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Disturbance, productivity and diversity in deep-sea canyons: A worm's eye view

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ABSTRACT

The abundance, diversity and assemblage structure of polychaetes from the Nazaré, Setúbal and Cascais Canyons along the Iberian Margin were studied as part of the EU project HERMES. A Dynamic Equilibrium Model (DEM) was used to identify the main environmental factors structuring the assemblages. Box corer and megacorer samples from upper (1000 m), middle (3400 m) and lower canyon (4300 m) settings were taken in each canyon. Polychaete abundances in the Nazaré and Setúbal Canyons were highest at 3400 m while in Cascais there were only slight differences between the various depths. Most of the polychaetes occurred in the top 5 cm of the sediment. Sample diversity both within and among the canyon sites did not differ statistically despite differences in the environmental settings, suggesting that small-scale heterogeneity at the scale of the sampler was similar at all sites. Species richness at the level of site was lowest at 3400 m sites in both the Nazaré and Setúbal Canyons. In contrast, species richness increased from 1000 m to ca. 3400 m and then again to 4300 m in the Cascais Canyon. The differences were linked to the physico-biogeochemical environment of each canyon. Analyses of physico-environmental variables indicated that the Nazaré mid-canyon sites were subject to high levels of disturbance and intermediate levels of productivity, accounting for high abundances and low species richness. Low disturbance and low productivity characterised the lower Nazaré Canyon site at 4300 m. Diversity results agreed with predictions of the DEM. However, the 4300 m site in the Setúbal Canyon did not conform to model predictions. Overall, while the Iberian Margin canyons demonstrated higher abundance and biomass than 'open slope' polychaete assemblages, they had lower species richness.

1. Introduction

Submarine canyons are deep incisions in the continental shelf and slope, and are important depocentres and major conduits of sediment and organic carbon to the abyss. They are also unstable deep-sea environments where down-slope processes such as sediment slumps and turbidite events can dominate (Gardner, 1989; de Stigter et al., 2007; Arzola et al., 2008). Canyons can also channel pollutants accumulated in costal-zone sediments to the deep sea (Gardner, 1989; Puig et al., 1999; Paull et al., 2006).

These conditions influence the biological communities found within the canyons. Indeed, several studies suggest that canyons are biodiversity 'hotspots', with biomass and abundance often higher than in similar depths in non-canyon environments, although diversity may be lower (Vetter and Dayton, 1998; Curdia et al., 2004). Studies comparing canyon and non-canyon assemblages also show that communities within canyons may be different to those found in nearby non-canyon areas suggesting the existence of 'canyon indicator species', which may often achieve high densities (Rowe, 1972; Vetter and Dayton, 1998).

Disturbance-nutrient (food availability) gradients have been implicated as primary factors in explaining patterns of species diversity/richness (e.g. Grime, 1973; Connell, 1978; Rex, 1983; Sousa, 1984; Picket and White, 1985; Huston, 1994; Abrams, 1995; Paterson and

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Lambshead, 1995; Cosson et al., 1998). Two main model-hypotheses have been developed from such observations. In the first model type one particular factor and its effect on diversity predicts a link between diversity and levels of productivity, for example, the Intermediate Disturbance Hypothesis (IDH Connell, 1978) or Intermediate Productivity Model (IPM Grime, 1973). The second type are models that combine predictions from varying disturbance and productivity regimes—Dynamic Equilibrium Models (DEM) (Huston, 1994; Kondoh, 2001; Kadmon and Benjamini, 2006; Svensson et al., 2007). Both IDH/IPM and DEM predict unimodal patterns of species diversity with changing levels of disturbance and/or productivity with highest diversity occurring at intermediate levels, although the model proposed by Kadmon and Benjamini (2006) shows other patterns depending on the levels of disturbance/productivity. Such models represent a conceptual framework within which to interpret the results of the canyons studies, although the HERMES sampling programmes were not designed to test specifically predictions from such models.

The underlying mechanisms driving such patterns are subject to debate. IDH models of Connell (1978) and Kondoh (2001) invoke competition as the main mechanism whereby low disturbance results in better competitors dominating an assemblage. In contrast, Kadmon and Benjamini (2006) postulate that competition is unnecessary and that similar patterns of species richness can be generated from neutral models. In this case, changes in species richness result from the interaction of mortality (caused by disturbance) and colonisation (from the regional species pool). Hence in areas with high productivity species richness declines because more individuals of existing species in the area colonise available space (termed the More Individuals Hypothesis). Similarly as disturbance changes so too does the mortality rate, providing an opportunity for colonisation by species from the regional pool. However, as disturbance increases the numbers of species ultimately will decline as mortality rates exceed colonisation rates. Predictions from these models are that high dominance should characterise high productivity/low disturbance areas, and that the community structure should differ from assemblages at each end of the gradients.

Recent studies on the canyons of the Iberian Margin suggest that canyons represent distinct gradients of disturbance and organic nutrient availability. Within the Nazaré Canyon, disturbance takes the form of down-slope events such as fast currents generated by internal tides leading to frequent resuspension of sediments in the upper canyon (50–1000 m); tidal transport, in the form of spring tides, in the middle sections; and gravity flows on time scales of a year or less which reach the deepest parts of the canyon (de Stigter et al., 2007; Koho et al., 2007; Garcia et al., 2008). Hence there is a change in the magnitude and the frequency of the disturbance events down the canyon. High food/organic nutrient availability occurs in upper canyons settings down to 1000 m with resuspension and elevated concentrations of suspended particles down to 2800 m (de Stigter et al., 2007). Below this depth, organic nutrient availability decreases. Within these canyon zones a uniform mud layer drapes the canyon terraces and thalweg (the central axis of the canyon). Subsurface sediment in the thalweg may have a higher proportion of sand. Therefore there may be smaller lateral gradients within canyons, such that terrace areas have finer sediments compared with the central canyon axis (de Stigter et al., 2007; Garcia and Thomsen, 2008; Lastras et al., 2009). In contrast to the Nazaré Canyon, the Setúbal Canyon has less hydrographic disturbance and Koho et al. (2008) showed that organic nutrient availability plays a more important role in structuring foraminiferan communities. The Cascais Canyon is considered to be a more quiescent canyon.

The objectives of this study were: (1) to determine patterns of polychaete abundance and species richness within and among the canyons and non-canyon sedimentary environments. (2) To investigate whether patterns of species richness can be explained within the conceptual framework of disturbance–productivity and agree with general predictions made by Dynamic Equilibrium Models (DEM, e.g. Huston, 1994; Kondoh, 2001; Kadmon and Benjamini, 2006). (3) To establish whether there was a distinct canyon polychaete assemblage by comparing the polychaete abundance, diversity and community structure among the canyons and non-canyon sediment habitats.

2. Methods

2.1. Study area

The Central Portuguese canyons (Nazaré, Cascais and Setúbal Canyons) of the Western Iberian Margin (Fig.1) cut through the continental shelf at water depths shallower than 50 m reaching down to the Tagus and Iberian Abyssal Plains, at depths exceeding 5000 m (Lastras et al., 2009). The Nazaré Canyon lies between 39°N and 40°N and it is one of Europe's largest marine canyon systems and has a relatively simple topography. Although this canyon is not connected to a river, it acts as major sediment sink (Arzola et al., 2008) because it cuts across all of the Portuguese continental shelf. The Setúbal-Lisbon Canyons are located south of the Nazaré Canyon and form a more complex system connected to two major river basins, the Tagus and Sado. The Cascais Canyon lies in close geographical proximity to Setúbal-Lisbon canyon, but its head is not connected directly to a river system. A more detailed description of the regional setting of the Western Iberian Margin is given by Arzola et al. (2008) and Lastras et al. (2009).

2.2. Field sampling

The polychaete samples were obtained during cruise R.R.S. *Discovery* Cruise 297 (D297; Weaver, 2005) in 2005 from Nazaré Canyon the R.R.S. *Charles Darwin* Cruise 179 (CD 179; Billett, 2006) in 2006 from Nazaré, Cascais and Setúbal Canyons and the R.V. *Pelagia* (NIOZ) Cruise (64PE252 2006) to all three canyons (Table 1). In the first two cruises samples were taken from the middle canyon at 3200–3500 m (hereafter termed 3400 m) and the lower canyon at 4000–4500 m (hereafter termed 4300 m). In addition samples were taken from upper canyon settings around 900–1000 m (hereafter termed 1000 m) on the R.V. *Pelagia* Cruise. The terminology – upper, middle and lower within the canyon – follows Vanney and Mougenot (1990). Samples were taken on the canyon terraces to the canyon axis

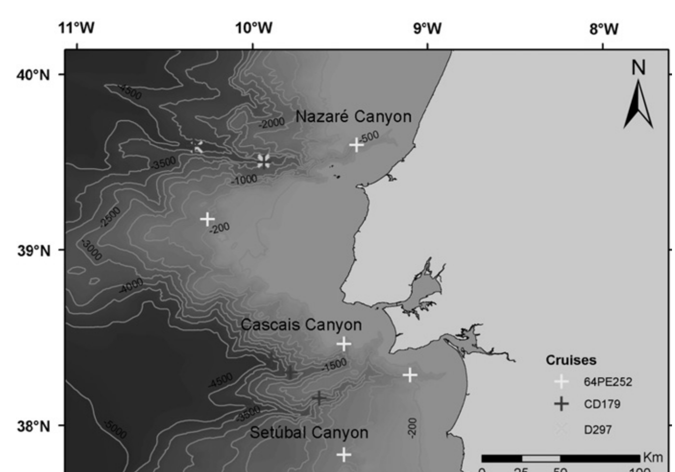

Fig. 1. Study area with sampling sites.