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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.

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; $O_2 < 0.5$ 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; Lambshead 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 g C m^{-2} 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; 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).

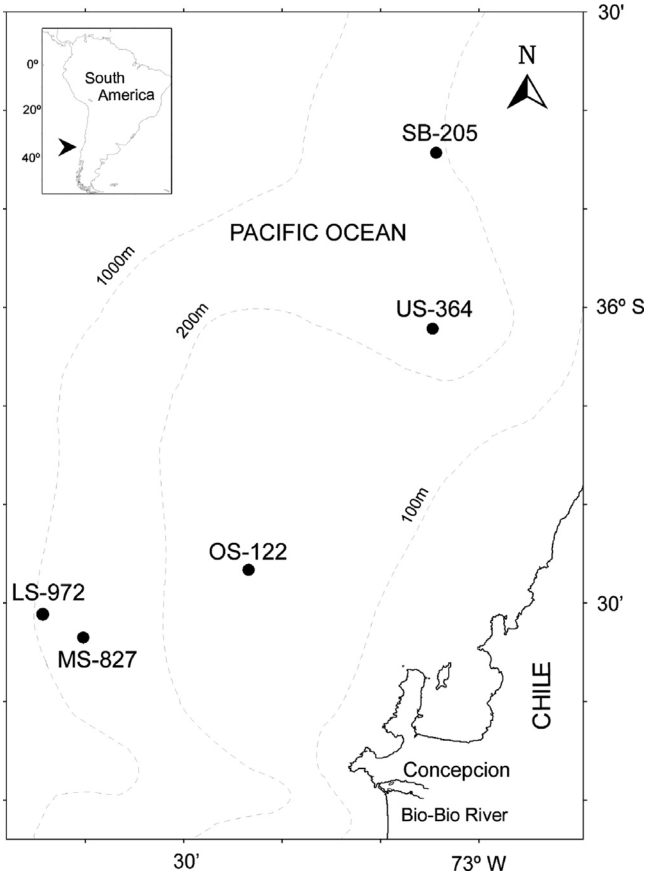

Fig. 1. Location of sampling sites across the continental margin off Concepción, central Chile (March 29–April 5, 1999).

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 (Pfannkuche 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).

Table 1
Abiotic properties of five benthic sites off central Chile within (sites OS-122 and SB-205) and beneath the oxygen minimum zone. Sedimentary parameters are given for the top 0–1 cm layer (means of 3 samples): TOC, total organic carbon; TN, total nitrogen; C-PRT, carbon proteins; C-CHO, carbon carbohydrates; C-LIP, carbon lipids; BPC, biopolymeric carbon (sum PRT, CHO and LIP); Chl a, chlorophyll a; Phae, phaeopigments; CPE, chloroplastic pigment equivalents; C-CPE/BPC, algal carbon contribution to BPC; C-PRT/BPC, carbon protein contribution to BPC; Eh, redox potential.

	SITES				
	OS-122	**SB-205**	**US-364**	**MS-827**	**LS-972**
Depth (m)	122	205	364	827	972
Bottom water temperature (°C)	10.8	10.4	8.9	3.7	3.4
Bottom water oxygen (ml L^{-1})	0.10	0.13	0.52	2.89	3.50
TOC (mg g^{-1})	46.91	11.88	35.04	25.7	29.59
TN (mg g^{-1})	6.64	1.53	4.62	3.63	3.87
C:N ratio	7.06	7.76	7.58	7.08	7.64
C-PRT (mg g^{-1})	15.49	4.89	9.65	6.75	8.34
C-CHO (mg g^{-1})	6.62	1.61	4.73	3.23	4.28
C-LIP (mg g^{-1})	5.57	0.88	2.44	1.29	1.65
BPC (mg C g^{-1})	27.69	7.37	16.81	11.28	14.27
BPC/TOC (%)	59.0	62.0	48.0	43.9	48.2
Chl *a* (μg g^{-1})	124.62	10.65	38.07	12.45	16.79
Phae (μg g^{-1})	196.76	58.32	108.54	63.05	73.93
CPE (μg g^{-1})	321.38	68.97	146.61	75.5	90.72
C-CPE/BPC (%)	46.43	37.42	34.88	26.78	25.42
C-PRT/BPC (%)	55.94	66.30	57.40	59.84	58.44
Eh (mV)	135	121	198	257	213
Water content (%)	68.52	44.1	66	60.2	68.5
Porosity (%)	85.63	68.9	86.8	82.1	87.5
pH	7.70	7.63	7.68	8.06	7.70
Sulfide (μM)	4.93	4.28	2.70	3.63	n.d.
Mud (%)	99.5	97.9	99.6	98.9	99.0
Sand (%)	0.5	2.1	0.4	1.1	1.0

Sediment redox potential was measured at 1-cm intervals using a platinum standard combination electrode with calomel internal reference. Measurements of pH were made with a Mettler Toledo glass combination electrode with $Ag/AgCl_2$ internal reference. For grain size analysis, aliquots of sediment were digested with hydrogen peroxide and wet sieved through a 63-μm mesh. After the fractions were dried, percent sand (>63 μm) and mud (<63 μm) were calculated. Sediment total organic carbon (TOC) and total nitrogen (TN) were determined from freeze-dried and homogenized sediment in a Heraeus-CHN elemental analyzer after acidification with 0.1 N HCl to remove carbonates. Proteins (PRT), carbohydrates (CHO) and lipids (LIP) were determined spectrophotometrically from freeze-dried sediment, as described by Danovaro and Gambi (2002). Blanks were obtained using precombusted sediments (500 °C for 4 h). Proteins, carbohydrates and lipid sediment content were converted into C equivalents using the conversion factors of 0.49, 0.40 and 0.75 mg C mg^{-1}, respectively (Fabiano et al., 1995), and their sum was referred as the biopolymeric carbon (BPC) (Fabiano et al., 1995; Neira et al., 2001a, b; Sellanes and Neira, 2006, Pusceddu et al., 2009). Pigments were determined spectrophotometrically from homogenized freeze-dried sediment (Hagerthey et al., 2006) after extraction with 90% acetone. After Chlorophyll *a* (chl *a*) determination, samples were acidified with 0.1 HCl to determine phaeopigment concentrations. Pigment concentrations are reported in μg g^{-1} DW. Chloroplastic pigment equivalent (CPE), i.e. the sum of chl *a* and phaeopigments, served as a measure of input of phytodetrital matter to the sediment (Pfannkuche and Soltwedel, 1998). The algal carbon contribution to BPC was calculated as the percentage of C-CPE to BPC concentrations, after converting phytopigment concentration into carbon equivalents using the conversion factor of 40 mg of C mg^{-1} (De Jonge, 1980; Cammen, 1991).

2.3. Meiofaunal and nematode analysis

Samples were processed for meiofauna analysis by suspension-decantation (Pfannkuche and Thiel, 1988) using a 40-μm sieve as the lower limit. The procedure was repeated five times and residual sediment was examined for extraction efficiency ($>98\%$). All meiofaunal specimens were counted and classified according to major taxon under a stereo dissecting microscope. To assess nematode assemblage composition per depth interval, all individuals were placed in a small (7 ml) vial. Immediately after resuspension, one aliquot (2 ml) was rapidly subsampled (method modified from Ólafsson and Elmgren, 1997). From each subsample all nematodes present were picked, mounted and identified to the genus level. To investigate the trophic structure of the nematode assemblages, the nematodes were divided in four feeding groups based on buccal morphology (Wieser, 1953a): (1A) selective deposit feeders—buccal cavity absent or fine tubular, (1B) non-selective deposit feeders—large but unarmed buccal cavity, (2A) epistrate or epigrowth (diatom) feeders—buccal cavity with scraping tooth or teeth and (2B) predators-omnivores—buccal cavity with large jaws. Meiofaunal and nematode biomass was estimated from the biovolume by using the formula $V = L \times W^2 \times C$, where V is the body volume in nl, L is the length (in mm), W is the maximum width (in mm), and C is the approximate conversion factor for each meiofaunal taxon (Feller and Warwick, 1988). For copepods, all individuals were measured. Measurements of length and width were made from digital micrographs, using the ImageJ 1.43 u software (http://rsb.info.nih.gov/ij—National Institute of Health, USA). Total biomass was estimated by multiplying the mean individual biomass by the total density in each vertical sediment fraction. Body biovolumes were converted to dry weight assuming a relative density of 1.13 g cm^{-3} and a dry:wet ratio of 0.25 (Wieser, 1960). Carbon content was considered to be 40% of the dry weight (Feller and Warwick, 1988).

2.4. Data analysis

Analysis of variance (ANOVA) and a *posteriori* Tukey HSD tests when differences were significant ($p<0.05$; Sokal and Rohlf, 1997) were used to compare sediment and meiobenthic parameters across sites. All data were tested for normality using goodness-of-fit tests, and were square root transformed when necessary. The non-parametric Wilcoxon's test was used when transformed data failed to fulfill parametric assumption. Analyses were carried out using the software package JMP 8.0.1. A Spearman's rank analysis was used to test the correlations between nematode and environmental data. Total density and biomass, as well as diversity indices such as Pielou's evenness (J′), Shannon-Wiener ($H' \log_2$) and rank 1 dominance (R_1D) (the proportion of the most abundant taxon), were used to describe nematode assemblage structure. Generic richness (G) was examined as a function of area (10 cm^{-2}), and rarefaction curves (number of genera per number of individuals sampled—Hurlbert, 1971). Rarefaction curves were created by randomly re-sampling the pool of N samples multiple times and then plotting the average number of genera found in each sample, by using PRIMER (6.0) and BiodiversityPro (v. 2). Canonical Correspondence Analysis (CCA) was used to explore multivariate relationships between nematode community structure and environmental variables (ter Braak and Šmilauer, 2002). A forward stepwise selection procedure was applied to select a set of explanatory variables (acceptance level: $p<0.05$), which could account for the maximum variation in the faunal data. These were used in the ordination model (ter Braak, 1988; ter Braak and Šmilauer, 1998). A Monte Carlo permutation test (999 permutations) was used to determine statistical significance of the genus–environment relationships (ordination axes). Genus densities were square-root transformed, while environmental variables were automatically centered and standardized by the CANOCO software (Jongman et al., 1995). Analysis was performed using CANOCO for Windows 4.5.

In order to identify any potential nematode assemblages and indicator genera characterizing the five study sites, the indicator value (IndVal) method (Dufrêne and Legendre, 1997) was used. This approach combines a genus' relative abundance with its relative frequency of occurrence at different sites. The IndVal is higher when all individuals of a species are found in a single sample or group of samples. A Monte Carlo permutation test was used to determine statistical significance of the indicator value (Dufrêne and Legendre, 1997). Indicator analysis was performed using the PC-ORD V. 4 (MJM) software package.

We used regression tree models (a non-parametric regression model) to describe the dependence of the response variable values on the values of the predictor variables (Lepš and Šmilauer, 2003). We modeled regression trees for nematode density and biomass (response variables) using the environmental data as predictor variables. Regression trees handle a single response variable and multiple explanatory predictors (Merler et al., 1996) without data transformation, and produce decision trees to display class memberships by recursive binary partitioning of the data set into subsets (also called nodes) that are successively more and more homogeneous in the values of the response variable (De'ath and Fabricius, 2000; Sutton, 2005). Regression trees were modeled using Statistica v.8 (StatSoft).

3. Results

3.1. Bottom-water and sediment properties

The shallowest sites within the OMZ (OS-122 and SB-205) exhibited the lowest bottom-water oxygen concentrations (0.10 and 0.13 ml L^{-1}, respectively), with temperatures over 10 °C (Table 1). At the upper slope (US-364), oxygen increased to 0.52 ml L^{-1}, and bottom-water temperature decreased to 8.9 °C. Toward the mid- and lower mid-slope (MS-827 and LS-972), oxygen increased to 2.89 ml L^{-1} and 3.50 ml L^{-1}, with bottom-water temperatures of 3.7 and 3.4 °C, respectively.

Overall, the shelf and slope sediments of the central Chile margin are characterized by their high content of mud (97.9–99.6%), and by their poor sorting (Gallardo et al., 2004). In the present study, the OMZ site (OS-122) had the highest TOC (4.69%) and TN (0.66%). Sediments were soupy brown and oxidized, with a relatively high water content and porosity and redox potential of 135 mV (Table 1). Filaments of *Thioploca* were observed in the sediment column. The SB-205 sediments were more compacted, with the lowest TOC, TN, porosity, water content and redox potential (121 mV). The US-364 site at the lower OMZ boundary showed the second highest TOC, TN and pigments content. Here and at the deeper more oxygenated sites (MS-827 and LS-972) sediments appeared highly oxidized, with redox potentials of 198, 257 and 213 mV, respectively. In general, the BPC represented 83% of the TOC variance. There was also a positive relationship between algal biomass expressed as carbon CPE (sum of chl *a* and phaeopigments) and the biopolymeric carbon fraction. Nearly 87% of the variance of BPC was explained by the total phytobenthic matter ($R^2=0.87$; $P<0.001$), and the phytopigment carbon contributed ~50% to the biopolymeric carbon ($R^2=0.49$; $P<0.001$). However, the phytopigments contribution varied between sites; it was lower in the deeper, more oxygenated sites and the shelf break than on the outer shelf and upper slope (ANOVA, $F_{4,49}=21.8$; $P<0.0001$, *a posteriori* Tukey HSD). The biopolymeric carbon (BPC) was highest at OS-122 and lowest at SB-205. Proteins (PRT) dominated the BPC pool at all sites, followed by carbohydrates (CHO) and lipids (LIP). On average, PRT, CHO and LIP accounted for 61.1%, 22.8% and 16.0% of BPC, for the sites within the OMZ, and 58.5%, 28.9% and 12.5% for the deeper oxygenated sites, respectively. The remaining material corresponded to the non-labile or more refractory fraction of the sedimentary organic carbon.

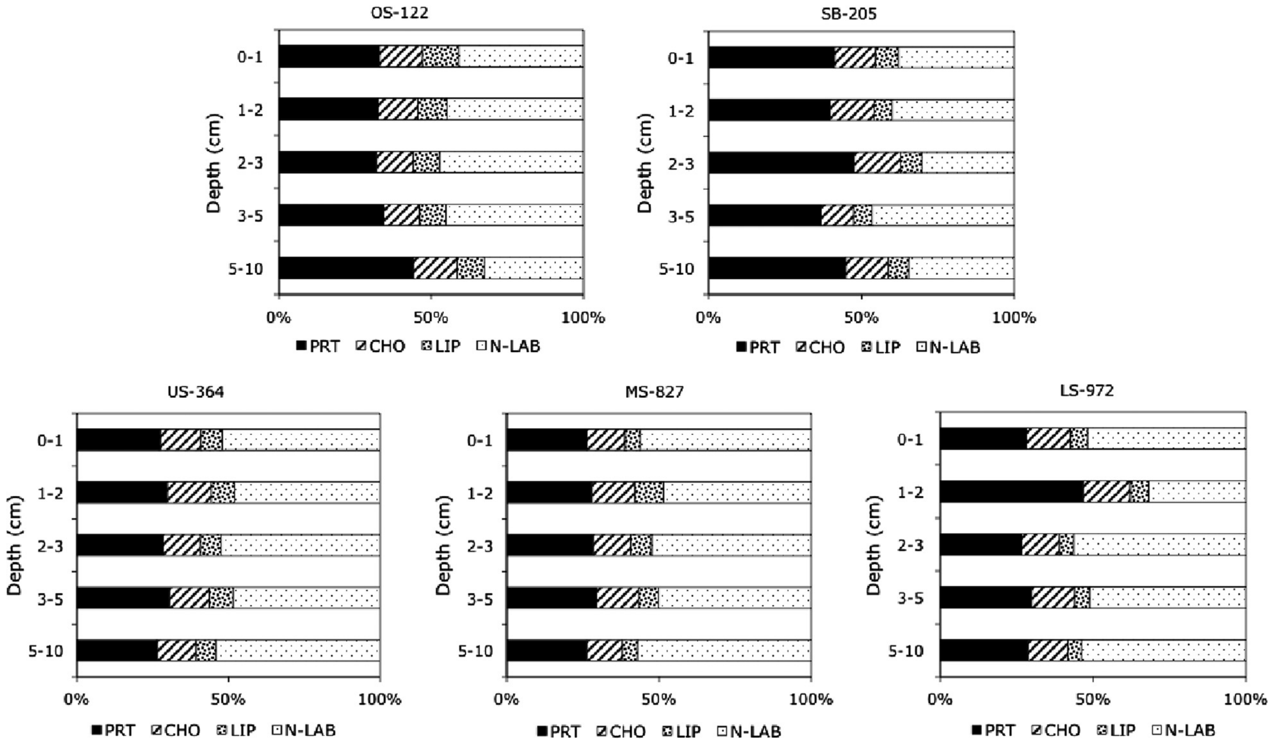

Fig. 2. Biochemical composition of the organic matter in the sediment column. (PRT=proteins, CHO=carbohydrates, LIP=lipids. N-LAB=non-labile organic matter).

Differences in organic matter composition in the sediment column led to changes in the proportion of specific biochemical compounds (Fig. 2). BPC/TOC varied on average from 59.0% at site OS-122 to 43.9% at site MS-827 (Table 1).

3.2. Meiobenthos

Overall, seventeen major metazoan meiobenthic taxa were recorded, with nematodes as the dominant taxon followed by harpacticoid copepods. Nematodes were dominant at all sites, dictating the patterns in total meiofaunal density. They accounted for over 99% of total meiofauna within the OMZ (OS-122), while downslope their relative numerical dominance declined to less than 84%. In contrast, copepods+nauplii density increased consistently with increasing bottom-water oxygen occurring at deeper sites, from 2 ind. 10 cm^{-2} at OS-122 to 97 ind. 10 cm^{-2} at LS-972. They were concentrated mainly in the top 1 cm. At the shelf break (SB-205), kinorhynchs had relatively high densities (45 ind. 10 cm^{-2}) as compared to the mid- and lower mid-slope sites, with ($\sim$8 and 6 ind. 10 cm^{-2}, respectively). Overall, meiobenthic taxa other than nematodes and copepods (i.e. polychaetes, gastrotrichs, ostracods, oligochaetes, turbellarians, halacarids, rotifers, nemerteans, tanaids, bivalves, cnidarians, amphipods, cumaceans and isopods) were poorly represented, with relative abundances lower than 1.7%.

3.3. Nematode density, community composition and diversity

Mean total nematode densities and biomass (0–10 cm) ranged between 677 and 2006 ind. 10 cm^{-2}, and 168.4 and 506.5 μg DW 10 cm^{-2}, respectively, with significant variation among sites ($F_{4,13}=6$; both $P<0.010$). The sites with lower oxygen (OS-122, SB-205 and US-364) had the highest densities, while biomass was highest at the upper (US-364) and mid-slope (MS-827). Nematodes were the main contributors to the total meiofaunal biomass, ranging from 54% (LS-972) to 88% (OS-122).

A total of 33 nematode genera belonging to 17 families was recorded along the transect (Table 2). At the OMZ site OS-122, *Pselionema* dominated, comprising over 60% of total nematodes, followed by *Desmoscolex* (sp. 1+2) with 33%. The OMZ shelf break site (SB-205) was dominated by *Microlaimus*, while *Halalaimus*, *Pselionema*, *Terschellingia* and *Dorylaimopsis* were co-dominant ($>10\%$). The upper slope site at the OMZ lower boundary (US-364) was dominated by *Parodontophora*, *Paracanthonchus, Paramonhystera*, and *Sabatieria*. The mid-slope site (MS-827) was dominated by *Sabatieria* and co-dominated by *Desmoscolex* (1+2), *Cervonema*, *Paracanthonchus* and *Theristus*. At the lower

Table 2
Nematode community genus composition, densities (ind. 10 cm^{-2}) relative abundances (%), genus richness, feeding types, and total biomass (μg DW 10 cm^{-2}) off central Chile. Feeding types: 1A, selective deposit feeders; 1B, non-selective deposit feeders; 2A, epistrate or epigrowth feeders; 2B, omnivores/predators. *Desmoscolex* species (1 & 2) are presented separately to show the differences in terms of presence, density and relative abundance. Value in brackets indicates ± 1SE.

		OS-122		SB-205		US-364		MS-827		LS-972	
	Feeding types	Density	%	Density	%	Density	%	Density	%	Density	%
Campylaimus	*1A*			9 (1)	0.54	4 (2)	0.21	16 (1)	2.36	20 (8)	1.86
Desmoscolex 1	*1A*	475 (13)	24.30					60 (3)	8.86	197 (119)	18.26
Desmoscolex 2	*1A*	174 (6)	8.91	43 (12)	2.70	155 (56)	7.72	59 (6)	8.70	142 (76)	13.21
Diplopeltula	*1A*					10 (2)	0.47			11 (4)	0.99
Eubostrichus	*1A*					45 (21)	2.23	12 (3)	1.72		
Halalaimus	*1A*	120 (3)	6.14	271 (21)	16.96	135 (41)	6.74	23 (2)	3.36	256 (78)	23.79
Litinium	*1A*			9 (1)	0.54	12 (1)	0.59			14 (5)	1.31
Oxystomina	*1A*					6 (0.4)	0.30			3 (2)	0.23
Pselionema	*1A*	1184 (18)	60.64	210 (25)	13.13	2 (1)	0.10	4 (0.4)	0.55	20 (1)	1.87
Quadricoma	*1A*							14 (1)	2.01	4 (2)	0.40
Terschellingia	*1A*			172 (9)	10.75	7 (0.9)	0.37	4 (1)	0.60		
Tricoma	*1A*							6 (0.6)	0.91	5 (4)	0.46
Cervonema	*1B*							66 (14)	9.72	100 (22)	9.26
Eumorpholaimus	*1B*					7 (1)	0.37	4 (1)	0.60		
Metalinhomoeus	*1B*			36 (4)	2.25	18 (1)	0.89	6 (2)	0.85	31 (11)	2.90
Odontophora	*1B*			39 (4)	2.43						
Paramonhystera	*1B*			59 (10)	3.67	208 (63)	10.38	40 (11)	5.97	68 (21)	6.32
Parodontophora	*1B*					527 (89)	26.29	4 (1)	0.60		
Sabatieria	*1B*			16 (2)	0.97	394 (33)	19.62	188 (39)	27.83	111 (29)	10.34
Steineria	*1B*					15 (2)	0.74				
Theristus	*1B*							46 (6)	6.74		
Actinonema	*2A*							17 (1)	2.56	25 (14)	2.29
Chromadorella	*2A*			135	8.43	6 (0.4)	0.30			18 (7)	1.66
Dichromadora	*2A*							12 (1)	1.81		
Dorylaimopsis	*2A*			164	10.24			12 (3)	1.80		
Microlaimus	*2A*			389	24.30	7 (1)	0.37			28 (15)	2.62
Neochromadora	*2A*			45	2.79						
Paracanthonchus	*2A*					401 (99)	20.01	54 (4)	7.91		
Paracomesoma	*2A*									3 (2)	0.23
Procamacolaimus	*2A*			5	0.29	34 (9)	1.70	6 (2)	0.85	11 (3)	0.98
Spirinia	*2A*					12 (1)	0.59				
Enoplolaimus	*2B*							9 (1)	1.40	11 (6)	1.01
Sphaerolaimus	*2B*							12 (3)	1.70		
Viscosia	*2B*							4 (1)	0.60		
Total density		1953		1599		2006		677		1077	
Total Biomass		169.14		228.80		506.48		299.13		168.44	
Genus richness		3		15		20		23		19	
Density / Richness ratio		651		107		100		29		57	

Table 3
Density (N), biomass (B), and diversity indices: taxon richness (G), evenness (J'), Shannon-Wiener (H'), and rank 1 dominance (R1D) for nematode genera (0–10 cm). (N=ind. 10 cm^{-2} ± 1SE; B=μg dry mass 10 cm^{-2}. Value in brackets indicates ± 1SE).

Sites	N	B	G	Pielou J'	$H'(\log_2)$	R1D (%)
OS-122	1953 (37)	169.1 (3.3)	3	0.75	0.05	60.6
SB-205	1599 (98)	228.8 (23.1)	15	0.81	0.32	24.4
US-364	2006 (383)	506.5 (88.4)	20	0.68	0.29	26.5
MS-827	677 (52)	299.1 (50.7)	24	0.80	1.00	27.3
LS-972	1077 (350)	168.4 (90.3)	20	0.77	1.03	24.8

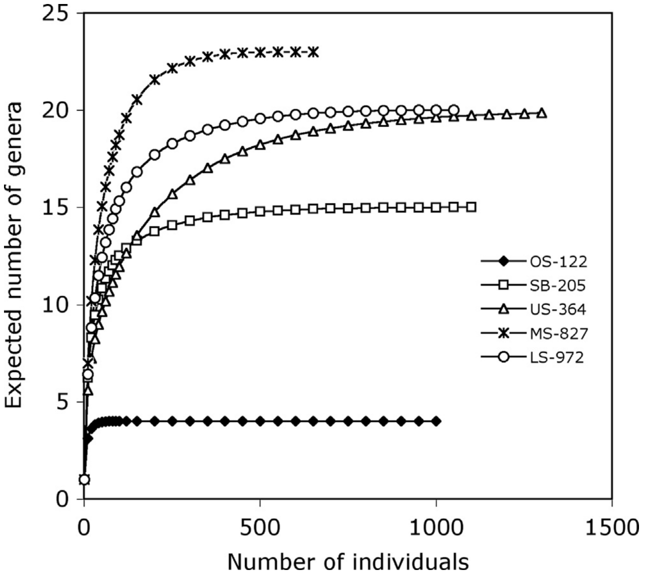

Fig. 3. Rarefaction curves showing richness of nematode genera (0–10 cm) at study sites off central Chile as a function of number of individuals sampled. (Plots are mean of 3 replicates). Steep slope on the left indicates that a large fraction of genus diversity remains to be found. Flattened curve on the right indicates fewer genera to be found per individuals sampled.

slope site (LS-972) *Halalaimus*, *Desmoscolex* (1+2), *Sabatieria*, *Cervonema*, and *Paramonhystera* were the dominant nematodes. Nematode generic richness (G) and diversity ($H' \log_2$) was lowest and rank 1 dominance (R_1D, an inverse indicator of assemblage evenness) was highest, at the OS-122. Inverse diversity patterns were observed at more oxygenated mid- and lower mid-slope sites (Table 3). Rarefaction diversity was lowest at the OMZ sites (OS-122 and SB-205), intermediate at the OMZ lower boundary (US-364), and greatest at the sites beneath the OMZ (MS-827 and LS-972) (Fig. 3).

3.4. Vertical distribution of nematodes

Nematodes were concentrated mainly in the subsurface sediment layers. At the shelf sites within the OMZ, over 61% were found in the 1–3 cm interval, while at the upper slope site (US-364), 74% were concentrated in the 2–5 cm layer, with 17% in the 5–10 cm interval. At the deeper, more oxygenated slope sites (MS-827 and LS-972), subsurface nematodes were dominant and more evenly distributed across the sediment column (Fig. 4). The vertical composition of the nematode community across the sediment column is shown for each site in Table 4. At the lowest oxygen site (OS-122), *Pselionema* contributed over 50% in subsurface layers while *Desmoscolex* was the main contributor in the top 1 cm. At slope sites, *Sabatieria* was widely distributed at all levels in the sediment column, and particularly dominant in the 5–10 cm interval at the MS-827 site. The deeper, more oxygenated sites had higher genus richness (19–23) than the OMZ sites (3–14).

Overall, the nematodes were on average 900 μm long and 33 μm wide, with a L:W ratio of 27.6 and a individual dry weight of 0.18 μg. The mean individual nematode biomass was lowest (0.08 μg) at the outer shelf site within the OMZ (OS-122), with a relatively homogeneous distribution of biomass across the sediment column, and highest (0.27 μg) below the OMZ at the mid-slope site (MS-827). There was a significant difference in individual biomass between the OMZ outer shelf (OS-122) and the mid-slope site (MS-827) (Wilcoxon χ^2=10.1; $P<0.001$, n=263). Mean (±1SE) individual weight for all nematodes in the sediment column at site MS-827 (0.27 ± 0.1 mg

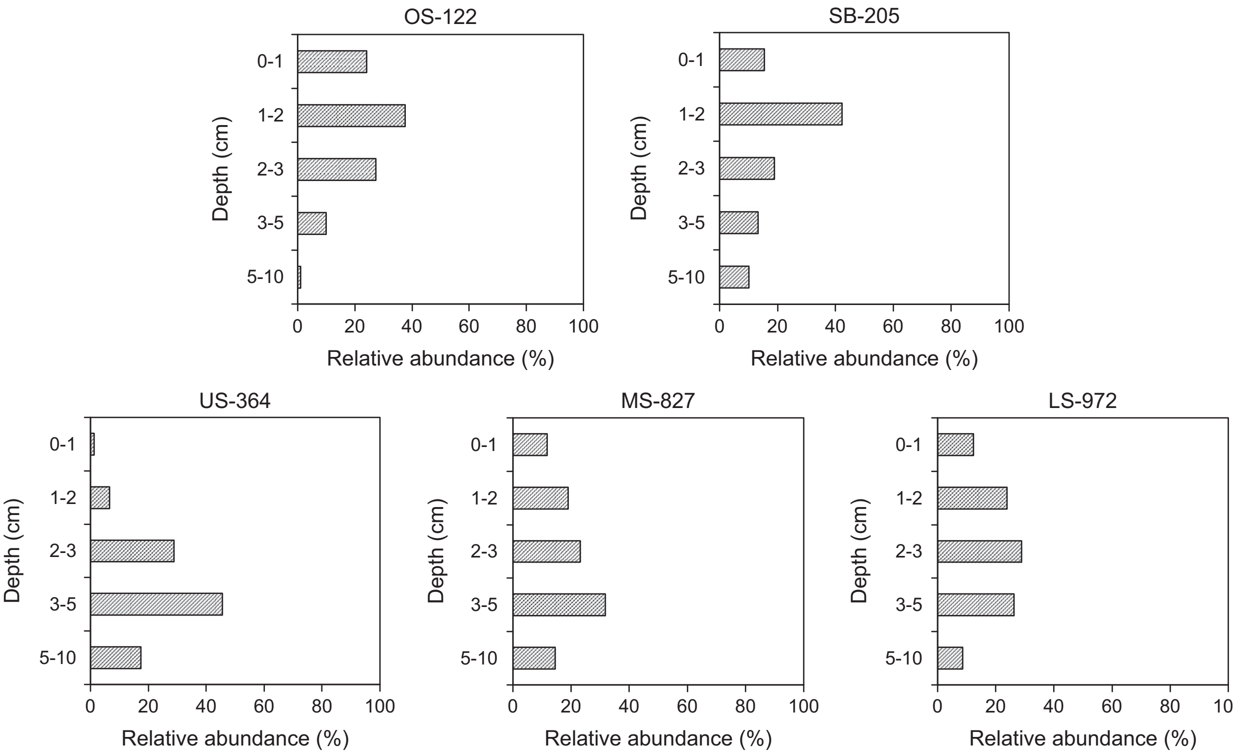

Fig. 4. Vertical distribution of nematode abundances (%) between 0 and 10 cm depth.

Table 4
Vertical composition of nematode community and relative contribution (%) of nematode genera at each study site. Genera are ordered alphabetically by feeding types.

Genera	0–1 %	1–2 %	2–3 %	3–5 %	5–10 cm %	Feeding types
OS-122						
Desmoscolex 1	58.97	20.79	0.00	22.73	3.85	1A
Desmoscolex 2	25.64	0.00	3.57	13.64	30.77	1A
Halalaimus	0.00	0.99	14.29	18.18	11.54	1A
Pselionema	15.38	78.22	82.14	45.45	53.85	1A
SB-205						
Desmoscolex 2	17.54	0.00	0.00	0.00	0.00	1A
Halalaimus	19.30	19.40	11.43	20.00	9.68	1A
Litinium	0.00	0.00	2.86	0.00	0.00	1A
Pselionema	3.51	16.42	8.57	30.00	0.00	1A
Terschellingia	0.00	0.00	34.29	10.00	29.03	1A
Metalinhomoeus	0.00	1.49	8.57	0.00	0.00	1B
Odontophora	0.00	4.48	2.86	0.00	0.00	1B
Paramonhystera	3.51	2.99	2.86	10.00	0.00	1B
Sabatieria	0.00	0.00	0.00	0.00	9.68	1B
Chromadorella	19.30	1.49	11.43	20.00	0.00	2A
Dorylaimopsis	0.00	11.94	0.00	0.00	51.61	2A
Microlaimus	21.05	40.30	14.29	10.00	0.00	2A
Neochromadora	14.04	1.49	0.00	0.00	0.00	2A
Procamacolaimus	1.75	0.00	0.00	0.00	0.00	2A
US-364						
Campylaimus	15.38	0.00	0.00	0.00	0.00	1A
Desmoscolex 2	7.69	0.00	1.28	15.91	0.00	1A
Eubostrichus	0.00	33.33	0.00	0.00	0.00	1A
Diplopeltula	7.69	0.00	1.28	0.00	0.00	1A
Halalaimus	0.00	0.00	1.28	11.36	6.78	1A
Litinium	0.00	0.00	0.00	0.00	3.39	1A
Oxystomina	0.00	0.00	0.00	0.00	1.69	1A
Pselionema	7.69	0.00	0.00	0.00	0.00	1A
Terschellingia	0.00	0.00	1.28	0.00	0.00	1A
Eumorpholaimus	0.00	0.00	1.28	0.00	0.00	1B
Metalinhomoeus	0.00	0.00	0.00	0.00	5.08	1B
Paramonhystera	23.08	0.00	7.69	15.91	3.39	1B
Parodontophora	15.38	33.33	20.51	25.00	37.29	1B
Sabatieria	15.38	33.33	33.33	6.82	25.42	1B
Steineria	0.00	0.00	2.56	0.00	0.00	1B
Chromadorella	0.00	0.00	0.00	0.00	1.69	2A
Microlaimus	0.00	0.00	1.28	0.00	0.00	2A
Paracanthonchus	7.69	0.00	26.92	22.73	10.17	2A
Procamacolaimus	0.00	0.00	1.28	2.27	1.69	2A
Spirinia	0.00	0.00	0.00	0.00	3.39	2A
MS-827						
Campylaimus	7.14	0.00	3.45	2.50	0.00	1A
Desmoscolex 1	21.43	24.32	6.90	0.00	0.00	1A
Desmoscolex 2	7.14	13.51	24.14	2.50	0.00	1A
Eubostrichus	0.00	0.00	0.00	2.50	5.56	1A
Halalaimus	0.00	8.11	0.00	2.50	5.56	1A
Pselionema	0.00	2.70	0.00	0.00	0.00	1A
Quadricoma	7.14	5.41	0.00	0.00	0.00	1A
Terschellingia	0.00	0.00	3.45	0.00	0.00	1A
Tricoma	7.14	0.00	0.00	0.00	0.00	1A
Cervonema	0.00	0.00	6.90	22.50	5.56	1B
Eumorpholaimus	0.00	0.00	3.45	0.00	0.00	1B
Metalinhomoeus	0.00	0.00	0.00	2.50	0.00	1B
Paramonhystera	0.00	0.00	0.00	15.00	5.56	1B
Parodontophora	0.00	0.00	3.45	0.00	0.00	1B
Sabatieria	14.29	2.70	3.45	37.50	77.78	1B
Theristus	0.00	24.32	10.34	0.00	0.00	1B
Actinonema	7.14	8.11	0.00	0.00	0.00	2A
Dichromadora	14.29	0.00	0.00	0.00	0.00	2A
Dorylaimopsis	0.00	0.00	10.34	0.00	0.00	2A
Paracanthonchus	14.29	8.11	20.69	2.50	0.00	2A
Procamacolaimus	0.00	0.00	0.00	2.50	0.00	2A
Enoplolaimus	0.00	2.70	0.00	2.50	0.00	2B
Sphaerolaimus	0.00	0.00	0.00	5.00	0.00	2B
Viscosia	0.00	0.00	3.45	0.00	0.00	2B
LS-972						
Campylaimus	0.00	0.97	5.66	0.00	0.00	1A
Desmoscolex 1	41.94	45.63	7.55	0.00	0.00	1A
Desmoscolex 2	9.68	25.24	20.75	0.00	0.00	1A
Diplopeltula	0.00	0.97	1.89	0.83	0.00	1A
Halalaimus	3.23	11.65	28.30	34.71	38.46	1A

Table 4 (*continued*)

Genera	**0–1** **%**	**1–2** **%**	**2–3** **%**	**3–5** **%**	**5–10 cm** **%**	**Feeding types**
Litinium	0.00	0.00	3.77	0.83	0.00	1A
Oxystomina	0.00	0.97	0.00	0.00	0.00	1A
Pselionema	0.00	0.00	1.89	0.00	15.38	1A
Quadricoma	3.23	0.00	0.00	0.00	0.00	1A
Tricoma	0.00	1.94	0.00	0.00	0.00	1A
Cervonema	0.00	0.00	1.89	28.10	15.38	1B
Metalinhomoeus	3.23	0.00	5.66	3.31	0.00	1B
Paramonhystera	3.23	2.91	3.77	13.22	7.69	1B
Sabatieria	3.23	0.97	13.21	14.88	23.08	1B
Actinonema	12.90	2.91	0.00	0.00	0.00	2A
Chromadorella	0.00	1.94	1.89	2.48	0.00	2A
Microlaimus	19.35	0.97	0.00	0.00	0.00	2A
Paracomesoma	0.00	0.97	0.00	0.00	0.00	2A
Procamacolaimus	0.00	0.00	1.89	1.65	0.00	2A
Enoplolaimus	0.00	1.94	1.89	0.00	0.00	2B

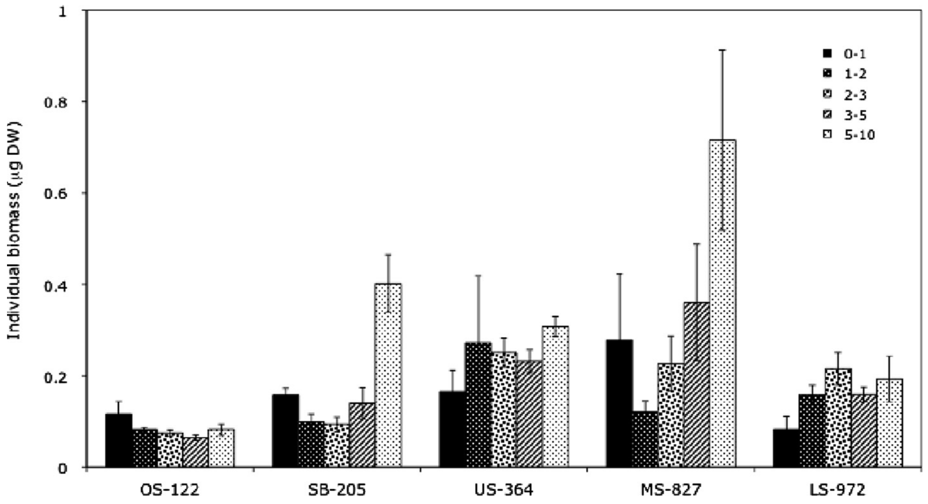

Fig. 5. Nematode mean individual biomass (µg DW) per sediment layer at the studied sites off central Chile. Bars indicate ±1SE.

DW) was 3.3 times of that of OS-122 (0.08±0.007 mg DW). Increasing individual biomass toward deeper sediment layers was correlated with body elongation. This correlation was significant at all sites (SB-205: $r=0.64$, $P<0.001$, $n=246$; US-364: $r=0.67$, $P<0.001$, $n=222$; MS-827: $r=0.60$, $P<0.001$, $n=136$; and LS-972: $r=0.53$; $P<0.001$, $n=369$) except the outer shelf (OS-122) ($P=0.34$). At SB-205, individual nematode biomass in the 5–10 cm sediment layer was ~3 times that in the upper layers, and body length almost doubled (Fig. 5).

3.5. *Trophic structure of the nematode community*

Nematode feeding groups (Wieser, 1953a) shifted along the transect and in the sediment column (Fig. 6). At the outer shelf within the OMZ (OS-122), only the 1A group (selective deposit feeders) was present, dominating downcore. At the shelf break (SB-205), group 2A (epistrate feeders) was dominant (>55%) in the upper layers (0–2 cm), while the 1A group was more important in the intermediate layers (2–5 cm). A small percentage (~10%) of the 1B group (non-selective deposit feeders) was present across the sediment column. At the lower OMZ boundary on the upper slope (US-364), the 1B group was dominant in all sediment layers. The deeper, more oxygenated slope sites (MS-827 and LS-972) were more diverse trophically, with the 2B group (predators/omnivores) present as well, although at a relatively low percentage and restricted to subsurface layers (Fig. 6).

3.6. *The nematode community in relation to the environment*

Spearman's rank correlation analysis showed the nematode densities to be significantly, positively correlated to sediment biopolymeric carbon, especially proteins ($r=0.64$) and lipids (0.74), as well as chl *a* ($r=0.95$) and phaeopigments ($r=0.72$), and inversely correlated with depth. Nematode biomass in the sediment column was positively correlated with sediment protein ($r=0.92$), carbohydrate ($r=0.97$) and lipids ($r=0.95$) content at the OS-122 site. At US-364, nematode biomass correlated positively with protein content ($r=0.86$) and negatively with carbohydrate content ($r=0.90$). No other significant correlation could be detected.

A CCA ordination plot for the nematode communities (0–10 cm) revealed that the first two axes explained 84.3% of the variance between nematode genera and environmental variables measured (Fig. 7A). The direction of the vectors indicates that oxygen and mud increased with the first axis (x), whereas the environmental vector temperature decreased with this axis. Sand decreased along the second axis (y), whereas biopolymeric components and CPE increased along the y-axis. A large number of genera (e.g. *Eumorpholaimus*, *Spirinia*, *Procamacolaimus*, *Sphaerolaimus*, *Viscosia*) occurring at the deeper slope sites (MS-827 and LS-972) were

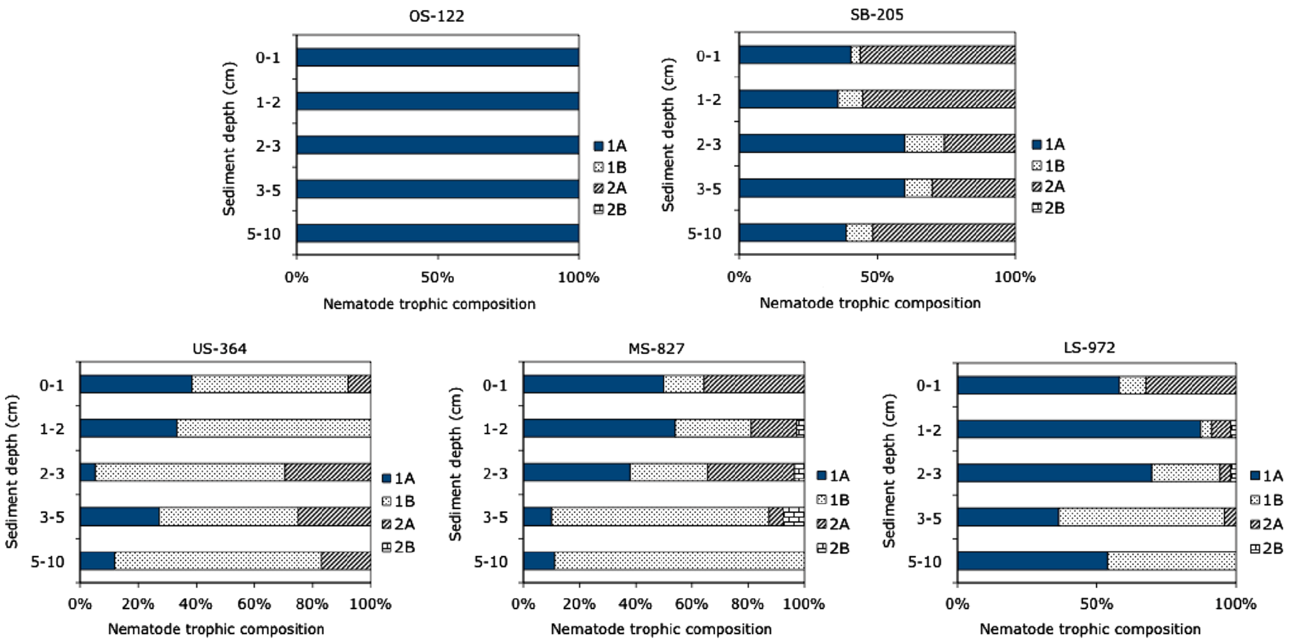

Fig. 6. Nematode trophic composition in the sediment column between 0 and 10 cm at sites on the central Chile margin. (1A), selective deposit feeders; (1B) non-selective deposit feeders; (2A) epistrate or epigrowth feeders; (2B) omnivores/predators.

clustered together along the *x*-axis, and were associated with increased bottom-water oxygen, mud and C-chl *a*/BPC. Genera occurring mainly at OS-122 (e.g. *Pselionema* and *Desmoscolex* 1) appear to be related to the biopolymeric fractions of organic matter. Other genera (e.g. *Chromadorella*, *Dorylaimopsis*, *Odontophora*, *Terschellingia*, *Microlaimus* and *Neochromadora*), occurring at the shelf break site (SB-205), appear to be related partially to variation in bottom-water temperature and sand content. A CCA plot based on nematode generic abundances grouped by feeding modes showed that the first two axes explained 91.5% of the variance between nematode trophic groups and the environmental variables measured (Fig. 7B). Selective deposit feeders (group 1A) appear to be associated with biopolymeric components of organic matter, best represented at the OMZ site. Non-selective deposit feeders (group 1B) and epistrate feeders (group 2A) seem to be related to sediment particle size. Predators and omnivores (group 2B) are present at the mid- (MS-827) and lower mid-slope (LS-972) sites associated with more oxygenated conditions.

By using regression trees (a non-parametric regression model), we describe the dependence of the response of nematode density and biomass (both community descriptors) on the explanatory environmental variables previously selected by the forward stepwise procedure. Because top sediment layers are more likely to be influenced by hydrographic variables such as bottom-water temperature and oxygen, we present the regression tree models for the nematodes in the top 1 cm of the sediment. Protein (C-PRT) appears to be one of the key explanatory variables associated with variation in nematode density and biomass (Fig. 8A-B, respectively). Differences occurred further along the successive node partitioning. Bottom-water oxygen and mud were the secondary explanatory variables for nematode density (Fig. 8A) whereas for nematode biomass, the pigment contribution to BPC and oxygen were secondary (Fig. 8B).

3.7. Nematode indicators

The approach applied to identify prospective nematode indicator genera or nematode assemblages characterizing sites (Dufrêne and Legendre, 1997), highlighted several genera (Table 5). Many of them can be visualized on the CCA plot (Fig. 7A). Based on the indicator value (IndVal), *Pselionema* was the main indicator of the OMZ, outer shelf (OS-122) assemblage, followed by *Desmoscolex* 1. The OMZ shelf-break (SB-205) assemblage was characterized by *Odontophora* and *Neochromadora*, along with four other genera (*Terschellingia*, *Dorylaimopsis*, *Microlaimus* and *Chromadorella*). The lower OMZ boundary on the upper slope (US-364) had *Steineria* and *Spirinia* with the highest indicator values, followed by other six nematode genera (*Parodontophora*, *Paracanthonchus*, *Eubostrichus*, *Oxystomina*, *Eumorpholaimus* and *Procamacolaimus*). The nematode assemblage below the OMZ was characterized by *Theristus*, *Dichromadora*, *Viscosia*, *Sphaerolaimus* and *Quadricoma* at MS-827. The indicator genus for the mid-lower slope (LS-972) was *Paracomesoma*, followed by *Cervonema*.

4. Discussion

4.1. Environmental settings and food availability

At central Chile, the poleward Equatorial Sub-Surface Water is the main source of upwelling waters (Ahumada, 1989) supporting high primary productivity (Fossing et al., 1995). About 25–40% of this material reaches the bottom sediments (Bernal et al., 1989). This is reflected in the low C/N ratios, which varied between 7 and 7.8 (Table 1), indicating little decomposition of nitrogenous organic compounds. Comparable C/N ratios (7.2 to 8.4) were reported for the shelf (Neira et al., 2001b; Sellanes and Neira, 2006), and for the upper slope (7.8) (Palma et al., 2005; Veit-Köhler et al., 2009) off central Chile. In addition, the relatively high biopolymeric (more labile) component of TOC, mostly of phytoplanktonic origin (C-CPE/BPC), along with a high C-PRT/BPC (Table 1, Fig. 8A–B), suggests that the OM potentially available for the benthic consumers is of high quality and fresh (e.g. Danovaro et al., 1995; Neira et al., 2001a,b; Bianchelli et al., 2010). The role of food availability and quality has been highlighted in many studies as one of the most important in controlling meiofaunal distribution, and in structuring nematode communities and spatial patterns of biodiversity (Danovaro et al., 1995; Neira et al., 2001a; Pusceddu et al., 2009; Danovaro et al., 2009; Ingels et al., 2009). Interactions with macrofauna or microbiota (Lambshead et al., 1994; Van Colen et al., 2009), habitat

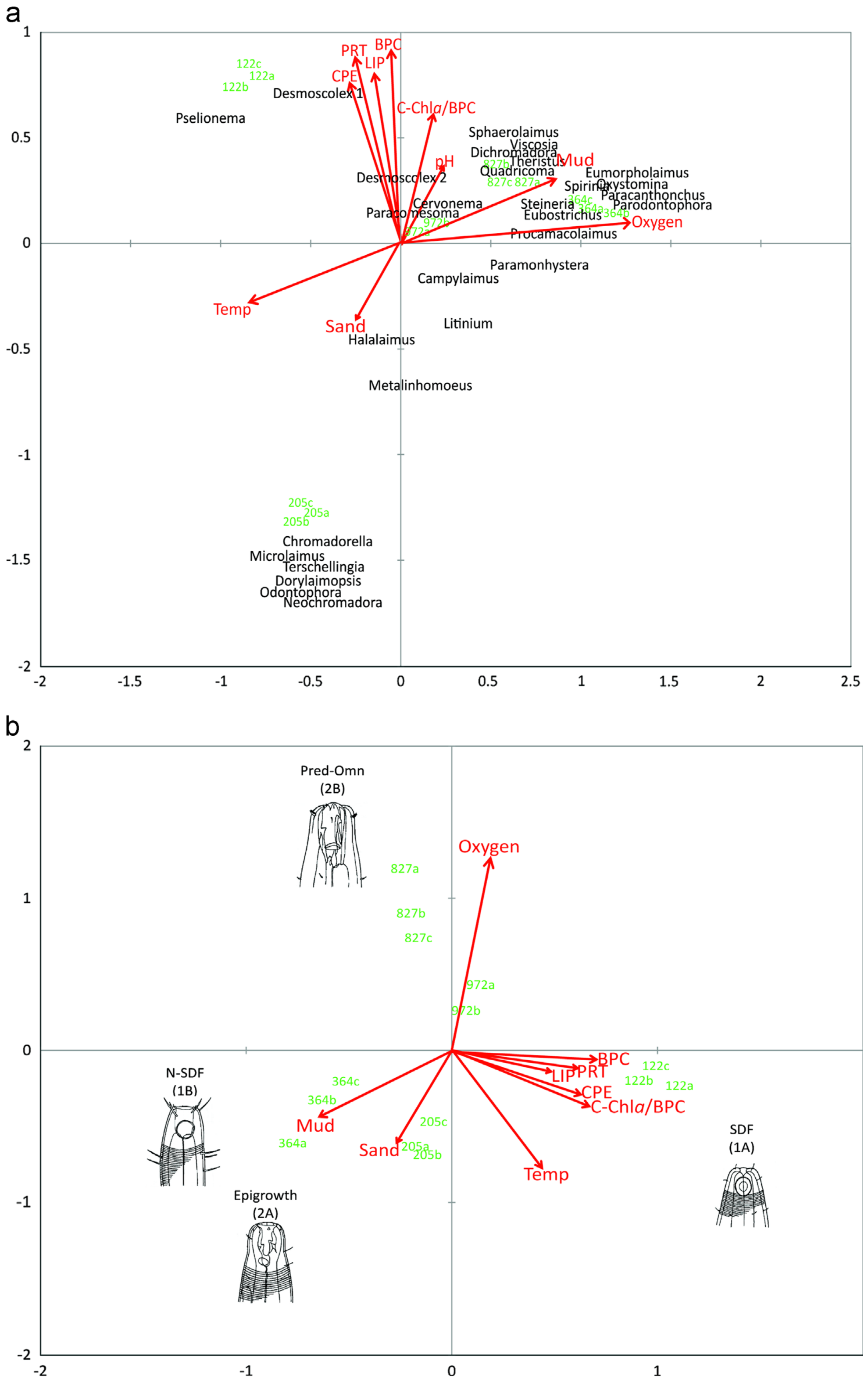

Fig. 7. Canonical correspondence analysis displaying (a) nematode genera and (b) nematode trophic groups in relation to environmental variables that best explain their distribution among sites (showed by their depths: 122 m=outer shelf, 205 m=shelf break, 364 m=upper slope, 827 m=mid-slope, and 972 m=lower mid-slope). Arrows are the environmental vectors. Arrows pointing in the same relative direction are correlated, and longer arrows indicate increasing values. The first two axes explained 84.3% and 91.5% of the variance of genus- and trophic groups-environment relationships. Both relationships were highly significant ($P=0.001$; 999 permutations in Monte Carlo test).

heterogeneity (Van Gaever et al., 2009), grain size (Heip et al., 1985), and oxygen (Levin et al., 2002) have also been mentioned as factors affecting meiofaunal distribution.

At all stations, the OM quality index (BPC/TOC) was ~3 times higher than that measured off Callao Peru (~17%) (Neira et al., 2001a) and ~2 times higher than that reported for the continental

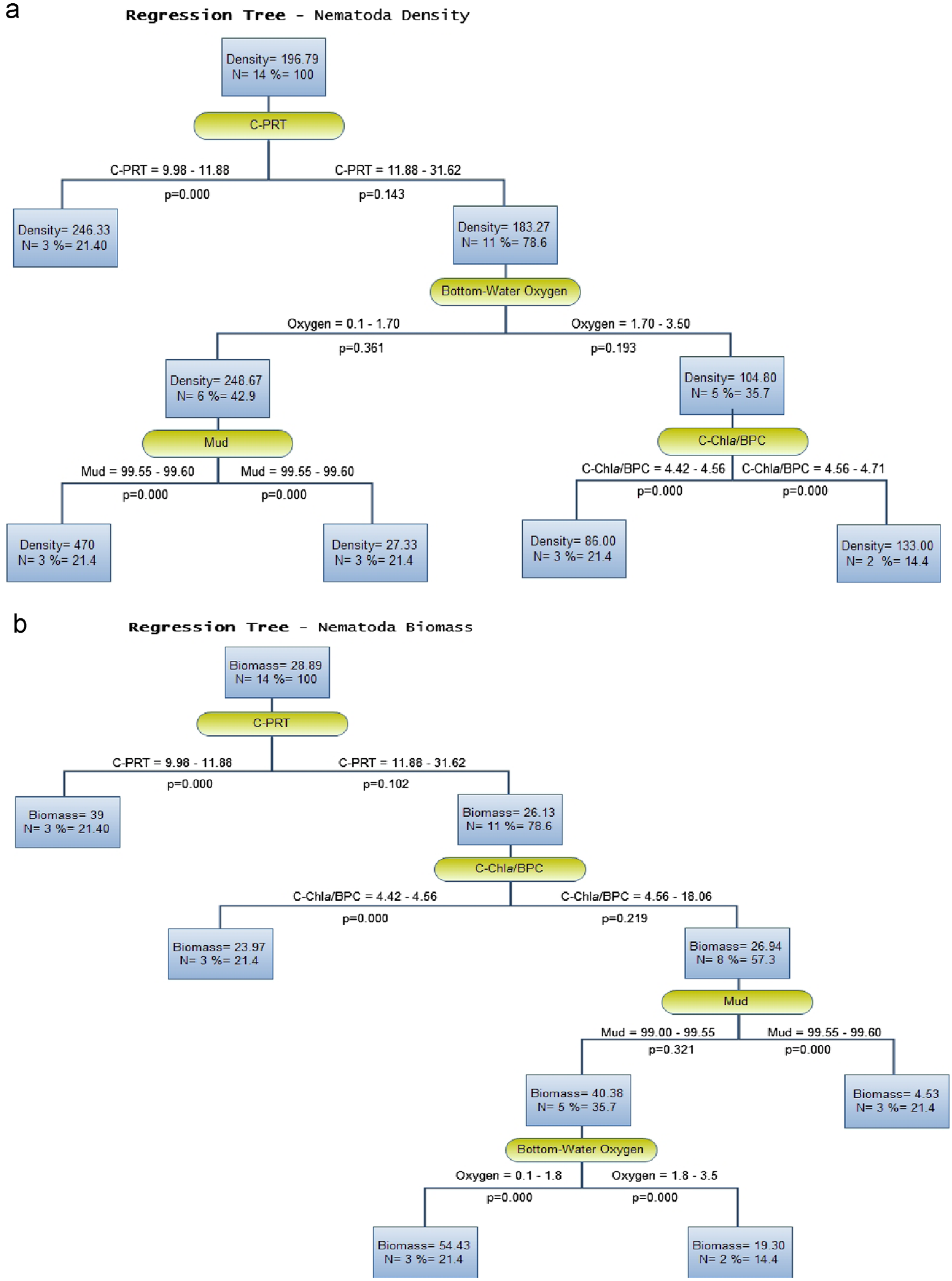

Fig. 8. Regression tree analysis for (a) nematode density (ind. 10 cm^{-2}) and (b) nematode biomass (mg dry weight). Density and biomass are single response variables while the multiple explanatory variables (predictors) are the environmental factors. Factors important in explaining variation appear at the terminal nodes along with the concentration range. Significance *P* of the split, as well as the number and percent observation in the group, are indicated. C-PRT (mg g^{-1}), Mud (%), C-Chl *a* of BPC (%), oxygen (ml L^{-1}).

shelf of central Chile (37% and 27%, before and after the 1997/98 El Niño, respectively) (Neira et al., 2001b). Along the transect, BPC was responsible for a large percentage (~83%) of the TOC variance. Other factors, such as presence of non-labile compounds and changes in OM composition, could explain the remaining variance (Middelburg et al., 1999; Zegouagh et al., 1999; Zonneveld et al., 2010). Changes in the OM composition and hence its quality along the depth gradient suggest that the productivity of the overlying water was an important factor, at least at the time of sampling, in controlling both quantity and quality of sedimentary organic

Table 5
Indicator genera characterizing the nematode community (0–10 cm) on the central Chile margin. The IndVal column shows the genus indicator value. Significance *P* for each IndVal is shown.

Site	Genus	IndVal (%)	P
OS-122	*Pselionema*	*83.4*	0.004
	Desmoscolex 1	64.9	0.009
SB-205	*Odontophora*	100	0.011
	Neochromadora	100	0.011
	Terschellingia	93.8	0.001
	Dorylaimopsis	93.2	0.005
	Microlaimus	91.7	0.011
	Chromadorella	85.1	0.011
SB-364	*Steineria*	100	0.009
	Spirinia	100	0.009
	Parodontophora	99.2	0.003
	Paracanthonchus	88.2	0.002
	Eubostrichus	79.4	0.044
	Oxystomina	70.6	0.017
	Eumorpholaimus	64.7	0.005
	Procamacolaimus	61.6	0.021
MS-827	*Theristus*	100	0.009
	Dichromadora	100	0.009
	Viscosia	100	0.009
	Sphaerolaimus	100	0.009
	Quadricoma	77.4	0.009
LS-972	*Paracomesoma*	100	0.009
	Cervonema	60.4	0.059

matter. The differences in feeding types (Fig. 6) and individual biomass (Fig. 5) along the transect and within the sediment column suggest that it is the composition or nutritional quality of the sedimentary organic matter, rather than its quantity, that is influencing nematode diversity.

4.2. Nematode community structure

Very little information has been published previously on free-living marine nematodes from Chile at the genus or species level (e.g. Wieser, 1953b, 1954, 1956; Gambi et al., 2003; Lee and Riveros, 2012). To our knowledge, ours is the first set of genus-level data on nematode communities on the upper continental margin off Chile, addressing influence by the OMZ. Enhanced total nematode densities in low-oxygen settings are consistent with other OMZs studies (e.g. Levin et al., 1991; Cook et al., 2000; Neira et al., 2001a,b). Total densities of nematodes at the low-oxygen sites (~2000 ind. 10 cm^{-2} at OS-122, SB-205 and US-364) were comparable to the those reported by Neira et al. (2001b) and Sellanes and Neira (2006) for the middle and outer continental shelf off Concepción, by Veit-Köhler et al. (2009) for the outer shelf off Concepción and upper slope off Antofagasta (22°S), and by Neira et al. (2001a) for the upper slope off Peru. These values are much higher than those reported for the western Indian shelf (Sajan et al., 2010). Cook et al. (2000) reported densities ranging from 494 to 2495 ind. 10 cm^{-2} for the Oman slope, with the maximum at the site of highest food quality. On the Volcano 7 seamount, Levin et al. (1991) found the highest densities of nematodes (~190 ind. 10 cm^{-2}) in the center of the OMZ intercepting the upper summit, where high concentrations of organic carbon and pigments were found. Off the Central West coast of India, nematode densities of 19–303 ind. 10 cm^{-2} were reported, with the genus *Desmoscolex* widely distributed (Nanajkar et al., 2010). At three Atacama slope sites (1050, 1140 and 1355 m), facing the Atacama trench off northern Chile, nematodes accounted for 90% of the community, with densities of ~498 ind. 10 cm^{-2} (Danovaro et al., 2002). At these three slope sites, the number of genera present were 55, 60 and 90, compared to only 29 in the Atacama Trench itself (Gambi et al., 2003). Interestingly, *Pselionema* was found at all Atacama sites, including the trench; however, relative abundances of this genus were much lower (1.7–4.2%) than in the central Chile OMZ (60%). *Halalaimus* and *Desmoscolex* were widely distributed along the transect off central Chile, as they were for the Atacama slope and Trench. However, relative abundances were substantially higher at the shelf break (SB-205) and lower mid-slope off central Chile. The steep increase of the total density/genus richness ratio (Table 2) in low-oxygen settings suggest that there is density compensation (e.g. McGrady-Steed and Morin, 2000; Longino and Colwell, 2011) through the population increase of possibly more hypoxia-tolerant taxa, and/or there is an indirect effect from reduction of hypoxia-intolerant predators and competitors, and enhanced preservation of available food (Neira et al., 2001a).

Our results revealed distinctly divergent nematode responses between OMZ-influenced settings and the deeper, more oxygenated ones. While the lowest nematode diversity, highest generic and trophic dominance occurred at the most oxygen-depleted site, the opposite was observed at the deeper, better-oxygenated sites. The increasing nematode diversity with depth was consistent with the general understanding that marine benthic diversity usually increases with increasing water depth along the upper continental slope (Rex, 1983; Rex and Etter, 2010; Menot et al., 2010). On the northeastern Pacific margin off Oregon, the lowest nematode diversity was observed at intermediate water depth (Guilini et al., 2012). Studies off Peru indicated that beyond the OMZ habitat, sediment heterogeneity has more relevance in shaping meiofaunal diversity than oxygen (Neira et al., 2001a; Levin et al., 2002; Sellanes et al., 2010).

4.3. Nematode trophic structure

Increased generic diversity at downslope sites can also be the result of the well-developed nutritional selectivity attributed to nematodes (Jensen, 1987a; Giere, 2009). Different oxygen and food requirements, as well as the wide range of buccal structures of the different feeding types, could be responsible for the vertical partitioning of nematodes in the sediment (Jensen, 1987a; Neira and Decraemer, 2009). This may effectively reduce interspecific competition and allow niche partitioning (Jumars et al., 1990). Trophic partitioning may favor those nematode genera broadly distributed across all sites (except OS-122) as well as across a wide vertical range in the sediment (Table 4) such as the genus *Sabatieria*. *Sabatieria* species have different microhabitats in the sediments thereby maximizing resources availability (Jensen, 1987a). They have been reported to thrive in disturbed sediments (Steyaert et al., 2007), near-anoxic muddy sediments (Vanreusel, 1990; Vincx et al., 1990), and have developed adaptation mechanisms to survive episodes of anoxia (Soetaert and Heip, 1995; Steyaert et al., 2007). In addition, it has been suggested that *Sabatieria* thrive only in sediments below the oxic zone containing a large amount of organic matter (Soetaert and Heip, 1995).

Further studies concerning nematodes suggest that carbon derived from microphytobenthos could be ingested via pathways other than direct grazing on microalgae (Moens et al., 2002), such as trans-cuticular uptake of dissolved organic matter (Jensen, 1987a; Ólafsson and Elmgren, 1997). The deep penetration of nematodes into the Chile margin sediments (Fig. 4) was most likely due to the relatively high amount of labile organic matter available (Fig. 2), as supported by the larger individual biomass observed in deeper sediment layers beyond the shelf break (Fig. 5). However, the presence of a substantial fraction of nematodes in deeper sediment layers could not be explained only by food availability. The vertical distribution of nematodes may reflect a combination of bacterial densities and oxygen supply (Vanreusel et al., 1995, 2000). Different diet and different kinds of food items, as well as predation pressure and hypoxic conditions, have been proposed to explain the vertical migration of nematodes to deeper sediment layers (Schratzberger et al., 2000; Steyaert et al., 2005; Braeckman et al., 2010; Maria et al., 2012). Large nematodes, such as those observed at upper- and mid-slope sites, may have the ability to maximize the oxygen absorption, migrate to oxic layers, or take advantage of oxic halo surrounding ventilated macrofaunal burrows (Wetzel et al., 1985; Neira et al., 2001c; 2005; Neira and Decraemer, 2009).

At the OMZ site OS-122, the nematode community comprised a single trophic group (1A), i.e. selective deposit (bacterial) feeders (Fig. 5). Loss of generic biodiversity along with trophic diversity can have consequences for ecosystem function (Danovaro et al., 2008). The absolute dominance of nematodes belonging to 1A (*Pselionema*, *Halalaimus* and *Desmoscolex*), especially at the outer shelf (OS-122), suggests that bacteria and biopolymeric carbon are the primary food sources for these nematodes.

The position of the epigrowth feeders (group 2A) on the opposite side of the CCA plot to the selective deposit feeders (group 1A), which are associated with the biopolymeric components (Fig. 7B), suggests trophic plasticity (Danovaro and Gambi, 2002), more likely relying both on phytobenthic biopolymeric carbon and bacteria. The non-selective deposit-feeding nematodes (group 1B), well represented at the US-364 site, are apparently unrelated to biopolymeric descriptors. Nematodes at this site had the highest length-width ratio (37.7), i.e. they were more slender and had an increased surface area, which has been suggested to enhance cuticular uptake of dissolved organic matter in deeper, hypoxic or anoxic sediments (Jensen, 1987a,b; Riemann et al., 1990).

The 2B (predator-omnivore) nematodes are typically associated with relatively large amounts of labile organic matter (Soetaert and Heip, 1995). The presence of the 2B genera *Enoplolaimus*, *Viscosia* and *Sphaerolaimus* in deep sediment layers at the oxygenated mid- and lower mid-slope sites may be explained by the relatively high biopolymeric carbon values ($\sim$13 mg g^{-1} and BPC/TOC $\sim$40%).

Members of the genus *Eubostrichus* (Stilbonematinae) were found in subsurface sediment layers on the upper (US-364) and mid-slope (MS-827). These are free-living nematodes with ectosymbiotic, sulfide-oxidizing bacteria (Ott et al., 1991) that migrate between the oxidized surface and the sulfidic deeper layers of the sediment to garden their symbionts (Ott et al., 1991). We did not observe other nematode species typical of OMZs such as the epsilonematid *Glochinema bathyperuvensis* found in the OMZ off Callao, Peru (Neira et al., 2001c), the selachinematid *Desmotersia levinae* (Neira and Decraemer, 2009), or the epsilonematid *G. spinithorni*, found in the OMZ off Baja California, Mexico (Neira et al., 2005).

4.4. Comparison of genera with other settings

In general, many of the nematode genera found on the central Chile margin have been found in other settings (e.g. Vanhove et al., 1999; Ingels et al., 2009; Vanreusel et al., 2010a,b; Muthumbi et al., 2004, 2011; Guilini et al., 2012), although they differ in our sample series both in terms of abundance and dominance. For instance, the ceramonematid *Pselionema*, with a relative abundance of over 60%, appears to characterize the most oxygen-depleted site (OS-122) (Table 5). *Pselionema* has been found in deep-sea sediments over a wide range of depths: in 6 sites between 100 and1000 m off North Carolina (Tietjen, 1976), in the Puerto Rico Trench (2217 m) and Hatteras Abbysal Plain (5411 m) (Tietjen, 1989), in slope sediments (1034 m) of the Goban Spur, NE Atlantic (Vanaverbeke et al., 1997), and Atacama Slope and Trench (Gambi et al., 2003). This genus has also been found at only 4 m depth in a *Posidonia oceanica* bed in the Gulf of Marconi (NW Mediterranean), coinciding with high bacterial densities (Danovaro and Gambi, 2002). The high dominance of *Pselionema* species (selective deposit feeders, with no buccal cavity) at the OMZ sites (OS-122 and SB-205) suggests the presence of an abundant bacteria community (Gallardo and Espinoza, 2007) associated with sediments rich in biopolymeric carbon.

5. Conclusions

This study provides novel baseline information on abundance, biomass, trophic structure, generic diversity and distribution patterns of free-living marine nematodes on the central Chile margin, spanning the outer shelf within the OMZ to the mid-lower slope beneath the OMZ. Overall, nematodes dominated the meiofauna in terms of abundance and biomass. The most oxygen-depleted site exhibited the lowest nematode genus richness, lower diversity (H') and lower taxonomic evenness (J'), highest rank 1 dominance (R_1D), and reduced individual biomass. The opposite occurred at downslope, more oxygenated sites. Mean total biomass was highest at the upper slope and decreased to the outer shelf and lower-mid slope. High densities of free-living nematodes at the organic-rich, oxygen-depleted sites were accompanied by very low structural and trophic diversity and biomass. At the site with lowest oxygen, only the nematode feeding group 1A (selective deposit feeders) was present. Changes in feeding types and individual biomass along the depth transect and within the sediment column strongly suggest that nematode diversity is influenced by the composition or nutritional quality of the sedimentary organic matter, rather than by its quantity. Climate-induced expansion of the OMZ (Stramma et al., 2010) may have important negative consequences at the ecosystem level. Density compensation by nematodes at lower oxygen levels might sacrifice key ecosystem functions (Danovaro et al., 2008). Loss of nematode generic and trophic diversity, as well as reduction in biomass, could be exacerbated under a scenario of OMZ shoaling and expansion. Understanding responses of dominant faunal groups such as nematodes to present-day environmental conditions and gradients along the eastern Pacific can help to make predictions about future responses to climate change.

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References

Ahumada, R., 1989. Producción y destino de la biomasa fitoplanctónica en un sistema de bahías en Chile Central: Una hipótesis. Biol. Pesquera 18, 53–66.

Barnett, P.R., Watson, J., Connely, D., 1984. A multiple corer for taking virtually undisturbed samples from shelf, bathyal and abyssal sediments. Oceanol. Acta 7, 399–408.

Bernal, P., Ahumada, R., González, H., Pantoja, S., Troncoso, A., 1989. Carbon flux in a pelagic trophic model to Concepción bay. Biol. Pesquera 18, 5–14.

Bianchelli, S., Gambi, C., Zeppilli, D., Danovaro, R., 2010. Metazoan meiofauna in deep-sea canyons and adjacent open slopes: a large scale comparison with focus on the rare taxa. Deep-Sea Res. I 57, 420–433.

Braeckman, U., Van Colen, C., Soetaert, K., Vincx, M., Vanaverbeke, J., 2010. Contrasting macrofaunal activities differentially affect nematode density and diversity in a shallow subtidal marine sediment. Mar. Ecol. Prog. Ser. 422, 179–191.

Buchanan, J.B., 1984. Sediment analysis. In: Holme, N.A., McIntyre, A.D. (Eds.), Methods for the Study of Marine Benthos, 2nd ed. Blackwell Scientific Publications, Oxford, London, pp. 41–65.

Cammen, L.M., 1991. Annual bacterial production in relation to benthic microalgal production and sediment oxygen uptake in an intertidal sandflat and an intertidal mudflat. Mar. Ecol. Prog. Ser 71, 13–25.

Cook, A.A., Lambshead, P.J., Hawkins, L.E., Mitchell, N., Levin, L.A., 2000. Nematode abundance at the oxygen minimum zone in the Arabian Sea. Deep-Sea Res. II 47, 75–85.

Cowie, G.L., 2005. The biogeochemistry of Arabian Sea surficial sediments: a review of recent studies. Prog. Oceanogr. 65, 260–289.

Danovaro, R., Della Croce, N., Eleftheriou, A., Papadopoulou, N., Smith, C., Tselepides, A., 1995. Meiofauna of the deep Eastern Mediterranean Sea: distribution and abundance in relation to bacterial biomass, organic matter composition and other environmental factors. Prog. Oceanogr. 36, 329–341.

Danovaro, R., Gambi, C., Dell'Anno, A., Corinaldesi, C., Frashetti, S., Vanreusel, A., Vincx, M., Gooday, A.J., 2008. Exponential decline of deep-sea ecosystem functioning linked to benthic biodiversity loss. Curr. Biol. 18, 1–8.

Danovaro, R., Canals, M., Gambi, C., Heussner, S., Lampadariou, N., Vanreusel, A., 2009. Exploring benthic biodiversity patterns and hotspots on European margin slopes. Oceanography 22, 16–25.

Danovaro, R., Gambi, C., 2002. Biodiversity and trophic structure of nematode assemblages in seagrass systems: evidence for a coupling with changes in food availability. Mar. Biol. 141, 667–677.

Danovaro, R., Gambi, C., Della Croce, N., 2002. Meiofauna hotspot in the Atacama Trench, eastern South Pacific Ocean. Deep-Sea Res. I 49, 843–857.

Danovaro, R., Tselepides, A., Otegui, A., Della Croce, N., 2000. Dynamics of meiofaunal assemblages on the continental shelf and deep-sea sediments of the Cretan Sea (NE Mediterranean): relationships with seasonal changes in food supply. Prog. Oceanogr. 46, 367–400.

De'ath, G., Fabricius, K.E., 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81, 3178–3192.

De Jonge, V.N., 1980. Fluctuations in the organic carbon to chlorophyll-a ratios for estuarine benthic diatom populations. Mar. Ecol. Prog. Ser. 2, 345–353.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Biol. Monogr. 67, 345–366.

Fabiano, M., Danovaro, R., Fraschetti, S., 1995. A three-year time series of elemental and biochemical composition of organic matter in subtidal sandy sediments of the Ligurian Sea (northwestern Mediterranean). Cont. Shelf Res. 15, 1453–1469.

Feller, R.J., Warwick, R.M., 1988. Energetics. In: Higgins, R.P., Thiel, H. (Eds.), Introduction to the Study of Meiofauna. Smithsonian Institution Press, Washington, D.C., London, pp. 181–196.

Fossing, H., Gallardo, V.A., Jørgensen, B.B., Hüttel, M., Nielsen, L.P., Schulz, H., Canfield, D., Foster, S., Glud, R.N., Gundersen, J.K., Ramsing, N.B., Teske, A., Thamdrup, B., Ulloa, O., 1995. Concentration and transport of nitrate by the mat-forming sulphur bacterium *Thioploca*. Nature 374, 713–715.

Galéron, J., Sibuet, M., Mahaut, L., Dinet, A., 2000. Variation in structure and biomass of the benthic communities at three contrasting sites in the tropical Northeast Atlantic. Mar. Ecol. Prog. Ser. 197, 121–137.

Gallardo, V.A., Espinoza, C., 2007. New communities of large filamentous sulfur bacteria in the eastern South Pacific. Int. Microbiol. 10, 97–102.

Gallardo, V.A., Palma, M., Carrasco, F.D., Gutiérrez, D., Levin, L.A., Cañete, J.I., 2004. Macrobenthic zonation caused by the oxygen minimum zone on the shelf and slope off central Chile. Deep-Sea Res. II 51, 2475–2490.

Gambi, C., Vanreusel, A., Danovaro, R., 2003. Biodiversity of nematode assemblages from deep-sea sediments of the Atacama slope and trench (South Pacific Ocean). Deep-Sea Res. I 50, 103–117.

Giere, O., 2009. Meiobenthology. The Microscopic Motile Fauna of Aquatic Sediments, 2nd edition Springer, Berlin Heidelberg.

Gooday, A.J., Bett, B.J., Escobar, E., Ingole, B., Levin, L.A., Neira, C., Raman, A.V., Sellanes, J., 2010. Habitat heterogeneity and its influence on benthic biodiversity in oxygen minimum zones. Mar. Ecol. 31, 125–147.

Gooday, A.J., Levin, L.A., Aranda da Silva, A., Bett, B.J., Cowie, G.L., Dissard, D., Gage, J. D., Hughes, D.J., Jeffreys, R., Lamont, P.A., Larkin, K.E., Murty, S.J., Schumacher, S., Whitcraft, C., Woulds, C., 2009. Faunal responses to oxygen gradients on the Pakistan margin: a comparison of foraminiferans, macrofauna and megafauna. Deep-Sea Res. II 56, 488–502.

Guilini, K., Levin, L.A., Vanreusel, A., 2012. Cold seep and oxygen minimum zone associated sources of margin heterogeneity affect benthic assemblages, diversity and nutrition at the Cascadian margin (NE Pacific Ocean). Prog. Oceanogr. 96, 77–92.

Gutiérrez, D., Gallardo, V.A., Mayor, S., Neira, C., Vásquez, C., Sellanes, J., Rivas, M., Soto, A., Carrasco, F., Baltazar, M., 2000. Effects of dissolved oxygen and fresh organic matter on the bioturbation potential of macrofauna in sublittoral sediments off central Chile during the 1997/1998 El Niño. Mar. Ecol. Prog. Ser. 201, 81–99.

Hagerthey, S.E., Louda, J.W., Mongkronsri, P., 2006. Evaluation of pigment extraction methods and recommended protocol for periphyton chlorophyll a determination and chemotaxonomic assessment. J. Phycol. 42, 1125–1136.

Heip, C., Vincx, M., Vranken, G., 1985. The ecology of marine nematodes. Oceanogr. Mar. Biol. Ann. Rev. 23, 399–489.

Hurlbert, S.H., 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52, 577–586.

Ingels, J., Konstadinos, K., Wolff, G.A., Vanreusel, A., 2009. Nematode diversity and its relation to the quantity and quality of sedimentary organic matter in the deep Nazaré Canyon, Western Iberian margin. Deep-Sea Res. I 56, 1521–1539.

Jensen, P., 1987a. Feeding ecology of free-living aquatic nematodes. Mar. Ecol. Prog. Ser. 35, 187–196.

Jensen, P., 1987b. Differences in microhabitat, abundance, biomass and body-size between oxybiotic and thibiotic free-living nematodes. Oecologia (Berlin) 71, 564–567.

Jongman, R.H.G., ter Braak, C.J.F., van Tongeren, O.F.R., 1995. Data Analysis in Community and Landscape Ecology. Cambridge University Press, Cambridge.

Jumars, P.A., Mayer, L.M., Deming, J.W., Baross, J.A., Wheatcroft, R.A., 1990. Deep-sea deposit-feeding strategies suggested by environmental and feeding constraints. In: Charnock, H., Edmond, J.M., McCave, I.N., Rice, A.L., Wilson, T.R.S. (Eds.). The Deep Sea Bed: Its Physics, Chemistry and Biology. Philos. Trans. R. Soc. London A, vol. 331, pp. 85–101.

Knap, A., Michaels, A., Dow, R., Johnson, R., Gundersen, K., Sorensen, J., Close, A., Howse, A., Hammer, F., Bates, N., Doyle, A., Waterhouse, T., 1993. Bermuda Atlantic Time Series Study Methods Manual (Version 3). Bermuda Biological Station for Research, Inc., US JGOFS108.

Lambshead, P.J.D., Boucher, G., 2003. Marine nematode deep-sea biodiversity—hyperdiverse or hype? J. Biogeogr. 30, 475–485.

Lambshead, P.J.D., Elce, B.J., Thistle, D., Eckman, J.E., Barnett, P.R.O., 1994. A comparison of the biodiversity of deep-sea marine nematodes from three stations in the Rockall Trough, Northeast Atlantic, and one station in the San Diego Trough, Northeast Pacific. Biodivers. Lett. 2, 21–33.

Lee, M.R., Riveros, M., 2012. Latitudinal trends in the species richness of free-living marine nematode assemblages from exposed sandy beaches along the coast of Chile (18–42°S). Mar. Ecol. 33, 317–325.

Lepš, J., Šmilauer, T., 2003. Multivariate Analysis of Ecological Data Using CANOCO. Cambridge University Press, Cambridge, UK.

Levin, L.A., 2003. Oxygen minimum zone benthos: adaptation and community response to hypoxia. Oceanogr. Mar. Biol. Ann. Rev. 41, 1–45.

Levin, L.A., Gutiérrez, D., Rathburn, A., Neira, C., Sellanes, J., Muñoz, P., Gallardo, V.A., Salamanca, M., 2002. Benthic processes on the Peru margin: a transect across the oxygen minimum zone during the 1997–98 El Niño. Prog. Oceanogr. 53, 1–27.

Levin, L.A., Huggett, C.L., Wishner, K.F., 1991. Control of deep-sea benthic community structure by oxygen and organic-matter gradients in the eastern Pacific Ocean. J. Mar. Res. 49, 763–800.

Levin, L.A., Sibuet, M., 2012. Understanding continental margin biodiversity: a new imperative. Annu. Rev. Mar. Sci. 4, 79–112.

Levin, L.A., Sibuet, M., Gooday, A.J., Smith, C.R., Vanreusel, A., 2010. The roles of habitat heterogeneity in generating and maintaining biodiversity on continental margins: an introduction. Mar. Ecol. 31, 1–5.

Longino, J.T., Colwell, R.K., 2011. Density compensation, species composition, and richness of ants on a neotropical elevation gradient. Ecosphere 2, 1–20.

Maria, T.F., Vanaverbeke, J., Esteves, A.M., De Troch, M., Vanreusel, A., 2012. The importance of biological interactions for the vertical distribution of nematodes in a temperate ultra-dissipative sandy beach. Estuar. Coastal Shelf Sci. 97, 114–126.

McGrady-Steed, J., Morin, P.J., 2000. Biodiversity, density compensation, and the dynamics of populations and functional groups. Ecology 81, 361–373.

Menot, L., Sibuet, M., Carney, R.S., Levin, L.A., Rowe, G.T., Billett, D.S.M., Poore, G.C.B., Kitazato, H., Vanreusel, A., Galéron, J., Lavrado, H.P., Sellanes, J., Ingole, B., Krylova, E.M., 2010. New perceptions of continental margin biodiversity. In: McIntyre, A.D. (Ed.) Life in the World's Oceans: Diversity, Distribution, and Abundance. pp. 79–101.

Merler, S., Furlanello, C., Cheminl, C., Nicolini, G., 1996. Classification tree methods for analysis of mesoscale distribution of *Ixodes ricinus* (Acari: Ixodidae) in Trentino, Italian Alps. J. Med. Entomol. 33, 888–893.

Middelburg, J.J., Niewenhuize, J., van-Breugel, P., 1999. Black carbon in marine sediments. Mar. Chem. 65, 245–252.

Moens, T., Luyten, C., Middelburg, J.J., Herman, P.M.J., Vincx, M., 2002. Tracing organic matter sources of estuarine tidal flat nematodes with stable carbon isotopes. Mar. Ecol. Prog. Ser. 234, 127–137.

Muthumbi, A.W., Vanreusel, A., Duineveld, G., Soetaert, K., Vincx, M., 2004. Nematode community structure along the continental slope off the Kenyan coast, Western Indian Ocean. Int. Rev. Hydrobiol. 89, 188–205.

Muthumbi, A.W., Vanreusel, A., Vincx, M., 2011. Taxon-related diversity patterns from the continental shelf to the slope: a case study on nematodes from the Western Indian Ocean. Mar. Ecol. 32, 453–467.

Nanajkar, M., Ingole, B., Chatterjee, T., 2010. Spatial distribution of the nematodes in the subtidal community of the Central West Coast of India with emphasis on *Terschellingia longicaudata* (Nematoda: Linhomoeidae). Indian J. Zool., 1–9 iFirst.

Neira, C., Decraemer, W., 2009. *Desmotersia levinae*, a new genus and new species of free-living nematode from bathyal oxygen minimum zone sediments off Callao, Peru, with discussion on the classification of the genus *Richtersia* (Chromadorida: Selachinematidae). Organisms. Divers. Evol. 9, 1–15.

Neira, C., Decraemer, W., Backeljau, T., 2005. A new species of *Glochinema* (Epsilonematidae: Nematoda) from the oxygen minimum zone off Baja California, NE Pacific and phylogenetic relationships at species level within the family. Cah. Biol. Mar. 46, 105–126.

Neira, C., Gad, G., Arroyo, N.L., Decraemer, W., 2001c. *Glochinema bathyperuvensis* sp. n. (Nematoda, Epsilonematidae): a new species from Peruvian bathyal sediments, SE Pacific Ocean. Contrib. Zool. 70, 147–159.

Neira, C., Rackemann, M., 1996. Black spots produced by buried macroalgae in intertidal sandy sediments of the Wadden Sea: effects on the meiobenthos. J. Sea Res. 36, 153–170.

Neira, C., Sellanes, J., Levin, L.A., Arntz, W.E., 2001a. Meiofaunal distributions on the Peru margin: relationship to oxygen and organic matter availability. Deep-Sea Res. I 48, 2453–2472.

Neira, C., Sellanes, J., Soto, A., Gutiérrez, D., Gallardo, V.A., 2001b. Meiofauna and sedimentary organic matter off central Chile: response to changes caused by the 1997–1998El Niño. Oceanol. Acta 24, 313–328.

Ólafsson, E., Elmgren, R., 1997. Seasonal dynamics of sublittoral meiobenthos in relation to phytoplankton sedimentation in the Baltic Sea. Estuar. Coastal Shelf Sci. 45, 149–164.

Ott, J.A., Novak, R., Schiemer, F., Hentschel, U., Nebelsick, M., Polz, M., 1991. Tackling the sulfide gradient: a novel strategy involving marine nematodes and chemoautotrophic ectosymbionts. P.S.Z.N.I. Mar. Ecol. 12, 261–279.

Palma, M., Quiroga, E., Gallardo, V.A., Arntz, W., Gerdes, D., Schneider, W., Hebbeln, D., 2005. Macrobenthic animal assemblages of the continental margin off Chile (22° to 42°S). J. Mar. Biol. Assoc. U.K. 85, 233–245.

Pfannkuche, O., Thiel, H., 1988. Sample processing. In: Higgins, R.P., Thiel., H. (Eds.), Introduction to the Study of Meiofauna. Smithsonian Institution Press, Washington, DC, London, pp. 134–145.

Pfannkuche, O., Soltwedel, T., 1998. Small benthic size classes along the N.W. European continental margin: spatial and temporal variability in activity and biomass. Prog. Oceanogr. 42, 189–207.

Pizarro, O., Shaffer, G., Dewitte, B., Ramos, M., 2002. Dynamics of seasonal and interannual variability of the Peru–Chile undercurrent. Geophys. Res. Lett. 29 (22-1), 22–24.

Platt, H.M., Warwick, R.M., 1980. The significance of free-living nematodes to the littoral ecosystem. In: Price, J.H., Irvine, D.E.G., Farnham, W.F. (Eds.), The Shore Environment, Ecosystems, vol. 2. Academic Press, London, pp. 729–759.

Pusceddu, A., Gambi, C., Zepelli, D., Bianchelli, S., Danovaro, R., 2009. Organic matter composition, metazoan meiofauna, and nematode biodiversity in sediments of the deep Mediterranean Sea. Deep-Sea Res. II 56, 755–762.

Rex, M.A., 1983. Geographic patterns of species diversity in deep-sea benthos. In: Rowe, G.T. (Ed.), The Sea, vol. 8. John Wiley & Sons Inc., New York, pp. 453–472.

Rex, M.A., Etter, R.J., 2010. Deep-Sea Biodiversity: Pattern and Scale. Harvard University Press354.

Riemann, F., Ernst, W., Ernst, R., 1990. Acetate uptake from ambient water by the free-living marine nematode *Adoncholaimus thalassophygas*. Mar. Biol. 104, 453–457.

Sajan, S., Joidas, T.V., Damodaran, R., 2010. Meiofauna of the western continental shelf of India, Arabian Sea. Estuar. Coastal Shelf Sci. 86, 665–674.

Schratzberger, M., Rees, H.L., Boyd, S.E., 2000. Effects of simulated deposition of dredged material on structure of nematode assemblages—the role of burial. Mar. Biol. 136, 519–530.

Sellanes, J., Neira, C., 2006. ENSO as a natural experiment to study meiofaunal communities. Mar. Ecol. 27, 31–43.

Sellanes, J., Neira, C., Quiroga, E., Teixido, N., 2010. Diversity patterns along and across the Chilean margin: a continental slope encompassing oxygen gradients and methane seep benthic habitats. Mar. Ecol 31, 111–124.

Soetaert, K., Heip, C., 1995. Nematode assemblages of deep-sea and shelf break sites in the North Atlantic and Mediterranean Sea. Mar. Ecol. Prog. Ser. 125, 171–183.

Sokal, R.R., Rohlf, F.J., 1997. Biometry: The Principles and Practice of Statistics in Biological Research, Third edition Freeman, New York887.

Steyaert, M., Moodley, L., Nadong, T., Moens, T., Soetaert, K., Vincx, M., 2007. Responses of intertidal nematodes to short-termanoxic events. J. Exp. Mar. Biol. Ecol. 345, 175–184.

Steyaert, M., Moodley, L., Vanaverbeke, J., Vandewiele, S., Vincx, M., 2005. Laboratory experiments on the infaunal activity of intertidal nematodes. Hydrobiologia 540, 217–223.

Stramma, L., Schmidko, S., Levin, L.A., Johnson, G.C., 2010. Ocean oxygen minima expansions and their biological impacts. Deep-Sea Res. I 57, 587–595.

Sutton, C.D., 2005. Classification and regression trees, bagging, and boosting. Data Mining and Data Visualization. Handbooks of Statistics 24.

ter Braak, C.J.F., 1988. CANOCO—A FORTRAN Program for Canonical Community Ordination by (partial) (detrended) (canonical) Correspondence Analysis, Principal Components Analysis and Redundancy Analysis (version 2.1). Technical Report LWA-88-02. Agricultural Mathematics Group, Wageningen95.

ter Braak, C.J.F., Šmilauer, P., 1998. CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4). Microcomputer Power, Ithaca, NY, USA.

ter Braak, C.J.F., Šmilauer, P., 2002. CANOCO Reference Manual and canoDraw for Windows User's guide: Software for Canonical Community Ordination (version 4.5), Ithaca, USA (⟨www.canoco.com⟩): Microcomputer Power.

Thistle, D., 1980. The response of a harpacticoid copepod community to a small-scale disturbance. J. Mar. Res. 38, 381–395.

Tietjen, J.H., 1976. Distribution and species diversity of deep-sea nematodes off North Carolina. Deep-Sea Res. 23, 755–768.

Tietjen, J.H., 1989. Ecology of deep-sea nematodes from the Puerto Rico Trench area and Hatteras Abyssal Plain. Deep-Sea Res. 36, 1567–1575.

Vanaverbeke, J., Martínez Arbizu, P., Dahms, H.U., Schminke, H.K., 1997. The metazoan meiobenthos along a depth gradient in the Arctic Laptev Sea with special attention to nematode communities. Polar Biol. 18, 391–401.

Van Colen, C., Monserrat, F., Verbist, K., Vincx, M., Steyaert, M., Vanaverbeke, J., Herman, P.M.J., Degraer, S., Ysebaert, T., 2009. Tidal flat nematode responses to hypoxia and subsequent macrofauna-mediated alterations of sediment properties. Mar. Ecol. Prog. Ser. 381, 189–197.

Van Gaever, D., Galéron, J., Sibuet, M., Vanreusel, A., 2009. Deep-sea habitat heterogeneity influence on meiofaunal communities in the Gulf of Guinea. Deep-Sea Res. II 56, 2259–2269.

Vanhove, S., Arntz, W., Vincx, M., 1999. Comparative study of the nematode communities of the southeastern Weddell Sea shelf and slope (Antarctica). Mar. Ecol. Prog. Ser. 181, 237–256.

Vanreusel, A., 1990. Ecology of free-living marine nematodes from the Voordelta (southern bight of the North Sea). 1. Species composition and structure of the nematode communities. Cah. Biol. Mar. 31, 439–462.

Vanreusel, A., Clough, L., Jacobsen, K., Ambrose, W., Jivaluk, J., Ryheul, V., Herman, R., Vincx, M., 2000. Meiobenthos of the central Arctic Ocean with special emphasis on the nematode community structure. Deep-Sea Res. I 47, 1855–1879.

Vanreusel, A., De Groote, A., Gollner, S., Bright, M., 2010a. Ecology and biogeography of free-living nematodes associated with chemosynthetic environments in the deep sea: a review. PLoS ONE 5 (8), e12449, http://dx.doi.org/10.1371/journal.pone.0012449.

Vanreusel, A., Fonseca, G., Danovaro, R., da Silva, M.C., Esteves, A.M., Ferrero, T., Gad, G., Galtsova, V., Gambi, C., da Fonsêca Genevois, C., Ingels, J., Ingole, B., Lampadariou, N., Merckx, B., Miljutin, D., Miljutina, M., Muthumbi, A., Netto, S., Portnova, D., Radziejewska, T., Raes, M., Tchesunov, A., Vanaverbeke, J., Van Gaever, S., Venekey, V., Martínez Arbizu, P., Galéron, J., 2010b. The contribution of deep-sea macrohabitat heterogeneity to global nematode diversity. Mar. Ecol. 31, 6–20.

Vanreusel, A., Vincx, M., Schram, D., van Gansbeke, D., 1995. On the vertical distribution of the metazoan meiofauna in shelf break and upper slope habitats of the NE Atlantic. Int. Rev. Gesamt. Hydrobiol. 80, 313–326.

Veit-Köhler, G., Gerdes, D., Quiroga, E., Hebbeln, D., Sellanes, J., 2009. Metazoan meiofauna within the oxygen-minimum zone off Chile: results of the 2001-PUCK expedition. Deep-Sea Res. II 56, 1105–1111.

Vincx, M., Bett, B.J., Dinet, A., Ferrero, T., Gooday, A.J., Lambshead, P.J.D., Pfannkuche, O., Soltwedel, T., Vanreusel, A., 1994. Meiobenthos of the deep Northeast Atlantic. Adv. Mar. Biol. 30, 2–88.

Vincx, M., Meire, P., Heip, C., 1990. The distribution of nematode communitiesin the southern bight of the North Sea. Cah. Biol. Mar. 31, 107–129.

Wetzel, M.A., Jensen, P., Giere, O., 1985. Oxygen.sulfide regime and nematode fauna associated with Arenicola marina burrows: new insights in the thiobios case. Mar. Biol. 124, 301–312.

Wieser, W., 1953a. Die Beziehung zwischen Mundhöhlengestalt, Ernährungsweise und Vorkommen bei freilebenden marinen Nematoden. Arkiv. Zool. 4, 439–484.

Wieser, W., 1953b. Free-Living Marine Nematodes. I. Enoploidea. Reports of the Lund University Chile Expedition 1948–1949. 10. C.W.K. Gleerup, Lund, Sweden, 155 pp.

Wieser, W., 1954. Free-living marine nematodes. II. Chromadoroidea. Reports of the Lund University Chile Expedition 1948–1949. 17. C.W.K. Gleerup, Lund, Sweden, 148 pp.

Wieser, W., 1956. Free-living marine nematodes. III. Axonolaimoidea and Monhysteroidea. Reports of the Lund University Chile Expedition 1948-1949. 26. C.W.K. Gleerup, Lund, Sweden, 115 pp.

Wieser, W., 1960. Benthic studies in Buzzards Bay. II. The meiofauna. Limnol. Oceanogr. 5, 121–137.

Williams, P., Jenkinson, N.W., 1982. A transportable microprocessor controlled precise Winkler titration suitable for field station and shipboard use. Limnol. Oceanogr. 27, 576–584.

Zegouagh, Y., Derenne, S., Largeau, C., Bertrand, P., Sicre, M.A., Saliot, A., Rousseau, B., 1999. Refractory organic matter in sediments from the North-West African upwelling system: abundance, chemical structure and origin. Org. Geochem. 30, 101–117.

Zonneveld, K.A.F., Versteegh, G.J.M., Kasten, S., Eglinton, T.I., Emeis, K.-C., Huguet, C., Kocj, B.P., de Lange, G.J., Leeuw, J.W., Middelburg, J.J., Mollenhauer, G., Prahl, F. G., Rethemeyer, J., Wakeham, S.G., 2010. Selective preservation of organic matter in marine environments: processes and impact on the sedimentary record. Biogeoscience 7, 483–511.