



Pergamon

Progress in Oceanography 53 (2002) 1–27

**Progress in  
Oceanography**

www.elsevier.com/locate/pocean

## Benthic processes on the Peru margin: a transect across the oxygen minimum zone during the 1997–98 El Niño

L. Levin<sup>a,\*</sup>, D. Gutiérrez<sup>b</sup>, A. Rathburn<sup>a 1</sup>, C. Neira<sup>c 2</sup>, J. Sellanes<sup>b</sup>,  
P. Muñoz<sup>b</sup>, V. Gallardo<sup>b</sup>, M. Salamanca<sup>b</sup>

<sup>a</sup> Integrative Oceanography Division, Scripps Institution of Oceanography, La Jolla, CA 92093-0218, USA

<sup>b</sup> University of Concepción, Project FONDAP-Humboldt, Casilla 160-C, Concepción, Chile

<sup>c</sup> Institute for Chemistry and Biology of the Marine Environment, University of Oldenburg, Postfach 2503, D-26111, Oldenburg, Germany

---

### Abstract

Oxygen minimum zones (OMZs) are widespread features in the most productive regions of the world ocean. A holistic view of benthic responses to OMZ conditions will improve our ability to predict ecosystem-level consequences of climatic trends that influence oxygen availability, such as global warming or ENSO-related events. Four stations off Callao, Peru (~12°S, Station A, 305 m; Station B, 562 m; Station C, 830 m and Station D, 1210 m) were sampled to examine the influence of the low bottom-water oxygen concentration and high organic-matter availability within the OMZ ( $O_2 < 0.5 \text{ ml L}^{-1}$ ) on sediments, benthic communities, and bioturbation. Sampling took place during early January 1998, an intense El Niño period associated with higher-than-normal levels of  $O_2$  on the shelf and upper slope.

Peru slope sediments were highly heterogeneous. Sediment total organic carbon content exceeded 16%, lamination was present below 6 cm depth, and filamentous sulfur bacteria (*Thioploca* spp.) were present at Station A, (305 m,  $O_2 < 0.02 \text{ ml L}^{-1}$ ). Deeper sites contained phosphorite crusts or pellets and exhibited greater bottom-water oxygenation and lower content and quality of organic matter. X-radiographs and  $^{210}\text{Pb}$  and  $^{234}\text{Th}$  profiles suggested the dominance of lateral transport and bioturbation over pelagic sedimentation at the mid- and lower slope sites. Macrofauna, metazoan meiofauna and foraminifera exhibited coherence of density patterns across stations, with maximal densities (and for macrofauna, reduced diversity) at Station A, where bottom-water oxygen concentration was lowest and sediment labile organic matter content (LOC: sum of protein, carbohydrate and lipid carbon) was greatest. Metazoan and protozoan meiofaunal densities were positively correlated with sediment LOC. The taxa most tolerant of nearly anoxic, organic-rich conditions within the Peru OMZ were calcareous foraminifera, nematodes and gutless phallodrilid (symbiont-bearing) oligochaetes. Agglutinated foraminifera, harpacticoid copepods, polychaetes and many other macrofaunal taxa increased in relative abundance below the OMZ. During the study (midpoint of the 1997–98 El Niño), the upper OMZ boundary exhibited a significant deepening (to 190 m) relative to 'normal', non-El Niño conditions (< 100 m), possibly causing a mild, transient oxygenation over the upper slope (200–300 m) and reduction of the organic particle flux to

---

\* \*Corresponding author. Tel.: +1-858-534-3579; fax: +1-858-822-0562.

E-mail address: llevin@ucsd.edu (L. Levin).

<sup>1</sup> Present address: Indiana State University, Dept. of Geography, Geology, and Anthropology, Terre Haute, IN 47809

<sup>2</sup> Present address: Integrative Oceanography Division, Scripps Institution of Oceanography, La Jolla, California 92093-0218, USA

the seabed. Future sampling may determine whether the Peru margin system exhibits dynamic responses to changing ENSO-related conditions. © 2002 Elsevier Science Ltd. All rights reserved.

*Keywords:* oxygen minimum zone; benthos; El Niño; macrofauna; meiofauna; foraminifera; organic matter composition

## Contents

|  |    |
|--|----|
| 1. Introduction  | 2  |
| 2. Materials and methods   | 4  |
| 2.1. Sediment properties   | 5  |
| 2.2. Radiochemical analyses  | 5  |
| 2.3. Protozoan meiofauna   | 6  |
| 2.4. Metazoan meiofauna  | 6  |
| 2.5. Macrofauna  | 7  |
| 2.6. Filamentous bacteria ( <i>Thioploca</i> spp.)                             | 7  |
| 2.7. Statistical methods   | 7  |
| 3. Results   | 7  |
| 3.1. Water column  | 7  |
| 3.2. Bottom descriptions   | 8  |
| 3.3. Water content and redox conditions  | 9  |
| 3.4. Content and quality of organic matter                                     | 9  |
| 3.5. Sedimentation and bioturbation  | 11 |
| 3.6. <i>Thioploca</i> spp.   | 11 |
| 3.7. Protozoan meiofauna   | 13 |
| 3.8. Metazoan meiofauna  | 13 |
| 3.9. Macrofauna  | 16 |
| 4. Discussion  | 18 |
| 4.1. Sediment characteristics  | 18 |
| 4.2. Sedimentation rates   | 18 |
| 4.3. Protozoan meiofauna   | 19 |
| 4.4. Metazoan meiofauna  | 20 |
| 4.5. Bioturbation and macrofauna   | 20 |
| 4.6. Overview and comparison of faunal patterns                                | 21 |
| 4.7. Hydrographic effects of the 1997–98 El Niño and possible benthic response | 22 |
| 5. Conclusions   | 22 |

## 1. Introduction

Oxygen minimum zones (OMZs) are significant midwater features in the eastern Pacific Ocean (Wyrski, 1973; Kamykowski & Zentara, 1990) that strongly influence the distribution and diversity of planktonic and benthic marine communities. Where OMZs intercept the continental margin or seamounts, strong gradients are formed in both bottom-water oxygen concentration and organic-matter input (Levin, Huggett, & Wishner, 1991; Levin, Gage, Martin, & Lamont, 2000). These gradients influence the biogeochemical

properties of sediments (Cowie, Calvert, Pedersen, Schulz, & von Rad, 1999) and the distributions and diversities of bacteria, meio-, macro- and megabenthic organisms (Sanders, 1969; Mullins, Thompson, McDougall, & Vercoutere, 1985; Wishner, Levin, Gowing, & Mullineaux, 1990; Tyson & Pearson, 1991). The location and intensity of the eastern Pacific OMZ varies spatially, from California to Chile, and temporally, on geological and ecological time scales. Naturally occurring climate variation (e.g., El Niño) can influence primary production and oxygen availability, and hence the size and distribution of benthic organisms in the eastern Pacific OMZ (Arntz & Fahrback, 1996).

Generally, oxygen-poor, organic-rich environments in the deep sea are dominated by meiofauna, mainly by calcareous foraminifera and nematodes (Levin et al., 1991; Gooday, Bernhard, Levin, & Suhr, 2000; Cook, Lamshead, Hawkins, Mitchell, & Levin, 2000; Neira, Sellanes, Levin, & Arntz, 2001a). When macrofauna are present, they are low-diversity, small-bodied, faunal assemblages (Levin et al., 1991, Levin, Plaia, & Huggett, 1994, Levin et al., 2000). Macrofauna in these settings often exhibit adaptive morphologies (e.g., enlarged gills; Lamont & Gage, 2000) or feeding strategies (e.g., surface deposit-feeding; Smith, Levin, Hoover, McMurtry, & Gage, 2000) suited to these conditions. Large benthic organisms are rare to absent in very low dissolved oxygen conditions ( $< 0.1 \text{ ml L}^{-1}$ ), while bacteria and meiofauna attain high abundances, possibly because of the high availability of food and the reduction in predation pressure (Levin et al., 1991; Cook et al., 2000; Neira et al., 2001a). At slightly higher oxygen levels (0.1 to  $0.2 \text{ ml L}^{-1}$ ), abundant, low-diversity, mega- and macrofaunal assemblages are present (Levin et al., 1991, 1994). Benthic community densities are reduced and diversities increase rapidly as oxygen levels increase and organic carbon levels decrease (Levin et al., 1991, 1994).

Understanding the modern fauna and their particle mixing activities (bioturbation) within OMZs can assist accurate reconstruction of historical climate regimes and population cycles. Biofacies models based on trace fossils, microfossils, and body fossils are a major source of inference about paleocirculation, productivity, oxygenation and global climate (e.g., Rhoads & Morse, 1971; Anderson & Gardner, 1989; Rhoads, Mulsow, Gutschick, Baldwin, & Stolz, 1991; Savrda & Bottjer, 1991; Behl & Kennett, 1996). Information about benthic communities within the Peru OMZ should be especially valuable because the Peru/Chile margin experiences some of the greatest organic matter inputs and oxygen stress in the world ocean (Wyrski, 1966; Walsh, 1981).

The Humboldt Current System (HCS) is one of the most productive eastern boundary systems in the world ( $\sim 1 \text{ kg C m}^{-2} \text{ y}^{-1}$ ) a result, in part, of persistent wind-driven upwelling cells that occur off central Peru ( $12\text{--}13^\circ\text{S}$ ) (Zuta & Guillén, 1970). In this region the HCS exhibits a thin but intense midwater oxygen minimum layer, which is a major source of upwelled water. This layer is generally associated with the equatorial subsurface water mass (Morales, Hormazábal, & Blanco, 1999). Variations in the temperature, nutrient and oxygen composition of upwelled water of Peru and Chile (Guillén, Lostanau, & Jacinto, 1985; Morales, Hormazábal, & Blanco, 1999) result from interannual events such as ENSO (Robles, Alarcón, & Ulloa, 1976; Huyer, Smith, & Paluszkiwicz, 1987). During the 1982–83 and 1997–98 El Niños, major shifts were observed on the Peru and Chile shelf in sediment organic matter availability, and macrofaunal and meiofaunal communities (Tarazona, Salzwedel, & Arntz, 1988a, 1988b; Gutiérrez, Gallardo, Mayor, Neira, Vásquez et al., 2000; Neira et al., 2001a, Neira, Sellanes, Soto, Gutiérrez, & Gallardo, 2001b).

This paper examines the general influence of oxygen and organic matter availability associated with the OMZ on the structure and function of animal communities inhabiting the Peru upper continental slope at  $12^\circ\text{S}$  (Fig. 1). The following questions were addressed: (1) How do sediment properties change with water depth and oxygenation across the OMZ? (2) Are OMZ conditions associated with shifts in faunal abundance, biomass, community structure, or bioturbation rates? (3) Do foraminifera, metazoan meiofauna, and metazoan macrofauna exhibit similar community-level responses to OMZ conditions? Based on previous studies examining infauna in oxygen minimum zones (Levin et al., 1991, 2000; Levin & Gage, 1998; Cook et al., 2000; Gooday et al., 2000; Gutiérrez et al., 2000; Neira et al., 2001a, b), we hypothesized that oxygen would mainly influence macrofaunal communities and bioturbation, while organic matter availability would

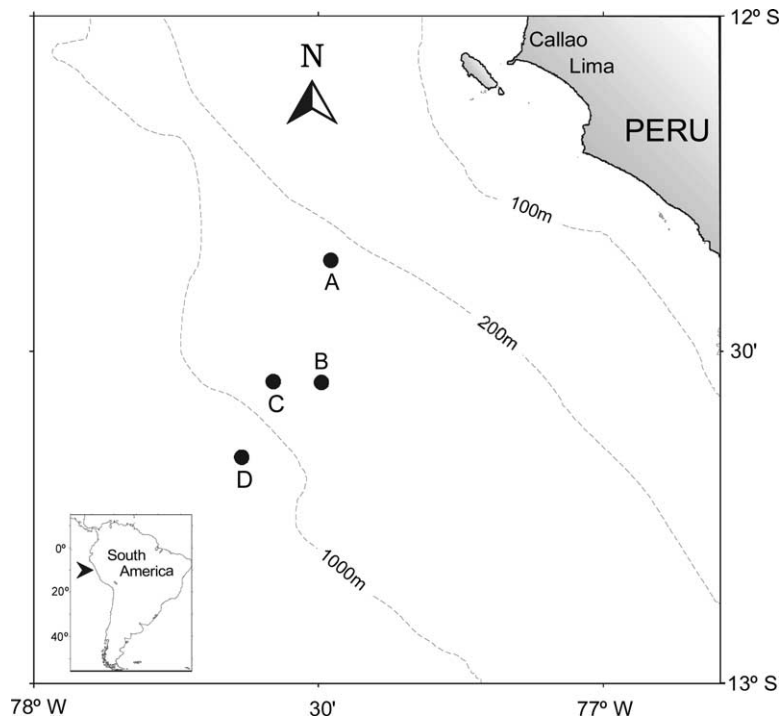


Fig. 1. Location of the sampling sites on the Peru margin (December 31 1997 – January 3 1998); Station A = 305 m depth, 12°22.7'S, 77°29.1'W; Station B = 562 m depth, 12°32.5'S, 77°29.6'W; Station C = 830 m depth, 12°32.8' S, 77°34.8'W; Station D = 1210 m depth, 12°40.3'S, 77°38.5'W.

strongly affect the structure of metazoan and protozoan meiofaunal communities. Sampling took place during the portion of the 1997–98 El Niño (McPhaden, 1999) with the greatest temperature anomaly off Callao (Sánchez, Calienes, & Zuta, 2000), allowing us to consider whether the El Niño might have influenced observed benthic patterns.

## 2. Materials and methods

Between December 31, 1997 and January 3, 1998, the slope sediment and water column were sampled off Callao, Peru during the expedition Panorama Leg 3a aboard the R/V *Melville*. Sampling took place at 4 stations: Station A, 305 m (12°22.70'S 77°29.07'W), Station B, 562 m (12° 32.54'S 77°29.58'W), Station C, 830 m (12°32.76'S 77°34.76'W) and Station D, 1210 m (12°40.31'S 77°38.49'W) (Fig. 1). Water column samples were collected for nitrate determination with a Niskin bottle rosette equipped with a Seabird CTD (1 drop per station). Bottom-water dissolved oxygen was measured with an oxygen sensor on the CTD and calibrated by Winkler titration of 3 replicates from rosette Niskin bottles. Sediments and sediment-dwelling faunas were sampled with a USNEL boxcorer (0.25 m<sup>2</sup>) and a multicorer (9.5 cm tube diameter) at Station A; the remaining stations were sampled only with the multicorer.

Samples were processed for subsequent analyses of porewater properties, macrofauna, metazoan meiofauna, foraminifera, grain size, sediment total organic carbon and nitrogen content, lipids, protein, carbohydrates, *Thioploca*, pigments, radiochemistry (<sup>210</sup>Pb, <sup>234</sup>Th), porosity, and other sediment measures. Ship-

board measurements included sediment redox and pH, x-radiography, Winkler titrations of bottom-water oxygen concentration, and some preliminary observations on benthic fauna.

### 2.1. 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  $2.65 \text{ g cm}^{-3}$  (quartz) and  $1.025 \text{ g cm}^{-3}$ , respectively (Buchanan, 1984). Sediment redox potential (Eh) and pH were measured at vertical intervals of 1 cm immediately after core collection with a portable Mettler Toledo pH-meter. 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. Surface sediment slices (0–1 cm) were kept deep-frozen at  $-20^\circ\text{C}$  until later analysis.

Total organic carbon and nitrogen were determined on freeze-dried, homogenized sediments, (after acidification with 1 N HCl to remove carbonates) in a Heraeus-CHN elemental analyser. Proteins (PRT) were determined photometrically by the Coomassie Blue reaction after incubation for 2 h at  $60^\circ\text{C}$  with NaOH 0.5 N (Boetius, Scheibe, Tselepidis & Thiel, 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), weighing the dry residue after complete evaporation of the solvent. Carbohydrate content in sediment was determined spectrophotometrically according to Taylor and Paterson (1998), with glucose as a reference. The biopolymeric (labile) fraction of sedimentary organic carbon (hereafter LOC), assumed to be potentially available to consumers, was defined as the sum of protein, carbohydrate and lipid carbon (Fabiano & Danovaro, 1994; Fabiano, Danovaro, & Frascchetti, 1995). Carbohydrates, proteins and lipids were converted into carbon equivalents using conversion factors of 0.40, 0.49 and 0.70, respectively (Fabiano et al., 1995). Chloroplastic pigment equivalents (CPE; sum of Chl *a* and phaeopigments), an estimate of the amount of organic matter derived from primary production, were measured photometrically according to Stal, Van Gamerden and Krumbein (1984).

### 2.2. Radiochemical analyses

To determine sedimentation rate, samples for  $^{210}\text{Pb}$  analyses were collected from a multicorer tube and a boxcore at 305 m, and from single multicorer tubes (9.5 cm diameter) at 562 m and 820 m. Cores were sectioned immediately after collection at 2 to 3 cm vertical intervals to depths of 18–40 cm and frozen at  $-20^\circ\text{C}$ . After thawing, samples were weighed and dried at  $60^\circ\text{C}$  to constant weight to determine porosity and bulk density. After homogenization,  $\sim 1.0 \text{ g}$  was used to determine total organic matter (TOM) (weight loss on ignition for 4 h at  $550^\circ\text{C}$ ).

The analysis of  $^{210}\text{Pb}$  was carried out by alpha spectrometry of its daughter  $^{210}\text{Po}$  according to Flynn (1968). Briefly, 0.5 g of dry sediment was digested in a Teflon beaker with a mixture of concentrated HCl,  $\text{HNO}_3$  and HF on a hot plate until dryness in the presence of  $^{209}\text{Po}$  yield tracer ( $2.22 \text{ dpm g}^{-1}$ ). After total dissolution, the samples were autoplated onto silver disks at  $\sim 75^\circ\text{C}$  for 2.5 h in the presence of ascorbic acid. The  $^{210}\text{Po}$  activity was counted in a CANBERRA QUAD alpha spectrometer (model 7404) for 24 to 48 h to achieve the desired counting statistics (4–10%  $1\sigma$  errors). The activity of  $^{210}\text{Po}$ , which is assumed to be in secular equilibrium with  $^{210}\text{Pb}$ , was calculated using the ratio between natural radionuclide and the tracer, multiplied by the activity of the tracer at the time of plating. The delay between plating and counting produces a decay of  $^{210}\text{Po}$  (half life: 138 days), and all data were corrected to the time of plating. The period between the collection date and the time of the analyses of the samples (six months) was compared to the half life of  $^{210}\text{Pb}$  (22.3 years). The calculated activities were corrected for this lag time.

Sedimentation rates were calculated from excess activities ( $^{210}\text{Pb}_{\text{xs}}$ ) according to the following equation (Turekian, Cochran, Benninger, & Aller, 1980):

$$A_z = A_0 e^{-\lambda/S * z};$$

where  $A_0$  and  $A_z$  are the activities in excess at surface and  $z$  depths, respectively,  $\lambda$  is a decay constant and  $S$  is the sedimentation rate.

The  $^{210}\text{Pb}_{\text{xs}}$  activities were estimated from the unsupported  $^{210}\text{Pb}$  data, using the constant rate of the supply model (CRS), originally applied to lake sediments (Appleby & Oldfield, 1978). This model assumes a constant rate of supply of  $^{210}\text{Pb}$ , which is unaffected by changes in sediment type or sedimentation rate and constant porosity. These assumptions for the study area are reasonable because sediment mixing frequently affects the upper 10 cm, but for some stations showing high sediment compaction, a modified model was used. This assumes an exponential bulk sediment density described by Christensen (1982). The  $^{210}\text{Pb}_{\text{xs}}$  was estimated from the unsupported  $^{210}\text{Pb}$ , which in turn was calculated from total  $^{210}\text{Pb}$  minus the asymptotic  $^{210}\text{Pb}$  activity at depth, assuming it to be in equilibrium with sediment  $^{226}\text{Ra}$  (Appleby & Oldfield, 1978; Binford & Brenner, 1986).

Excess  $^{234}\text{Th}$  profiles were used to estimate particle mixing in one core per station. Sediment slices from the top 15 cm were processed within 20 days of sampling. The samples were dried and the organic matter was removed by ignition before leaching with 8N HCl. A fraction of each leachate was spiked with an aliquot of known  $^{232}\text{U}/^{228}\text{Th}$  activity in order to calculate the chemical yield. Uranium and thorium species were separated through ionic exchange using a column of DOWEX 1  $\times$  8 100–200 resin as the solid phase and successive concentrated HCl and  $\text{HNO}_3$  solutions as mobile phases. Electrolytic solutions were prepared from the final eluants and were electroplated on stainless steel planchets (Aller & Cochran, 1976). Beta spectrometry was used to measure  $^{234}\text{Th}$  and alpha spectrometry was used to measure its parent  $^{238}\text{U}$ ,  $^{232}\text{U}$  and other thorium species. All  $^{234}\text{Th}$  activities were corrected for background radiation, chemical yield and for decay since the sampling date. Statistical errors include the propagation of specific counting errors and chemical yield calculations for both  $^{234}\text{Th}$  and  $^{238}\text{U}$ . Mixing rates were calculated as a volumetric process, using activities on a per volume basis (Mulsow, Boudreau, & Smith, 1998). Sedimentation was assumed to be zero, and flux of  $^{234}\text{Th}$  was assumed to be constant over the past 100 days. Bioturbation was modeled using the hierarchical approach of Soetaert, Herman, Middelburg, Heip, DeStigter et al. (1996), which allows estimation of both local and non-local mixing. Only the models with an  $R^2$  value above 0.60 were compared.

### 2.3. Protozoan meiofauna

Foraminifera were sampled from the top 1 cm of multicorer tubes. Samples were preserved in 4% buffered formalin, using procedures described in Rathburn and Corliss (1994) and were stained with rose Bengal ( $1\text{g L}^{-1}$ ) for at least one week before processing. One tube-core from each site was examined. Stained benthic foraminifera from the  $> 150\text{-}\mu\text{m}$  fraction of the 0–1 cm interval were sorted wet, placed on micropaleontological slides, identified, and counted. Because of the large amount of time required to process and pick stained foraminifera, station samples were not replicated. This methodology and data set are comparable to those of other foraminiferal studies of living assemblages. However, because of the lack of replication, we adopt the trends indicated by our foraminiferal data as hypotheses suitable for future testing.

### 2.4. Metazoan meiofauna

To sample metazoan meiofauna (defined here as metazoans that pass through a  $500\text{-}\mu\text{m}$  mesh sieve but are retained on a  $40\text{-}\mu\text{m}$  sieve (Giere, 1993), three to four replicate subcores, each from different multicorer drops, were taken by gently inserting a perspex tube of  $3.6\text{ cm}$  inner diameter ( $10\text{ cm}^2$ ) into the original cores. Sediment from the subcores was sectioned into five vertical fractions (0–1 cm, including some

overlying water; 1–2; 2–3; 3–5; and 5–10 cm depth). A 6% solution of magnesium chloride was added to each of these fractions, and after 20 min, 10% buffered formalin containing Rose Bengal ( $0.2 \text{ g L}^{-1}$ ) was added for fixation and staining. Meiofaunal taxa were sieved following the suspension-decantation method (Wieser, 1960) with a few modifications (Neira & Rackemann, 1996). The efficiency of this method has been documented by Murrell & Fleeger (1989). All meiofaunal animals were sorted into major taxa and counted under a stereo dissecting microscope.

## 2.5. Macrofauna

Macrofauna ( $> 300 \mu\text{m}$ ) were examined from one boxcore and two multicore drops at Station A (305 m), and from three multicore drops at each of three stations at other depths. We examined two  $9.6 \times 9.6 \text{ cm} \times 10 \text{ cm}$  deep subcores from the box core, and from each multicore drop we examined two tubes ( $9.5 \text{ cm diameter} \times 10 \text{ cm deep}$ ). Sediments were sectioned vertically at 0–1, 1–2, 2–5, and 5–10 cm intervals. The upper two fractions were preserved unsieved in 8% buffered formalin and the 2–5 cm fraction was sieved on a  $63\text{-}\mu\text{m}$  mesh in order to retain small organisms for other studies. The 5–10 cm fraction was sieved through a  $300\text{-}\mu\text{m}$  mesh. In the laboratory, all samples were stained with Rose Bengal and re-sieved with a  $300\text{-}\mu\text{m}$  mesh to separate the macrofauna. Invertebrates were sorted under a dissecting microscope, counted, weighed on an analytical balance, and identified to the lowest taxon possible, which in most cases was to putative species.

## 2.6. Filamentous bacteria (*Thioploca* spp.)

*Thioploca* spp. were examined in three multicore tubes (each from different drops) for each depth station (A–D). Subcores of 3.6 cm inner diameter ( $10 \text{ cm}^2$ ) were used. The biovolume of *Thioploca* trichomes was measured at 1-cm sections in the top 15 cm, according to Schulz, Jørgensen, Fossing and Ramsing (1996). The integrated biomass was calculated assuming a cytoplasm density of  $1 \text{ g cm}^{-3}$ .

## 2.7. Statistical methods

Analysis of variance and *a posteriori* Tukey's HSD tests were used to compare geochemical, sediment and faunal parameters across stations. Relationships between environmental variables (oxygen, organic matter) and faunal parameters were examined with simple linear regressions. Spatial differences in vertical distribution of metazoan meiofauna were assessed using a factorial ANOVA. Contrasts were performed using *a posteriori* Tukey's tests. The raw data were square root-square root transformed to correct for heteroscedasticity. In order to study the vertical distribution of macrofaunal density and biomass, the cumulative percentage of the pooled replicates with sediment depth at each station was calculated. Then all the medians were determined as well as the global median from all stations. Spatial changes were examined with G-tests comparing the percent density or percent biomass above or below the global median (Sokal & Rohlf, 1998), under the null hypothesis of independence of the vertical distribution with site location. Pairwise comparisons were done by the Fisher's exact independence test (Sokal & Rohlf, 1998). Macrofaunal diversity statistics (rarefaction,  $H'$ ,  $J'$ ) were calculated using Biodiversity Pro (MacAleece, Lambshead, Paterson, & Gage, 1997).

# 3. Results

## 3.1. Water column

The upper 100 m of the water column exhibited salinities  $> 35.30$ , temperatures  $> 21^\circ\text{C}$  and oxygen  $> 3 \text{ ml L}^{-1}$ . The oxycline was located between 110 and 150 m, with oxygen values around  $1.1 \text{ ml L}^{-1}$  at

the base of the layer. A weak subsurface peak of oxygen was located from 150 to 180 m, where salinity and temperature were 35.2 and 16°C, respectively (Fig. 2). The OMZ ( $< 0.5 \text{ ml L}^{-1}$ ) extended from 170–195 m to 600–700 m. The upper boundary was deepest at the shallower (inshore) stations. Within the OMZ (Stations A, B), nitrate increased with depth from 15 to 35  $\mu\text{M}$ , while salinity decreased with depth, from 35.02 to 34.55, and temperature from 15°C to 6.7°C. Below the OMZ, nitrate values remained very high ( $> 32 \mu\text{M}$ ), salinity was rather constant (34.55–34.60), temperature decreased to 3.5°C and oxygen increased to  $1.78 \text{ ml L}^{-1}$  at 1200 m depth. The lowest oxygen concentrations in bottom water were encountered at Station A (305 m), where minimum values were  $< 0.02 \text{ ml L}^{-1}$ ; below this station, oxygen concentration increased with depth (Table 1).

### 3.2. Bottom descriptions

Sediments at each station varied considerably in texture, composition and geochemical conditions; phosphorite crusts, nodules or pellets were present at all except the shallowest station (Table 1, Fig. 3). Sediments at 305 m (Station A) were typically soupy, dark olive-green muds. The upper 5–6 cm was fairly homogenized, as determined by x-radiography; below 6 cm, laminated sediments were evident to the bottom of the core at 13 cm (Fig. 3A). Large numbers of vertebrate teeth, fish scales and other skeletal parts were present. The sea floor at 562 m (Station B) was characterized by a discontinuous crust of well-cemented, irregular-shaped phosphorite nodules covered by a thin veneer ( $< 0.5 \text{ cm}$ ) of fine sediment. No laminae were present. In some cores, below the phosphorite crust, the upper 8–10 cm of sediment consisted of non-laminated, olive green mud. This sediment intermixed with filled-in burrows within a lighter colored sediment matrix of foraminiferal sand. In most of the cores the three facies (phosphorite nodules, foraminiferal sands and organic-rich muds) were distributed in patches downcore (Fig. 3B). The substrates at this site supported both hard- and soft-substrate organisms. Below the OMZ, Station C (830 m) had sediments formed of phosphoritic sand (pellets), foraminiferal sand and olive-green mud (Fig. 3C). Sediments of Station D (1210 m) contained phosphoritized pellets, recemented rip-up clasts, and olive-green mud. Sediments were bioturbated within the upper 8–9 cm (Fig. 3D). Many tubes and ophiuroids (6–8 cm diameter) were visible on the sediment surface.

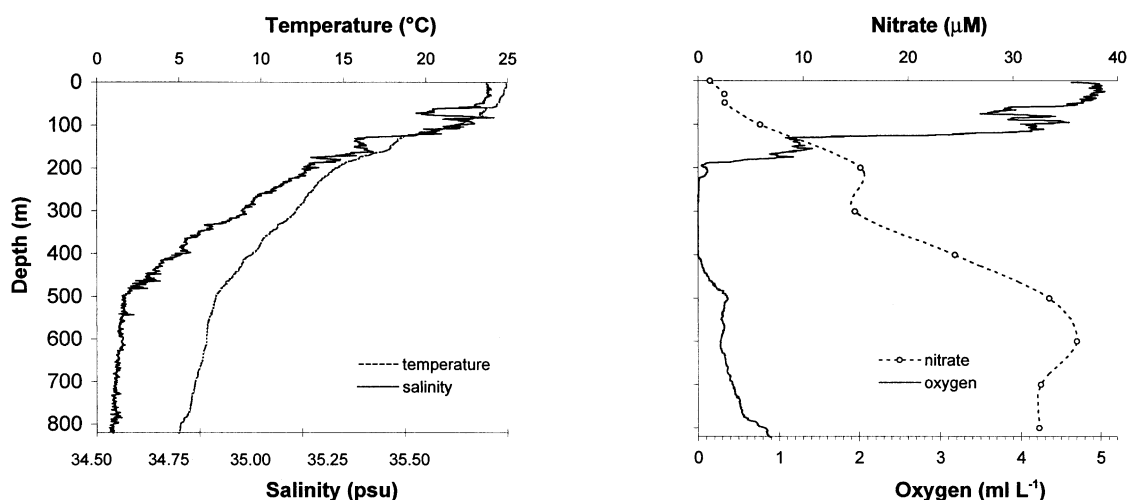


Fig. 2. Structure of the water column above the 830 m depth station; (a) Temperature ( $^{\circ}\text{C}$ ) and Salinity; (b) Nitrate ( $\mu\text{M}$ ) and Oxygen ( $\text{ml L}^{-1}$ ).



Table 1

Abiotic properties of benthic stations along a transect off Callao, Peru passing within (Station A & B) and beneath (Station C & D) the oxygen minimum zone. Sedimentary parameters are given for the top 0–1 cm of the sediment column: TOM, total organic matter; TOC, total organic carbon; C-PRT, proteins in carbon units; C-LIP, lipids in carbon units; C-CHO, carbohydrates in carbon units; LOC, labile organic carbon (sum of protein, lipid, and carbohydrate carbon); C/N, Carbon/Nitrogen ratio; CPE, chloroplastic pigment equivalents; Eh, redox potential. Values in parentheses represent the standard error of 2–3 replicates taken from within a single multicore tube

|   | STATION        |              |            |            |
|---|----------------|--------------|------------|------------|
|   | A              | B            | C          | D          |
| Depth (m)                                 | 305            | 562          | 827        | 1210       |
| Temperature (°C)                          | 10.2           | 7.1          | 5.2        | 3.5        |
| Salinity                                  | 34.73          | 34.56        | 34.55      | 34.59      |
| Bottom-water Oxygen (ml L <sup>-1</sup> ) | 0.02           | 0.26         | 0.84       | 1.78       |
| TOM (mg g <sup>-1</sup> )                 | 327            | 116          | 160        | 105        |
| TOC (mg g <sup>-1</sup> )                 | 169.0 (8.5)    | 49.5 (3.3)   | 83.0 (1.7) | 53.0 (3.9) |
| C-PRT (mg g <sup>-1</sup> )               | 18.3 (0.9)     | 2.9 (0.6)    | 8.0 (0.8)  | 4.9 (0.2)  |
| C-LIP (mg g <sup>-1</sup> )               | 15.9 (1.3)     | 2.6 (0.8)    | 2.8 (0.6)  | 2.7 (0.1)  |
| C-CHO (mg g <sup>-1</sup> )               | 2.7 (0.5)      | 0.5 (0.1)    | 0.5 (0.1)  | 0.5 (0.1)  |
| LOC (mg g <sup>-1</sup> )                 | 36.9 (2.6)     | 6.0 (1.5)    | 11.3 (1.5) | 8.0 (0.4)  |
| LOC/TOC (%)                               | 21.8 (2.6)     | 12.1 (1.7)   | 13.6 (1.7) | 15.1 (2.4) |
| C:N ratio                                 | 9.8 (0.1)      | 10.8 (0.3)   | 10.0 (0.1) | 10.3 (0.1) |
| CPE (µg g <sup>-1</sup> )                 | 99.4 (2.3)     | 11.2 (0.6)   | 23.3 (2.0) | 10.5 (0.9) |
| Eh (mV)                                   | 210            | 155          | 452        | 396        |
| Laminations                               | Present > 5 cm | Absent       | Absent     | Absent     |
| Phosphorites                              | Absent         | Crusts/Rocks | Pellets    | Pellets    |

### 3.3. Water content and redox conditions

Highest values of porosity and water content within the top 15 cm were observed at Station A (on average 0.95 and 0.83, respectively); values declined slightly with depth in the sediment. Station B exhibited the lowest porosity and water content (0.65 and 0.39, respectively). Although sulfide was not measured, only at Station A did the sediment smell of sulfide. Redox values at Stations A and B indicated sub-oxic conditions, ( $100 < Eh < 300$  mV; Graf, Schulz, Peinert, & Meyer-Reil, 1983; Jørgensen & Revsbech, 1989) (Table 1). The relatively high Eh values measured at Station A may reflect the presence of iron, manganese and nitrate (Froelich, Arthur, Burnett, Deakin, Hensley et al., 1988), possibly mixed and made available by the high densities of oligochaetes at this station (see below). In contrast, the upper 2 cm and 1 cm of Station C (830 m) and D (1210 m), respectively, were more oxidized and possibly contained free oxygen.

### 3.4. Content and quality of organic matter

Total organic carbon content of near surface sediments (0–1 cm) was two or three times greater at Station A (16.9%) than at the other stations (5.8%) (Table 1). In general, organic carbon and nitrogen content decreased with depth in the sediment at all stations except the shallowest where maximal organic carbon values of over 20% occurred at 10–12 cm (Levin et al., unpublished data); C:N ratios ranged from 9.8–10.8 (Table 1).

Labile biopolymeric carbon concentrations (LOC) in the upper cm (as the sum of protein, lipid and

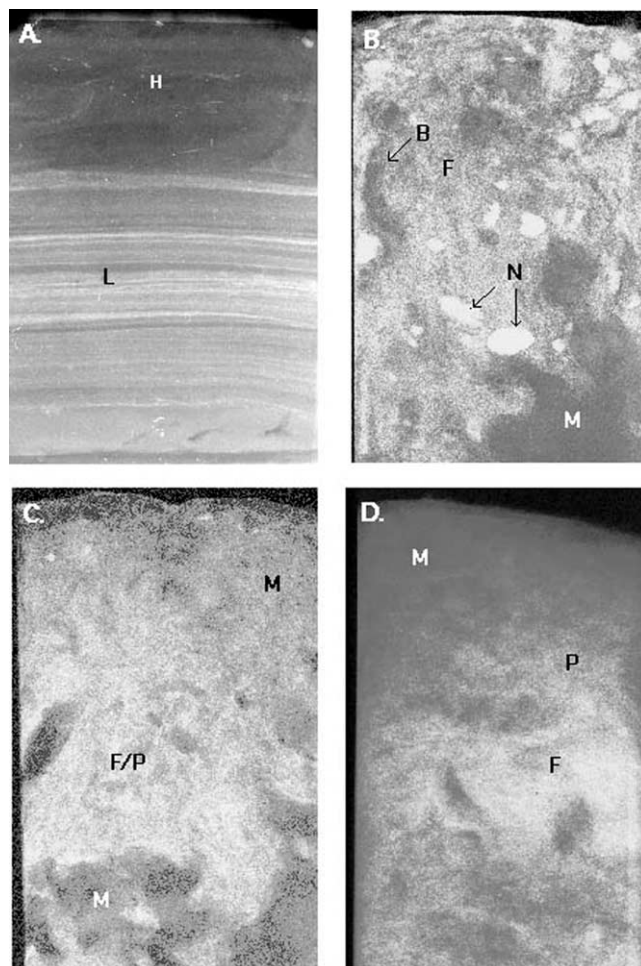


Fig. 3. X-radiographs of the sediment structure at (a) Station A, 305 m, (b) Station B, 562 m (c) Station C, 830 m and (d) Station D, 1210 m depth. Key features are shown: homogenized sediment (H), Laminations (L), burrows (B), phosphorite nodules (N), foraminiferal sand (F), olive-green mud (M), phosphorite sands (P).

carbohydrate carbon equivalents) ranged from  $36.9 \text{ mg g}^{-1}$  to  $6 \text{ mg g}^{-1}$ . Proteins dominated the biopolymeric carbon pool at all sites. In the topmost 1-cm layer, proteins on average accounted for 57.5% of LOC, followed by lipids (36.1%) and carbohydrates (6.2%) (Neira et al., 2001a). The nutritional quality of the sediment organic matter for benthic fauna is reflected in the proportion of specific labile compounds within the topmost 1 cm (Table 1). The biopolymeric carbon fraction (LOC) of the total organic carbon (LOC/TOC,%) was used as a measure of the fraction of the sediment organic carbon potentially available to benthic heterotrophs. This fraction was 1.5 to 1.8 times greater at station A than at the other stations. However, refractory material constituted the main fraction of the sedimentary organic carbon at all stations (Fig. 4, Table 1).

Chloroplasmic pigment equivalents in the top 1 cm were 5–10 times greater at Station A than at the other stations (Table 1). Sediment-bound pigments were mainly phaeopigments, which ranged from  $3.0$  to  $95.1 \text{ } \mu\text{g g}^{-1}$  DW. Chl a, a measure of fresh organic matter of photosynthetic origin, ranged from  $0.14$  to  $4.30 \text{ } \mu\text{g g}^{-1}$  DW, and represented less than 10% of the total pigment content. At Station A, Chl a concentration

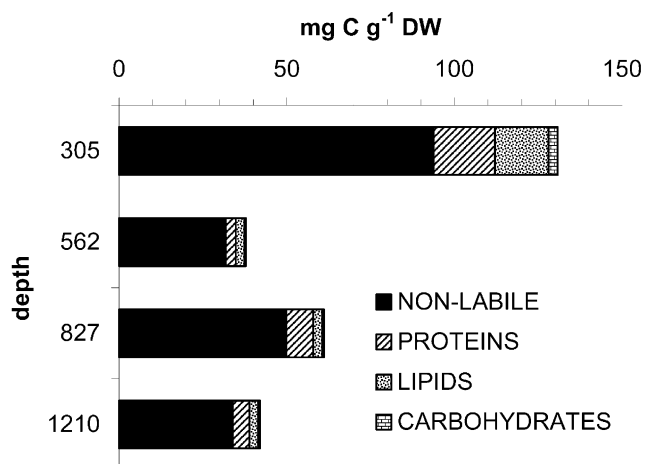


Fig. 4. Organic carbon content and its labile components at 4 stations on the Peru margin.

was greatest in the top 1 cm ( $4.30 \mu\text{g g}^{-1} \text{DW}$ ), and decreased to  $1\text{--}2 \mu\text{g g}^{-1}$  at 5–15 cm within the sediment column. Sediments at the deeper stations exhibited less than  $1 \mu\text{g g}^{-1}$  Chl a throughout the sediment column.

### 3.5. Sedimentation and bioturbation

Apparent sediment accumulation rates in the cores analyzed on the Peru margin ranged from  $0.10$  (Station C) to  $0.15 \text{ cm y}^{-1}$  (Station B) (Fig. 5). At Station A, the top  $^{210}\text{Pb}$  activity and the excess inventory (data not shown) in the boxcore sample were significantly lower than in the multicore tube, suggesting the loss of 2–3 cm of sediment surface. However sediment accumulation rates below the 8-cm mixed layer calculated from the multicore sample ( $0.13 \pm 0.01 \text{ cm y}^{-1}$ ) and from the boxcore ( $0.11 \pm 0.01 \text{ cm y}^{-1}$ ) did not differ significantly. The estimates accounted for 96–99% of the model variance; estimated profiles had an error of less than 4% from observed minus estimated values.

Within the OMZ, excess  $^{234}\text{Th}$  was present to depths of 1 cm (Station A) and 2 cm (Station B), excluding subsurface spikes. Excess  $^{234}\text{Th}$  was present down to 12 cm (Station C) and 8 cm (St. D) in the two cores collected beneath the OMZ. Bioturbation modeling was not possible for the boxcore sample from Station A. For the rest of the stations, the best fit to bioturbation models included diffusive (Station B) and diffusive + non-local processes (Station C and D) (Fig. 6). The biodiffusive mixing coefficients ( $D_b$ ) were 6–7 times higher at Station C ( $100 \text{ cm}^2\text{y}^{-1}$ ) and D ( $80 \text{ cm}^2\text{y}^{-1}$ ) than at Station B ( $14 \text{ cm}^2\text{y}^{-1}$ ).

### 3.6. *Thioploca* spp.

Large sulfide-oxidizing, nitrate-reducing bacteria *Thioploca* spp. (Gallardo, 1977; Henrichs & Farrington, 1984) were found only at Station A, in two of the three cores examined. *Thioploca* reached a trichome biomass of  $7.9$  and  $3.1 \text{ g m}^{-2}$  (wet weight) in the two cores. Most of the *Thioploca* trichomes were located 3–8 cm below the sediment-water interface (Fig. 7) and were not visible as mats on the surface.

### 3.7. Protozoan meiofauna

Density of benthic foraminifera in the 0–1 cm interval was 28–36 times higher in the core from Station A than at the other stations (Table 2). Proportions of agglutinated taxa in the 0–1 cm interval increased

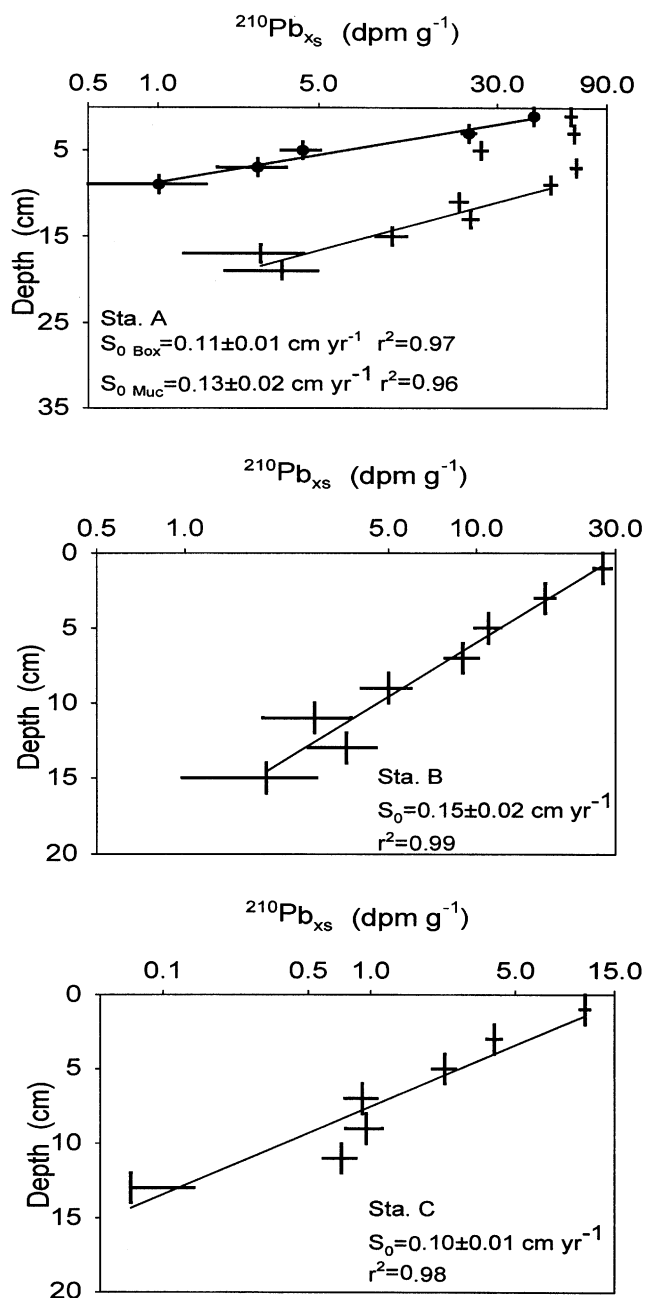


Fig. 5.  $^{210}\text{Pb}$  excess profiles in Peruvian slope sediments. The sedimentation rates were estimated according Turekian et al. (1980) and corrected by compaction (Christensen, 1982). The logarithmic scale shows the depth penetration of the excess and the similarity between the slopes, representative of the sedimentation rates.  $r^2$  is a measure of the goodness of fit of the models.  $S_0$  denotes apparent sedimentation rates, given that the models do not take into account bioturbation explicitly. Filled circles: boxcore (Station A).

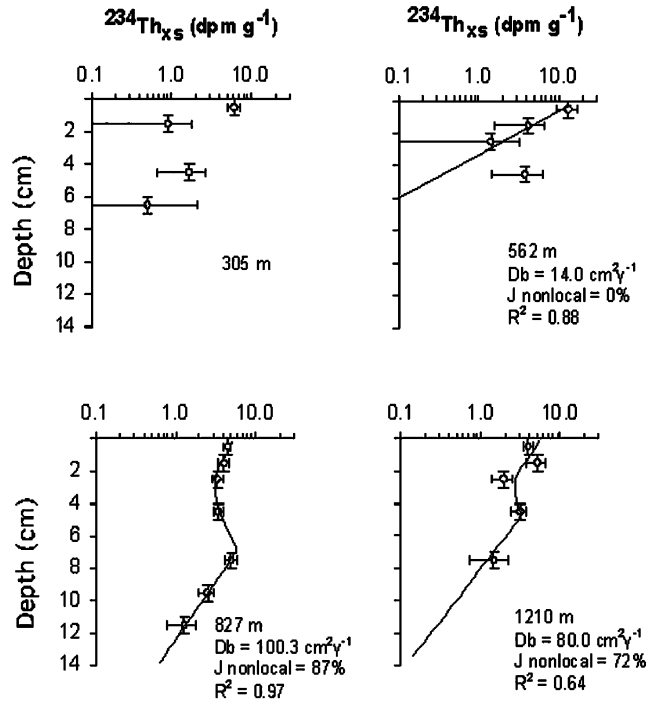


Fig. 6. Depth profiles of excess  $^{234}\text{Th}$ . The curves correspond to fitted bioturbation models (from Soetaert et al., 1996), corrected by bulk density: model '2' (diffusive only) at 562 m, and model '3' (including a nonlocal flux  $J$ ) at 827 m and at 1210 m. The percent of total flux explained by nonlocal injection is indicated as  $J_{\text{nonlocal}}$ .

with water depth, comprising 8.5% of the assemblage at Station A, and about 89% at Station D. Thus, the foraminiferal assemblage was dominated by calcareous foraminifera ( $29\ 820/50\ \text{cm}^3$ ) in the core from the shallowest station (Station A), while the core from the deepest station (Station D) was dominated by agglutinated taxa ( $818/50\ \text{cm}^3$ ).

### 3.8. Metazoan meiofauna

Detailed analyses of metazoan meiofaunal communities are given in Neira et al. (2001a), so the key features are only discussed briefly here. Total metazoan meiofaunal density (0–10 cm) was highest at Station A ( $1517 \pm 431\ \text{ind. } 10\ \text{cm}^{-2}$ ; mean  $\pm 1$  SE) and lowest at Station C ( $440 \pm 73\ \text{ind. } 10\ \text{cm}^{-2}$ ). Densities at Station A (305 m) were significantly higher than those at the three deeper sites ( $F_{3,10} = 4.54$ ,  $P = 0.029$ ). The densities of harpacticoid copepods and nauplii were positively correlated with bottom-water oxygen concentration (Pearson's  $r = 0.991$ ,  $P = 0.008$ ), but nematode densities were not (Pearson's  $r = 0.57$ ,  $P = 0.430$ ).

Overall, fifteen major meiofaunal taxa were found, with Nematoda dominant at all sites (Table 3). Station A was the least diverse, with only 7 higher taxa, whereas the deeper stations harbored 14–15 taxa. Nematoda comprised more than 99% (0–10 cm) of total metazoan meiofauna abundance at Station A. Downslope, their relative dominance decreased to less than 80%. Harpacticoid copepods and nauplii formed the next most abundant group. They were restricted to the top 1 cm and increased in percent representation with increasing water depth (Fig. 8). Other taxa that were relatively abundant in the upper cm of sediment at

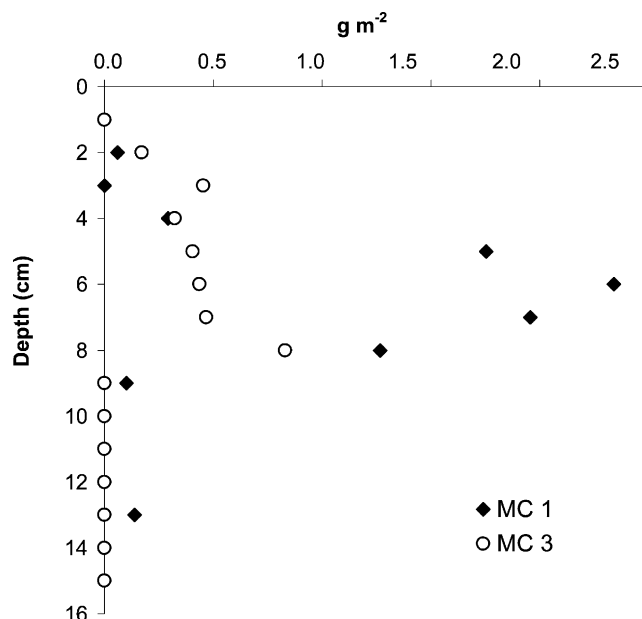


Fig. 7. Vertical distribution of the sulfide-oxidizing bacteria *Thioploca* spp. in terms of trichome biomass ( $\text{g m}^{-2}$ ), determined in two independent cores (MC1 and MC3) at 305 m depth.

Table 2  
Foraminifera ( $> 150 \mu\text{m}$ ) along the margin transect off Callao, Peru (Jan 1998). Data are for 0–1 cm sediment fractions

| Station                             |                | A (305m) | B (563 m) | C (831m) | D (1211m) |
|-------------------------------------|----------------|----------|-----------|----------|-----------|
| Density<br>(# 50 $\text{cm}^{-3}$ ) | Calcareous     | 29 820   | 1093      | 542      | 103       |
|                                     | Agglutinated   | 2783     | 133       | 314      | 818       |
|                                     | Total          | 32 603   | 1227      | 855      | 921       |
|                                     | Calc/agg ratio | 10.72    | 8.20      | 1.73     | 0.13      |
|                                     | % agglutinate  | 8.5      | 10.9      | 36.7     | 88.8      |
| Standing                            | Calcareous     | 29 043   | 926       | 497      | 96        |
| Stock<br>(# 50 $\text{cm}^{-2}$ )   | Agglutinated   | 2710     | 113       | 288      | 762       |
|                                     | Total          | 31 753   | 1034      | 785      | 858       |

the deeper stations were polychaetes, gastrotrichs, kinorhynchs, and ostracods (Fig. 8); together these comprised on average 6.6% of the total metazoan meiofauna at these stations.

The vertical distribution of metazoan meiofauna differed significantly between Station A and the downslope stations (factorial ANOVA  $F_{3,50} = 18.04$ ;  $P < 0.001$ ). At Sta. A metazoan meiofauna exhibited a subsurface density peak (2–5 cm), whereas densities declined consistently with depth in the sediment at the downslope stations (Fig. 9).

### 3.9. Macrofauna

Macrofaunal density ranged from  $16,233 \pm 4,440 \text{ ind. m}^{-2}$  (mean  $\pm 1$  SE) at Station A to  $8,493 \pm 1811$  at Station C (Table 4), but did not differ significantly among stations ( $F_{3,11} = 1.91$ ,  $P = 0.207$ ). Total macrofaunal biomass was over 7 times higher at Station D than at either Stations A or C (Table 4) ( $F_{3,15} = 5.92$ ;

Table 3  
Densities of meiofauna along the Peru margin (no. ind.10 cm<sup>-2</sup> ± 1 SE)

|              | Sta A (305 m)  | Sta B(562 m)  | Sta C (830 m) | Sta D (1210 m) |
|--------------|----------------|---------------|---------------|----------------|
| Nematoda     | 1506.5 ± 428.3 | 405.7 ± 200.9 | 375.3 ± 58.6  | 438.0 ± 47.2   |
| Copepoda     | –              | 6.7 ± 2.3     | 26.5 ± 6.2    | 43.0 ± 5.3     |
| Nauplii      | –              | 8.0 ± 4.6     | 12.0 ± 5.1    | 23.0 ± 7.6     |
| Tanaidacea   | 1.5 ± 0.9      | 1.7 ± 0.9     | 5.0 ± 1.1     | 20.0 ± 3.5     |
| Ostracoda    | 3.25 ± 1.8     | 4.7 ± 4.2     | 7.8 ± 2.6     | 5.0 ± 3.5      |
| Kinorhyncha  | –              | 11.7 ± 6.9    | 1.5 ± 0.9     | 3.7 ± 2.0      |
| Halacarida   | –              | 3.3 ± 0.7     | 2.0 ± 0.7     | 8.7 ± 3.5      |
| Rotifera     | 0.5 ± 0.3      | 9.3 ± 5.8     | –             | 0.7 ± 0.7      |
| Gastrotricha | 3.25 ± 1.3     | 1.3 ± 0.9     | 1.3 ± 0.5     | 0.7 ± 0.7      |
| Turbellaria  | –              | 0.3 ± 0.6     | 1.3 ± 0.7     | 0.3 ± 0.3      |
| Polychaeta   | 1.0 ± 0.4      | 1.0 ± 0.6     | 1.8 ± 0.8     | 1.7 ± 0.3      |
| Oligochaeta  | 1.0 ± 0.6      | 1.3 ± 0.7     | 2.0 ± 1.4     | –              |
| Priapulida   | –              | 0.7 ± 0.3     | 0.5 ± 0.5     | 2.7 ± 0.9      |
| Nemertina    | –              | 0.3 ± 0.3     | 2.5 ± 2.5     | 0.3 ± 0.3      |
| Bivalvia     | –              | –             | 0.5 ± 0.5     | 0.7 ± 0.7      |
| Tardigrada   | –              | –             | 0.3 ± 0.3     | –              |
| TOTAL        | 1517.0 ± 431.7 | 456.0 ± 216.4 | 440 ± 73.3    | 548 ± 67.6     |
| n            | 4              | 3             | 4             | 3              |
| No of Taxa   | 7              | 14            | 15            | 14             |

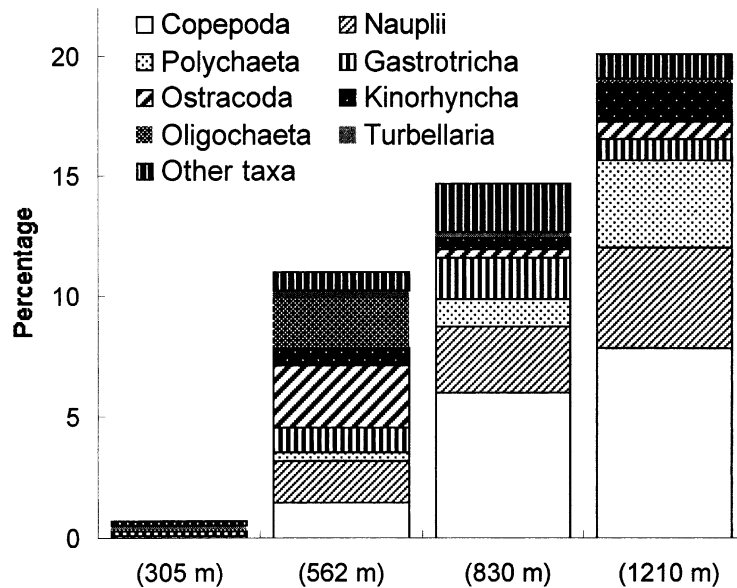


Fig. 8. Density of major meiofaunal taxa (> 40 µm) at 4 stations on the Peru margin. Nematodes were not included for clarity, but constitute the remaining portion of organisms at each station.

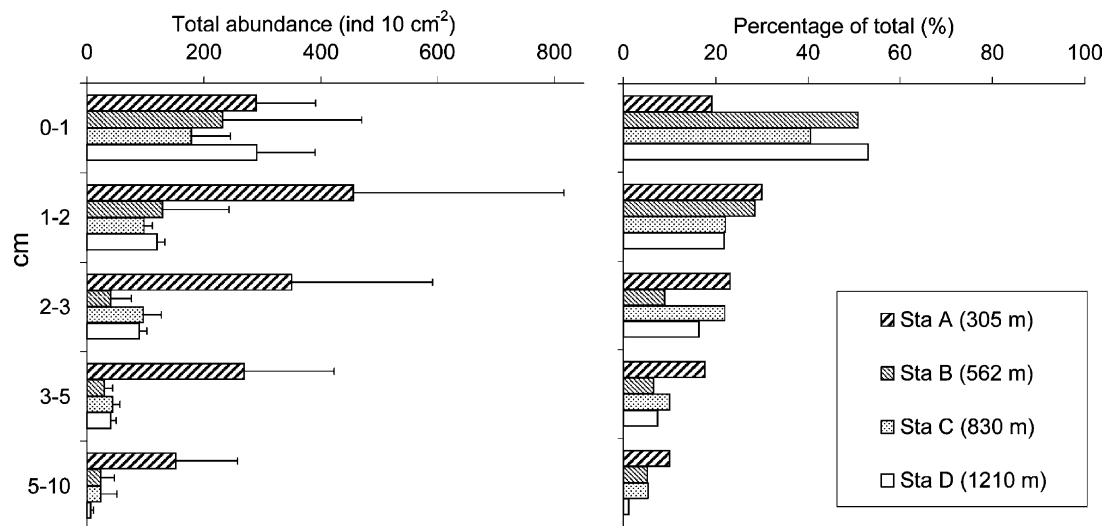


Fig. 9. Vertical distribution of the metazoan meiofauna (> 40 µm) within the sediment column at each of 4 depth stations on the Peru margin. Error bars correspond to 1 SE.

Table 4

Macrofaunal properties at stations within (A & B) and below (C & D) the oxygen minimum zone off Callao, Peru. (Jan. 1998)

| Station<br>Depth (m)                                   | A<br>305         | B<br>562       | C<br>827       | D<br>1210        |
|--|------------------|----------------|----------------|------------------|
| No. Macrofauna (no. ind. m <sup>-2</sup> )<br>(1 S.E.) | 16 233<br>(4440) | 9151<br>(816)  | 8493<br>(1811) | 11 762<br>(1493) |
| Macrofaunal biomass (g m <sup>-2</sup> )<br>(1 S.E.)   | 8.6<br>(3.0)     | 52.0<br>(21.0) | 8.5<br>(1.6)   | 65.4<br>(11.6)   |
| Body Size/Individual (mg)<br>(1 S.E.)                  | 0.5<br>(0.1)     | 5.5<br>(2.1)   | 1.2<br>(0.4)   | 5.7<br>(1.0)     |
| % of macrofauna in top 1 cm                            |                  |                |                |                  |
| by density   | 17.8             | 49.6           | 52.4           | 50.4             |
| by biomass   | 71.0             | 66.7           | 24.8           | 44.0             |
| Taxon Composition (%)                                  |                  |                |                |                  |
| Polychaeta   | 1                | 34             | 53             | 74               |
| Oligochaeta  | 85               | 16             | 2              | 1                |
| Crustacea  | 0                | 36             | 31             | 10               |
| Mollusca   | 2                | 5              | 2              | 4                |
| Echinodermata  | 0                | <1             | 4              | 2                |
| Other vermes   | 11               | 4              | 4              | 4                |
| Other taxa   | <1               | 4              | 1              | 5                |
| Diversity measures                                     |                  |                |                |                  |
| Rank 1 Dominance (%)                                   | 85               | 37             | 14             | 18               |
| H' (log <sub>2</sub> )                                 | 2.28             | 4.52           | 4.36           | 2.58             |
| J'   | 0.22             | 0.66           | 0.90           | 0.93             |
| E(S20)   | 2.38             | 7.33           | 14.13          | 14.69            |



$P = 0.020$ ). Biomass at Station B was highly variable and did not differ from any of the other stations. Average individual body size was 5 to 10 times greater at Station B and D than at Station A or C ( $F_{3, 15} = 5.62$ ;  $P = 0.023$ ). The largest organisms were amphipods at Station B and ophiuroids at Station D.

Species composition of macrofauna differed among stations. Annelids comprised over 50% of the macrofauna at all 4 stations (Table 4). However, the relative importance of oligochaetes and polychaetes exhibited opposite depth trends. The gutless, tubificid oligochaete, *Olavius crassitunicatus*, dominated the fauna at Station A (85%), but oligochaetes declined in importance with depth (Table 4). Other taxa present at Station A included the epifaunal gastropod *Astyris permodesta*, nemerteans, and sigambrid polychaetes. Polychaetes increased in proportion with depth, comprising 74% of the macrofauna at Station D (Table 4). Ampeliscid amphipods were dominant at Station B, and with annelids, comprised over 30% of the macrofauna at this site. The deeper stations had increased representation of tanaids and isopods. The importance of taxa with calcified body parts increased with increasing oxygen (and depth). Large ophiuroids were extremely abundant (one per 71 cm<sup>-2</sup> multicore tube = 140 ind. m<sup>-2</sup>) at Station D.

Significant differences in the vertical distribution of macrofauna within the sediment column were observed among the four stations ( $G = 37.2 > \chi^2_3$ ,  $P < 0.001$ ). The vertical distribution was similar at the 3 deepest stations, where ~50% of the animals were concentrated in the uppermost 1 cm. However, at Station A, >55% of the macrofauna (mainly oligochaetes) were found in the 2–5 cm fraction (Fig. 10) and only 18% occurred in the upper 1 cm. Thus, macrofauna at Station A had a significantly deeper vertical distribution than at the other stations ( $P < 0.05$ , Fisher's exact test). At all sites only a small fraction of the individuals (generally < 5%) occurred below 5 cm.

Macrofaunal species richness, evaluated by rarefaction, was lowest at Station A, intermediate at Station B, and similar at Stations C and D (Table 4). Evenness exhibited a similar trend. Dominance exhibited the reverse pattern, with exceptionally high (Rank 1) dominance (85%) at Station A (Table 4).

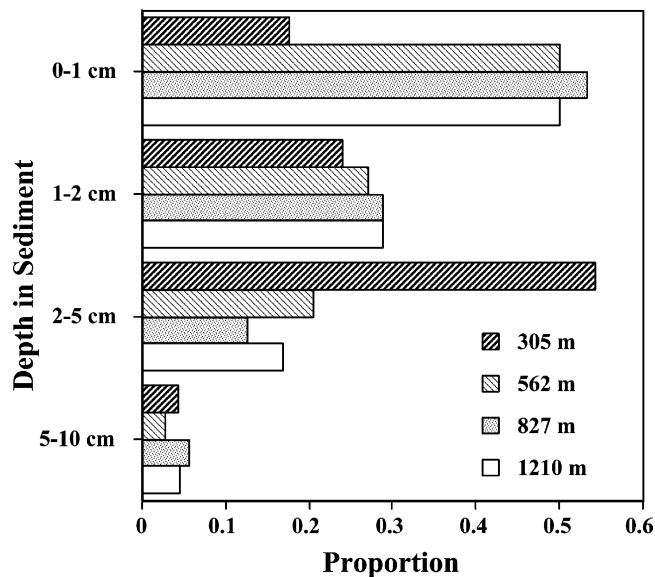


Fig. 10. Vertical distribution of the macrofauna (> 300 µm) within the sediment column at each of 4 depth stations on the Peru margin.

## 4. Discussion

### 4.1. Sediment characteristics

Previous studies off central Peru (Suess, 1981; DeVries & Percy, 1982; Reimers, 1982; Henrichs & Farrington, 1984; Froelich et al., 1988) have indicated that sediments associated with upwelling areas are typically organic-rich (up to 20% org C), rapidly accumulating muds. The sediment organic matter includes fish debris, fecal material, sheaths and diatom frustules (DeVries & Percy, 1982). The high porosities and water content in sediment recorded at 305 m appear to be typical characteristics of the upper slope muds from this region. This results from a dual macropore/micropore space system formed by organo-mineral aggregates associated with fecal material, sheath structures, and microporous siliceous tests and clay minerals (Reimers, 1982). At the deeper stations, the bottom was structurally heterogeneous as a result of the presence of phosphorite nodules. Biogenic structures such as sediment-mucus aggregates, fecal pellets, and macrofauna as well as agglutinating, arborescent foraminifera contributed to this heterogeneity.

The presence of living *Thioploca* spp. within the Peru OMZ has been reported previously (Rosenberg, Arntz, Chumán de Flores, Flores, Carbajal et al., 1983; Henrichs & Farrington, 1984; Arntz, Tarazona, Gallardo, Flores, & Salzwedel, 1991; Suits & Arthur, 2000). The deepest record was reported by Henrichs and Farrington (1984) at 506 m water depth, but only Arntz et al. (1991) gave biomass values (1–5 g m<sup>-2</sup> at 300–499 m depth). The values of trichome biomass reported here are not directly comparable, because the values of Arntz et al. (1991) include trichomes and sheaths. If a trichome: trichome + sheath conversion factor of ~3 is used (V. A. Gallardo et al., unpubl. data), the values we reported in this study become 5 to 10 times higher, but are still much lower than the maximal records for the eastern Pacific margin (1 kg m<sup>-2</sup>; Gallardo, 1977). In fact, thick mats have only been observed on shelf and uppermost slope sediments (< 300 m) (Arntz et al., 1991; Henrichs & Farrington, 1984; Suits & Arthur, 2000). The absence of this sulfide-oxidizing, nitrate-reducing bacterium at all but the 305-m station may result from the decreasing reactivity of the organic matter with increasing bottom depth (Table 1, Fig. 4).

Results indicate that part of the organic matter accumulating on the Peru slope has undergone preferential decomposition of nitrogenous organic compounds. C:N ratios at the sediment surface are similar to previous records at 250–1000 m depth, 15°S (9.2 to 10.1; Henrichs & Farrington, 1984). However, 2–3 times higher concentrations of TOC and 3–6 times higher concentrations of the main biochemical components were present at the 305-m site relative to the deeper stations. These values rank among the highest levels of organic carbon ever reported for the Peruvian slope (e.g., Henrichs, Farrington, & Lee, 1984; Froelich et al., 1988) and are comparable to a similar highly productive coastal system off Chile (Neira et al., 2001b). Sediment characteristics were related only in part to depth and oxygen since the lowest organic content and the poorest quality organic matter were found at Station B, within the OMZ (Table 1).

### 4.2. Sedimentation rates

Kim & Burnett (1988), using <sup>210</sup>Pb profiles and <sup>14</sup>C chronologies, reported a range of sedimentation rates between 0.028 and 0.18 cm yr<sup>-1</sup> for the Peruvian shelf and slope (10–15°S). Other authors have reported <sup>210</sup>Pb-sedimentation rates in the range of 0.03 to 0.9 cm yr<sup>-1</sup> for the same zone (Koide & Goldberg, 1982; DeMaster, 1981; Reimers & Suess, 1983; Henrichs & Farrington, 1984), but the values of Henrichs and Farrington (0.6–0.9 cm yr<sup>-1</sup>) may have been overestimated since they did not take into account bioturbation (Kim & Burnett, 1988). Off northern Chile (Mejillones Bay, 23°S), Ortlieb, Escribano, Follegai, Zuñiga, Kong et al. (2000) estimated average sedimentation rates from <sup>14</sup>C dating in the range of 0.02 to 0.04 cm yr<sup>-1</sup> for the last 2000 years, but with periods of enhanced sedimentation reaching 0.18 cm yr<sup>-1</sup>. Off central Chile, Salamanca (1993) estimated sedimentation rates from 0.1 to 0.2 cm yr<sup>-1</sup> for shelf sediments. In this study, the estimated sedimentation rates were rather similar for all the analyzed cores (Fig. 5),

which is surprising given the different sediment properties at each station. With the exception of the  $^{210}\text{Pb}$  profile from the multicore sample at Station A, none of the profiles exhibited an upper mixed layer, and sedimentation rates were estimated disregarding bioturbation effects. Nevertheless, most of the cores analyzed for excess  $^{234}\text{Th}$  showed clear evidence of bioturbation, especially those collected beneath the OMZ (Fig. 6). If the actual sedimentation rates are very low, the  $^{210}\text{Pb}$  downcore profiles may indicate mainly biomixing effects, and therefore the sedimentation rates may be overestimated, particularly at Station C. This would not be the case for Station A where the sedimentation rate calculation from the multicore profile ( $0.13\text{ cm y}^{-1}$ ) was based on points below the  $^{210}\text{Pb}$  mixed layer.

We note, however, that estimated  $^{210}\text{Pb}$ -sedimentation rates do not always reflect the sediment accumulation regime on the Peru slope (Kim & Burnett, 1988). Erosive processes, such as winnowing, and slumps are common along the Peru margin (Kim & Burnett, 1988; Froelich et al., 1988). At Station B, x-radiographs and field observations revealed a patchy vertical structure of the sediment column, with some phosphorite nodules present well below the sediment-water interface (Fig. 3). It is possible that the nodules may have formed elsewhere under a low and stable sedimentation regime and had then been transported to the 562-m station. The highest excess  $^{210}\text{Pb}$  inventory ( $164\text{ dpm cm}^{-2}$ , D. Gutiérrez & P. Muñoz, unpub. data) and the highest apparent sedimentation rates were recorded at Station B (Fig. 5). In contrast, this station had the lowest content and quality of organic matter in surface sediment (Table 1, Fig. 4). Therefore the particles reaching the seafloor appear to be composed of a greater amount of detrital particles and old, possibly reworked organic matter. The observed spatial trends of sediment and organic matter features across stations are consistent with the idea that the preservation and composition of organic matter within the Peruvian OMZ are more influenced by physical reworking (winnowing, resuspension, redeposition) than by the anoxic or oxic conditions during deposition at the sediment/water interface (Emeis, Whelan, & Tarafa, 1991). This physical reworking appears to be most intense near the lower OMZ boundary. Similar processes have been proposed to regulate organic matter preservation on the Oman margin (Pederson, Shimmield, & Price, 1992).

#### 4.3. Protozoan meiofauna

Although the foraminiferal results are based on a single core from each station, valuable insight can be gained and hypotheses can be generated by comparing these results with similar foraminiferal studies in other regions, particularly those that have examined the  $> 150\text{ }\mu\text{m}$  fraction separately. Calcareous assemblage densities in the 0–1 cm interval at 563 m ( $1093/50\text{ cm}^3$ ) and at 831 m ( $542/50\text{ cm}^3$ ) off Peru were higher than or similar to those of a 720-m site ( $311\text{ to }634/50\text{ cm}^3$ ) in the San Pedro Basin off California (Silva, Corliss, Rathburn, & Thunell, 1996). At 1211 m off Peru, calcareous assemblage densities ( $103/50\text{ cc}$ ) were comparable to those from similar depths at two sites along the California margin ( $58\text{--}126/50\text{ cm}$  and  $204\text{--}497/50\text{ cm}$ ) (Rathburn, Perez, & Lange, 2001) and the Sulu Sea ( $67/50\text{ cm}^3$ ) (Rathburn & Corliss, 1994). We expect that the density differences we observed between the shallow Peru station (Station A) and deeper stations would be greater still if the  $63\text{--}150\text{ }\mu\text{m}$  fraction had been considered, because foraminiferal assemblages found in low-oxygen, organic-rich environments typically have a smaller average test size than those in other environments (Sen Gupta & Machain-Castillo, 1993). Our results suggest that calcareous foraminiferal assemblages thrive under conditions of low oxygen and high organic loading and that agglutinated assemblages prevail under conditions of greater oxygenation. These observations are consistent with those of Gooday et al. (2000) in their examination of  $> 63\text{ }\mu\text{m}$  fraction foraminifera in the Arabian Sea and Gooday and Rathburn (1999) along the California margin. Given the high food availability and the low pH conditions associated with OMZs, it is not clear why agglutinated taxa fail to thrive in these settings. Our data support the hypothesis of Gooday et al. (2000) that, as a group the agglutinated taxa are much less tolerant of hypoxic conditions than their adaptive counterparts with calcareous tests.

#### 4.4. Metazoan meiofauna

Off the South American coast, nematodes and cirratulid polychaetes have been reported to be numerous in low oxygen areas (Frankenberg & Menzies, 1968; Rowe, 1971a, 1971b). The high dominance of nematodes within the OMZ may be related to their ability (1) to tolerate low oxygen conditions, (2) to take advantage of abundant food, (3) to flourish in the absence of most predators, and, (4) to tolerate highly fluid sediment, such as that of Station A (305 m). The enhanced nematode abundances found at Station A suggest that very low oxygen concentration has a positive effect on density, possibly as a result of reductions in predation pressure or enhanced preservation of organic matter. Nematode density was positively correlated with food availability and quality (Pearson's  $r = 0.79$ ,  $P < 0.001$ ) (Neira et al., 2001a). The finding of a new nematode species, *Glochinema bathyperuvensis* sp. n, living exclusively in the soupy, muddy surface sediments of the 305-m site (Station A), extended the range of known habitats for the family Epsilonematidae from sandy intertidal sediments to muddy slope sediments (Neira, Gad, Arroyo & Decraemer, 2001c). The occurrence in these sediments of representatives of Epsilonematidae, otherwise present only in sandy sediments (Lorenzen, 1973; Gourbault & Decraemer, 1996), was interpreted as effective adaptation to this habitat. Harpacticoid copepods are known to be highly sensitive to low oxygen and normally are restricted to the oxygenated upper sediment layers (Wells, 1988). The absence of these animals at Station A, as well as their increase with greater oxygenation (Pearson's  $r = 0.99$ ,  $P < 0.05$ ) (Fig. 8), suggests that oxygen limitation may control meiofauna composition at higher taxonomic levels within the OMZ (Station A, 305 m) (Neira et al., 2001a).

#### 4.5. Bioturbation and macrofauna

Although we cannot derive definitive information about bioturbation from the single core samples taken at each site, we can observe patterns that can be verified by future sampling. We were unable to calculate a bioturbation rate at Station A, but there was clear evidence of mixing in some of the samples. X-radiographs revealed a homogenous layer 6 cm deep (Fig. 3) and the multicore profile of  $^{210}\text{Pb}$  indicated an upper mixed layer of 8–10 cm (Fig. 5). The dominant macrofauna (gutless oligochaetes) inhabited relatively deep depths within this sediment (Fig. 10), possibly in order to gain access to the sulfide required by their symbiotic bacteria (Giere & Krieger, 2001). However, the boxcore  $^{210}\text{Pb}$  samples show no mixed layer (Fig. 5) and there was an excess of  $^{234}\text{Th}$  only at the top of the boxcore sample from this station (Fig. 6). We conclude that either some of the surficial sediment was lost during boxcore sampling or that bioturbation activity may have been patchy.

Typically bioturbation rates are found to be poorly correlated with macrofaunal parameters but are positively correlated with organic matter flux to the seabed (Smith, 1992; Wheatcroft & Martin, 1996; Smith et al., 2000). Bioturbation rates were higher in cores taken beneath the OMZ; nevertheless, neither macrofaunal density, nor biomass nor mean body size changed significantly across the OMZ (Table 4). Instead, TOC content of the surficial sediment and radionuclide profiles suggest that organic matter accumulation rates were lower beneath the OMZ (see above).

Wheatcroft, Jumars, Smith and Nowell (1990) suggested that biomixing may depend mainly on the presence of rare, large deposit-feeders, rather than on the abundant, small-sized individuals. Other authors have indicated that the community bioturbation potential may be related to the presence of specific lifestyles rather than to total biomass or vertical distribution. For example, the shallow mixed depths within the OMZ on the Oman slope coincided with high dominance of surface feeding, tube-dwelling spionid polychaetes in the genera *Prionospio* and *Paraprionospio* (Smith et al., 2000). During the 1997–98 El Niño, a central Chilean, spionid-dominated shelf assemblage was replaced with a mixed assemblage, having a higher relative abundance of large burrowing organisms and subducting deposit-feeders. This community change coincided with enhanced bioturbation rates (Gutiérrez et al., 2000). Among the three stations at which we

were able to estimate bioturbation, the 830-m station exhibited the highest bioturbation rate (Fig. 6). Maldanid polychaete densities were exceptionally high at this station (average = 426 ind. m<sup>-2</sup>). Maldanid polychaetes are known to act as both conveyor belt feeders, bringing subsurface sediments up to the surface (Wheatcroft et al., 1990) and as reverse conveyor belt feeders, rapidly subducting organic matter and inorganic particles from the surface to depths of 5–15 cm (Levin, Blair, DeMaster, Plaia, Fornes, Martin, & Thomas, 1997). Since most of the other macrofaunal taxa present at the 830-m station were small, except for some epifaunal ophiuroids, we hypothesize that the maldanids were responsible for the high mixing rate.

The Peru margin macrofauna differ from several other OMZ transect studies in exhibiting uniform densities over a broad range of depths, organic-matter, and bottom-water oxygen concentrations. Depression of macrofaunal densities has been observed at very low oxygen sites off Walvis Bay (Sanders, 1969), in the NW Arabian Sea (Levin et al., 2000), on a seamount off Mexico (Levin et al., 1991), and in the Santa Barbara Basin (Levin et al., unpublished data), but was not evident at our Station A off Peru (305 m). Our observations of exceptionally high dominance and low species richness within the core of the OMZ, however, were consistent with findings of other studies. Annelids dominated, as in the Arabian Sea OMZ (Levin et al., 2000), but off Peru these were gutless, symbiont-bearing phalloporinid oligochaetes (Giere & Krieger, 2001), rather than the spionids characteristic of the upper slope on the Oman margin. Ampeliscid amphipods (*Ampelisca* sp.) were abundant at Station B (562 m). This group was also common off Oman (700 m) (Levin et al., 2000) and in the Santa Barbara Basin (550 m) (Levin, unpublished data).

Although Station A exhibited exceptionally low macrofaunal diversity (Table 4), at Station B a surprisingly diverse fauna occurred, possibly reflecting the greater substrate heterogeneity. The phosphorite nodules provided hard-substrates for tunicates, limpets, chitons and polychaetes so that in the same cores they co-occurred with soft-sediment fauna. Indeed the diversity at Station B ranks high among global OMZ sites (Levin & Gage, 1998). Macrofauna of the deeper stations below the OMZ resembled that of other bathyal settings; key features were dominance by paraonid and maldanid polychaetes, and increasing representation of tanaid and isopod crustaceans.

#### 4.6. Overview and comparison of faunal patterns

Perhaps the most surprising result of this study is that all the faunal groups examined (agglutinated and calcareous foraminifera, metazoan meiofauna and macrofauna) exhibited their highest densities at Station A, where bottom-water oxygen concentration was lowest but where food availability, measured as labile organic carbon or chloroplastic equivalents (Table 1), was highest. These results might suggest that food rather than oxygen, controls infaunal densities. However, for at least one group (the macrofauna), the dominant taxon was a non-feeding, oligochaete that utilizes energy from sulfide-oxidizing, endosymbiotic bacteria (Giere & Krieger, 2001), and thus indirectly relies on high organic matter inputs (and sulfate reduction) to generate reduced compounds. Although we have no direct evidence that symbiont-bearing forms dominate the protozoan and metazoan meiofaunal assemblages off Peru, such symbioses are very prevalent in at least one other hypoxic basin, off California (Bernhard, Buck, Farmer & Browser, 2000). We hypothesize that chemoautotrophy may represent a significant trophic pathway for metazoans within OMZs and merits further examination.

The different taxonomic entities considered in this study exhibit many similarities and some differences in their response to environmental factors. For none of the meiofaunal or macrofaunal groups was total density correlated with bottom-water oxygen concentration ( $P > 0.05$ ). However taxonomic representation was clearly affected. Polychaete ( $r^2 = 0.87$ ;  $P = 0.065$ ), copepod ( $r^2 = 0.92$ ;  $P = 0.041$ ), and agglutinated foraminiferan representation ( $r^2 = 0.98$ ;  $P = 0.012$ ) were positively correlated with bottom-water oxygen concentration while nematode ( $r^2 = 0.82$ ;  $P = 0.097$ ) and calcareous foraminiferan percentage ( $r^2 = 0.98$ ;  $P = 0.012$ ) were negatively correlated. The protozoan and metazoan meiofaunal taxa exhibited positive correlations with food availability measured as labile organic carbon (metazoan meiofauna:  $r^2 = 0.96$ ;  $P$

= 0.020, total foraminifera:  $r^2 = 0.97$ ;  $P = 0.014$ , calcareous foraminifera:  $r^2 = 0.97$ ;  $P = 0.014$ ; agglutinated foraminifera:  $r^2 = 0.093$ ;  $P = 0.036$ ), but the macrofauna did not ( $P \gg 0.05$ ).

When we compare similarities among taxa in density variation across stations, we find total foraminiferan and metazoan meiofaunal densities to be tightly, positively correlated ( $r^2 = 0.99$ ;  $P = 0.005$ ). The relationship is positive but weaker between macrofauna densities and metazoan meiofauna ( $r^2 = 0.90$ ;  $P = 0.052$ ) or protozoan meiofauna ( $r^2 = 0.88$ ;  $P = 0.085$ ). Similarity of macrofaunal and meiofaunal responses to oxygen and food availability have been previously noted for the Oman margin (Gooday et al., 2000; Cook et al., 2000) and the North Carolina margin (Gooday, Hughes & Levin, 2001); in all cases organic input was thought to be a primary structuring agent. Cook et al. (2000) reported a particularly strong, positive correlation between polychaete and nematode densities on the Oman margin. Off Peru the percentage polychaetes among macrofauna and percent nematodes among meiofauna were strongly negatively correlated ( $r^2 = 0.99$ ;  $P = 0.007$ ).

#### 4.7. Hydrographic effects of the 1997–98 El Niño and possible benthic response

During non-El Niño years the OMZ ( $< 0.5 \text{ ml L}^{-1}$ ) lies between 50–100 m and 700 m depth off Callao (Zuta & Guillén, 1970). The shift observed in the January 1998 position of the OMZ was similar to that of the 1982–83 El Niño, when the upper boundary deepened to nearly 300 m (Guillén, Lostanau & Jacinto, 1985). According to the hydrographic measurements made in this study, three water masses were easily distinguishable following the classification of Wyrski (1963). The top 100 m of the water column was occupied by the saline Subtropical Surface Water (SSW) of high oxygen content ( $> 3 \text{ ml L}^{-1}$ ); the OMZ extension coincided with the Equatorial Subsurface Water (ESSW); and the Antarctic Intermediate Water (AIW) was present below 800 m depth.

Based on the water column structure and the temporal development of the 1997–98 El Niño (Ulloa, Escribano, Hormazábal, Quiñones, Gonzalez and Ramoset al., 2001), we hypothesize that the oxygen increase in the bottom water at the 305-m station was probably a recent event, limited in duration to a few weeks and that maximum values reached no more than  $0.05 \text{ ml L}^{-1}$ . Our current knowledge of El Niño oceanographic effects on the southeast Pacific (Strub, Mesías, Montecino, Rutllant & Salinas, 1996) indicates that a significant increase of oxygen levels at deeper waters in the OMZ could not have occurred. However, a reduction in the input of fresh organic carbon is expected to have occurred at all stations, given the lowering of productivity in the surface waters reported during past El Niños (Barber & Chávez, 1983, 1986; Tarazona, Arntz & Canahuire, 1996). Reduced carbon flux should have consequences for the standing stock of benthos, for survival and establishment of certain species, taxonomic groups and lifestyles, and for their vertical distribution and bioturbation activities (Gutiérrez et al., 2000; Neira et al., 2001b). It may also increase bottom-water oxygen concentrations and sediment redox potential. These hypotheses can only be tested by sampling at comparable stations within the Peruvian OMZ during non El Niño and subsequent El Niño conditions.

## 5. Conclusions

1. Sediments of the Peru slope are highly heterogeneous; authigenic precipitation of phosphorites as well as lateral transport, bioturbation and erosive processes are dominant processes superceding effects of depth (pelagic sedimentation) or bottom-water oxygenation on sediment properties.
2. Low oxygen concentrations do not appear to result in a reduction in faunal standing stock. Rather, metazoan and protozoan meiofaunal densities were both highly correlated with availability of labile organic carbon. All size-categories of fauna exhibited maximal densities (and for macrofauna, reduced diversity) at the station where bottom-water oxygen concentrations were lowest but the sediments had

the greatest labile organic matter content. There was general coherence of densities across stations among the macrofauna, metazoan meiofauna and foraminifera.

3. Calcareous foraminifera, nematodes, and oligochaetes were the dominant forms under low-oxygen conditions; nematode and calcareous foraminiferan representation in the community was negatively correlated with bottom-water oxygen concentration. Representation of polychaetes, copepods and agglutinated foraminifera exhibited positive correlations with oxygen availability.
4. El Niño influence on the Peru margin OMZ is expected to take the form of mild oxygenation of the upper slope (300 m) and reduced input of labile organic matter to all stations. Further sampling, particularly during non-El Niño conditions, is required to substantiate these effects and their biotic consequences.

## Acknowledgements

We thank the captain and crew of the R/V *Melville*, Panorama Expedition Leg 3A. Shipboard technical assistance was provided by R. Wilson. Assistance at sea was provided by J. Crooks, D. Fields, L. Quipuzcoa, L. Romero, A. Shankle, A. Soto, and F. Velazco. Ship time support was provided by the University of California Ship Funds. Research and logistical support was provided by NSF Grant OCE 98–03861 to L. Levin and the project FONDAP-Humboldt for Oceanography and Marine Biology (Chile). Travel expenses for D. Gutiérrez and J. Sellanes were provided by DAAD. P. Muñoz, as well as other researchers that participated in the expedition, received support from the Graduate School of the University of Concepción. G. Sánchez (IMARPE) provided valuable information about the development of the 1997–98 El Niño off Callao. Assistance with macrofaunal processing and identifications were provided by J. Hillman, S. Kalyra, and C. Martin. C. Erséus provided help with oligochaete identification and background. We thank T. Höpner (ICBM, Univ. Oldenburg) for support and laboratory facilities and two anonymous reviewers for helpful critique of the manuscript.

## References

- Aller, R., & Cochran, K. (1976).  $^{234}\text{Th}/^{238}\text{U}$  disequilibrium in near shore sediment particle reworking and diagenetic time scales. *Earth and Planetary Science Letters*, 29, 37–50.
- Anderson, R. Y., & Gardner, J. V. (1989). Variability of the late Pleistocene–early Holocene oxygen minimum zone off Northern California. In D. H. Peterson (Ed.), *Aspects of climate variability in the Pacific and the Western Americas*, vol. 55 (pp. 75–84). Washington, DC: American Geophysical Union: Geophysical Monographs.
- Appleby, P. G., & Oldfield, F. (1978). The calculation of lead-210 dates assuming a constant rate of supply of unsupported  $^{210}\text{Pb}$  to the sediment. *Catena*, 5, 1–8.
- 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 R. V. Tyson, & T. H. Pearson (Eds.), *Modern and ancient continental shelf anoxia*, No. 58 (pp. 31–154). Tulsa, Oklahoma: Geological Society Special Publication.
- Arntz, W. & Fahrback, Y.E. (1996). El Niño: experimento climático de la naturaleza. Causas físicas y efectos biológicos. *Fondo de Cultura Económica, México*, D.F.
- Barber, R. T., & Chávez, F. P. (1983). Biological consequences of El Niño. *Science*, 222, 1203–1210.
- Barber, R. T., & Chávez, F. P. (1986). Ocean variability in relation to living resources during the 1982–83 El Niño. *Nature, London*, 319, 279–285.
- Behl, R. J., & Kennett, J. P. (1996). Brief interstadial events in the Santa Barbara Basin, NE Pacific, during the past kyr. *Nature, London*, 379, 243–246.
- Bernhard, J. M., Buck, K. R., Farmer, K. R., & Browser, S. S. (2000). The Santa Barbara Basin is a symbiosis oasis. *Nature, London*, 403, 77–80.
- Binford, M. W., & Brenner, M. (1986). Dilution of  $^{210}\text{Pb}$  by organic sedimentation in lakes of different trophic states, and application to studies of sediment-water interactions. *Limnology and Oceanography*, 31, 584–595.

- Boetius, A., Scheibe, S., Tselepidis, A., & Thiel, H. (1996). Microbial biomass and activities in deep-sea sediments of the Eastern Mediterranean: trenches are benthic hotspots. *Deep-Sea Research I*, 43, 1439–1460.
- Buchanan, J. B. (1984). Sediment analysis. In N. A. Holme, & A. D. McIntyre (Eds.), *Methods for the study of marine benthos* (2nd ed) (pp. 41–65). Oxford London: Blackwell Scientific Publications.
- Christensen, E. R. (1982). A model for radionuclides in sediments influenced by mixing and compaction. *Journal of Geophysical Research*, 87, 566–572.
- Cook, A. A., Lamshead, P. J., Hawkins, L. E., Mitchell, N., & Levin, L. (2000). Nematode abundance at the oxygen minimum zone in the Arabian Sea. *Deep-Sea Research II*, 47, 75–85.
- Cowie, G. L., Calvert, S. E., Pedersen, T. F., Schulz, H., & von Rad, U. (1999). Organic content and preservational controls in surficial shelf and slope sediments from the Arabian Sea (Pakistan margin). *Marine Geology*, 161, 23–38.
- DeMaster, D. J. (1981). The supply and accumulation of silica in the marine environment. *Geochimica and Cosmochimica Acta*, 45, 1715–1732.
- 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 I*, 29, 87–109.
- Emeis, K. -C., Whelan, J. K., & Tarafa, M. (1991). Sedimentary and geochemical expressions of oxic and anoxic conditions on the Peru shelf. In R. V. Tyson, & T. H. Pearson (Eds.), *Modern and ancient continental shelf anoxia*, No. 58 (pp. 155–170). Tulsa, Oklahoma: Geological Society Special Publication.
- 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., & Frascchetti, 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.
- Flynn, W. W. (1968). The determination of low levels of  $^{210}\text{Po}$  in environmental materials. *Analytica Chimica Acta*, 43, 221–227.
- Frankenberg, D., & Menzies, R. J. (1968). Some quantitative analysis of deep sea benthos off Peru. *Deep-Sea Research I*, 15, 623–626.
- Froelich, P. N., Arthur, M. A., Burnett, W. C., Deakin, M., Hensley, V., Jahnke, R., Kaul, L., Kim, K., Roe, K., Soutar, A., & Vathakanon, C. (1988). Early diagenesis of organic matter in Peru continental margin sediments: phosphorite precipitation. *Marine Geology*, 80, 309–343.
- Gallardo, V. A. (1977). Large benthic microbial communities in sulfide biota under Peru-Chile subsurface countercurrent. *Nature, London*, 268, 331–332.
- Guillén, O., Lostanau, N. & Jacinto, M. (1985). Características del Fenómeno El Niño 1982–83. In W. Arntz, A. Landa & J. Tarazona. *El Niño y su impacto en la fauna marina. Inst. Mar Perú—Callao (Boletín Extraordinario)*, 11–21.
- Giere, O. (1993). Meiobenthology. In *The microscopic fauna in aquatic sediments*. Springer-Verlag: Berlin.
- Giere, O., & Krieger, J. (2001). A triple bacterial endosymbiosis in a gutless oligochaete (Annelida). Ultrastructural and immunocytochemical evidence. *Invertebrate Biology*, 120, 41–49.
- Gooday, A. J., & Rathburn, A. E. (1999). Temporal dynamics in deep-sea benthic foraminifera. *Earth Sciences Review*, 46, 187–212.
- 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*, 57, 25–54.
- Gooday, A. J., Hughes, A. J., & Levin, L. A. (2001). The protozoan macrofauna (foraminifers and xenophyophores) from three North Carolina (USA) slope sites with contrasting carbon flux, and a comparison with the metazoan macrofauna. *Deep-Sea Research I*, 48, 1709–1739.
- Gourbault, N., & Decraemer, W. (1996). Marine nematodes of the family Epsilonematidae: a synthesis with phylogenetic relationships. *Nematologica*, 42, 133–158.
- Graf, G., Schulz, R., Peinert, R., & Meyer-Reil, L. -A. (1983). Benthic response to sedimentation events during autumn to spring at a shallow-water station in the Western Kiel Bight. I. Analysis of processes on a community level. *Marine Biology*, 77, 235–246.
- Greiser, N., & Faubel, A. (1988). Biotic factors. In R. P. Higgins, & H. Thiel (Eds.), *Introduction to the study of meiofauna* (pp. 79–114). Washington, D.C. London: Smithsonian Institution Press.
- 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 bottoms off central Chile, during the 1997–98 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.
- Henrichs, S. M., Farrington, J., & Lee, C. (1984). Peru upwelling region sediments near 15°S. 2. Dissolved free and total hydrolyzable amino acids. *Limnology and Oceanography*, 29, 20–34.
- Huyer, A., Smith, R. L., & Paluszkiwicz, T. (1987). Coastal upwelling off Peru during normal and El Niño times, 1981–1984. *Journal of Geophysical Research*, 92, 14297–14307.
- Jørgensen, B. B., & Revsbech, N. P. (1989). Oxygen uptake, bacterial distribution, and carbon-nitrogen-sulfur cycling in sediments from the Baltic Sea–North Sea transition. *Ophelia*, 31, 29–49.



- Kamykowski, D., & Zentara, S. J. (1990). Hypoxia in the world ocean as recorded in the historical data set. *Deep-Sea Research I*, 37, 1861–1874.
- Kim, K. H., & Burnett, W. (1988). Accumulation and biological mixing of Peru margin sediments. *Marine Geology*, 80, 181–194.
- Koide, M., & Goldberg, E. D. (1982). Transuranic nuclides in two coastal marine sediments off Peru. *Earth & Planetary Science Letters*, 57, 263–277.
- Lamont, P. A., & Gage, J. D. (2000). Morphological responses of macrobenthic polychaetes to low oxygen on the Oman continental slope, NW Arabian Sea. *Deep-Sea Research II*, 47, 9–24.
- 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.
- Levin, L. A., Plaia, G. R., & Huggett, C. L. (1994). The influence of natural organic enhancement on life histories and community structure of bathyal polychaetes. In C. M. Young, & K. J. Eckelbarger (Eds.), *Reproduction, larval biology, and recruitment of the deep-sea benthos* (pp. 261–283). New York: Columbia University Press.
- Levin, L. A., Blair, N., DeMaster, D. J., Plaia, G., Fornes, W., Martin, C., & Thomas, C. (1997). Rapid subduction of organic matter by malmanid polychaetes on the North Carolina slope. *Journal of Marine Research*, 55, 595–611.
- Levin, L. A., & Gage, J. D. (1998). Relationships between oxygen, organic matter and the diversity of bathyal macrofauna. *Deep-Sea Research I*, 45, 129–163.
- Levin, L. A., Gage, J. D., Martin, C., & Lamont, P. A. (2000). Macrobenthic community structure within and beneath the oxygen minimum zone, NW Arabian Sea. *Deep-Sea Research II*, 47, 189–226.
- Lorenzen, S. (1973). Die Familie Epsilonematidae (Nematodes). *Mikrofauna des Meeresboden*, 25, 1–86.
- McAleece, N., Lamshead, P.J.D., Paterson, G.L.J. & Gage, J.D. (1997). BioDiversity Professional, copyright Natural History Museum, London and Scottish Association for Marine Sciences, Oban. [Beta Version].
- McPhaden, M. J. (1999). Genesis and evolution of the 1997–98 El Niño. *Science*, 283, 950–954.
- Morales, C., Hormazábal, S., & Blanco, J. (1999). Interannual variability in the mesoscale distribution of the depth of the upper boundary of the oxygen minimum layer off Northern Chile (18–24°S): implications for pelagic system and biogeochemical cycling. *Journal of Marine Research*, 57, 909–932.
- Mullins, H. T., Thompson, J. B., McDougall, K., & Vercoutere, T. L. (1985). Oxygen-minimum zone edge effects, evidence from the central California coastal upwelling system. *Geology*, 13, 491–494.
- Murrel, M. C., & Fleeger, J. W. (1989). Meiofauna abundance on the Gulf of Mexico continental shelf affected by hypoxia. *Continental Shelf Research*, 9, 1049–1062.
- Mulrow, S., Boudreau, B., & Smith, J. (1998). Bioturbation and porosity gradients. *Limnology and Oceanography*, 43, 1–9.
- 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., Levin, L. A., & Arntz, W. E. (2001a). Meiofaunal distributions on the Peru margin: relationship to oxygen and organic matter availability. *Deep-Sea Research 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 1997–98 El Niño. *Oceanologica Acta*, 24, 313–328.
- 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. *Contributions to Zoology*, 70, 147–159.
- Ortlieb, L., Escribano, R., Follegati, R., Zuñiga, O., Kong, I., Rodríguez, L., Valdes, J., Guzman, N., & Iratchet, P. (2000). Recording of ocean-climate changes during the last 2000 years in a hypoxic marine environment off Northern Chile. *Revista Chilena de Historia Natural*, 73, 221–242.
- Pederson, T. F., Shimmield, G. B., & Price, N. B. (1992). Lack of enhanced preservation of organic matter in sediments under the oxygen minimum on the Oman margin. *Geochimica Cosmochimica Acta*, 56, 454–551.
- Rathburn, A. E., Perez, M. E., & Lange, C. E. (2001). Benthic–pelagic coupling in the southern California Bight: relationships between sinking organic material, diatoms and benthic foraminifera. *Marine Micropaleontology*, 43, 261–271.
- Rathburn, A. E., & Corliss, B. H. (1994). The ecology of deep-sea benthic foraminifera from the Sulu Sea. *Paleoceanography*, 9, 87–150.
- 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.
- Reimers, C. E., & Suess, E. (1983). Spatial and temporal patterns of organic matter accumulation on the Peru continental margin. In J. Thiede, & E. Suess (Eds.), *Coastal Upwelling: Its sediment record. Part B: Sedimentary records of ancient coastal upwelling* (pp. 311–346). New York: Plenum.
- Rhoads, D. C., & Morse, J. W. (1971). Evolutionary and ecologic significance of oxygen-deficient marine basins. *Lethaia*, 4, 413–428.
- Rhoads, D. C., Mulrow, S. G., Gutschick, R., Baldwin, C. T., & Stolz, J. F. (1991). The dysaerobic zone revisited: A magnetic facies? In R. V. Tyson, & T. H. Pearson (Eds.), *Modern and ancient continental shelf anoxia*, No. 58 (pp. 187–199). Tulsa, Oklahoma: Geological Society Special Publication.

- Robles, F., Alarcón, E., & Ulloa, A. (1976). Water masses in the northern Chilean zone and their variations in the cold period (1967) and warm periods (1969, 1971–1973). *FAO Fisheries Report*, 185, 94–196.
- Rosenberg, R., Arntz, W., 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 J. D. Costlow (Ed.), *Fertility of the sea*, vol. 2 (pp. 441–454). New York: Gordon and Breach Science.
- Salamanca, M.A. (1993). *Sources and sinks of <sup>210</sup>Pb in Concepcion Bay, Chile*. Ph.D. thesis. MSRC- SUNY, USA.
- Sánchez, G., Calienes, R., & Zuta, S. (2000). The 1997–98 El Niño and its effects on the coastal marine ecosystem off Peru. *CalCOFI Report*, 41, 62–86.
- Sanders, H. L. (1969). Benthic marine diversity and stability-time hypothesis. In Brookhaven Symposium. *Diversity and Stability in Ecological Systems*, 22, 71–81.
- Savrdá, C., & Bottjer, D. (1991). Oxygen-related biofacies in marine strata: an overview and update. In R. V. Tyson, & T. H. Pearson (Eds.), *Modern and ancient continental shelf anoxia*, No. 58 (pp. 201–220). Tulsa, Oklahoma: Geological Society Special Publication.
- Schulz, H., Jørgensen, B. B., Fossing, H., & Ramsing, R. (1996). Community structure of filamentous, sheath-building sulfur bacteria, *Thioploca* spp., off the coast of Chile. *Applied Environmental Microbiology*, 62, 1855–1862.
- Sen Gupta, B. K., & Machain-Castillo, M. L. (1993). Benthic foraminifera in oxygen-poor habitats. *Marine Micropaleontology*, 20, 183–201.
- Silva, K. A., Corliss, B. H., Rathburn, A. E., & Thunell, R. C. (1996). Temporal variation in benthic foraminifera in the San Pedro Basin (California Borderland). *Journal of Foraminifera Research*, 26, 71–93.
- Smith, C. R. (1992). Factors controlling bioturbation in deep-sea sediments and their relation to models of carbon diagenesis. In G. T. Rowe, & V. Pariente (Eds.), *Deep-sea food chains and the global carbon cycle* (pp. 375–393). Boston: Kluwer.
- 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.
- Sokal, R., & Rohlf, F. J. (1998). *Biometry. The principles and practice in biological research* (3rd ed). New York: W.H. Freeman & Co.
- Soetaert, K., Herman, P., Middelburg, J., Heip, C., DeStigter, H., Van Weering, T., Epping, E., & Helder, W. (1996). Modeling <sup>210</sup>Pb-derived mixing activity in ocean margin sediments: diffusive versus nonlocal mixing. *Journal of Marine Research*, 54, 1207–1227.
- Stal, L. J., Van Gamerden, H., & Krumbein, W. E. (1984). The simultaneous assay of chlorophyll and bacteriochlorophyll in natural microbial communities. *Journal of Microbiological Methods*, 2, 295–306.
- Strub, T., Mesías, J., Montecino, V., Rutllant, J., & Salinas, S. (1998). Coastal ocean circulation off western South America. In A. Robinson, & K. Brink (Eds.), *The Sea*, vol. 11 (pp. 29–67). New York: John Wiley and Sons, Inc.
- Suits, N., & Arthur, M. (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.
- Suess, E. (1981). Phosphate regeneration from sediments of the Peru continental margin by dissolution of fish debris. *Geochimica and Cosmochimica Acta*, 45, 577–588.
- 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.
- Tarazona, J., Arntz, W. E., & Canahuire, E. (1996). Impact of two ‘El Niño’ events of different intensity on the hypoxic soft bottom macrobenthos off the central Peruvian coast. *Marine Ecology*, 17, 425–446.
- Taylor, I. S., & Paterson, D. M. (1998). Microspatial variation in carbohydrate concentrations with depth in the upper millimetres of intertidal cohesive sediments. *Estuarine Coastal Shelf Science*, 46, 359–370.
- Turekian, K., Cochran, K., Benninger, L., & Aller, R. (1980). The sources and sinks of nuclides in Long Island Sound. *Advances in Geophysics*, 22, 129–163.
- Tyson, R. V., & Pearson, T. H. (1991). Modern and ancient continental shelf anoxia: an overview. In R. V. Tyson, & T. H. Pearson (Eds.), *Modern and ancient continental shelf anoxia*, No. 58 (pp. 1–24). Tulsa, Oklahoma: Geological Society Special Publication.
- Ulloa, O., Escribano, R., Hormazábal, S., Quiñones, R., Gonzalez, R., & Ramos, M. (2001). Evolution and biological effects of the 1997–98 El Niño in the upwelling ecosystem of northern Chile. *Geophysical Research Letters*, 28, 1591–1594.
- Walsh, J. J. (1981). A carbon budget for overfishing off Peru. *Nature, London*, 290, 300–304.
- Wells, J. B. J. (1988). Copepoda. In R. P. Higgins, & H. Thiel (Eds.), *Introduction to the study of meiofauna* (pp. 380–388). Washington, D.C. London: Smithsonian Institution Press.
- Wheatcroft, R. A., Jumars, P. A., Smith, C. R., & Nowell, A. R. M. (1990). A mechanistic view of the particulate bioturbation coefficient: step lengths, rest periods and transport directions. *Journal Marine Research*, 48, 177–207.

- Wheatcroft, R. A., & Martin, W. (1996). Spatial variation in short term ( $^{234}\text{Th}$ ) sediment bioturbation intensity along an organic-carbon gradient. *Journal Marine Research*, 54, 763–792.
- Wieser, W. (1960). Benthic studies in Buzzards Bay. II. The meiofauna. *Limnology and Oceanography*, 5, 121–137.
- Wishner, K., Levin, L. A., Gowing, M., & Mullineaux, L. (1990). Involvement of the oxygen minimum in the benthic zonation on a deep seamount. *Nature, London*, 346, 57–59.
- Wyrski, K. (1963). The horizontal and vertical field of motion in the Peru current. *Bulletin of Scripps Institution of Oceanography*, 8, 313–346.
- 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 B. Zeitzschel (Ed.), *The biology of the Indian Ocean* (pp. 18–36). Berlin: Springer-Verlag.
- Zuta, S., & Guillén, O. (1970). Oceanografía de las aguas costeras del Perú. *Boletín Instituto del Mar de Perú*, 2, 41–62.