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Meiofaunal distributions on the Peru margin: relationship to oxygen and organic matter availability

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Abstract

A quantitative study of metazoan meiofauna was carried out on bathyal sediments (305, 562, 830 and 1210 m) along a transect within and beneath the oxygen minimum zone (OMZ) in the southeastern Pacific off Callao, Peru (12°S). Meiobenthos densities ranged from 1517 (upper slope, middle of OMZ) to 440–548 ind. 10 cm⁻² (lower slope stations, beneath the OMZ). Nematodes were the numerically dominant meiofaunal taxon at every station, followed by copepods and nauplii. Increasing bottom-water oxygen concentration and decreasing organic matter availability downslope were correlated with observed changes in meiofaunal abundance. The 300-m site, located in the middle of the OMZ, differed significantly in meiofaunal abundance, dominance, and in vertical distribution pattern from the deeper sites. At 305 m, nematodes amounted to over 99% of total meiofauna; about 70% of nematodes were found in the 2–5 cm interval. At the deeper sites, about 50% were restricted to the top 1 cm. The importance of copepods and nauplii increased consistently with depth, reaching ~12% of the total meiofauna at the deepest site. The observation of high nematode abundances at oxygen concentrations <0.02 ml l⁻¹ supports the hypothesis that densities are enhanced by an indirect positive effect of low oxygen involving (a) reduction of predators and competitors and (b) preservation of organic matter leading to high food availability and quality. Food input and quality, represented here by chloroplastic pigment equivalents (CPE) and sedimentary labile organic compounds (protein, carbohydrates and lipids), were strongly, positively correlated with nematode abundance. By way of contrast, oxygen exhibited a strong negative correlation, overriding food availability, with abundance of other meiofauna such as copepods and nauplii. These taxa were absent at the 300-m site.

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The high correlation of labile organic matter (C-LOM, sum of carbon contents in lipids, proteins and carbohydrates) with CPE (Pearson's $r = 0.99$, $p < 0.01$) suggests that most of the sedimentary organic material sampled was of phytodetrital origin. The fraction of sediment organic carbon potentially available to benthic heterotrophs, measured as C-LOM/Total organic carbon, was on average 17% at all stations. Thus, a residual, refractory fraction, constitutes the major portion of organic matter at the studied bathyal sites. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Meiofauna; Nematodes; Oxygen minimum zone; Organic matter composition; Continental slope; Peru margin; El Niño

1. Introduction

Oxygen minimum zones (OMZs) are midwater regions in the open ocean where dissolved oxygen concentrations fall below 0.5 ml l^{-1} (Kamykowski and Zentara, 1990; Levin et al., 1991). They result from oxygen depletion through biological oxygen demand and are well developed in areas where upwelling promotes very high surface production such as the southeastern Pacific Ocean (Wyrтки, 1966), the Arabian Sea (Wyrтки, 1973), and the southeastern Atlantic off West Africa (Bailey, 1991). In midwater regions with low oxygen, the consumption of primary production is often reduced, which means that much sinking organic material reaches the bottom relatively undegraded (Wishner et al., 1990, 1995). Where OMZs intercept the continental seabed or seamounts, strong gradients of bottom-water oxygen concentration and organic-matter input are created (Levin et al., 1991). These gradients influence the biogeochemical properties of sediments and the structure and distribution of bacterial, meio-, macro- and megafaunal communities (Sanders, 1969; Rosenberg et al., 1983; Mullins et al., 1985; Arntz et al., 1991; Levin et al., 1991, 2000).

The southeastern Pacific Ocean contains one of the most extensive OMZs of the world oceans, from the latitude of Galapagos Islands ($\sim 1^\circ\text{S}$) to southern Chile ($\sim 40^\circ\text{S}$) (Gallardo, 1963; Rosenberg et al., 1983; Arntz et al., 1991). This OMZ develops beneath the highly productive surface waters (over $1000 \text{ g C m}^{-2} \text{ yr}^{-1}$, Walsh, 1981; Chávez and Barber, 1985) of the Humboldt Current System (HCS). In contrast to coastal areas that typically experience episodic hypoxia, the continental margin intercepted by the OMZ of the HCS experiences permanently hypoxic conditions in the deep sublittoral to bathyal benthic environment. Dissolved oxygen concentrations of $< 0.5 \text{ ml l}^{-1}$ occur in the heart of the OMZ between 100 and 500 m depth off Peru and values of $< 1 \text{ ml l}^{-1}$ occur at 800 m (Zuta et al., 1983). At greater depths, the oxygen concentration gradually increases (Rosenberg et al., 1983).

Large areas of the oxygen-deficient bottom beneath the HCS are inhabited by a conspicuous prokaryotic community made up mainly of the sulphur bacterium *Thioploca* (Gallardo, 1977; Rosenberg et al., 1983). Sometimes and in some places, *Thioploca* forms mats on the bottom that make up a large portion of the benthic biomass (Gallardo, 1977, 1985). Because of its nitrate-reducing, sulphide-oxidizing metabolism, *Thioploca* could be an important detoxicator of the sediment, facilitating the establishment of zoobenthos (Gallardo et al., 1996; Neira et al., 2001a).

In recent years considerable attention has been directed towards the study of the OMZs of the world's oceans (Mullins et al., 1985; Kamykowski and Zentara, 1990; Levin et al., 1991; Arntz

et al., 1991; Bailey, 1991; Gage, 1995; Lallier-Vergès et al., 1993; Wishner et al., 1990, 1995; Levin et al., 2000). Enhanced biological and biogeochemical activity is often observed near upper and lower OMZ boundaries (Mullins et al., 1985; Thompson et al., 1985; Wishner et al., 1990; Levin et al., 1991). Where OMZs intercept the bottom, benthic ecosystems are characterized by a strong faunal zonation, severe reduction of macro- and megafauna abundance and diversity as well as a reduction of bioturbation (Wishner et al., 1990; Levin et al., 1991, 2000; Smith et al., 2000). However, there is evidence that protozoan and metazoan meiofauna are less affected than macrofauna, and that oxygen apparently plays a minor role in determining total meiofaunal abundance (Gooday et al., 2000; Bernhard et al., 2000; Levin et al., 1991; Cook et al., 2000).

To date, there are few studies on the meiofauna of the Peru margin. In part, these have been semi-quantitative, considering only shallow-water nematodes of sandy sediments (Nichols and Musselman, 1979; Nichols, 1980), or deep-sea nematodes beyond the OMZ (Bussau, 1993). Several studies have related faunal data to water depth rather than oxygen concentration or organic matter (Rowe, 1971a,b; Karpinski, 1985).

The objectives of the present paper are (1) to describe the gross taxonomic composition, numerical abundance and vertical distribution patterns of bathyal metazoan meiofauna on the Peruvian slope, and (2) to determine the biochemical composition of sedimentary organic matter and its potential relationship to meiofaunal abundance. The study transect, located at 12°S off Callao, Peru, extends from the core of the OMZ, across the lower OMZ boundary, and beneath the OMZ. Correlations of the meiofaunal assemblage with oxygen and organic-matter gradients are examined in order to test the hypotheses that (i) low oxygen concentration does not reduce nematode abundance, and (ii) metazoan meiobenthos exhibit distinct patterns of abundance, vertical distribution, and gross taxonomic composition within the OMZ, relative to better oxygenated, downslope sites.

2. Materials and methods

2.1. Study area and sampling

From December 31, 1997, to January 3, 1998, four stations with depths of 305 m (Station A), 562 m (Station B), 830 m (Station C) and 1210 m (Station D) were investigated during the expedition Panorama Leg 3a aboard the R/V *Melville*. Stations formed a transect through and beneath the oxygen minimum zone off Callao, Peru (Fig. 1). Sampling was conducted in the midst of the 1997–98 El Niño, when temperature anomalies in surface waters off Callao were at their maximum (Sánchez et al., 2000). This El Niño (hereafter EN) was one of the strongest of the century (McPhaden, 1999). The area is characterized by intense and persistent coastal upwelling resulting in a well-developed, mid-water OMZ. Samples were collected using a multiple corer (Barnett et al., 1984), with tubes having a 9.5 cm diameter. Only undisturbed cores with clear overlying water were used. Bottom-water dissolved oxygen was measured by Winkler titration in 3 replicates from Niskin bottles of a CTDO. Table 1 shows the location of the study sites and physico-chemical characteristics of the near-bottom water.

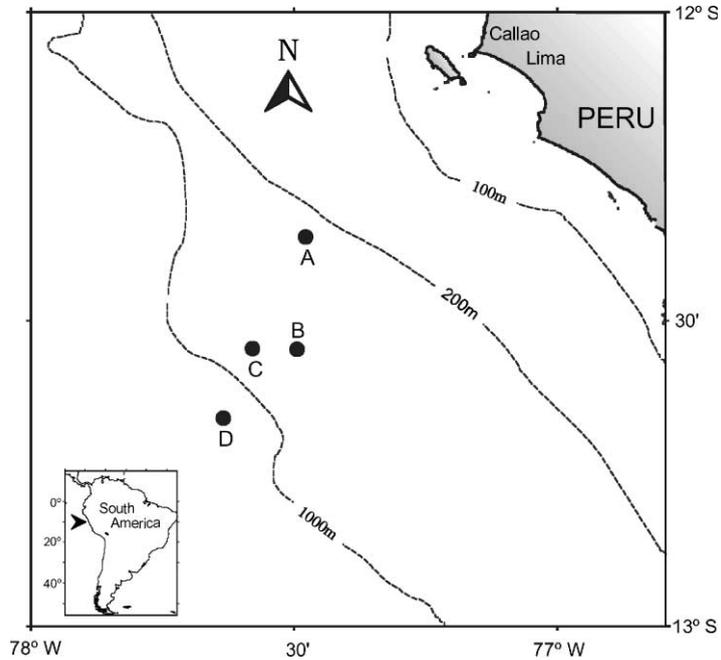


Fig. 1. The investigated area and the sampling sites in the southeastern Pacific off Callao, Peru. Isobaths in meters.

Table 1

Water depth, location, bottom-water temperature (BWT), salinity and bottom-water dissolved oxygen (BWO) along the transect off Callao, Peru

Station	Depth (m)	Latitude (S)	Longitude (W)	BWT (°C)	Salinity	BWO ₂ (ml l ⁻¹)
A	305	12°22.70'	77°29.07'	10.15	34.73	0.013
B	562	12°32.54'	77°29.58'	7.06	34.56	0.227
C	830	12°32.76'	77°34.76'	5.18	34.55	0.745
D	1210	12°40.31'	77°38.49'	3.40	34.59	1.624

2.2. Meiofauna

For metazoan meiofauna, defined here as metazoans that pass through a 0.5-mm mesh sieve, but are retained on a 0.040-mm mesh sieve (Giere, 1993), three to four replicate cores (different multicore drops) were collected. From each replicate, one subsample was taken from the central

area by gently inserting a perspex tube of 3.6 cm inner diameter (10 cm^2). To examine meiofaunal distribution, cores were sectioned vertically (0–1; 1–2; 2–3; 3–5; and 5–10 cm) immediately after recovery, treated with a solution of magnesium chloride, and preserved in 10% buffered formalin containing Rose Bengal (Pfannkuche and Thiel, 1988). Meiofauna were separated by the suspension-decantation method (Wieser, 1960) with a few modifications (Neira and Rackemann, 1996). The efficiency of this method has been documented by Murrell and Fleeger (1989). All meiofaunal individuals were sorted into major taxa and counted under a stereo dissecting microscope.

2.3. Sediment properties

Porosity and water content were determined at 1-cm intervals by weight loss after freeze-drying a known volume of sediment assuming a sediment and water density of 2.65 g cm^{-3} (quartz) and 1.025 g cm^{-3} , respectively (Buchanan, 1984). Redox profiles (Eh) were measured at intervals of 1 cm immediately after collection using an Eh-meter (Mettler Toledo). Additional cores were subsampled for chlorophyll *a* (Chl *a*) and phaeopigments, total organic carbon and nitrogen, and the principal biochemical components of organic matter: lipids, carbohydrates, and proteins. Cores were sectioned at depth intervals of 0–1, 1–3, 3–5, 5–7, 7–9, 9–11, 11–13, 13–15 cm and were kept deep-frozen until later analysis.

Sediment organic carbon and nitrogen were determined in a Heraeus-CHN elemental analyser (model TMT CHN-O-RAPID) after treatment with diluted hydrochloric acid to remove carbonates. Proteins (PRT) were determined photometrically by the Coomassie Blue reaction after incubation for 2 h at 60°C with NaOH 0.5 N (Boetius et al., 1996) and further centrifugation, and expressed as albumin equivalents. Lipid (LIP) content was determined in methanol-chloroform extracts as described by Greiser and Faubel (1988); the dry residue was weighed after complete evaporation of the solvent. Carbohydrate quantification was made photometrically using phenol-sulfuric acid and expressed as glucose equivalents. The carbohydrate material was separated into two operational fractions before quantification as described by Taylor and Paterson (1998): the colloidal fraction (CHO) (Underwood et al., 1995), which represents the most labile carbohydrates, and the bulk fraction, which comprises a complex of more refractory carbohydrate material that remains in the sediment after the colloidal fraction has been removed by centrifugation (Taylor and Paterson, 1998). If not otherwise indicated, carbohydrates (CHO) refer exclusively to the colloidal fraction. Carbohydrates, proteins and lipids were converted into carbon equivalents assuming conversion factors of 0.40, 0.49 and 0.70, respectively (Fabiano et al., 1995). The sum of the three biochemical classes in terms of carbon is reported here as a measure of the sediment biopolymeric carbon fraction (C-LOM) potentially available to benthic heterotrophs (Fabiano and Danovaro, 1994; Fabiano et al., 1995; Danovaro et al., 2000). This fraction, when related to sedimentary total organic carbon, is considered as an index of sediment quality (Fichez, 1991; Relexans et al., 1992, 1996).

Chloroplastic pigment equivalents reaching the bottom (Chl *a* and phaeopigments), an estimate of the amount of organic matter that is derived from primary production, were measured photometrically according to Stal et al. (1984).

2.4. Statistics

Pearson product-moment correlations were used to test for relationships between meiofaunal distribution and environmental variables. Parametric ANOVA was used to detect differences in meiofauna abundances between sites. When necessary, square root or log transformed data were used in order to remove heteroscedasticity and to correct residuals. After a significant ANOVA, Tukey HSD test or the non-parametric Mann–Whitney U-test were used for contrasts. Correlations were considered significant when $p < 0.05$. All tests were performed using the SYSTAT 8.0 software package (Wilkinson et al., 1992) or Statistica 5.1 (StatSoft Inc.).

3. Results

3.1. Sampling sites

Sediments of the mid-OMZ site (Sta. A) were organically rich (12.8–20.5% org C), dark olive-green muds, mixed with abundant sand-sized foraminifera. The high porosities and water content at Sta. A (on average, 94.8% and 82.9%, respectively), even in deeper sediments, seem to be a typical feature for the upper slope muds from this region (Reimers, 1982; Suits and Arthur, 2000). At the downslope sites (Stations B, C and D), porosity and water content were lower (on average 69.3% and 44.3%, respectively). This was reflected by structurally more heterogeneous and compact sediments composed of well-cemented phosphorite (Diester-Haass, 1978; Froelich et al., 1988), phosphatic pellets (formerly fecal pellets) (Romankevich, 1984), and foraminiferal sand mixed with sediment-mucus aggregates and agglutinating arborescent foraminifera. Redox potential analysis indicated the presence of sub-oxic conditions (generally < 200 mV) in the whole sediment column (0–15 cm) at Sta. A. However, the upper 2 and 1 cm of Sta. C and D, respectively, presented values over 300–400 mV, indicating oxic conditions. The lowest Eh value (47 mV) was measured at 15 cm depth at Sta. B. The giant sulphide-oxidizing, nitrate-reducing bacteria *Thioploca* spp. (Gallardo, 1977; Henrichs and Farrington, 1984; Fossing et al., 1995) were scarce. *Thioploca* occurred only in a single core from Sta. A, with biomass $< 10 \text{ g m}^{-2}$ (biovolume of trichomes, Schulz et al., 1996) and was concentrated mainly at a depth of 2–10 cm in the sediment column (Gallardo and Soto, pers. comm.).

The study transect was characterized by a strong bottom-water oxygen concentration gradient, from 0.013 ml l^{-1} in the core of the OMZ (Sta. A), to 0.027, 0.745 and 1.624 ml l^{-1} , at stations B, C and D, respectively. Table 2 shows the range of values of physico-chemical sediment parameters measured in the uppermost 15 cm of the study sites sediments.

3.2. Sediment pigments and organic matter composition

Concentrations of sediment-bound pigments were measured to obtain a general idea of sedimentation patterns of phytoplankton-derived organic material from the euphotic zone. Chloroplastic pigment equivalent (CPE) concentrations in the top 1 cm were highest at Sta. A ($99.43 \mu\text{g g}^{-1}$ DW), 4–9 times of the CPE at all other stations (Fig. 2). In general, phaeopigments made up more than 90% of total pigment equivalents at all stations. Vertical distribution of CPE

Table 2

Physico-chemical features of the bathyal sediments off Callao, Peru. Values are the extreme ranges measured in the upper 15 cm sediment column. C-LOM is the sum of carbon content in lipids, proteins and carbohydrates

	Sta. A (305 m)	Sta. B (562 m)	Sta. C (830 m)	Sta. D (1210 m)
Sediment				
Porosity (%)	93.46–96.13	56.52–67.52	68.86–84.67	65.95–78.67
Water content (%)	80.43–85.31	31.72–41.68	43.42–62.91	39.95–57.44
Eh (mV)	210–159	155–47	452–142	396–126
Percent organic C	10.42–20.55	4.20–6.01	5.54–8.59	3.55–5.29
Percent total N	0.81–2.20	0.32–0.48	0.56–0.94	0.40–0.60
C : N ratio (weight)	8.99–12.86	10.77–17.84	9.14–9.89	8.82–9.59
C-LOM (mg g^{-1})	17.77–38.07	3.72–7.07	9.89–11.59	7.00–7.99

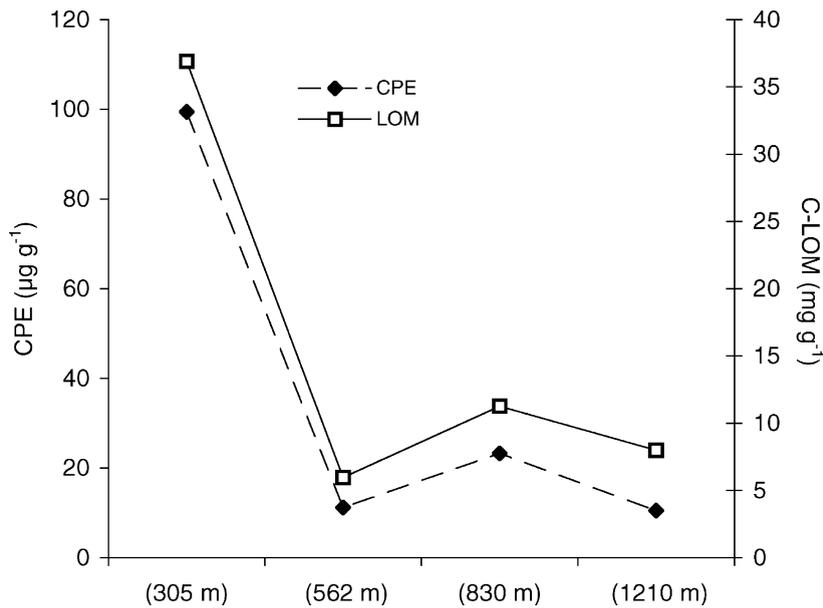


Fig. 2. Horizontal distribution of chloroplasic pigment equivalents (CPE, sum of chl *a* + phaeopigments) and of carbon labile organic matter (C-LOM, sum of carbon contents of proteins, carbohydrates and lipids) in the top 1 cm sediment.

exhibited an irregular decreasing trend with sediment depth (Fig. 3). At the shallower site (Sta. A, 305 m), Chl *a* concentrations were highest ($4.30 \mu\text{g g}^{-1}$) in the top 1 cm, decreasing to values close to $1 \mu\text{g g}^{-1}$ at 10 cm depth. Sediments at all the deeper sites exhibited levels of Chl *a* below $1 \mu\text{g g}^{-1}$ in all vertical fractions within the sediment column. Phaeopigments, instead, accounted for concentrations ranging from 3 to $10 \mu\text{g g}^{-1}$ at 10 cm depth.

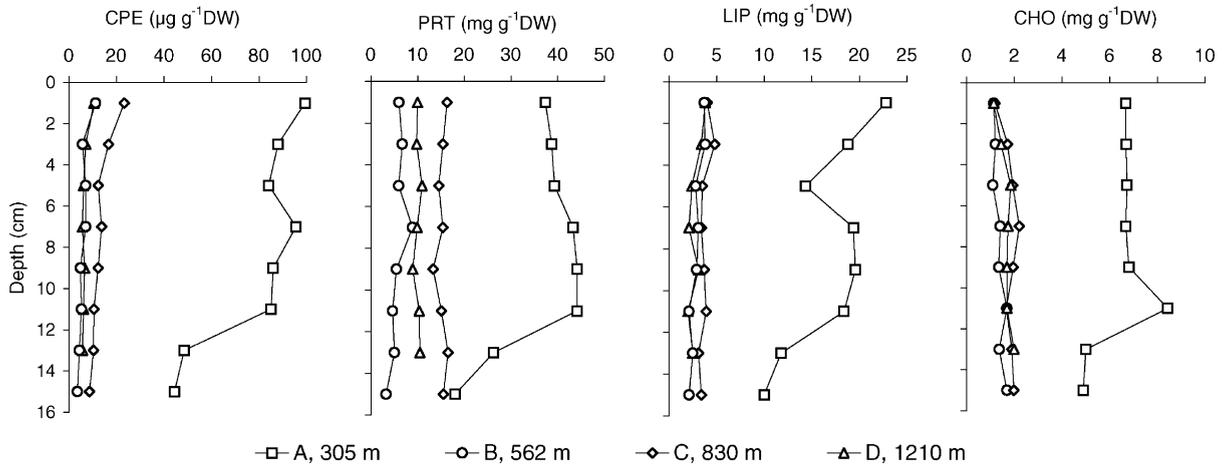


Fig. 3. Vertical distribution of chloroplasmic pigment equivalents (CPE), proteins (PRT), lipids (LIP) and carbohydrates (CHO) at the sampling sites.

The sediment biopolymeric carbon concentrations (C-LOM, as the sum of protein, lipid and carbohydrate carbon) followed the same trend with water depth (Pearson's $r = 0.99$; $p < 0.01$) along the transect as those for CPE (see Fig. 2). Each specific biochemical component correlated very well with CPE (Pearson's $r = 0.92$ for protein; 0.97 for lipid; 0.90 for carbohydrate, all $p < 0.01$) (Fig. 4). The vertical distribution of proteins (PRT), lipids (LIP) and carbohydrates (CHO) within the sediment column (Fig. 3) was rather irregular at all sites. For instance, at Sta. A (305 m), proteins increased slightly in the uppermost layers, but decreased further in deeper sediments. Likewise, at 562 and 830 m, lipid content first increased to 3 cm and then decreased. In contrast, a reduction of lipids occurred in the upper 3 cm of Sta. A (305 m) and D (1210 m). Carbohydrates fluctuated less with depth. Concentrations of protein, carbohydrate and lipid were about 2–6 times higher at Sta. A than at all other sites. Proteins dominated the labile carbon pool at all sites. In the upper 1 cm layer, proteins accounting for, on average, 57.5% of C-LOM, followed by lipids (36.1%) and carbohydrates (6.2%). At 15 cm depth, this picture was 57.4%, 30.9% and 11.7%, for protein, lipids and carbohydrates, respectively. However, differences in organic matter composition between sites were evident due to changes in the proportion of specific biochemical compounds. The food quality index (C-LOM/TOC, %) for the whole sediment column amounted to 20.2%, 10.4%, 16.4%, and 19.1%, for the 305, 562, 830, and 1210 m stations, respectively. This means that the residual, more refractory fraction (Fichez, 1991), constitutes the major portion (on average, over 83%) of the sedimentary organic matter for all sites.

3.3. Meiofauna

The densities (0–10 cm) of total meiofauna, nematodes, copepods+nauplii and other taxa (tanaidaceans, ostracods, kinorhynchs, halacarids, rotifers, gastrotrichs, turbellarians, polychaetes, oligochaetes, priapulids, nemertines, bivalves and tardigrades) along the depth transect

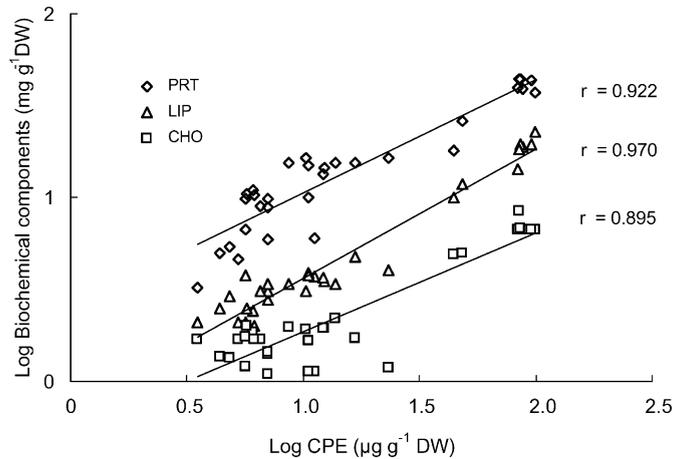


Fig. 4. Relation between concentrations (log transformed) of the principal biochemical components of sedimentary organic matter (PRT=protein; CHO=carbohydrates; LIP=lipids) and chloroplactic pigment equivalents (CPE) ($p < 0.1$).

are shown in Fig. 5. Total metazoan meiofaunal density differed significantly among sites (ANOVA $F_{3,10} = 4.54$; $p = 0.029$). Higher densities were found at Sta. A (1517 ± 431 ind. 10 cm^{-2} ; mean \pm SE) than at the deeper stations (Mann Whitney U-test $p < 0.05$). No significant differences were found among the 562 m (456 ± 216 ind. 10 cm^{-2}), the 830 m (440 ± 73 ind. 10 cm^{-2}) and the 1210 m (548 ± 67 ind. 10 cm^{-2}) stations. Nematodes were dominant at all stations, dictating the patterns in total meiofaunal density. They accounted for over 99% of total meiofauna in the OMZ core (Sta. A, 305 m). Downslope, their relative dominance declined to less than 80%. By way of contrast, copepods + nauplii exhibited downslope density patterns different from those of nematodes. They increased consistently with increasing water depth from 0 ind. 10 cm^{-2} at Sta. A to a maximum of 66 ± 12 ind. 10 cm^{-2} at Sta. D. Other taxa (mentioned above) were strongly reduced at Sta. A (10 ± 4 ind. 10 cm^{-2}) and increased towards the deepest site (45 ± 9 ind. 10 cm^{-2}). Table 3 shows the relative dominance (%) of each taxon within the whole sediment column (0–10 cm).

Patterns of vertical distribution of meiofaunal abundance within the sediment differed (factorial ANOVA $F_{3,50} = 18.04$; $p < 0.001$, followed by Tukey multiple comparisons) between the OMZ core station (Sta. A, 305 m) and the downslope sites (Fig. 6). At the deeper stations, over 48% of the metazoan meiofauna occurred in the top 1 cm, decreasing to less than 5% of the total at the 5–10 cm interval. In contrast, over 70% of the meiofauna (mainly nematodes) of Sta. A were concentrated between 2 and 5 cm, with 10% found at the 5–10 cm level. Only 19% of the meiofauna was present in the upper 1 cm at this station. Harpacticoid copepods + nauplii occurred only at stations B, C, and D (up to 12% at Sta. D, 1210 m). There they were restricted to the uppermost 1 cm and formed the second dominant group. Other taxa that were relatively important at Stations B, C, and D were polychaetes, gastrotrichs, kinorhynch, and ostracods. Together these made up, on average, 6.6% of the meiofauna at these stations (Table 3).

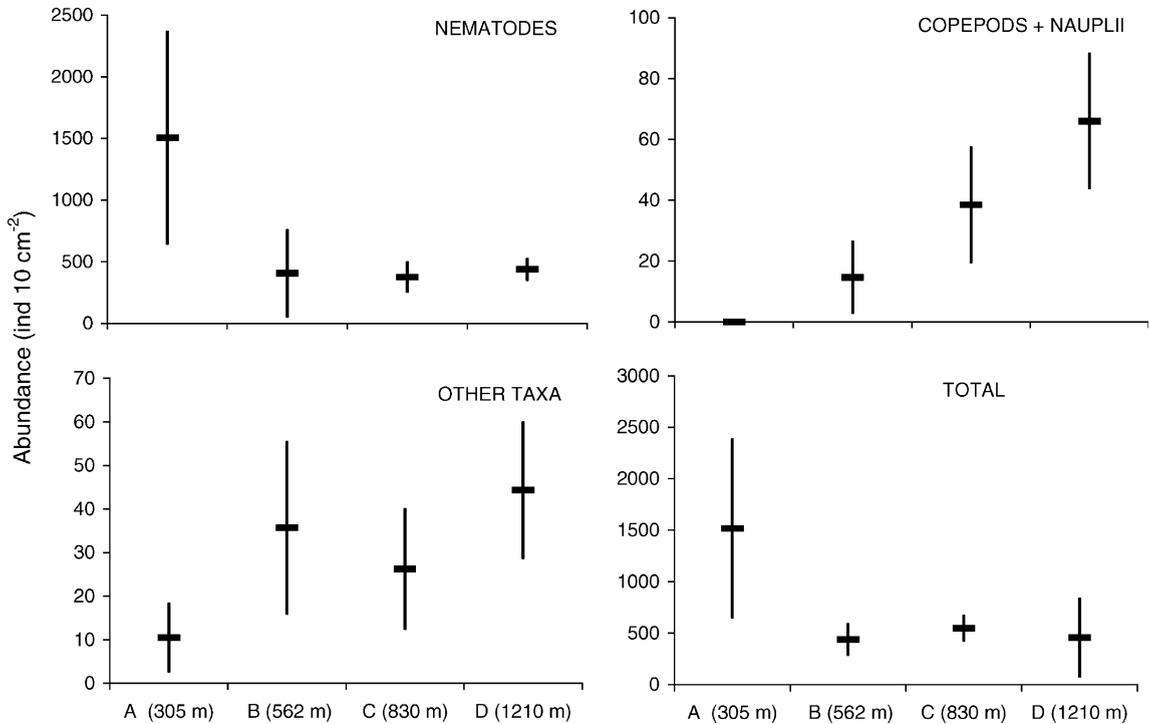


Fig. 5. Horizontal distribution of nematode, copepod + nauplii, other taxa, and total meiofauna abundances (mean \pm 1 SE) of the upper 10 cm. Other taxa are tanaidaceans, ostracods, kinorhynchs, halacarids, rotifers, gastrotrichs, turbellarians, polychaetes, oligochaetes, priapulids, nemertines, bivalves and tardigrades.

4. Discussion

4.1. Physical settings

Previous studies off central Peru (Suess, 1981; DeVries and Pearcy, 1982; Reimers, 1982; Froelich et al., 1988) have indicated that sediments associated with upwelling are typically organic-rich (up to 20% org C). As observed in other studies, the Peru margin sediments collected in this study contained fish debris (vertebrae and teeth), faecal material, sheath structures, and abundant diatom frustules. Where the OMZ reached the minimum bottom-water oxygen concentration (Sta. A, 305 m), laminated sediments were present below 5 cm. The upper 5 cm displayed evidence of bioturbation (Levin et al., unpublished). The highest densities of macro-fauna (>0.3 mm, Levin et al., unpublished) and metazoan meiofauna were found at Sta. A. Macrofauna included tubificid oligochaetes (Subfamily Phallodrilinae) *Olavius crassitunicatus* ($\sim 13,000$ ind. m⁻²), and low numbers of gastropods, polychaetes and nemertines (Levin et al., unpublished). Downslope sites exhibited no lamination (upper 8–9 cm), presumably as a result of bioturbation by macrofauna (e.g. polychaetes, amphipods and others) (Levin et al., unpublished).

Table 3

Relative dominance (%) of higher meiofauna taxa at the studied sites off Callao, Peru

	Sta A (305 m)	Sta B (562 m)	Sta C (830 m)	Sta D (1210 m)
	Relative dominance %			
Nematoda	99.30	88.95	85.30	79.93
Copepoda	—	1.47	6.02	7.85
Nauplii	—	1.75	2.73	4.20
Tanaidacea	—	0.07	0.30	0.05
Ostracoda	—	2.54	0.34	0.68
Kinorhyncha	—	0.72	0.45	1.59
Malacarida	0.07	0.22	0.41	0.31
Rotifera	0.07	0.29	0.45	—
Gastrotricha	0.21	1.01	1.77	0.91
Turbellaria	0.21	0.29	0.30	0.13
Polychaeta	0.10	0.35	1.14	3.65
Oligochaeta	0.03	2.04	—	0.13
Priapulida	—	0.13	0.11	0.49
Nemertina	—	0.07	0.57	0.05
Bivalvia	—	—	0.11	0.13
Tardigrada	—	—	0.07	—
<i>n</i>	4	3	4	3
No. of Taxa	7	14	15	14

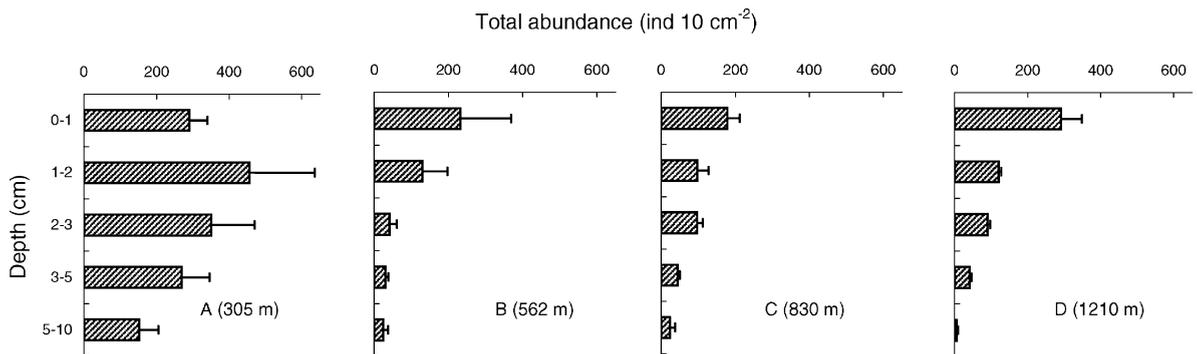


Fig. 6. Patterns of vertical distribution of total meiofaunal abundance in five sediment intervals down to 10 cm. Bars indicate mean (± 1 SE) abundances.

4.2. Oxygen and meiofauna

The control of deep-water benthic community structure by oxygen has been proposed previously for regions of intense upwelling, such as those off Chile and Peru (Thiel, 1978), Mexico

(Levin et al., 1991), SW Africa (Sanders, 1969), and in the Arabian Sea (Gooday et al., 2000; Levin et al., 2000), or in basins where sharp oxygen gradients are formed, such as the Black Sea (Rhoads and Morse, 1971) or those off Southern California (Thompson et al., 1985; Bernhard et al., 2000). In the present paper, nematode densities were similar to those reported by Cook et al. (2000) for the bathyal Oman margin (range: 494–2495 ind. 10 cm^{-2}). However, they found the highest abundances not in the centre of the OMZ (400 m; $0.13\text{ ml O}_2\text{ l}^{-1}$), but inside the OMZ (700 m; $0.16\text{ ml O}_2\text{ l}^{-1}$) at the site of highest food quality. Levin et al. (1991) found the highest densities of nematodes ($\sim 190\text{ ind. }10\text{ cm}^{-2}$) in the centre of the OMZ (upper summit of a seamount at 745 m; $0.09\text{ ml O}_2\text{ l}^{-1}$), where high concentrations of organic carbon and pigments were found. On the flank and base of the seamount (below the OMZ) densities were 2–8 times lower.

On the upper Peru slope (Sta. A, 305 m), where oxygen concentration was lowest, there are weak bottom currents and low mixing of the entire water column (Barber and Smith, 1981). This results in efficient nutrient trapping, oxygen depletion, and high organic matter deposition, in development of benthic, filamentous bacteria (*Thioploca* spp.) and in a relatively dense meiofaunal assemblage, composed almost entirely of nematodes. A plot of nematode density versus bottom-water oxygen concentration suggests that oxygen has a positive effect on density at very low oxygen concentrations (Fig. 7, Table 4). We hypothesize that the bathyal nematode abundance at Sta. A, within the core of the OMZ, is strongly enhanced by indirect effects of hypoxia that act to (a) reduce the densities of predators (especially larger taxa) and competitors, and (b) preserve organic matter, enhancing the quantity and quality of available food. The absence of forms unable to tolerate low oxygen concentration, such as harpacticoid copepods and nauplii (Hicks

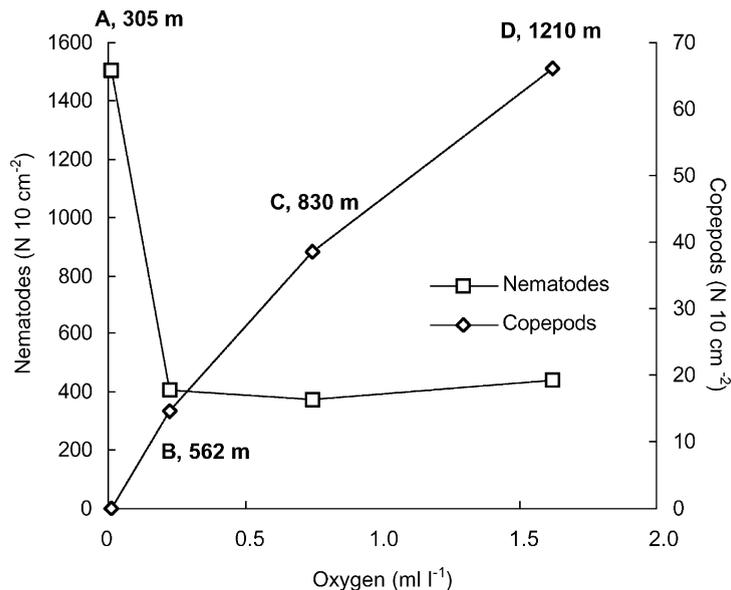


Fig. 7. Distribution of nematode and copepod+nauplii abundances along the bottom-water dissolved oxygen gradient.

Table 4

Pearson product–moment correlations and significance level between total meiofaunal and nematode abundances versus bottom oxygen, pigments and sediments biochemical parameters^a

	BWDO	TOC	PRT	CHO	LIP	C-LOM	CPE
Total meiofauna	−0.59 ^{ns}	0.72**	0.67*	0.68*	0.73**	0.70*	0.73**
Nematodes	−0.57 ^{ns}	0.78**	0.75**	0.77**	0.80**	0.79**	0.80**

^a Note: ns = non significant, * = $p < 0.01$, ** = $p < 0.001$; $n = 4$ for BWDO and 20 for the remaining parameters. BWDO = bottom water dissolved oxygen; TOC = total organic carbon; PRT = protein; CHO = carbohydrate; LIP = lipid; C-LOM = sum of PRT + CHO + LIP in terms of carbon; CPE = chloroplastic pigment equivalents.

and Coull, 1983; Murrell and Fleeger, 1989; Wells, 1988) at Sta. A (305 m), and their consistent increase (Pearson's $r = 0.99$, $p < 0.05$) with greater oxygenation (see Fig. 7), suggest that oxygen limitation might directly control meiofauna composition at higher taxonomic levels within the OMZ (Sta. A, 305 m).

Early investigations off the coast of South America revealed numerous nematodes and cirratulid polychaetes in areas of low oxygen levels (Frankenberg and Menzies, 1968; Rowe, 1971b). The tolerance of benthic animals to low oxygen concentration has been a topic of experimental studies on both macrofauna (Dales and Warren, 1980; Theede, 1984; Diaz et al., 1992) and meiofauna (Lasserre and Renaud-Mornant, 1973; Josefson and Widbom, 1988). It has been recognized that macrofauna tend to be more sensitive than meiofauna to hypoxia (Josefson and Widbom, 1988; Giere, 1993) and that nematodes exhibit a higher tolerance than other meiofaunal taxa to oxygen deficiency (Giere, 1993; Levin et al., 1991; Moodley et al., 1997). Recent studies (Cook et al., 2000; Gooday et al., 2000) carried out along a transect (400–3400 m) through and beneath the OMZ off Oman in the Arabian Sea, indicated that among the benthic fauna, nematodes and calcareous foraminifera were the most tolerant to low oxygen concentration (0.13 ml l^{-1}). A. Rathburn (pers. comm.) has obtained similar results off Peru, finding calcareous foraminifera dominant at Sta. A. The dominance of these groups may be related to their ability to tolerate low oxygen conditions, abundant food supply, and absence of most predators (which are intolerant to hypoxia). Wishner et al. (1990, 1995) noted a significance decrease in the type of epibenthic fishes and invertebrates that might consume nematodes within the OMZ on the summit of Volcano 7, off Mexico.

Although data do not exist to identify which, if any, of the factors mentioned above is most significant, we note that food input and quality were highly correlated with nematode density in the present study (Pearson's $r = 0.79$, $p < 0.001$) (Table 4). Several other OMZ investigations have noted a correlation between food quality and meiofaunal abundance and the absence of an oxygen effect. Cook et al. (2000) reported a strong positive correlation between nematode density and food quality, measured as the hydrogen index ($r^2 = 0.93$), along a transect through the Oman margin OMZ. Meiofaunal densities quantified along a similar OMZ transect on Volcano 7, a seamount off Mexico, were correlated only with sediment chlorophyll *a* concentration ($r^2 = 0.38$), and not with oxygen or other sediment parameters (Levin et al., 1991). In all three OMZ investigations, highest nematode densities were observed within the OMZ. Additional research is clearly necessary to separate the direct and indirect effects of low oxygen concentration on

meiofaunal communities, and to distinguish indirect bottom-up (food increase) versus top-down (predation decrease) oxygen effects.

4.3. *Sedimentary organic matter quality and meiofaunal distributions*

C/N ratios (weight) ranging from 8.82 to 17.84 indicate that part of the organic matter accumulating on the Peru margin has undergone preferential decomposition of nitrogenous organic compounds. This is consistent with the relatively low quality of the sedimentary organic matter (average 17% food quality index) in spite of the very high organic carbon content of sediments (up to 20% at Sta. A). In muddy sediments off central Chile (27–120 m), the food quality index was over 27% (Neira et al., 2001a). The positive correlation between CPE and biochemical components (see Fig. 4) suggests that the most bioavailable fraction was of phytoplanktonic origin. A rough calculation of biomass of filamentous bacteria (A. Soto, pers. comm.), meiofauna (this study), and macrofauna (Levin et al., unpublished.) from Stations A–D in terms of carbon, revealed that their contribution to the organic carbon pool (for the upper 15 cm) was low. It accounted for a maximum of only 0.22% at the deeper station (Sta. D), and 0.049, 0.084 and 0.017% for Stations A, B and C, respectively.

The sum of proteins, carbohydrates, and lipids provides a good measure of the nutritional value of sedimentary organic matter, although it has some limitations (Fichez, 1991; Relexans et al., 1992, 1996; Danovaro et al., 1993, 1998; Fabiano and Danovaro, 1994; Danovaro and Fabiano, 1997). The strong decrease in lipid content with increasing sediment depth reveals the importance of these highly energetic compounds as a nutritional resource for the heterotrophic metabolism in the sediment (Salonen et al., 1976; Sargent et al., 1983; Fichez, 1991; Fabiano and Danovaro, 1994). Proteins and carbohydrates decrease as well, but more gradually. According to their degradation coefficients (data not shown) calculated from the difference in concentration between the top 1 and the 15 cm layers, and related to the initial concentration of the upper layer, photosynthetic pigments, lipids, proteins and carbohydrates were more efficiently degraded than the refractory fraction or, in other words, displayed in that order decreasing nutritional values (Fichez, 1991). Shirayama (1984) showed that meiofaunal organisms concentrate in the surface layer of the sediment where flux of organic carbon into the sediment is low. Vertical distribution patterns of meiofauna exhibited a similar trend in this study. Nematodes were concentrated in the top 1 cm at Stations B–D), where sediments had lower organic carbon content. In contrast, at Sta. A, which contained the highest sediment organic carbon content, nematodes were distributed deeper in the sediments (19% in the top 1 cm of the sediment). Similar observations were made in the Arabian Sea (Sommer and Pfannkuche, 2000). In the present study, nematode abundance was positively correlated with biochemical indicators of sediment quality (Table 4).

4.4. *The 1997–98 El Niño*

Most of the studies on effects of El Niño have considered the macro- and megafauna (e.g. Gallardo, 1985; Arntz et al., 1991; Tarazona et al., 1988a,b, 1996), whereas the meiofauna have been neglected (Neira et al., 2001a, b). To our knowledge, this is the first quantitative study on bathyal meiofauna carried out within the Peru margin OMZ during an El Niño event. Hence, the results presented in this paper may eventually be useful as a basis for meiofaunal

comparisons with non-El Niño periods and with future El Niño events. However, without comparable data during non-El Niño years, it is not possible to directly evaluate the effects of the 1997–98 El Niño.

Research off central Chile during 1997–98 offers insight into important processes that can affect infauna during El Niño events and can be used to generate predictions for future testing on the Peru margin. During the 1997–98 El Niño, Gutiérrez et al. (2000) observed increasing penetration of macrofauna in the sediment at a 27-m station (Bay of Concepción) and a 120-m station (outer shelf) relative to non-El Niño periods. Neira et al. (2001a) also observed increasing penetration of meiofauna at the 27-m station and at a 64-m station (inner shelf) in the same region. This was attributed by both authors to increased oxygenation and reduced quality of organic inputs associated with El Niño conditions.

We suggest that the vertical pattern of meiofauna observed on the upper slope off Peru (Sta. A, 305 m) might be the consequence of a combination of changes in abiotic and biotic factors triggered by El Niño: a strong increase in bottom-water oxygen concentration (Arntz et al., 1991; Tarazona et al., 1996; Tarazona pers. comm.), increasing bioturbation by burrowing oligochaetes (Levin et al., unpublished), strongly reduced primary production in the surface waters (Barber and Chávez, 1986; Wallace and Vogel, 1994) and hence decreasing food quality of the material deposited on the bottom, and increasing competition for food among the nematodes (Thiel, 1983). Nematodes at the deeper margin stations are likely to be unaffected by these processes. Salzwedel et al. (1988) and Arntz et al. (1991) indicated that El Niño effects on Peruvian benthos may be limited mainly to the shelf and uppermost slope. Subsurface meiofaunal density peaks, such as those observed at Sta. A, have been reported from water depths between 80 and 1000 m in the NE African upwelling region, the central northern Pacific (5850 m), the Red Sea (500–1500 m), the NW Atlantic off South Carolina (4000 m) (Coull et al., 1977; Burnett, 1979; Thiel, 1983), and in the Arabian Sea (4414 m) (Sommer and Pfannkuche, 2000). Biotic factors such as predation, competition for suitable microhabitat, interaction with macrofauna, microbiota and adaptation to different physical properties of the sediment, and food supply were offered as explanations (Thiel, 1983; Shirayama, 1984; Pfannkuche and Thiel, 1987; Danovaro et al., 1995; Sommer and Pfannkuche, 2000).

Studies of the Peru margin meiofauna indicate that nematode abundance is enhanced in low oxygen ($<0.02 \text{ ml l}^{-1}$) bathyal sediments, while in better oxygenated conditions, it is not. Although the data do not support a direct effect of oxygen on the physiology of nematodes, we hypothesize that bathyal nematode abundance within the OMZ is strongly enhanced by high food availability and quality and, potentially, by an indirect positive effect of very low oxygen availability through the removal of predators and competitors. In contrast, low dissolved oxygen concentration seems to eliminate copepods and nauplii on the upper Peruvian slope (Sta. A, 305 m). Changes in oxygenation and organic matter inputs associated with the 1997–98 El Niño may have been manifested as lowered quality of organic matter and a deepened vertical distribution of nematodes at the upper slope site (Sta. A, 305 m). We predict that during non-El Niño conditions, sediment organic matter quality within the Peru OMZ should be higher than observed in this study and that meiofaunal vertical distributions should be correspondingly shallower within the sediment column. Under conditions of increased oxygenation, densities of predatory and competitor species might increase and nematode densities might decline.

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References

- Arntz, W.E., Tarazona, J., Gallardo, V.A., Flores, L.A., Salzwedel, H., 1991. Benthos communities in oxygen deficient shelf and upper slope areas of the Peruvian and Chilean Pacific coast, and changes caused by El Niño. In: Tyson, R.V., Pearson, T.H. (Eds.), *Modern and ancient Continental Shelf Anoxia*. Geological Society Special Publication No. 58, London, pp.131–154.
- Bailey, G.W., 1991. Organic carbon flux and development of oxygen deficiency on the modern Benguela continental shelf south of 22°S, spatial and temporal variability. In: Tyson, R.V., Pearson, T.H. (Eds.), *Modern and Ancient Continental Shelf Anoxia*. Geological Society Special Publication No. 58, London, pp. 171–183.
- Barber, R.T., Chávez, F.P., 1986. Ocean variability in relation to living resources during the 1982–83 El Niño. *Nature* 319, 279–285.
- Barber, R.T., Smith, R.L., 1981. Coastal upwelling ecosystems. In: Longhurst, A.R. (Ed.), *Analysis of Marine Ecosystems*. Academic Press, New York, pp. 31–68.
- Barnett, P.R.O., Watson, J., Connelly, D., 1984. A multiple corer for taking virtually undisturbed samples from shelf, bathyal and abyssal sediments. *Oceanologica Acta* 7, 339–408.
- Bernhard, J.M., Buck, K.R., Farmer, M.A., Bowser, S.S., 2000. The Santa Barbara Basin is a symbiosis oasis. *Nature* 403, 77–80.
- Boetius, A., Scheibe, S., Tselepides, A., Thiel, H., 1996. Microbial biomass and activities in deep-sea sediments of the Eastern Mediterranean: trenches are benthic spots. *Deep-Sea Research I* 43, 1439–1460.
- 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.
- Burnett, B.R., 1979. Microbiota and meiofauna. In: Talbert, D.M. (Ed.), *Benthic Biological Studies*. Seabed Disposal Program Annual Report, January–December 1978. Sandia Laboratories, Albuquerque, NM, 19pp.
- Bussau, C., 1993. *Taxonomische und ökologische Untersuchungen an Nematoden des Peru-Beckens*. Diss. Fakultät Mathematik und Naturwissenschaft, Univ. Kiel, 519 pp.
- Chávez, F., Barber, R.T., 1985. La productividad de las aguas frente a la costa del Perú. *Boletín ERFEN* 15, 9–13.
- Cook, A.A., Lamshead, P.J., Hawkins, L.E., Mitchell, N., Levin, L.A., 2000. Nematode abundance at the Oxygen Minimum Zone in the Arabian Sea. *Deep-Sea Research II* 47, 75–85.
- Coull, B.C., Ellison, R.L., Fleeger, J.W., Higgins, R.P., Hope, W.D., Hummon, W.D., Rieger, R.M., Sterrer, W.E., Thiel, H., Tietjen, J.H., 1977. Quantitative estimates of the meiofauna from the deep sea off North Carolina, USA. *Marine Biology* 39, 233–240.

- Dales, R.P., Warren, L.M., 1980. Survival of hypoxic conditions by the polychaete *Cirriformia tentaculata*. *Journal of Marine Biology Association of the United Kingdom* 60, 509–516.
- Danovaro, R., Fabiano, M., 1997. Seasonal changes in quality and quantity of food available for benthic suspension-feeders in the Golfo Marconi (North-western Mediterranean). *Estuarine, Coastal and Shelf Science* 44, 723–736.
- Danovaro, R., Fabiano, M., Albertelli, G., della Croce, N., 1995. Vertical distribution of meiobenthos in bathyal sediments of the eastern Mediterranean Sea: Relationship with labile organic matter and bacterial biomasses. *P.S.Z.N.I.: Marine Ecology* 16, 103–116.
- Danovaro, R., Fabiano, M., Della Croce, N., 1993. Labile organic matter and microbial biomass in deep-sea sediments (Eastern Mediterranean Sea). *Deep-Sea Research I* 40, 953–965.
- Danovaro, R., Gambi, C., Manini, E., Fabiano, M., 2000. Meiofauna response to a dynamic plume front. *Marine Biology* 137, 359–370.
- Danovaro, R., Marrale, D., Della Croce, N., Dell'Anno, A., Fabiano, M., 1998. Heterotrophic nanoflagellates, bacteria, and labile organic compounds in continental shelf and deep-sea sediments of the eastern Mediterranean. *Microbial Ecology* 35, 244–255.
- DeVries, T.J., Percy, W.G., 1982. Fish debris in sediments of the upwelling zone off central Peru: a late Quaternary record. *Deep-Sea Research* 29, 87–109.
- Diaz, R.J., Neubauer, R.J., Schaffner, L.C., Phil, L., Baden, S.P., 1992. Continuous monitoring of dissolved oxygen in an estuary experiencing periodic hypoxia and the effect of hypoxia on macrobenthos and fish. *Scientific Total Environment, Supplement*. Elsevier Science Publishers B.V., Amsterdam, pp. 1055–1068.
- Diester-Haass, L., 1978. Sediments as indicators of upwelling. In: Boje, R., Tomczak, M. (Eds.), *Upwelling Ecosystems*. Springer, Berlin, pp. 261–281.
- Fabiano, M., Danovaro, R., 1994. Composition of organic matter in sediments facing a river estuary (Tyrrhenian Sea): relationships with bacteria and microphytobenthic biomass. *Hydrobiologia* 277, 71–84.
- 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). *Continental Shelf Research* 15, 1453–1469.
- Fichez, R., 1991. Composition and fate of organic matter in submarine cave sediments: implications for the biogeochemical cycle of organic carbon. *Oceanologica Acta* 14, 369–377.
- Fossing, H., Gallardo, V.A., Jørgensen, B.B., Hüttel, M., Nielsen, L.P., Schulz, H., Canfield, D.E., Forster, S., Glud, R.N., Gundersen, J.K., Küver, J., 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.
- Frankenberg, D., Menzies, R.J., 1968. Some quantitative analysis of deep sea benthos off Peru. *Deep-Sea Research* 15, 623–626.
- Froelich, P.N., Arthur, M.A., Burnett, W.C., Deakin, M., Hensley, V., Jahnke, R., Kaul, L., Kim, K.-H., Roe, K., Soutar, A., Vathakanon, C., 1988. Early diagenesis of organic matter in Peru continental margin sediments: phosphorite precipitation. *Marine Geology* 80, 309–343.
- Gage, J.D., 1995. Benthic community and fluxes in relation to the oxygen minimum zone in the Arabian Sea. *Cruise Report: R.R.S. Discovery 211/94 9 October–11 November 1994 Muscat to Owen Basin and adjacent continental slope of Masirah Island to Muscat*. Scottish Association for Marine Sciences, Oban, Scotland, UK, 71 pp.
- Gallardo, V.A., 1963. Notas sobre la densidad de la fauna bentónica en el sublitoral del norte de Chile. *Gayana* 10, 3–15.
- Gallardo, V.A., 1977. Large benthic microbial communities in sulfide biota under Peru-Chile subsurface countercurrent. *Nature* 268, 331–332.
- Gallardo, V.A., 1985. Efectos del fenómeno de El Niño sobre el bentos sublitoral frente a Concepción, Chile. In: Arntz, W.E., Landa, A., Tarazona, J. (Eds.), *El Niño y su impacto en la fauna marina*. Inst. Mar Perú–Callao (Boletín Extraordinario), pp. 79–85.
- Gallardo, V.A., Soto, A., Personal communication.
- Gallardo, V.A., Carrasco, F.D., Roa, R., Quiñones, R., Ulloa, O., Cañete, J.I., Mesías, J., Sobarzo, M., Pineda, V., Baltazar, M., 1996. Benthic habitat detoxification by a bacterial biomat (*Thioploca* spp.)? Observations on the recruitment of the squat lobster (*Pleuroncodes monodon*) off central Chile. *Proceedings of the Ninth Southern*

- African Marine Science Symposium, Marine Science in southern Africa. Past perspectives and future challenges, 21–23 November 1996, Univ. Cape Town, South Africa (Programme, Abstracts and Directory).
- Giere, O., 1993. Meiobenthology. The Microscopic Fauna in Aquatic Sediments. Springer, Berlin, 328 pp.
- Gooday, A.J., Bernhard, J.M., Levin, L.A., Suhr, S., 2000. Foraminifera in the Arabian Sea oxygen minimum zone and other oxygen deficient settings: taxonomic composition, diversity and relation to metazoan faunas. *Deep-Sea Research II* 47, 25–54.
- Greiser, N., Faubel, A., 1988. Biotic factors. In: Higgins, R.P., Thiel, H. (Eds.), *Introduction to the Study of Meiofauna*. Smithsonian Institution Press, Washington, DC, London, pp. 79–114.
- 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. *Marine Ecology Progress Series* 202, 81–99.
- Henrichs, S.M., Farrington, J.W., 1984. Peru upwelling region sediments near 15°S. 1. Remineralization and accumulation of organic matter. *Limnology and Oceanography* 29, 1–19.
- Hicks, G.F.R., Coull, B.C., 1983. The ecology of marine meiobenthic harpacticoid copepods. *Oceanography and Marine Biology Annual Review* 21, 67–175.
- Josefson, A.B., Widbom, B., 1988. Differential response of benthic macrofauna and meiofauna to hypoxia in the Gullmar Fjord basin. *Marine Biology* 100, 31–40.
- Kamykowski, D., Zentara, S.J., 1990. Hypoxia in the world ocean as recorded in the historical data set. *Deep-Sea Research* 37, 1861–1874.
- Karpinski, M.G., 1985. Particularidades de la distribución del bentos en los límites submarinos de las aguas peruanas. Ministerio de Pesquería de la URSS, Instituto General de Investigación Científica de Pesquería y Oceanografía VNIRO, Informe científico del Tema No. 2, 78 pp.
- Lallier-Vergès, E., Bertrand, P., Despraires, A., 1993. Organic matter composition and sulfate reduction intensity in Oman Margin sediments. *Marine Geology* 112, 57–69.
- Lasserre, P., Renaud-Mornant, J., 1973. Resistance and respiratory physiology of intertidal meiofauna to oxygen-deficiency. *Netherlands Journal of Sea Research* 7, 290–302.
- Levin, L.A., Gage, J.D., Martin, C., Lamont, P.A., 2000. Macro-benthic community structure within and beneath the oxygen minimum zone, NW Arabian Sea. *Deep-Sea Research II* 47, 189–226.
- 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. *Journal of Marine Research* 49, 763–800.
- McPhaden, M.J., 1999. Genesis and evolution of the 1997–98 El Niño. *Science* 283, 950–954.
- Moodley, L., van der Zwaan, G.L., Herman, G.L., Breugel, P., 1997. Differential response of benthic meiofauna to anoxia with special reference to foraminifera (Protista: Sarcodina). *Marine Ecology Progress Series* 158, 151–163.
- Mullins, H.T., Thompson, J.B., McDougall, K., Vercoetere, T.L., 1985. Oxygen-minimum zone edge effects, evidence from the central California coastal upwelling system. *Geology* 13, 491–494.
- Murrell, M.C., Fleegeer, J.W., 1989. Meiofauna abundance on the Gulf of Mexico continental shelf affected by hypoxia. *Continental Shelf Research* 9, 1049–1062.
- Neira, C., Gad, G., Arroyo, N.L., Decraemer, W., 2001b. *Glochinema bathyperuvensis* sp. n. (Nematoda, Epsilonematidae): a new species from Peruvian bathyal sediments, SE Pacific Ocean. *Contributions to Zoology*, in press.
- Neira, C., Rackemann, M., 1996. Black spots produced by buried macroalgae in intertidal sandy sediments of the Wadden Sea: effects on the meiobenthos. *Journal of Sea Research* 36, 153–170.
- Neira, C., Sellanes, J., Soto, A., Gutiérrez, D., Gallardo, V.A., 2001a. Meiofauna and sedimentary organic matter off central Chile: response to changes caused by the 1997–98 El Niño. *Oceanologica Acta*, Vol. 24.
- Nichols, J.A., 1980. Spatial pattern of a free-living marine nematode community off the coast of Peru. *Internationale Revue der gesamten Hydrobiologie* 65, 249–257.
- Nichols, J.A., Musselman, M.R., 1979. Free-living marine nematodes from sandy sediments off the the coast of Peru. *Cahiers de Biologie Marine* 20, 449–459.

- Pfannkuche, O., Thiel, H., 1987. Meiobenthic stocks and benthic activity on the NE-Svalbard Shelf and in the Nansen Basin. *Polar Biology* 7, 253–266.
- 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.
- Reimers, C.E., 1982. Organic matter in anoxic sediments off central Peru: relations of porosity, microbial decomposition and deformation properties. *Marine Geology* 46, 175–197.
- Relexans, J.-C., Deming, J., Dinet, A., Gaillard, J.-F., Sibuet, M., 1996. Sedimentary organic matter and micro-meiofauna with relation to trophic conditions in the tropical northeast Atlantic. *Deep-Sea Research I* 43, 1343–1368.
- Relexans, J.-C., Lin, R.G., Castel, J., Etcheber, H., Laborde, P., 1992. Response of biota to sedimentary organic matter quality of the West Gironde mud patch, Bay of Biscay (France). *Oceanologica Acta* 15, 639–649.
- Rhoads, D.C., Morse, J.W., 1971. Evolutionary and ecological significance of oxygen-deficient marine basins. *Lethaia* 4, 413–428.
- Romankevich, E.A., 1984. *Geochemistry of Organic Matter in the Ocean*. Springer, Berlin, Heidelberg, 334 pp.
- Rosenberg, R., Arntz, W.E., Chumán de Flores, E., Flores, L.A., Carbajal, G., Finger, I., Tarazona, J., 1983. Benthos biomass and oxygen deficiency in the Peruvian upwelling system. *Journal of Marine Research* 41, 263–279.
- Rowe, G.T., 1971a. Benthic biomass in the Pisco, Peru upwelling. *Investigación Pesquera* 35, 127–135.
- Rowe, G.T., 1971b. Benthic biomass and surface productivity. In: Costlow, J.D. (Ed.), *Fertility of the Sea*, Vol. 2. Gordon and Breach, New York, pp. 442–454.
- Salonen, K., Sarvala, J., Hakala, I., Viljanen, M.L., 1976. The relation of energy and organic carbon in the aquatic invertebrates. *Limnology and Oceanography* 21, 724–730.
- Salzwedel, H., Flores, L.A., Chumán de Flores, E., Zafra, A., Carbajal, G., 1988. Macrozoobenthos del sublitoral peruano antes, durante y después de El Niño 1982–83. In: Salzwedel, H., Landa, A. (Eds.), *Recursos y dinámica del ecosistema de afloramiento peruano*. Boletín Instituto del Mar del Perú (Boletín especial), pp. 77–98.
- Sáncuez, G., Calienes, R., Zuta, S., 2000. The 1997–98 El Niño and its effects on the coastal marine ecosystem off Peru. *Calcofi Reports* 41, 62–86.
- Sanders, H.L., 1969. Benthic marine diversity and the stability-time hypothesis. *Brookhaven Symposium in Biology* 12, 71–81.
- Sargent, J.R., Hopkins, C.C.E., Seiring, J.V., Youngson, A., 1983. Partial characterization of organic material in surface sediments from Balsfjorden, northern Norway, in relation to its origin and nutritional value for sediment-ingesting animals. *Marine Biology* 76, 87–94.
- Schulz, H.N., Jørgensen, B.B., Fossing, H.A., Ramsing, N.B., 1996. Community structure of filamentous, sheath-building sulfur bacteria *Thioploca* spp., off the coast of Chile. *Applied Environmental Microbiology* 62, 1855–1862.
- Shirayama, Y., 1984. Vertical distribution of meiobenthos in the sediment profile in bathyal, abyssal and hadal deep sea systems of the Western Pacific. *Oceanologica Acta* 7, 123–129.
- Smith, C.R., Levin, L.A., Hoover, D.J., McMurtry, G., Gage, J.D., 2000. Variations in bioturbation across the oxygen minimum zone in the northwest Arabian Sea. *Deep-Sea Research II* 47, 227–257.
- Sommer, S., Pfannkuche, O., 2000. Metazoan meiofauna of the deep Arabian Sea: standing stocks, size spectra and regional variability in relation to monsoon induced enhanced sedimentation regimes of particulate organic matter. *Deep-Sea Research II* 47, 2957–2977.
- Stal, L.J., Van Gamberden, H., Krumbein, W.E., 1984. The simultaneous assay of chlorophyll and bacteriochlorophyll in natural microbial communities. *Journal of Microbiological Methods* 2, 295–306.
- Suess, E., 1981. Phosphate regeneration from sediments of the Peru continental margin by dissolution of fish debris. *Geochimica et Cosmochimica Acta* 45, 577–588.
- Suits, N.S., Arthur, M.A., 2000. Bacterial production of anomalously high dissolved sulfate concentrations in Peru slope sediments: steady-state sulfur oxidation, or transient response to end of El Niño? *Deep-Sea Research I* 47, 1829–1853.
- Tarazona, J., Arntz, W.E., Canahuire, E., 1996. Impact of two El Niño events of different intensity on the hypoxic soft bottom macrobenthos off central Peruvian coast. *P. S. Z. N. I: Marine Ecology* 17, 425–446.
- Tarazona, J., Salzwedel, H., Arntz, W.E., 1988a. Positive effects of El Niño on macrobenthos inhabiting hypoxic areas of the Peruvian upwelling system. *Oecologia* 76, 184–190.

- Tarazona, J., Salzwedel, H., Arntz, W.E., 1988b. Oscillations of macrobenthos in shallow waters of the Peruvian central coast induced by El Niño 1982–83. *Journal of Marine Research* 46, 593–611.
- Taylor, I.S., Paterson, D.M., 1998. Microspatial variation in carbohydrate concentrations with depth in the upper millimetres of intertidal cohesive sediments. *Estuarine, Coastal and Shelf Science* 46, 359–370.
- Theede, H., 1984. Physiological approaches to environmental problems of the Baltic. *Limnologica* 15, 443–458.
- Thiel, H., 1978. Benthos in upwelling regions. In: Boje, R., Tomczak, M. (Eds.), *Upwelling Ecosystems*. Springer, Berlin, pp. 124–138.
- Thiel, H., 1983. Meiobenthos and nanobenthos of the deep sea. In: Rowe, G.T. (Ed.), *The Sea*. Vol. 8. Wiley-Interscience Publication, Wiley, New York, pp. 167–230.
- Thompson, J.B., Mullins, H.T., Newton, C.R., Vercoutere, T., 1985. Alternative biofacies model for dysaerobic communities. *Lethaia* 18, 167–179.
- Underwood, G.J.C., Paterson, D.M., Parkes, R.J., 1995. The measurement of microbial carbohydrate exopolymers from intertidal sediments. *Limnology and Oceanography* 40, 1243–1253.
- Walsh, J.J., 1981. A carbon budget for overfishing off Peru. *Nature* 290, 300–304.
- Wallace, J.M., Vogel, S., 1994. *El Niño and Climate Prediction*. Reports to the Nation, on our Changing Planet, No. 3, Springer, Berlin, 25 pp.
- Wells, J.B.J., 1988. Copepoda. In: Higgins, R.P., Thiel, H. (Eds.), *Introduction to the Study of Meiofauna*. Smithsonian Institution Press, Washington, DC, pp. 380–388.
- Wieser, W., 1960. Benthic studies in Buzzards Bay. II. The meiofauna. *Limnology and Oceanography* 5, 121–137.
- Wilkinson, L., Hill, M., Welna, J.P., Birkenbeuel, G.K., 1992. *Systat for Windows: Statistics, Version 5 Edition*. Evanston, IL: Systat, Inc., 750 pp.
- Wishner, K., Levin, L.A., Gowing, M., Mullineaux, L., 1990. Involvement of the oxygen minimum in the benthic zonation on a deep seamount. *Nature* 346, 57–59.
- Wishner, K.F., Ashjian, C.J., Gelfman, C., Gowing, M., Kann, L., Levin, L.A., Mullineaux, L., Saltzman, J., 1995. Pelagic and benthic ecology of the lower interface of the Eastern Tropical Pacific oxygen minimum zone. *Deep-Sea Research I* 42, 93–115.
- Wyrski, K., 1966. Oceanography of the eastern Pacific Ocean. *Oceanography and Marine Biology Annual Review* 4, 33–68.
- Wyrski, K., 1973. Physical oceanography of the Indian Ocean. In: Zeitzschel, B. (Ed.), *The Biology of the Indian Ocean*. Springer, Berlin, pp. 18–36.
- Zuta, S., Tsukayama, I., Villanueva, R., 1983. El ambiente marino y las fluctuaciones de las principales poblaciones pelágicas de la costa peruana. *FAO Fisheries Reports* 291, 179–253.