Deep-Sea Research I 93 (2014) 131–144

Contents lists available at ScienceDirect

Deep-Sea Research I

journal homepage: www.elsevier.com/locate/dsri

Meiofaunal abundances and faunal similarity on the continental rise off the coast of California

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ARTICLE INFO

Article history:
Received 23 January 2014
Received in revised form
2 July 2014
Accepted 7 July 2014
Available online 19 July 2014

Keywords:
Deep sea
Meiofauna
Nematoda
Desmoscolecidae
Harpacticoida
Ostracoda
Kinorhyncha
Pacific

ABSTRACT

Metazoan meiofauna (e.g., nematodes, benthic copepods) play important roles in deep-sea sediment communities, but information as basic as standing stocks is not known for much of the world ocean. We therefore sampled six stations: one near the 2700-m isobath and one near the 3700-m isobath off northern, central, and southern California. We counted benthic copepods, both Desmoscolecidae and nondesmoscolecid nematodes, kinorhynchs, nauplii, and ostracods from multiple-corer samples. Nematodes from our 2700-m and 3700-m stations, and ostracods and nauplii from our 3700-m stations, were unusually abundant compared to those from other stations from comparable depths in the Pacific.

Off California, the abundances of benthic copepods, kinorhynchs, and nondesmoscolecids at the 2700-m stations were significantly greater than those at the 3700-m stations. Abundance of benthic copepods was correlated with the percentage of medium sand in the sediment, so sediment texture could be important to them. That of kinorhynchs was correlated with the concentration of chloroplastic-pigment equivalents and percentage nitrogen, so consumable material from the euphotic zone could be important to them. In contrast to the usual pattern of decreasing abundance with depth, Desmoscolecidae abundance in the central region was greater at the 3700-m than at the 2700-m station.

The three regions differed significantly in both kinorhynch and ostracod abundances, independently of depth. In the food-poor deep sea, animals are expected to be more abundant where food is plentiful. Unexpectedly, ostracod abundance was negatively correlated with all food variables. A possible explanation is that the natural enemies of ostracods are abundant where food is abundant.

Multivariate faunal similarity at 2700 m differed significantly from that at 3700 m, independently of regions. Benthic copepods were most responsible for the difference. Regions also differed in multivariate faunal similarity independently of depth. In general, faunal similarity is expected to decrease as separation distance increases, but unexpectedly, the northern- and southern-region faunas were more similar to each other than to the central-region fauna. Kinorhynchs were most responsible for this pattern.

1. Introduction

The deep-sea floor is a huge habitat, and mud covers most of it (Gage and Tyler, 1991). It is of ecological interest for many reasons. For example, the resident organisms perform important ecosystem services, such as recycling organic matter (Snelgrove et al., 1997; Snelgrove, 1999). Because conditions at the deep-sea floor are extreme, it provides an end point for the study of ecological gradients of variables such as temperature and pressure (see, e.g., Young and Tyler, 1993). Still, the study of the deep-sea fauna is far from complete; in particular, abundances are unknown for large areas (Snelgrove et al., 1997).

Meiofauna are abundant and species rich in deep-sea sediments (Vincx et al., 1994; Lambshead et al., 2003). Some consume microbes (Ingels et al., 2010a,b), and most are thought to be consumed by larger animals (Dayton and Hessler, 1972). The presence of hundreds of meiofaunal species in 100-cm^2 samples presents a challenge to our understanding of diversity maintenance (Thistle, 1978; Leduc et al., 2012). For these and other reasons, an adequate understanding of the ecology of the communities of deep-sea sediments requires the inclusion of

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http://dx.doi.org/10.1016/j.dsr.2014.07.004
0967-0637/

substantial information about the meiofauna. Unfortunately, even such basic facts as their abundance are unknown for 1000-km-scale areas (Baguley et al., 2006b, and references therein).

Here we describe the distribution of the abundant groups of metazoan meiofauna (hereafter meiofauna) along the continental rise off California, a region where such research is just beginning (see, e.g., Barry et al., 2004; Carman et al., 2004). In addition, we searched our data for patterns with depth and region, which are of ongoing interest to deep-sea ecologists (Shirayama, 1984; Danovaro et al., 1995; Baguley et al., 2006b; Itoh et al., 2011).

We first asked (1) whether our abundances differed from others at comparable depths in the Pacific. Then, focusing on our data from the California rise, we asked these questions: (2a) does the abundance of a meiofaunal group differ significantly with depth independently of regional differences, and if so, (2b) are the differences correlated with environmental variables? From the literature (reviewed by Soltwedel, 2000), we expected abundances to decrease with depth. (3a) Do regions differ significantly in abundance of a meiofaunal group independently of depth, and if so, (3b) are the differences correlated with environmental variables? We expected abundances to be greater where food was more abundant (see Vincx et al., 1994, for a review). (4) Do depths or regions differ in multivariate faunal similarity? If so, (5a) are the differences correlated with environmental variables (Vanhove et al., 1995; Soltwedel et al., 2000; Brown et al., 2001; Baguley et al., 2006a), and (5b) which meiofaunal groups account for the dissimilarity?

2. Materials and methods

2.1. Stations

We sampled near the 3700-m and 2700-m isobaths in a northern, a central, and a southern region on the continental rise off California and designated the six stations A through F (Fig. 1). We used a version of the Barnett et al. (1984) multiple corer (Ocean Instruments MC 800 Multi Core, San Diego, CA) with 10-cm inner-diameter cores.

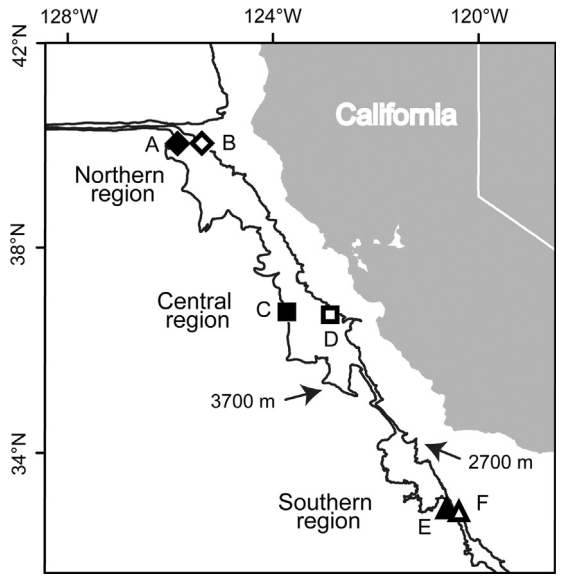

Fig. 1. A portion of the northeast Pacific off the United States, showing the locations of the regions studied (northern, central, and southern). The 3700-m stations are A, C, and E. The 2700-m stations are B, D, and F.

2.2. Sampling and processing of meiofauna

We processed the cores from each deployment in a predetermined, random order; we imaged the sediment through the side of the transparent core tube, noted any unusual features, collected the water overlying the sediment, imaged the sediment surface, and collected the top 1 cm of sediment. The water and sediment samples were combined, preserved with cold 95% ethyl alcohol, and stored at −20 °C.

In the laboratory, we randomly selected a station, a deployment from that station, and an undisturbed core from that deployment. We repeated this procedure until we had selected a sample from each station and repeated the entire process three times. The 18 samples were processed in the order selected. For each sample, we separated the 300-μm fraction from the 30-μm fraction and stained both with rose bengal. Under a stereomicroscope (25 ×), a sorter removed and counted benthic copepods, kinorhynchs, nauplii, nematodes, and ostracods and noted which nematodes belonged to the family Desmoscolecidae from both size fractions. Other taxa were too rare to be analyzed. A second person sorted each sample to ensure accuracy.

In studies of the distribution of deep-sea meiofauna, the desire to work with groups that are as homogenous as possible conflicts with the cost in time and money to do so. Many workers have been able to afford to separate the nauplii of benthic copepods from copepodites (e.g., Carman et al., 2004; Shimanaga et al., 2000), which makes ecological sense because these life stages differ dramatically in morphology and should respond differently to environmental differences. In our study, we could afford to separate nauplii from copepodites and Desmoscolecidae from other nematodes. We did the latter because desmoscolecids appear to be an ecologically coherent group within the Nematoda, e.g., their body walls have ring-like expansions that are reinforced with sediment in many species (see Giere, 2009, fig. 5.16 for an image), they are plumper than most other nematodes (Soetaert et al., 2002), they have very small buccal cavities and cannot feed on particles larger than bacteria (Soetaert et al., 2002), and they appear to prefer well-oxygenated sediments (Soetaert et al., 2002).

2.3. Sampling and processing for environmental variables

2.3.1. Sample handling at sea

A second core from each deployment (chosen at random) was used for the measurement of environmental variables. We removed and discarded the water above the sediment and inserted five subcorers (cut-off syringes). All were inserted before any was removed. We sliced the 0–1-cm layer from each. Samples for particle-size distribution were preserved in 10% formalin and reagent-grade NaCl in distilled water (salinity = 35), which was buffered to neutrality with $NaHCO_3$. Those for enzyme-hydrolyzable amino acids (see Mayer et al., 1995) were frozen at −20 °C. Those for pigments (chlorophyll *a* and phaeopigments), percentage organic carbon, and percentage nitrogen were frozen at −20 °C in new, foil-closed, scintillation vials that had been heated at 450 °C for 4 h. The pigment samples were stored in the dark.

2.3.2. Sample processing in the laboratory

2.3.2.1. Particle-size distributions. We separated the sediment into a coarse and a fine fraction by pouring the sample into a 30-μm sieve and gently moving the sieve up and down for 5 min in a container of deionized water. To separate the sediment retained on the 30-μm sieve into size fractions, we dried Whatman GF/D filters overnight at 60 °C, let them cool, and weighed them. We then rinsed the sediment remaining on the 30-μm sieve through nested