Rise than Challenger Plateau, likely reflecting differences in food supply between the two regions; this contrast in megafaunal biomass was mainly due to differences in mean body weight rather than abundance. Meio- and macrofauna made similar contributions to SCOC and together accounted for 12% of benthic metabolism on average. In contrast, the estimated contribution of megafauna never exceeded 1.5%. Significant positive correlations between faunal respiration and food availability indicate a link between food supply and benthic community function. Our analyses also show that fauna made a greater contribution to SCOC in conditions of high food availability, and that microorganisms (i.e., the proportion of SCOC not accounted for by the fauna) tended to be more dominant at sites with low food availability. These findings provide support for the concept that large organisms are more strongly affected by a reduction in food resources than small organisms, which in turn underlies one of the most widely described patterns in the deep-sea benthos, i.e., the reduction in organism body size with depth. Because metabolism in deep-sea sediments is typically dominated by microorganisms and small fauna, the absence of a relationship between bottom trawling intensity and the respiration of benthic fauna in the present study may be explained by benthic communities shifting towards smaller body size following physical disturbance. Future studies of deep-sea benthic ecosystem function will need to quantify the indirect influence of fauna on microbial metabolism through activities such as feeding and bioturbation in order to better understand the total contribution of benthic fauna to benthic processes.

1. Introduction

Soft sediments cover the vast majority of the deep-sea floor and play an important role in global carbon cycling (Jahnke and Jackson, 1992; Archer and Maier-Reimer, 1994). Benthic metabolism in deep-sea sediments is largely dependent on the input of particulate organic carbon (POC) from surface waters (Smith, 1987; Pfannkuche, 1993), which in turn is influenced by surface (e.g., seasonal and inter-annual variability in climate; Lampitt et al., 2001; Smith et al., 2006), and water column processes (e.g., hydrodynamics, POC recycling and remineralisation by bacteria; Lampitt and Antia, 1997; Turner, 2002). Climate change is likely to impact the structure and function of deep-sea benthic communities through changes in POC flux to the benthos (Coma et al., 2009; Smith et al., 2009; Lewandoska et al., 2014), but predicting these impacts will require more in-depth knowledge on the ecology of deep-sea benthic organisms and their role in ecosystem function (Smith et al., 2008).

Processing of organic material and overall metabolism in deep-

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sea sediments are typically dominated by bacteria and small fauna (e.g., Schwinghamer et al., 1986; Pfannkuche, 1993; Beaulieu, 2002; Hubas et al., 2006). Data on the relative contributions of the different size groups to deep-sea benthic metabolism are scarce, but analyses based on sediment community oxygen consumption (SCOC) measurements and estimated faunal respiration rates based on body size suggest that metazoan meio-, macro-, and megafauna may each contribute up to a quarter or more of total benthic community respiration in continental slope environments (Piepenburg et al., 1995; Heip et al., 2001; Baguley et al., 2008; Rowe et al., 2008; van Oevelen et al., 2011). The contribution of mega- and macrofauna to benthic metabolism decreases rapidly with water depth (Piepenburg et al., 1995; Rowe et al., 2008), reflecting the proportionally greater decline in biomass with depth of the larger fauna relative to meiofauna and bacteria as POC fluxes decrease (Rex et al., 2006). Factors other than POC flux, such as food quality (Wigham et al., 2003) and sediment granulometry (Hubas et al., 2006), may also influence the relative importance of the different faunal groups to benthic metabolism.

Bottom trawling is the most widespread and pervasive source of disturbance on continental margins (Cryer et al., 2002; Puig et al., 2012). Vulnerability of benthic organisms to this type of disturbance is to a large extent dictated by body size, with megafaunal organisms more likely to suffer deleterious effects than the smaller macro- and meiofauna (Duplisea et al., 2002). High trawling intensity has been linked with shifts in community size spectra and greater relative abundance of small organisms, which translate into lower benthic biomass and secondary productivity (Jennings et al., 2001; Queiros et al., 2006), and affects marine biodiversity (Thrush and Dayton, 2002). The effects of shifts in community size spectra on overall benthic secondary productivity, however, may differ depending on sediment physical characteristics (Queiros et al., 2006). Estimated benthic secondary productivity may even temporarily increase in more heavily trawled areas due to increased dominance of small organisms, which are characterised by higher mass-dependent respiration rates than larger organisms (Mahaut et al., 1995; Jennings et al., 2001). Understanding and predicting change in deep-sea benthic metabolism (ecosystem function) remains a significant challenge given the potentially complex relationships between environmental variables, anthropogenic disturbance, and the abundance, biomass, and size spectra of benthic communities, and the paucity of data on continental margins.

A recent study on the New Zealand continental margin revealed some marked contrasts in the abundance and biomass of meio- and macrofauna between the Chatham Rise, which is situated below the highly productive Subtropical Front, and the Challenger Plateau, which lies in an area of relatively low productivity (Pilditch et al., 2015). The abundance and biomass of both size groups were 1.9–3.5 times greater in Chatham Rise than Challenger Plateau, reflecting regional differences in food availability (e.g. Cummings et al., 2013). Total infaunal biomass was dominated by macrofauna, particularly on the oligotrophic Challenger Plateau where meiofauna accounted for only 2.1% of total infaunal biomass on average, compared to 3.6% on Chatham Rise (Pilditch et al., 2015). Contrary to previous findings, the relative contribution of meiofauna to total infaunal biomass at the Chatham Rise and Challenger Plateau study sites was not correlated with water depth but was positively correlated with sediment chlorophyll *a* content, which may reflect the ability of meiofauna to respond more quickly to food input than macrofauna (Pilditch et al., 2015). The meiofauna:macrofauna biomass ratio has also been found to vary between the southern and northern flanks of Chatham Rise, potentially due to differences in food quality and sediment characteristics (Berkenbusch et al., 2011). In contrast to patterns in the distribution of benthic fauna, variation in sediment community oxygen consumption (SCOC) on the New Zealand continental margin appears to be mainly associated with water depth, likely reflecting temperature effects on microbial metabolism, although food availability is also likely to play a role (Pilditch et al., 2015).

The relative contributions of meio-, macro-, and megafauna to overall benthic metabolism on the continental slope of New Zealand have not yet been estimated, and data on the biomass of benthic megafauna are lacking. These data, however, are necessary for the development of trophic models and for predicting the consequences of natural and anthropogenic change on deep-sea ecosystems and understanding how these ecosystems function (Rowe et al., 2008). In the present study, samples of benthic megafauna on Chatham Rise and Challenger Plateau were obtained using beam trawl tows as part of the 2007 Ocean Survey 20/20 Chatham-Challenger Hydrographic Biodiversity and Seabed Habitat Project (Bowden, 2011). These data, as well as literature data on meiofauna, macrofauna, and SCOC from Chatham Rise and Challenger Plateau (Berkenbusch et al., 2011; Pilditch et al., 2015), were used to estimate and make regional comparisons of: (1) megafaunal abundance and biomass, (2) meio-, macro-, and megafaunal respiration, and (3) the contributions of meio-, macro-, and megafauna to total benthic metabolism (SCOC)). Potential relationships between environmental factors, trawling intensity, and the respiration of benthic fauna were also investigated.

2. Methods

2.1. Study area

The present study focused on the Chatham Rise and Challenger Plateau, two major features of the New Zealand Exclusive Economic Zone (EEZ) (Leduc et al., 2010). The Chatham Rise is a submarine ridge that extends eastwards from the South Island of New Zealand at depths ~250–3000 m (Fig. 1). It lies under the Subtropical Front (STF), a region where warm subtropical surface water to the north meets cold, high nutrient-low chlorophyll subantarctic surface water to the south (Boyd et al., 1999). The STF appears to be bathymetrically locked onto the southern flank of the Rise near 44°S (Uddstrom and Oien, 1999; Sutton, 2001), and is associated with heightened primary productivity (Bradford-Grieve et al., 1997; Murphy et al., 2001). The Challenger Plateau encompasses water depths ranging from ~250–3000 m in subtropical waters in an area of generally low biological productivity to the northwest of the South Island, New Zealand (Murphy et al., 2001).

2.2. Megafauna

Megafauna was sampled at 25 sites on the Chatham Rise (NIWA voyage TAN0705) and 14 sites on the Challenger Plateau (TAN0707) using a beam trawl with a cod end lined with a 10 mm mesh (Fig. 1, Table 1). The surface area sampled by the beam trawl ranged from 732 to 3059 m^2 (mean=2055 m^2). Samples were processed at sea immediately after collection; organisms were first sorted into broad taxonomic groups, counted, and weighed wet before fixing. The entire content of each sample was processed for megafauna, except for one sample on the western Chatham Rise (site 18) containing large quantities of fine sediments, of which only a known proportion (21%) was processed due to time constraints. Pelagic organisms, (e.g., salps) and highly mobile demersal taxa (i.e., fish and squid) were not included in the analyses. Megafaunal wet weights were converted to carbon weight by using taxon-specific conversion factors (Lampitt et al., 1986; Ricciardi and Bourget, 1998; Barthel, 1995) and assuming an organic carbon content to ash-free dry weight ratio of 1:2 (Salonen et al., 1976).