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Nematode community zonation in response to environmental drivers in Blanes Canyon (NW Mediterranean)

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ABSTRACT

Within the framework of the DosMares project, we investigated the standing stocks, structural and functional diversity and community structure of the nematode assemblages both along a bathymetric gradient, and the vertical sediment profile (0–5 cm) in the Blanes Canyon (NW Mediterranean) during autumn 2012.

The standing stocks (total density and biomass) did not follow the traditional pattern of bathymetric decline, showing disrupting peaks at 1200 and 1750 m depth. Along the sediment profile, high densities occurred in surface sediment layers, mainly due to increased nematode abundance, while biomass did not show clear general trends.

Structural and functional diversity did not exhibit consistent bathymetric gradients, and were not related to sedimentary variables, except for positive correlations with clay and silt contents. However, structural and functional diversity decreased significantly along the vertical sediment profile.

The analysis of the nematode community assemblages allowed us to identify three different community structure zones along the canyon axis: upper (ca. 500–1200 m depth), middle (ca. 1500–1750 m depth) and deeper (ca. 2000 m depth), which were 1) followed the canyon topographic heterogeneity, 2) supported by the environmental analyses (food sources and grain size), and 3) were reflected in the variable sediment and organic matter inputs from canyon walls and adjacent margins. The nematode distribution along the vertical sediment profile also varied in the three zones, mainly owing to differences in the respective surface sediment layers. Deeper sediment layers were similar, mainly caused by to the high abundance of *Sabatieria*.

Our results indicate that, in addition to the expected influence of the canyon's topography and hydrodynamic regimes, the nematode community from Blanes Canyon were controlled by the sedimentary characteristics and available food sources. Moreover, our results and additional data from other research in and around Blanes Canyon suggest that observed anthropogenic pressure in the surrounding areas (mainly derived from regular and persistent trawling activities) plays a key role in explaining the sedimentary pattern along the canyon axis and the observed nematode assemblage distribution.

1. Introduction

Deep-sea ecosystems cover nearly two-thirds of the Earth's surface and represent the largest biome in the biosphere. The perception that the deep sea is relatively homogeneous is outdated, and it is now acknowledged that habitat heterogeneity and species diversity are among the highest on the planet. Despite this, deep-sea spatial and temporal patterns as well as its biological and ecological diversity are among the least explored, while our knowledge on the functions and services it provides to humankind remains very poor (Rex, 1981; Danovaro et al., 2010; Vanreusel et al., 2010; Ramirez-Llodra et al., 2010; Thurber et al., 2014). Among the various deep-sea habitats, submarine canyons have recently gained much interest from marine ecologists. Their topographical uniqueness, alongside tremendous environmental heterogeneity and hydrodynamic variability, and their prevalence along productive continental margins make them ideal subjects to study ecological patterns and faunal drivers in the deep sea.

In deep-sea sediments worldwide, nematodes are generally the most abundant and diverse metazoan component (Jensen, 1988; Tietjen, 1992; Heip et al., 1985) and this is certainly true for canyons as well (Ingels and Vanreusel, 2013; Ingels et al., 2011a; Leduc et al., 2014). Deep-sea habitat heterogeneity greatly influences nematode diversity

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and assemblage structure and functional characteristics (Vanreusel, 2010). This includes the small-scale vertical distribution patterns along the sediment profile that are still poorly understood (Snelgrove and Smith, 2002; Gorska et al., 2014). At larger scales, the highest levels of heterogeneity in deep-sea habitats are known to occur around major geomorphological structures such as seamounts and submarine canyons, which lead to modifications in bathymetric patterns generally observed along the shelf-slope-abyss gradient. Nematode densities and biomass, along with those of meiofauna in general, typically decrease with water depth in response to food availability (Muthumbi et al., 2004; Soetaert et al., 1995; Vanaverbeke et al., 1997), but canyon meiofauna studies have shown that such a bathymetric decrease is not universal, and that it depends on the local topographical and related environmental conditions (Bianchelli et al., 2010; Romano et al., 2013; Román et al., 2016). Therefore, insights into nematode assemblage structure and functional characteristics have the potential to provide relevant information for understanding the environmental forces driving many aspects of the ecology of deep-sea benthos (e.g., Ingels et al., 2009; Hasemann and Soltwedel, 2011; Pusceddu et al., 2013).

Submarine canyons can modify the local oceanographic regime, by altering current directions and speed and/or by increasing the turbidity flows for instance (Martín et al., 2006; Puig et al., 2012). They also enhance the exchange of water and sediments between the shelf and slope, acting as preferential conduits of organic matter towards the abyss and serving as deep-sea deposition areas for large quantities of sediment and particular matter (Puig et al., 2000; Pasqual et al., 2010; Heussner et al., 2006; Lopez-Fernandez et al., 2013). Benthic communities, including the meiobenthos, are known to reflect these unstable and organically enriched conditions in canyon systems (Aller, 1997; Garcia et al., 2007; Ingels et al., 2009; Van Gaever et al., 2009; Romano et al., 2013; Román et al., 2016). Indeed, enhanced particle transport along canyons makes for an effective food supply to benthic organisms, resulting in higher faunal densities and biomass compared to non-incised slopes (Rowe et al., 1982; Soltwedel, 2000; De Leo et al., 2010; Leduc et al., 2014; Gambi and Danovaro, 2016). High habitat heterogeneity, coupled with an enhanced food supply, results in submarine canyons being biomass hotspots that consequently boost local fisheries (e.g., Rowe et al., 1982; Vetter et al., 2010; Company et al., 2008; De Leo et al., 2010). As a result, canyons and adjacent areas are targeted for fish and shellfish and may subsequently suffer anthropogenic impacts. Some of them are caused by local fisheries, mainly by bottom trawling (Company et al., 2012; Pusceddu et al., 2014; Román et al., 2016), while some others are related with channelling and accumulation of pollutants such as litter (Ramirez-Llodra et al., 2013) or chemicals (Sanchez-Vidal et al., 2015). These additional disturbances certainly play an important role in the canyon system dynamics.

Mediterranean margins are frequently and deeply incised by submarine canyons, and have received increased attention in recent years. For some of them, nematode diversity patterns in these ecosystems have been studied along bathymetric gradients at different spatial scales (Bianchelli et al., 2013). Identifying and quantifying the importance of the factors that drive local and turnover diversity and would allow – to an extent – prediction of (inter)spatial patterns and species composition in deep-sea assemblages and have been highlighted as priorities to advance our understanding of biodiversity dynamics in the deep sea and in submarine canyons. However, the available information on nematode community structure related to its environmental drivers in canyons is still limited (Snelgrove and Smith, 2002; Ingels et al., 2013; Vanreusel, 2010). This knowledge is essential to increase our understanding about the benthic functioning of these highly heterogeneous habitats.

The Blanes Canyon, located at the NW Mediterranean coast of the Iberian Peninsula, has been the subject of several benthic studies in the past (e.g., Zúñiga et al., 2009; Canals et al., 2013; Lopez-Fernandez et al., 2013). Higher meiofauna and nematode densities were found in the canyon compared to the adjacent open slope (Ingels et al., 2013; Román et al., 2016; Romano et al., 2013), while abundances did not show a clear bathymetric pattern along the canyon axis, owing in part to changes and heterogeneity in spatial and temporal availability of organic matter (Román et al., 2016). A key role in the disruption at greater water depths (e.g. 1200 m) of the expected bathymetric decrease in meiofauna densities has been attributed to lateral advection of food-enriched sediment, resuspended as a result of the daily bottom trawling activities on the canyon flanks. These sediments are assumed to be transported and accumulated down the canyon, resulting in an anthropogenic depocenter in the canyon axis (Román et al., 2016). Nematode communities from the Blanes Canyon system have been studied within the framework of the project RECS (2003–2004) by Ingels et al. (2013). However, on the report is limited to the nematode standing stocks, feeding types and gender-life stage distributions from specific stations in the upper canyon head (500 m depth), flanks (900 m depth) and axis (1600 m depth). A more comprehensive nematode analysis of the whole canyon axis is presented here.

Here, we provide a comprehensive analysis of the spatial patterns of nematode community structure, and functional diversity in Blanes Canyon, while considering its relationships with the main biogeochemical and environmental factors. Differences in assemblage composition, structure and diversity are assessed at six stations along a bathymetric gradient (500 to 2000 m depth), as well as along the vertical sediment profile (0–5 cm), to identify the main driving factors of canyon infaunal community patterns. The lack of clear bathymetric gradients in higher-taxa meiofauna canyon assemblages (Román et al., 2016; Romano et al., 2013) is assessed further by investigating the following questions for nematodes: 1) Are elevated densities at specific water depths in the canyon explained by the increase in particular genera or trophic groups? 2) Are these elevated densities associated with the surface and/or subsurface sediments? 3) Are the same environmental factors that explain density changes also associated with changes in nematode genera composition, structure and diversity? By answering these questions we aim to identify spatial nematode community patterns that are related to the canyon environment.

2. Material and methods

2.1. Study area and sampling

The Blanes submarine canyon is located in the NW Mediterranean Sea (Fig. 1). The canyon is 184 km long and its head incises the continental shelf at 60 m depth, < 4 km offshore, in a NW-SE direction (Lastras et al., 2011). The width increases with depth and reaches a maximum width of 20 km wide when the canyon meets the Valencia Channel at 2400 m water depth. The upper course of the canyon is characterized by a V-shaped cross-section, indicative of intense erosion processes, and is flanked by several gullies; the lower course has a U-shaped cross-section, indicative of high sediment deposition (Lastras et al., 2011). Mesoscale circulation is dominated by the North Current (NC) which is mainly forced by the entrance of Atlantic Water (AW) into the Mediterranean through the Gibraltar Strait and extending from the surface down to 100–200 m depth. The more saline Levantine Intermediate Water (LIW), originating in the eastern Mediterranean basin, extends down to approximately 600 m depth, while the Western Mediterranean Deep Water (WMDW), which forms during the winter in the Gulf of Lion, extends down to the seafloor (Millot, 1999). The Blanes Canyon area is exposed to intense natural disturbance due to the typical NW Mediterranean atmospheric forcing which includes Eastern wet storms (Guillén et al., 2006; Bonnin et al., 2008) and Northern dry storms, as well as, episodic dense shelf water cascading (DSWC) (Canals et al., 2006; Heussner et al., 2006). Moreover, the canyon is particularly exposed to deep-sea fisheries, mainly bottom trawling on the canyon flanks (Company et al., 2008; Puig et al., 2012). Sediments resuspended by trawling are transported down to the canyons´ axis through lateral gullies or tributaries causing altered patterns of sediment deposition at

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