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Note

Further evidence for the effect of particle-size diversity on deep-sea benthic biodiversity

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ABSTRACT

The positive correlation between sediment particle-size diversity (a measure of habitat heterogeneity) and deep-sea macrofaunal diversity was first demonstrated two decades ago. The causality of this relationship was not elucidated because of the potential influence of macrofauna on sediment granulometry. Here we test the generality of this correlation using smaller organisms with limited mobility and limited ability to change the physical structure of sediments. Results of partial regressions accounting for the effect of water depth and food availability showed that nematode species and genus diversity were positively correlated with sediment particle-size diversity on the continental slope of New Zealand. Trophic diversity was not correlated with sediment particle-size diversity, however, which could suggest that the relationship between habitat heterogeneity and diversity was not the result of food partitioning between species/genera. Our findings provide support for the importance of small-scale habitat heterogeneity in the maintenance of local diversity in the deep sea, one of the few known environmental factors that may directly influence species co-existence in this biome.

1. Introduction

The deep sea (i.e., >200 m water depth) is the largest ecosystem on Earth and is characterized by highly diverse benthic communities (Gray, 2002; Mokievsky and Azovsky, 2002). Overall, the ecological factors responsible for large-scale diversity trends in the deep sea remain poorly understood relative to the much better studied terrestrial ecosystems, which is hardly surprising given the challenging nature of deep-sea research (e.g., Snelgrove and Smith, 2002; Danovaro et al., 2008). Productivity is by far the most widely studied factor in deep-sea diversity investigations (though mostly via proxy measures, such as organic matter input to the seafloor), and appears to be important in shaping bathymetric and regional diversity trends (e.g., Rex et al., 2005). Though it has only received more recent attention, habitat heterogeneity (e.g., seep, vent, slope, and abyssal plain habitats) has also been found to contribute to global deep-sea diversity (Vanreusel et al., 2010). Besides productivity and habitat heterogeneity, other factors such as disturbance (e.g., Paterson and Lambshead, 1995), oxygen concentrations (e.g., Levin et al., 2000), predation (e.g., Dayton and Hessler, 1972), and combinations thereof (e.g., Rex, 1976; Huston, 1979; Jorissen et al., 1995; McClain and Barry, 2010) have been investigated, but the supporting evidence is often indirect (see Levin et al., 2001; Rex and Etter, 2010 for reviews).

One of the most compelling explanations for patterns of infaunal diversity in deep-sea soft sediments was provided by Etter and Grassle (1992). Their study was the first to show that regional and bathymetric trends in species diversity could be explained by variation in sediment particle-size diversity. The likely mechanisms behind the positive correlation between particle-size diversity and species diversity were increased partitioning of food resources based on particle size (e.g., Whitlatch, 1981) and/or greater habitat heterogeneity (Gray, 1974). However, as noted by Etter and Grassle (1992), the feeding and burrowing activities of diverse faunal communities could lead to a wider range of particle sizes rather than the other way around (Eckman and Nowell, 1984; Nowell et al., 1984). Sediment granulometry can also be correlated with organic matter input (Snelgrove and Butman, 1994), the effect of which needs to be accounted for in order to produce convincing analyses. Moreover, it is not clear why species diversity should peak at intermediate values of sediment particle size diversity once the effect of depth is taken

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into account (Etter and Grassle, 1992). A high proportion of deep-sea diversity studies include sediment characteristics in their analyses, but surprisingly very few have explicitly examined the generality of the sediment particle size diversity–species diversity relationship (Thistle, 1998; Netto et al., 2005). To our knowledge, no attempts have been made to test robustly the hypothesis nor address the weaknesses (i.e., potential circularity, correlation with food availability) in the analysis of Etter and Grassle (1992).

Most of what is known about the ecological drivers of deep-sea biodiversity is based on studies of macrofauna (see review by Rex and Etter, 2010). Much less is known about meiofaunal organisms, mostly due to their small size, high abundance, high diversity, and lack of taxonomic expertise to process samples of these organisms. Nematodes are by far the most abundant metazoan organisms in marine soft sediments (usually representing $>90\%$ of total metazoan abundance (Giere, 2009)) and differ from larger macrofaunal taxa in several fundamental ways: they (1) possess relatively limited abilities to modify the structure of their habitats (but see Cullen (1973) and Pike et al. (2001)), (2) lack pelagic larvae and therefore are expected to have very limited dispersal abilities, and (3) experience their environment at a much more fine-grained level due to their small size. These characteristics mean that a given individual is expected to spend its entire lifespan in a very small area (although passive dispersal can occur; Commito and Tita, 2002); ecological processes influencing diversity are, therefore, likely to operate at small spatial scales (<10 cm, Gallucci et al., 2009). In addition, the potential for niche partitioning based on particle size distribution is greater for nematodes than for larger macrofaunal organisms (Schwinghamer, 1981; Tita et al., 1999). Thus, nematodes are expected to respond more strongly to changes in the physical structure of deep-sea sediments at the local scale than larger organisms, and are therefore suited to the study of sediment-diversity relationships in the deep sea. In addition, nematodes can be classified into feeding types based on buccal morphology (Wieser, 1953; Moens and Vincx, 1997), allowing the relationship between sediment particle size diversity and trophic diversity to also be investigated.

Many studies of deep-sea diversity patterns are conducted along depth transects (see reviews by Gage and Tyler, 1991 and Rex and Etter, 2010). One common problem associated with such a sampling strategy is the predictable way in which organic matter input and sediment grain size tend to co-vary with increasing water depth (i.e., both often decrease). As a result, disentangling the effects of food supply and sediment characteristics can be problematic. The sampling strategy used in the present study resulted in minimal correlation between environmental variables, which allowed us to evaluate the separate effects of sediment particle-size diversity, food availability, and water depth on local nematode species-, genus-, and trophic diversity on the upper continental slope of New Zealand.

2. Methods

2.1. Sampling and laboratory methods

The present study focused on two major bathymetric features of the New Zealand Exclusive Economic Zone (EEZ), the Chatham Rise in the SW Pacific Basin, and the Challenger Plateau in the eastern Tasman Sea (Fig. 1). The Chatham Rise is a broad submarine ridge extending eastwards from the South Island of New Zealand at water depths ~350–3000 m. The highly productive Subtropical Front (STF), a region where warm subtropical surface water to the north meets cold, subantarctic surface water to the south, is geographically constrained near the southern flank of the rise near 44°S (Murphy et al., 2001; Sutton, 2001). The Challenger Plateau encompasses water depths ~400–3000 m in an area of generally low biological

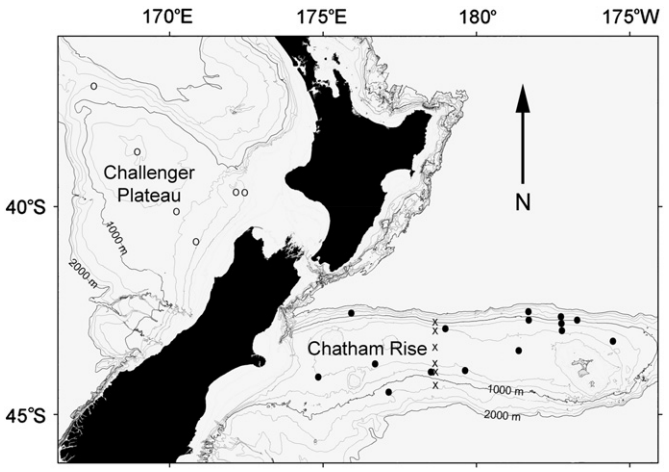

Fig. 1. Map of New Zealand showing bathymetric contours (left blank at depths >2000 m) and sites on the Chatham Rise (bottom right) and Challenger Plateau (top left) sampled during NIWA voyages TAN0116 (marked by Xs, September–October 2001), TAN0705 (filled circles, March–April 2007), and TAN0707 (circles, May–June 2007).

productivity to the northwest of the South Island, New Zealand (Murphy et al., 2001).

Samples were collected from a total of 27 sites. Six sites were sampled in September–October 2001 along a transect at 178°30′E across the Chatham Rise (350–1200 m water depth) during National Institute of Water and Atmospheric Research (NIWA) cruise TAN0116 (Nodder et al., 2007). Samples were collected from 21 additional sites (240–1250 m water depth) on the Chatham Rise and Challenger Plateau in March–April and May–June 2007, during NIWA cruises TAN0705 and TAN0707, respectively, as part of the Ocean Survey 20/20 initiative (Leduc et al., 2010). All the sites in the present study were situated on the open slope, and not on any conspicuous geomorphological features such as canyons, pockmarks, or seamounts. Samples were collected from sites and water depths that are likely to experience a wide range of organic matter input from surface productivity. Silt/clay content at the study sites ranged from 6% to 93% (Leduc et al., 2010), thus providing a wide range of sediment characteristics for the analysis of sediment particle size diversity–species diversity relationships.

Samples were taken using an Ocean Instruments MC-800A multicorer (MUC; core i.d.$=9.52$ cm). For faunal analyses, one–three replicates (i.e., samples from different MUC deployments) per site were obtained. Each faunal sample consisted of a subcore (i.e.$=2.6$ cm) taken to a sediment depth of 5 cm. All samples were preserved in 10% buffered formalin and stained with Rose Bengal. Samples were rinsed through a 1-mm mesh to remove macrofauna and through a 45 μm mesh to retain nematodes. Nematodes were extracted from the remaining sediment by Ludox flotation, transferred to pure glycerol, and mounted on slides (Somerfield and Warwick, 1996). The fraction of sediments left behind after Ludox extraction of meiofauna was inspected with a stereomicroscope at $50\times$ magnification and any remaining nematodes were added to the sample prior to mounting on slides.

Physical and biogeochemical parameters were determined from one core per site. Methods for the analyses of sediment parameters are given in Nodder et al. (2003) and Grove et al. (2006). Three parameters, i.e., %TOM (total organic matter content of the sediments), CPE (chloroplastic pigment equivalents; sum of chlorophyll *a* and phaeopigments), and %chl *a* (proportion of chlorophyll *a* relative to chloroplastic pigment equivalents) were used as proxies for food availability. CPE provided a measure of the amount of photosynthetically derived organic matter available to