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Temporal and spatial variation in the Nazaré Canyon (Western Iberian margin): Inter-annual and canyon heterogeneity effects on meiofauna biomass and diversity

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ABSTRACT

The Nazaré Canyon on the Portuguese Margin (NE Atlantic) was sampled during spring-summer for three consecutive years (2005–2007), permitting the first inter-annual study of the meiofaunal communities at the Iberian Margin at two abyssal depths (~3500 m and ~4400 m). Using new and already published data, the meiofauna standing stocks (abundance and biomass) and nematode structural and functional diversity were investigated in relation to the sediment biogeochemistry (e.g. organic carbon, nitrogen, chlorophyll *a*, phaeopigments) and grain size. A conspicuous increase in sand content from 2005 to 2006 and decrease of phytodetritus at both sites, suggested the occurrence of one or more physical disturbance events. Nematode standing stocks and trophic diversity decreased after these events, seemingly followed by a recovery/recolonisation period in 2007, which was strongly correlated with an increase in the quantity and bioavailability of phytodetrital organic matter supplied. Changes in meiofauna assemblages, however, also differed between stations, likely because of the contrasting hydrodynamic and food supply conditions. Higher meiofauna and nematode abundances, biomass and trophic complexity were found at the shallowest canyon station, where the quantity, quality and bioavailability of food material were higher than at the deeper site. The present results suggest that even though inter-annual variations in the sedimentary environment can regulate the meiofauna in the abyssal Nazaré Canyon, heterogeneity between sampling locations in the canyon were more pronounced.

1. Introduction

In contrast to earlier ideas of the deep sea as a remote faunal desert, we now know that it harbours diverse assemblages of animals and protists. Organisms inhabiting this environment are subjected to variable regulating disturbance and seasonal/episodic productivity regimes related to upper water-column processes (Gage and Tyler, 1991). Understanding benthic community responses to such events allows insights into deep-sea diversity and dynamics (Gage and Tyler, 1991; Gooday, 2002; Billett et al., 2010). There is evidence that smaller benthic organisms tend to respond quickly to pulses of organic-rich detritus, with increases in standing stocks and enhanced metabolic responses (Gooday, 2002; Guidi-Guilvard et al., 2009). Nevertheless we are still confronted with a lack of knowledge on the scales (temporal and spatial) at which different processes regulate deep-sea communities, including conclusive insights into the cause–effect relationships (Glover et al., 2010; Ingels and Vanreusel, 2013). In addition, for certain relatively homogeneous deep-sea habitats it is possible to roughly predict faunal response to, for instance, yearly peaks in organic matter (OM) fluxes (Gooday, 2002), while for other, more complex and dynamic habitats, patterns are more challenging to investigate. This is particularly the case for submarine canyons, where different regulating processes and heterogeneous environmental conditions act in concert, in time and space, to structure faunal communities (e.g. Bianchelli et al., 2008; Ingels and Vanreusel, 2013; McClain and Barry, 2010).

Submarine canyons are pervasive, large-scale geological features that cut the continental shelf and slope, and form a direct

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pathway from shallow waters to the deep sea. Characterised by complex topography, hydrology, disturbance regimes (e.g. strong near-bottom currents, turbidity flows) and locally enhanced organic matter availability, canyons act as important sediment and organic material conduits to the abyssal plain (Canals et al., 2006; de Stigter et al., 2007; Masson et al., 2010). In general, higher faunal densities, biomass, local diversity and trophic complexity are found in canyons compared to the adjacent slope (e.g. Soetaert and Heip, 1995; Soltwedel, 2000; Danovaro et al., 2009; Ingels et al., 2009, 2011c; De Leo et al., 2010; McClain and Barry, 2010), although occasionally very low densities are also found (Van Gaever et al., 2009; Garcia et al., 2007).

The number of studies on meiofauna in submarine canyons has increased in recent years, providing a better insight into how benthic communities respond to environmental conditions within canyons (e.g. Soetaert et al., 1991; Soltwedel, 2000; Soltwedel et al., 2005; Koho et al., 2007; Bianchelli et al., 2008, 2010, Ingels et al., 2009, 2011a, 2011b, 2011c; Danovaro et al., 2010; Pusceddu et al., 2013). Nematodes, as the most abundant meiobenthic taxon, are considered a useful tool to obtain information on ecosystem characteristics and functioning (Heip et al., 1985; Vincx et al., 1994). Due to their ecological and biological characteristics (high abundance, sensitive to different types of disturbance, short generation time, limited mobility and lack of pelagic life stages), it is expected that the structural and functional diversity of nematode communities reflect variability in habitats, physical disturbance and food availability throughout canyon systems over time (Giere, 2009; Vanreusel et al., 2010). Still, many of the canyon studies only address spatial patterns (e.g. Danovaro et al., 1999, 2009; Garcia et al., 2007; Ingels et al., 2009, 2011b, 2011c; Bianchelli et al., 2010; Ingels and Vanreusel, 2013).

The relative inaccessibility and the logistical challenges of maintaining a long-term monitoring programme are among the main factors restricting temporal studies in canyons. Information on temporal variability of meiofauna within canyons is therefore sparse and generally limited to seasonal studies (Danovaro et al., 1999; Gooday, 2002; Fontanier et al., 2005). The few studies that use nematodes to investigate intra- and inter-annual variability, focus solely on abundances (de Bovée et al., 1990; Soetaert et al., 1991; Guidi-Guilvard et al., 2005) and to our knowledge only one study has investigated patterns based on nematode diversity as well as biomass (Pusceddu et al., 2013) from canyons in the Mediterranean Sea. All studies indicate high variability over time, probably related with fluctuations of the food supply in the context of bentho-pelagic coupling. Additionally, alterations to the sedimentary environment caused by physical disturbance (e.g. turbidity currents, benthic storms, etc.) may be responsible for some of the faunal temporal changes observed (Guidi-Guilvard et al., 2009; Pusceddu et al., 2013). Meiofaunal abundances can decrease markedly after physical disturbance events and are usually followed by a short recovery time (Ingels et al., in press; Romano et al., in press; Pusceddu et al., 2013). The causes for the evident standing stocks decrease could be the result of one or a set of factors such as an increase in mortality, resuspension and transport of the individuals entrained with sediments, and migration to deep sediment layers (Guidi-Guilvard et al., 2009). Nevertheless, limited information is available on how meiobenthic, and in particular nematode community composition, and structural and functional diversity are altered by temporal changes in canyons.

As part of the HERMES project (Hotspot Ecosystem Research on the Margins of European Seas), the NE Atlantic margin's largest canyon, the Nazaré Canyon, was sampled in three consecutive years (2005–2007), permitting us to perform the first inter-annual meiobenthic study in canyons along the Iberian coast. Using already published (Ingels et al., 2009, 2011b; Kiriakoulakis et al., 2011) and new data, the main aim of this study was to investigate inter-annual patterns of the meiofaunal communities, with emphasis on free-living marine nematodes at two distinct abyssal canyon locations (representing two different water depths; ca. 3500 m and ca. 4400 m). We hypothesised that potential changes in environmental conditions between the two canyon sites and over the years would be reflected in the meiofauna/nematodes standing stocks and structural and functional diversity. The following null hypotheses were tested for meiofauna and nematode abundance, community composition, biomass, diversity, and trophic composition: (1) there are no significant differences between the different years, 2005, 2006, and 2007; (2) there are no significant differences between the canyon sites (ca. 3500 and ca. 4400 m); (3) there is no relation between environmental conditions and meiofauna and nematode community parameters.

2. Material and methods

2.1. Study area

The Western Iberian Margin in the Northeast Atlantic is characterised by a narrow shelf adjacent to a steep irregular slope and is incised by numerous canyons. The largest canyon along the Western Iberian Margin is the Nazaré Canyon (Fig. 1), originating on the shelf at a water depth of 50 m near the Portuguese coast and extending to 5000 m water depth at the edge of the Iberian Abyssal Plain (Masson et al., 2011). There is no connection to a large river system, but the canyon intersects a significant part of the shelf, and traps large quantities of sediments with high OM content that are moving along the coast (de Stigter et al., 2007; Oliveira et al., 2007; Arzola et al., 2008; Lastras et al., 2009; Masson et al., 2011). The canyon is usually divided into three parts on the basis of its morphology (de Stigter et al., 2007; Lastras et al., 2009). The upper and mid-canyon sections are characterised by the presence of moderately strong tidal currents (maximum of 35 cm/s), causing resuspension, transport and redistribution of particulate matter (de Stigter et al., 2007; Masson et al., 2011). The transport towards the lower part of the canyon takes place predominantly in nepheloid layers or less frequently through the flushing of sediments by gravity flows, providing irregular OM input to the deeper section (Van Weering et al., 2002; de Stigter et al., 2007; Lastras et al., 2009). The mid-canyon site was located in the central part of the canyon on a terraced slope next to the axial channel (thalweg), with high sediment accumulation rates (Arzola et al., 2008; Lastras et al., 2009). The deep-canyon site was located in the flat-floored lower canyon valley.

2.2. Sampling

The sampling was conducted during the late spring/early summer of 2005, 2006 and 2007, at ca. 3500 m and ca. 4400 m, corresponding to the mid and deeper sections of the canyon, respectively (Fig. 1; Weaver, 2005; Billett, 2006; Masson, 2009). At each sampling site and in each year, 6 sediment cores were recovered (3 for meiofauna analysis and 3 for environmental analyses). The sediment samples from 2005 and 2006 were obtained using a multicorer (MUC, Plexiglas tubes with 57 mm internal diameter) and a megacorer (MGC, Ocean Scientific International Ltd, Plexiglas tubes with 100 mm internal diameter), the latter subsampled with a core of 60 mm internal diameter, in order to maintain relative consistency in sample surface area for all replicates. The 2007 samples were taken using push cores (with internal diameter of 57 mm) by the Remotely Operated Vehicle (ROV) ISIS. At each sampling event the top 1 cm of 3 replicate cores (each core from independent deployments) were placed in Petri dishes and frozen at $-20\,^{\circ}C$, for later determination of environmental characteristics in the lab. The other 3 replicate cores from independent deployments, with exception of the deep site in 2006