Functional diversity patterns of abyssal nematodes in the Eastern Mediterranean: A comparison between cold seeps and typical deep sea sediments

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ABSTRACT

Spatial patterns in deep sea nematode biological trait composition and functional diversity were investigated between chemosynthetic and typical deep sea ecosystems as well as between different microhabitats within the chemosynthetic ecosystems, in the Eastern Mediterranean. The chemosynthetic ecosystems chosen were two mud volcanoes, *Napoli* at 1950 m depth and *Amsterdam* at 2040 m depth which are cold seeps characterized by high chemosynthetic activity and spatial heterogeneity. Typical deep sea ecosystems consisted of fine-grained silt-clay sediments which were collected from three areas located in the south Ionian Sea at 2765 to 2840 m depth, the southern Cretan margin at 1089 to 1998 m depth and the Levantine Sea at 3055 to 3870 m depth. A range of biological traits (9 traits; 31 categories) related to buccal morphology, tail shape, body size, body shape, life history strategy, sediment position, cuticle morphology, amphid shape and presence of somatic setae were combined to identify patterns in the functional composition of nematode assemblages between the two habitats, the two mud volcanoes (macroscale) and between the microhabitats within the mud volcanoes (microscale). Data on trait correspondence was provided by biological information on species and genera. A total of 170 nematode species were allocated in 67 different trait combinations, i.e. functional groups, based on taxonomic, morphological and behavioral characteristics. The Biological Trait Analysis (BTA) revealed significant differences between the mud volcanoes and the typical deep sea sediments indicating the presence of different biological functions in ecologically very different environments. Moreover, chemosynthetic activity and habitat heterogeneity within mud volcanoes enhance the presence of different biological and ecological functions in nematode assemblages of different microhabitats. Functional diversity and species richness patterns varied significantly across the different environmental gradients prevailing in the study areas. Biological trait analysis, with the addition of newly introduced trait categories, and functional diversity outcomes provided greater explanatory power of ecosystem functioning than species richness and taxonomic diversity.

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1. Introduction

Mud volcanoes are cold seep geological structures characterized by mud and gas emissions whose main component is methane (Dimitrov, 2002; Kopf, 2005). Gas hydrates emissions are known to be utilized by bacteria and archaea during their chemoautotrophic processes, the derivatives of which are used by several invertebrates to increase their biomass (Olu-Le Roy et al., 2004). These highly active geological structures enhance the spatial heterogeneity of the deep sea habitats, at a mega- (regionally), macro- (within regions) and micro- (within habitats) scale, increasing the abundance and biomass of benthic fauna (Soltwedel et al., 2005), and consequently altering the ecology and functioning of benthic ecosystems (Zeppilli et al., 2011). Mud volcanoes have a worldwide distribution (Milkov, 2000), however the exploration of these structures is limited mostly to geological, geophysical and geochemical studies (Charlou et al., 2003; Etiope et al., 2009; Lykousis et al., 2009; Zitter et al., 2005) whereas ecology and biology of those ecosystems are much less investigated. Additionally, the majority of the limited ecological studies are mainly focusing on the microbial activity and on macro- and megafaunal communities (Bouloubassi et al., 2006; Niemann et al., 2006a; Olu-Le Roy et al., 2004; Ritt et al., 2012; Werne et al., 2004) whereas even fewer studies are associated with meiofaunal assemblages (Lampadariou et al., 2013; Soltwedel et al., 2005; Van Gaever et al., 2009b; Zeppilli et al., 2011).

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Nematodes are among the most common, abundant and speciose metazoan taxa on earth occurring in more habitats than any other group (Heip et al., 1985). They comprise 70–90% of the total meiofauna, often numbering millions of individuals per square meter (Mokievskii et al., 2007) and their species composition reflects habitat heterogeneity in marine environments, including the deep sea, being in close contact with seafloor related processes (Van Gaever et al., 2009a,b; Vanreusel et al., 2010). They contribute directly to ecological processes through their feeding activities and their metabolism (Yeates et al., 2009) playing a major role in the energetic pathways of the small food web (Giere, 2009). Nematodes, due to their ubiquity and numerical dominance, underpin ecosystem processes (Murray et al., 2002). They are active burrowers, bioturbators, very common and diverse and their relationship with sediment properties is complex (Heip et al., 1985; Reichelt, 1991) having a major impact on geomorphology (Murray et al., 2002). Nematodes are capable of biogeomorphological activity that will express itself at a scale of millimeters to large-scales of meters indicated by the mucus tube-building and functions such as sediment pelletization, increased pore water exchange, and elimination of macro-faunal traces (Reichelt, 1991). However, our knowledge of nematode natural history, feeding ecology, their contribution to carbon mineralization processes in the deep sea is yet poor (Soetaert et al., 1997). One approach to this problem has been to combine species into functional groups, i.e. groups consisting of species that share morphological traits thought or known to imply similarity in an important ecological function. For example, Wieser (1953) showed that the buccal structures of marine nematode genera allow a relatively easy classification into feeding guilds which has since found application in a variety of marine habitats (Giere, 2009 and references therein). Similarly, Thistle and Sherman (1985) noted that nematode tails are important in locomotion and reproduction and proposed a functional grouping of species based on tail shapes. Both feeding guilds (i.e. deposit feeding) and tail shapes (i.e. movement through the sediment) reflect ecological functions classifying different nematode activities and are associated with several sediment processes, i.e. sediment mixing, slope stability, etc. (Murray et al., 2002). Shaikh et al. (1998) confirmed that the morphology of structures produced by sediment failure is a function of the nature of the biological communities. More recently, there have been studies which attempt to follow a complete functional group approach, however they are still very few (Alves et al., 2014; Armenteros et al., 2010; Brustolin et al., 2012; Da Rocha et al., 2006; Fraschetti et al., 2006; Schratzberger et al., 2007; Somerfield et al., 2006), while the published studies in regard to the deep sea ecosystems are even less (Hasemann and Soltwedel, 2011; Ingels et al., 2011; Sharma et al., 2011; Thistle et al., 1995).

Species richness alone cannot entirely explain the ecosystem processes and functioning (Hooper et al., 2005). For this reason, Biological Trait Analysis (BTA) has become an indicative measure of the ecosystem functioning (Cadotte et al., 2011; Hooper et al., 2005; Norling et al., 2007). The creation of a functional group requires the appropriate choice of biological–functional trait combination shown by the species (Petchey and Gaston, 2006). The traits that have so far been used in several studies focus on a single or few biological traits such as the feeding types, tail shape or the size spectra of the organisms (Ingels et al., 2011; Vanaverbeke et al., 2004). According to Bremner et al. (2006), the BTA, which includes a series of traits related to the life history and morphological and behavioral characteristics of species, is a useful method for the assessment of the ecological processes as long as the selection of the traits is associated with important ecosystem processes. In the present study a number of measures of meiofaunal functional diversity have been created, quantifying the spatial distribution of 9 biological traits of the nematode assemblages between chemosynthetic habitats and typical deep sea habitats as well as between different microhabitats. These measures are intuitively useful for understanding ecological patterns and thus could be important for management (Cadotte et al., 2011; Petchey and Gaston, 2006). We also try to examine whether functional diversity and species richness varies across different environmental gradients and whether the former offers greater explanatory power of ecosystem functioning than species richness alone. We address the questions below by combining a range of biological traits based on buccal morphology, tail shape, body size, body shape, life history strategy, sediment position, cuticle morphology, amphid shape and presence of somatic setae. 1) Do nematode functional diversity and biological trait categories vary spatially at the deep sea, when comparing extreme ecosystems (e.g. mud volcanoes) and typical deep sea sediments? 2) Do nematode communities exhibit similar functional patterns at a microscale (i.e. between different microhabitats)? 3) Do nematode functional and taxonomical diversity reveal similar information about the ecosystem functioning?

2. Materials and methods

2.1. Study areas and microhabitats

2.1.1. Mud volcanoes

Two different mud volcanoes in the eastern Mediterranean were sampled: *Amsterdam* and *Napoli*. *Amsterdam* is an elliptical seafloor formation, up to 3 km wide and 100 m high, located in the area southwest of Turkey (Fig. 1). The geomorphology is rough characterized by depressions and abrupt scarps, particularly on its summit (2040 m depth) due to an erupted mud flow (300 m thick). The substratum is characterized by the presence of carbonate crusts, muddy areas and rock clasts. Temperature is reaching 36 °C, 7 m deep within the sediments indicating the presence of a high seepage activity; however no brine pools have ever been observed (Zitter et al., 2005). Bivalve shells belonging to the families Mytilidae and Vesicomyidae as well as to the genus *Idas* and live specimens of *Lamellibrachia* tubeworms have been observed close or under the carbonate crusts. *Napoli* is a dome-shaped formation at 1950 m depth, up to 1000 m wide and 200 m high, located in the area south of Crete (Fig. 1), surrounded by irregular mud flows and circular depressions. Fresh mud flows and brine pools were observed on the summit, indicating intense degassing (Charlou et al., 2003). Benthic assemblages, as bivalves of the Lucinidae family and tubeworms (i.e. *Lamellibrachia anaximandri*), have been observed at the periphery of the center of the mud volcano (Charlou et al., 2003).

In total, eight different microhabitats were sampled, that is four from each of the mud volcanoes, *Amsterdam* and *Napoli*: the sampled microhabitats at the *Amsterdam* mud volcano were: (i) brown sediments with high density of bivalve shells (denoted hereafter as Biv); (ii) the periphery of carbonate crusts (Pcc); (iii) a gas emission area, the reduced sediment area (Red); and (iv) the summit of the mud volcano (Top); the sampled microhabitats at the *Napoli* mud volcano were: (i) brown sediments with bivalve shells (Biv); (ii) the *Lamellibrachia* microhabitat (Lam); (iii) the periphery of the carbonate crusts (Pcc); and (iv) the periphery of the *Lamellibrachia* microhabitat (Plam). Detailed information on the two areas and their microhabitats as well as the sampling methodology can be found in Ritt et al. (2012) and Lampadariou et al. (2013).

2.1.2. Deep sea sediments

Three areas were chosen as typical deep sea ecosystems (Table 1) in the Eastern Mediterranean Sea. In total, data from nine sampling stations were employed (Fig. 1) with five of them being located in the south Ionian Sea (stations 18–21) (Sevastou et al., 2013), two in the southern Cretan margin (stations 16–17) (Polymenakou et al., 2008) and the remaining two stations in the Levantine Sea (stations 14–15) (Danovaro et al., 2008). All of them, consisted of typical fine-grained Mediterranean sediments characterized by the dominance of the silt-clay fraction (>70%). They are all located at abyssal depths, which ranged from 2765 to 3870 m, except the two stations at the southern Cretan margin which are located on bathyal slopes with depths ranging from 1089 to 1998 m (Table 1).