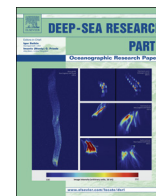




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Bathymetric and regional changes in benthic macrofaunal assemblages on the deep Eastern Brazilian margin, SW Atlantic



Angelo Fraga Bernardino^{a,*}, Vanessa Berenguer^b, Venina P. Ribeiro-Ferreira^c

^a Grupo de Ecologia Bentônica, Departamento de Oceanografia, Universidade Federal do Espírito Santo, Av. Fernando Ferrari, 514 Goiabeiras, Vitória-ES 29075-910, Brazil

^b Benthos Ambiental, Rio de Janeiro, RJ, Brazil

^c Puc-Rio, CENPES, Petrobras, Rio de Janeiro, RJ, Brazil

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ABSTRACT

Deep-sea continental slopes have valuable mineral and biological resources in close proximity to diverse, undersampled and fragile marine benthic ecosystems. The eastern Brazilian Continental Margin (19.01°S to 21.06°S, 37.88°W to 40.22°W) is an important economic region for both fishing and oil industries, but is poorly understood with respect to the structure of the soft-sediment benthic fauna, their regional distribution and their bathymetric patterns. To identify spatial and temporal patterns of benthic macrofaunal assemblages on the slope (400 to 3000 m), the Espírito Santo Basin Assessment Project (AMBES, coordinated by Cenpes-Petrobras) sampled 42 stations across the Brazilian Eastern Slope during both Summer 2012 and Winter 2013. We found a significant decrease in macrofaunal abundance at the 400 m isobath along the slope near the northern region of the Espírito Santo Basin, suggesting benthic responses to upwelling events towards the south in Campos Basin and southern Espírito Santo Basin. The taxonomic diversity and assemblage composition also changed significantly across depth zones with mid-slope peaks of diversity at 1000–1300 m. In general, macrofaunal assemblages were strongly related to slope depth, suggesting a strong influence of productivity gradients and water mass distribution on this oligotrophic margin. Sediment grain size was marginally important to macrofaunal composition on the upper slope. In general, macrofaunal assemblages on the slope of Espírito Santo Basin are similar to other areas of the SE Brazilian margin, but regional changes in response to productivity and depth need to be considered for management strategies in the face of increasing economic activities off-shore.

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1. Introduction

Continental margins cover roughly 11% of the ocean floor, are characterized by strong depth gradients, high habitat heterogeneity and high biological diversity as well as providing important ecosystem services (Gage and Tyler, 1991; Ramirez-Llodra et al., 2010; Levin and Sibuet, 2012; Thurber et al., 2014). Continental margins host a number of ecological processes that are important to global biogeochemical cycles (Danovaro et al., 2008), and offer food provision and other mineral resources in the vast and species-rich deep-sea (Grassle and Maciolek, 1992; Ramirez-Llodra et al., 2010; Mora et al., 2011; Levin and Sibuet, 2012). The growing economic interests and human activities along continental margins worldwide offer an opportunity to understand diversity and ecology in areas of biological and economic relevance.

Benthic assemblages on deep-sea slopes typically show bathymetric patterns of decreasing abundance and regional changes in taxonomic composition and diversity, related to decreasing food availability, oceanographic processes and local-scale ecological processes (Hessler and Sanders, 1967; Dayton and Hessler, 1972; Rowe et al., 1974; Levin et al., 2001; Carney, 2005). The limited organic input to the deep-sea benthos has a fundamental influence on assemblage abundance; the flux of particulate organic carbon (POC) is often a good proxy for community attributes (e.g. abundance and biomass), and function (e.g. bioturbation; Smith et al., 2008). Species diversity on continental slopes usually peaks at intermediate depths (2000–3000 m), as a result of multiple depth-related factors (Rex, 1981; Levin and Dayton, 2009). Habitat heterogeneity, biogeographic ranges and other biological factors are important at regional scales (meters to kilometers) and have an effect on whether diversity is maintained on continental margins worldwide (Glover et al., 2002; Snelgrove and Smith, 2002; McClain and Hardy, 2010; McClain et al., 2011; Levin and Sibuet, 2012). Bathymetric gradients also influence assemblage composition on continental margins, which may be

* Corresponding author.

E-mail address: angelo.bernardino@ufes.br (A.F. Bernardino).

associated with habitat heterogeneity (e.g. sediment grain size and covariables), water masses (Carney, 2005; Menot et al., 2010; Narayanaswamy et al., 2010) and other regional oceanographic parameters.

The physical oceanography and geological structure of the Brazilian margin in the SW Atlantic are well studied, but the biological communities on the slope are less well known (De Madron and Weatherly, 1994; Campos et al., 1995; Viana et al., 1998; Calado et al., 2006; Mello e Souza et al., 2006; Miloslavich et al., 2011). The slope off E-SE Brazil has over 90% of the country's deep-sea oil reserves and production, which are distributed along Santos Basin, Campos Basin and Espirito Santo Basin (ESB) (Carvalho et al., 1995; Viana et al., 1998; Mohriak, 2003). These three basins are under typically oligotrophic conditions with minor continental input (Mahiques et al., 2004). However, there is a region at the edge of both the Santos and Campos Basins that is influenced by strong summer upwelling, resulting in higher productivity and the intensification of food export to sediments (Valentin, 2001). Effects of this upwelling have been extensively studied from shelf to upper slope depths and have significant influences on benthic assemblages (Sumida et al., 2005; De Leo and Pires-Vanin, 2006; Quintana et al., 2015). In the Eastern region of the margin, Espirito Santo basin is also typically oligotrophic, economically important and geomorphologically diverse (Viana et al., 1998).

The benthic biota of the ESB and the deep Eastern Brazilian margin were initially surveyed by international expeditions in the 1980s, then characterized more recently (1996–2002) as part of the Brazilian government's efforts to recognize living resources within its Exclusive Economic Zone (REVIZEE program). Sparsely distributed sampling along the eastern margin between 50 and 1000 m depth revealed slope megafaunal communities dominated by epifaunal deposit-feeders including ophiuroids, echinoids, holothurians and decapod crustaceans, and by suspension-feeders including sponges and cold-water corals (Lavrado and Ignacio, 2006; Pires, 2007). Macrofaunal assemblages were also initially characterized, dominated by typical deep-sea peracarid crustaceans, polychaetes, molluscs and sipunculids (Lavrado and Ignacio, 2006). Patterns of distribution and bathymetric trends were not investigated in detail, but species richness and composition were mostly associated with variable grain size, depth and the presence of a number of hard bottom habitats (e.g. rhodolith beds) on the shelf and upper slope. The taxonomic richness on the upper slope (250–500 m; $ES_{25} = 10$) was lower than on the shelf ($ES_{25} = 14$), but that assessment relied on a limited sampling effort in deeper areas ($N = 10$; Lavrado and Ignacio, 2006). Although REVIZEE program efforts contributed to the quantification of deep biodiversity on the Brazilian margin, the effect of regional and bathymetric changes on benthic faunal structure along most regions of the slope remains poorly understood. Those patterns of change in benthic assemblages over deep-sea basins off Brazil have gained importance in light of the country's recent economic interest in exploring multiple natural resources.

To understand patterns within the macrofaunal assemblage structure for this northern portion of the SE Brazilian margin in the SW Atlantic, the Espirito Santo Basin Assessment Project (AMBES, coordinated by Petrobras) quantitatively sampled the continental slope of Espirito Santo and the northern Campos Basin. Given the high environmental heterogeneity and steep depth gradients on the slope, we expected to find marked spatial differences on macrofaunal assemblages in the study region. We hypothesized that macrofaunal density would be strongly reduced and species composition altered with increased depth in response to food limitation on the slope. We also hypothesized that regional differences in productivity would have minor effects on community structure (i.e. assemblage composition and diversity), if compared to depth effects.

2. Materials and methods

2.1. Study site and sampling

The eastern Brazil margin is one of the most studied regions of the SW Atlantic, with approximately 60% of Brazil's oil production in the Campos Basin (22.58°S to 20.19°S and 42.1°W to 40.2°W) and the Espirito Santo/Mucuri Basin (20.19°S to 19°S and 37.88°W to 40.22°W) (Carvalho et al., 1995; Viana et al., 1998; Mohriak, 2003). In the northern part of the margin, the Espirito Santo Basin (ESB) is limited to the north by the Abrolhos Coral Reef banks and to the south by the Campos Basin. To the east, the Vitória-Trindade seamount chain stretches eastward from the slope at 21°S. Eddy formation between the Vitoria-Trindade Seamount chain to the east and the slope to the west may intensify upwelling events at the southern and central areas of the basin (Schmid et al., 1995; Calado et al., 2006). The northern and central oceanic regions of ESB are typically oligotrophic (pigment concentrations of 0.06–2.0 mg m⁻³, (Gonzalez-Silveira et al., 2004)), with complex topography near the Abrolhos Bank. The slope in the study region is influenced by four main water masses with distinct flow directions: (i) the South Atlantic Central Water (SACW; T = 18–6 °C) flowing northward between 300 and 550 m depth; (ii) Antarctic Intermediate Water (AAIW; T = 6–2 °C) flowing northward between 550 and 1200 m depth; (iii) North Atlantic Deep Water (NADW; T = 4–2 °C) flowing southward between 1200 and 3500 m; and (iv) Antarctic Bottom Water (AABW; T < 2 °C) flowing northward below 3500 m (De Madron and Weatherly, 1994).

The Espirito Santo Basin Assessment Project (AMBES, Cenpes/Petrobras) sampled the continental slope of Espirito Santo and northern Campos Basin during two oceanographic cruises in Summer 2012 and Winter 2013. Seven transects (where transect A represented northern Campos Basin and B–G represented ESB) were evenly distributed in the study region; Triplicate box core (USNEL) samples were collected at depths of 400, 1000, 1300, 1900, 2500 and 3000 m from 42 stations during each cruise (Fig. 1). The presence of hard bottoms limited box core sampling for sediments at 400–1000 m in the northern part of the basin (Transect G, Table 1). Each box corer was processed on board for sediment properties (grain size and total organic matter) and macrofauna (top 10 cm over an area of 0.09 m⁻² per replicate). Sediment samples (top 5 cm) were frozen after sampling (–20 °C) for later laboratory analysis. Macrofaunal samples were preserved unsieved on board (10% formalin with neutral pH).

2.2. Laboratory and statistical analysis

Sediment samples (0–5 cm) were analyzed for particle size and total organic matter (TOM). Sediment particle size and composition were analyzed by standard wet sieving methods and carbonate content by weight difference after acidification (1N HCl). Sediment TOM was determined by the difference between dry (60 °C) and ash free dry weight (400 °C). Spatial differences in sediment particle size and TOM were determined by Kruskal-Wallis tests due to non-normality of variances (BioEstat statistical package).

Macrofaunal samples were washed in fresh water in the laboratory through 300 µm mesh sieves and preserved in ETOH (70% v/v) until sorting. Organisms were identified to family (Polychaeta), order (Crustacea, Mollusca), or higher levels for less abundant groups (e.g. Sipuncula, Nemertea, Echinodermata). Spatial and seasonal changes in macrofaunal assemblages were tested based on total density (normalized to individuals m⁻²), dominance (Pielou J') and diversity indices (rarefaction, PRIMER v6) that were appropriate for changes in the number of individuals with depth (Hulbert, 1971; Magurran, 2004). Patterns of faunal

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