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Nematode community structure along a central Chile margin transect influenced by the oxygen minimum zone



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ABSTRACT

Nematodes are among the metazoans most tolerant of low-oxygen conditions and play major roles in seafloor ecosystem processes. Nematode communities were studied in sediments off Concepción, Central Chile, spanning the outer shelf within the OMZ (122 m) to the mid-lower continental slope (972 m) beneath the OMZ. The total density and biomass of nematodes (core depth 0–10 cm) ranged from 677 to 2006 ind. 10 cm⁻², and 168.4 to 506.5 μg DW 10 cm⁻², respectively. Among metazoan meiofaunal taxa, nematodes predominated at all sites both in terms of relative abundance (83.7–99.4%) and biomass (53.8–88.1%), followed by copepods, nauplii and polychaetes. Nematodes were represented by 33 genera distributed among 17 families, with densities greatest at low oxygen sites (122–364 m; ~2000 ind. 10 cm⁻²). Nematode generic and trophic diversity, and individual biomass were lowest, and Rank 1 dominance was highest, at the most oxygen-depleted site (122 m), despite the fact that the organic carbon content of the sediment was maximal at this depth. At the most oxygenated slope sites (827 and 972 m), all of Wieser's nematode feeding groups were represented. In contrast, at the lowest-oxygen site, only selective deposit (bacterial) feeders (1A) were present, indicating a reduction in trophic complexity. A large percentage of nematodes inhabited subsurface sediment layers (> 1 cm). At deeper, more oxygenated sites (827 and 972 m), nematode individual biomass increased downcore, while within the OMZ, nematode biomass was low and remained relatively uniform through the sediment column. The concentration of nematodes in deeper sediment layers, the vertical distribution of the feeding groups, as well as the high nutritional quality of the deeper layers, suggest a differential resource partitioning of the food available, which may reduce interspecific competition.

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1. Introduction

Habitat heterogeneity is now understood to play a key role in promoting taxon diversity across continental margins (Levin et al., 2010; Levin and Sibuet, 2012). In this regard, bottom-water oxygen concentrations and organic matter input exhibit some of the steepest gradients, especially in sediments underlying oxygen minimum zones (OMZs; O₂ < 0.5 ml L⁻¹). These gradients can be highly heterogeneous (Gooday et al., 2010), influencing biogeochemical properties of sediments (Cowie, 2005) as well as the abundance, biodiversity and distribution of the benthic fauna (Levin, 2003; Gooday et al., 2009; Gooday et al., 2010). For most

larger benthic organisms, the oxygen gradient represents a barrier to dispersal that leads to distinct benthic communities within and outside the OMZ (Levin, 2003). The general consensus is that metazoan meiofauna are less affected by hypoxia than macrofauna and megafauna in OMZs, and that oxygen plays a minor role in determining meiofaunal abundance (Levin et al., 1991; Neira et al., 2001a). Meiofauna also seem to cope well with unconsolidated sediments that often co-occur with hypoxia (Thistle, 1980; Neira and Rackemann, 1996). Indeed, the core of OMZs is often dominated by fine grained, soupy and fluffy sediments, with high water and organic matter (OM) content and a large phytodetrital component while the upper boundary of OMZs, located on the shelf, is often dominated by coarse substrate (Neira et al., 2001a). Furthermore, within the meiofauna, nematodes have been suggested to be the most tolerant to low oxygen concentrations (Cook et al., 2000; Giere, 2009; Van Colen et al., 2009).

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Organic matter supply decreases with increasing water depth. To date, organic matter has been considered the main limiting factor for meiofauna assemblages in non-upwelling ecosystems, which generally receive organic input of low nutritional quality (e.g. Vincx et al., 1994; Galéron et al., 2000). Assemblages of deep-sea meiobenthos appear to be structured by the labile components of organic matter (Danovaro et al., 2000; Danovaro et al., 2009). Several transitional settings, including the outer shelf influenced by the OMZ, the shelf break (a physiographical boundary between shallow shelf and deep-sea faunas), the lower OMZ boundary located on the slope, and the area below the OMZ, provide multiple oxygen and organic matter gradients that allow us to examine their correlations with changes in meiobenthos. Here we consider the nematode community response to those gradients. No previous taxonomic study has been made of nematodes from central Chile margin sediments influenced by the oxygen minimum zone. These settings allow us to investigate how oxygen and food availability affect and modulate the abundance and community structure of nematodes, the most ubiquitous, abundant and diverse meiofaunal component. As a result of their numerical dominance, diversity, varied trophic modes, sensitivity to environmental conditions, small size and limited dispersal capabilities (Platt and Warwick, 1980; Lamshead and Boucher, 2003), nematodes provide a good model for examining biotic response to changes in food availability, both horizontally along the transect and vertically within the sediment column. From a trophodynamic perspective, we predict that spatial variability in food quantity and quality (i.e. availability) of OM (i.e. food-forced heterogeneity) should be reflected in changes in nematode community composition, trophic structure, and biodiversity both horizontally and vertically. We also predict that nematode diversity and density will be directly correlated to oxygen gradients. We expect nematode density to be higher in low oxygen sites, and diversity to display a reverse pattern.

The present paper examines (1) the community composition, generic biodiversity, biomass, trophic structure and vertical distribution of free-living nematodes in the sediment, and (2) the key environmental variables controlling nematode communities. We test the hypotheses that (i) nematode generic diversity and nematode trophic diversity are reduced in the shallower, oxygen-depleted sites compared with deeper, more oxygenated settings, and (ii) vertical patterns of community composition and trophic structure within the sediment are associated with changes in the quantity and quality of organic matter.

2. Material and methods

2.1. Study area and sampling

Coastal waters off central Chile are considered to be among the most productive worldwide (Fossing et al., 1995). Wind-driven upwelled water, mostly Equatorial Subsurface Water (ESSW), contributes to high primary production rates. Production can reach up to $9.9 \text{ g C m}^{-2} \text{ d}^{-1}$, resulting in relatively high input to the sediments off central Chile (Gutiérrez et al., 2000). Furthermore, a pronounced OMZ, associated with the ESSW and located at depths between 50 and 250 m, partially covers the continental shelf (Pizarro et al., 2002). From March 29 to April 5, 1999 we sampled sites along a transect covering a depth range from 122 m to ~1000 m across the continental margin off Concepción, central Chile (~36°S). Sampling was conducted aboard the R/V *Vidal Gormáz* at the following five sites: (1) the outer shelf at 122 m (OS-122; 36°26.04'S; 73°23.12'W), (2) the shelf break at 205 m, within the OMZ (SB-205; 35°45.07'S; 73°04.10'W), (3) on the upper slope at 364 m, located at the lower OMZ boundary (US-364;

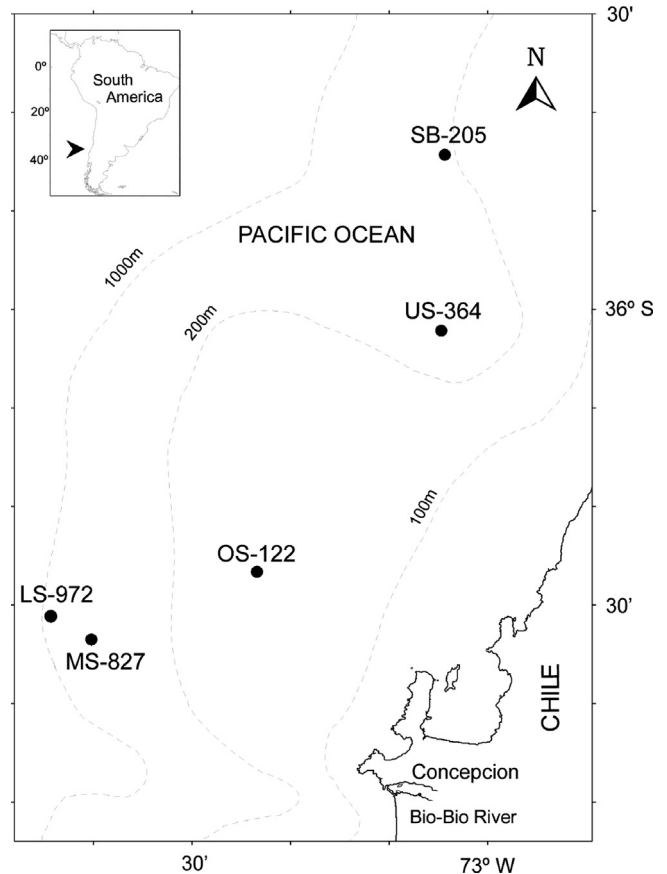


Fig. 1. Location of sampling sites across the continental margin off Concepción, central Chile (March 29–April 5, 1999).

36°03.31'S; 73°05.17'W), (4) on the mid-slope at 827 m (MS-827; 36°32.37'S; 73°40.14'W), (5) and on the lower mid-slope at 972 m (LS-972; 36°32.58'S; 73°41.93'W). MS-827 and LS-972 were both located beneath the OMZ (Fig. 1).

Water column temperature, salinity and dissolved oxygen (DO) were measured using a CTDO. In addition, DO measurements were made on water samples collected with the CTD-rosette using a semi-automatic Winkler method (Knap et al., 1993; Williams and Jenkinson, 1982). Sediment samples were collected using a multiple corer (tube i.d. 9.5 cm) (Barnett et al., 1984). Only undisturbed cores with clear overlying water were used. At each site, three different multicorer drops were made (except site LS-972 where two drops were made). From one tube of each drop, two subsamples were taken simultaneously, for meiofauna and sediment, using Plexiglas liners (i.d. 3.6 cm; 10 cm depth). To examine meiofaunal distribution, cores were sectioned vertically (0–1, 1–2, 2–3, 3–5, and 5–10 cm), treated with 6% magnesium chloride for 10 min to relax fauna, and then preserved in 4% buffered formalin containing Rose Bengal (Pfanckuche and Thiel, 1988). For sediment parameters, cores were sectioned at 1 cm intervals and kept frozen until analysis.

2.2. Sediment properties, elemental and biochemical composition of organic matter

A suite of analyses was conducted on sediment samples from the study sites (Table 1). Water content and porosity were determined by weight loss after freeze drying the frozen 1-cm vertical fractions, assuming a sediment and water density of 2.65 g cm^{-3} (quartz) and 1.025 g cm^{-3} , respectively (Buchanan, 1984).

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