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ENSO as a natural experiment to understand environmental control of meiofaunal community structure

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Abstract

The sediments of the Bay of Concepción and the adjacent shelf underlie one of the most productive upwelling areas in the SE Pacific margin. Reports on factors controlling meiofaunal community structure in these kinds of organic-rich and oxygen-deficient habitats are scarce in the literature. In this study, five sites along a transect from the mid-Bay of Concepción (27 m) to the outer shelf (120 m) were studied on fives dates (May, August, November 1997, and March and May 1998) in order to assess the dynamic relationships between sedimentary organic matter and metazoan meiofauna. The sampling period coincided with the 1997–1998 El Niño event. Sediment parameters investigated were the redox potential discontinuity depth, photosynthetic pigment concentrations (chlorophyll *a* and phaeopigments), organic carbon, nitrogen, total lipids, carbohydrates, and proteins. In general, lowest values of meiofauna abundance and biomass were found within the naturally eutrophic Bay of Concepción and towards the shelf break, while maximum values occurred at intermediate depths. During the whole period, the meiofaunal abundance was negatively correlated with the concentration of most of the biochemical components of organic matter, as well as with the sediment phaeopigment content. However, positive correlations were found with chlorophyll *a* derived indices and with bottom-water oxygen content. Most of the sediment parameters displayed a seasonal cycle, but towards the beginning of 1998, an effect of the 1997–1998 El Niño was evident. Typical austral-summer (*i.e.* oxygen-deficient) conditions did not develop, and sedimentary parameters reflected a decreased input of phytodetritus. Along the transect, the magnitude of this effect on meiofauna varied among sites. An overall positive response, in terms of meiofaunal abundance was observed, probably due to the amelioration of low oxygen conditions in the sediment.

Problem

The mechanisms controlling abundance and biomass of meiofauna in marine sub-littoral systems are still poorly known. The structure of a meiobenthic community is the product of an intricate network of abiotic factors, which interact with biotic factors like food availability, intra- and interspecific interactions and predation (Giere 1993). In spite of this inherent complexity, the temporal variation of meiobenthic communities in coastal systems might be quite predictable in relation to seasonal variation of primary production (*i.e.* food availability) and environmental conditions (*e.g.* temperature and oxygen) (Coull 1988; Giere 1993; Olafsson & Elmgren 1997). Nevertheless, there are stochastic or incidental factors that may alter the expected normal seasonal cycle of animal populations. In coastal systems of the SE Pacific, the ENSO-cycle (El Niño Southern Oscillation), related to the variability of the oceanographic conditions, and in particular its unpredictable warm phase 'El Niño', can profoundly alter environmental conditions and hence benthic communities (Gallardo 1985; Arntz *et al.* 1991; Tarazona *et al.* 1996). Main environmental alterations associated with El Niño that have been reported off Peru and Chile are (i) the deepening of the upper boundary of the oxygen minimum zone (OMZ), effectively oxygenating the shelf waters; (ii) the intrusion of warmer and nutrient-depleted waters that cover the shelf; and (iii) the occurrence of low rates of pelagic primary production and consequently reduced phytodetrital fluxes to the sediments (Arntz *et al.* 1991; Gutiérrez *et al.* 2000; Neira *et al.* 2001b; Levin *et al.* 2002).

Most studies on the benthic communities of the Chilean shelf deal with macro- (Carrasco & Arcos 1980; Gallardo 1985; Gallardo *et al.* 1995; Gutiérrez *et al.* 2000) and megabenthos (Gallardo *et al.* 1996b). Only recently have surveys been carried out on meiobenthos, including their relationships with other faunal components (*i.e.* filamentous bacteria and macrofauna) and with environmental factors such as food availability and oxygen (Neira *et al.* 2001c). Part of this work reports also on the effect of the 1997–1998 El Niño on meiofaunal community structure, but based on sampling off Concepción on just two dates (austral falls of 1997 and 1998). More recently, the role of the meiobenthos on the energy flux through the benthos was assessed, based in three samplings dates during the 1997–1998 period (Sellanes *et al.* 2003).

The present study complements and expands these previous observations, reporting relationships between metazoan meiobenthos and sediment environmental conditions (oxygen, sediment physico-chemical conditions and sedimentary organic matter) in the Bay of Concepción and in the adjacent shelf from the onset to the end of the 1997–1998 El Niño event.

The 1997–1998 warm event provided a 'natural' experiment, which allowed us to examine meiofaunal response to temporal changes in the sediment organic matter, bottom-water oxygen regime and redox conditions at several sampling sites located at different depths. The aim of this study was thus to identify which environmental factors might be controlling meiofaunal community structure and its spatial and temporal distribution. We hypothesize that during non-El Niño conditions, low oxygen would control the meiofauna abundance and biomass while during El Niño conditions organic matter quality would become more important for meiofauna. This hypothesis is based on the observation that when continental margins are intercepted by OMZs, strong gradients of bottom-water oxygen concentration and organic-matter input are formed (Levin *et al.* 1991). These gradients influence the biogeochemical properties of sediments and the structure and distribution of benthic fauna (reviewed by Levin 2003). Neira *et al.* (2001b) reported a strong positive correlation between nematode abundance and organic matter (both in term of quantity and quality) in the Peru margin during the most intense part of the 1997–1998 El Niño, while oxygen exhibited a positive correlation with harpacticoid copepods and their nauplii, masking the influence of food availability.

Study area

This study is part of a multidisciplinary project whose aim is to study the spatial space-temporal variations of benthic communities (including the mat-forming bacteria *Thioploca*, meio- and macrofauna) and their response to changing environmental conditions. Methodological details concerning *Thioploca*, and macrofauna, and sediment biogeochemical processes are reported elsewhere (see Gutiérrez *et al.* 2000; Muñoz *et al.* 2004).

Five sites located along a transect between the mid-bay of Concepción and the shelf-break were sampled in May, August and November 1997, March and May 1998 (Table 1). The sampling period coincided with the strong El Niño 1997–1998 event (McPhaden 1999). All sampling was conducted on board the R/V Kay Kay (University of Concepción) and samples for hydrographic, sediment and meiofaunal analyses were collected at each station (Fig. 1). The stations were categorized as mid-bay (27 m), bay mouth (34 m), inner shelf (64 m), mid-shelf (88 m) and outer shelf (120 m).

Hydrographic conditions during the study period are reviewed in detail elsewhere (Gutiérrez *et al.* 2000; Sellanes 2002; Muñoz *et al.* 2004), but are summarized briefly here. Surface temperature along the transect ranged from 13.2 ° to 17.6 °C with the highest average values in November 1997 (15.3 ± 2.1 °C; mean ± SD). Average bottom water nitrate concentrations were in general $<10\ \mu\text{mol}\cdot\text{L}^{-1}$ at the mid-bay site while at the shelf,

Table 1. Location of the sampling sites, depth and dates of the seasonal cruises carried out during 1997 and 1998.

location	station	depth (m)	1997 May	1997 August	1997 November	1998 March	1998 May/June
mid-bay	MB	27	22	22	13	14	28
bay mouth	BM	34	22	22	13	14	28
inner shelf	IS	64	20	24	19	10	26
mid-shelf	MS	88	24	26	21	12	01
outer shelf	OS	120	26	26	16	17	03

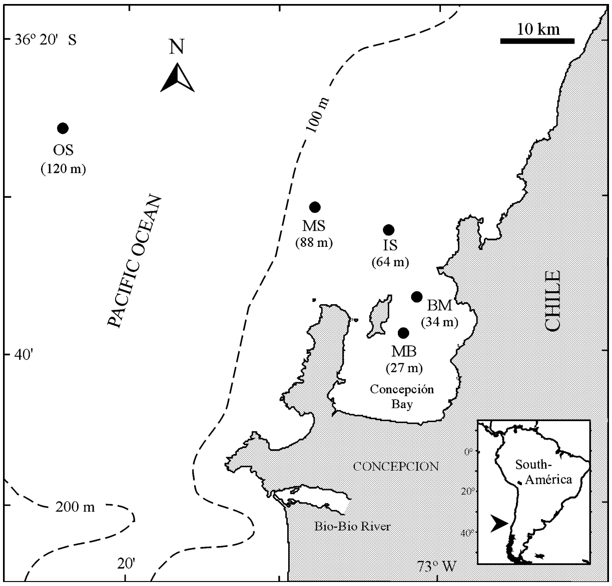

Fig. 1. Study sites on the continental margin off Concepción Bay, central Chile: MB, mid-Bay; BM, bay mouth; IS, inner shelf; MS, mid-shelf; OS, outer shelf.

nitrate concentrations were over 20 μmol·l^{-1} (Muñoz *et al.* 2004). All this indicated a deepening of waters with characteristics typical of Sub-surface Equatorial Waters (SSEW) during El Niño. SSEW are the main source of upwelling waters at this latitude (Ahumada 1989).

Material and methods

Bottom-water dissolved oxygen and sedimentary settings

Bottom-water samples were taken using Niskin bottles and dissolved oxygen was measured in three replicates by a modified Winkler method (Williams & Jerkinson 1982) using a DOSIMAT for titration and a photoelectric cell for end point detection.

Sediments, sampled with a mini-multiple-corer (Barnett *et al.* 1984), were analysed (top 1 cm) at each site and date for chlorophyll *a* (Chl *a*) and phaeopigments content (Phaeop), total organic carbon (TOC) and total nitrogen (TN). Only undisturbed cores with clear overlying water were processed. Pigments from freeze-dried sediment samples were analysed spectrophotometrically according to Stal *et al.* (1984). The sum of Chl *a* and phaeopigment is reported as the chloroplastic pigment equivalent (CPE). TOC and TN were determined on freeze-dried, homogenized sediment using a Heraeus TMT CHN-O-Rapid elemental analyser. Prior to analysis, carbonates were removed with 1 N HCl.

Chlorophyll *a* is a good indicator of 'fresh' material derived from primary production. To assess the contribution, in terms of carbon, of this 'fresh' organic matter source for consumers, a C/Chl *a* value of 42.5 was used (Bernal *et al.* 1989). Then, ratios of carbon Chl *a* to TOC content (Chl *a*: TOC; in μg Chl *a*·mg^{-1} C) were calculated. The contribution of Chl *a* to the CPE (% Chl *a* CPE) was also estimated.

The biochemical composition of sedimentary organic matter, in terms of proteins (PRT), lipids (LIP) and carbohydrates (CHO), was assessed according to the methods of Hartree (1972), modified by Rice (1982); Greiser & Faubel (1988) and Taylor & Paterson (1998), respectively. Proteins, lipids, and carbohydrates were converted into carbon equivalents using conversion factors of 0.49, 0.70, and 0.40, respectively, and the sum of the three components was assumed to be the labile fraction of the total organic carbon (LC) (Fabiano *et al.* 1995).

Pore water dissolved sulphide was extracted from 1- and 2-cm sediment slices (down to 15 cm) under a N_2 atmosphere, using a pneumatic squeezer. Sulphide was determined colorimetrically at 670 nm using the methylene blue technique (Cline 1969). Sulphide inventory values were expressed as the total amount integrated for the upper 15 cm of the sediment and corrected for porosity. Sediment redox potential was measured at vertical intervals of 1 cm immediately after core collection using a platinum standard combination electrode with a calomel internal reference (Mettler Toledo). Redox potential discontinuity depth (RPD) was the depth at which the transition from positive to negative values occurred.

Meiofauna

At each site, three sub-samples from independent multicore drops were taken using Plexiglas liners (10 cm^2) for the analysis of meiofauna. In the laboratory, the upper 15 cm of each core was kept in buffered 10% formalin. Sieving (40–500 μm) was performed according to the resuspension–decantation methodology (Wieser 1960). The efficiency of extraction was checked by inspection of the residual sediment. Preservation was done in 10% buffered formalin stained with Rose Bengal; sorting was done under a low-power stereo-microscope. All metazoan meiofaunal animals were sorted to major taxon and counted under a stereo dissecting microscope. The body volume of nematodes was derived from measurements of body length and width using the Andrassy formula (Andrassy 1956):

$$V = \frac{LW^2}{16 \times 10^5}$$

where V is the volume in nanolitres, L the length, and W the maximum width (L and W expressed in μm). For other taxa, the body volume was estimated as described by Feller & Warwick (1988), using basically the same formula:

$$V = LW^2C$$

where V is also in nanoliters, L and W in mm and C is an approximate conversion factor for each taxon (*e.g.* 400 for pyriform copepods). Dry weight values were estimated to be 25% of the wet weight (Jensen 1984).

Data analysis

Spatial and temporal changes, both in total abundance and in biomass of major metazoan meiofaunal groups, were evaluated by a two-way Analysis of Variance (ANOVA; $\alpha = 0.05$). Sampling sites were taken as fixed factors, and months as random factors. The raw data were square-root transformed and the homoscedasticity (Bartlett's test), as well as the normality of residuals was checked (Zar 1974). When significant differences were observed, contrasts were performed by *a posteriori* Tukey's HSD tests (Zar 1974).

To estimate which environmental factors play a key role in structuring the meiofaunal community, relationships between abiotic factors and the fauna were assessed using uni- and multivariate methods. Spearman rank-correlations between surface sediment parameters and abundance for each major taxonomic level were performed.

In order to identify suites of environmental variables that best explain the meiofaunal structure, the relationships between multivariate community structure and environmental data were analysed by the BIOENV procedure (Clarke & Ainsworth 1993) included in the PRIMER statistical package (Carr 1996). This procedure compares iteratively the biotic and abiotic similarity matrices and identifies the sub-group of environmental variables that has a higher weighted Spearman rank-correlation (ρ_w) between both. Biotic similarity matrices were constructed using the Bray–Curtis similarity index (Bray & Curtis 1957) on fourth root transformed abundance data of major groups (Nematoda, Copepoda and their Nauplii, Polychaeta and others). For the environmental data matrix, Euclidean distance over log-transformed data was used (Clarke & Ainsworth 1993). The significance of the weighted Spearman correlation between the abiotic distance matrix, identified by the BIOENV procedure, and the faunistic similarity matrix was estimated by the permutation procedure RELATE (Clarke & Warwick 1994). To corroborate that the environmental variables identified by these analyses explain the multivariate faunal structure, sites were also ordered by non-metric multidimensional scaling (NMDS; Clarke & Warwick 1994) according to their biotic and abiotic characteristics. NMDS ordination was performed over similarity matrices of biotic and abiotic variables. Grouping of sites with similar biotic or environmental characteristics was performed by the Unweighted Pair-Group Method using Arithmetic averages (UPGMA; Sneath & Sokal 1973). Model fits and statistical analysis were performed with Sigmaplot 6.10 (SPSS Inc.), Statistica 5.1 (Statsoft Inc.) and Primer 5.1.2. (Primer-E Ltd) software.

Results

Bottom water oxygen and sediment characteristics

Bottom water dissolved oxygen was relatively high for this area (≥ 0.19 ml·l^{-1}) during the study period and no events of anoxia were observed in summer 1998 (Table 2).

In general, all investigated sediment parameters, except for sulphide inventories, Chl *a* and RPD, showed a trend with the highest values at the mid-bay and outer shelf sites and the lowest values at the inner shelf site (Table 2). As an example, TOC ranged from 25.3 to 55.5 mg·g^{-1} from the inner shelf to the outer shelf site, respectively. On the other hand, the C/N ratio highest values were in general observed at the inner shelf site.

Sulphide inventories were fairly low at the bay mouth and shelf sites with a slight decreasing trend towards the outer shelf. The mid-bay site showed very high levels of sulphide in May 1997 (192.4 mmol·m^{-2}), reflecting typical non-El Niño summer conditions, decreasing drastically (over one order of magnitude) during the course of El Niño (11.4 mmol·m^{-2} in May 1998). The Chl *a* content showed the same decreasing trend, both temporal and bathymetric, with values ranging from 20.3 μg·g^{-1} at the mid-bay in May 1997 to 0.9 μg·g^{-1} at the outer shelf in May 1998 (Table 2). The RPD tended to deepen towards the shelf sites (up to 12 cm). At the mid-bay, surface sediment, otherwise permanently reduced (Gallardo 1985), showed oxidized conditions during 1998 at the uppermost layer (Table 2).

Meiofauna

Total abundance of major meiofaunal groups and total meiofauna biomass are reported in Table 2. Spatial and temporal variation of total meiofauna abundances during the study period are shown in Fig. 2.

A total of 16 higher meiofaunal taxa were identified (nematodes, copepods + nauplii, polychaetes, ostracods, halacarids, gastrotrichs, turbellarians, oligochaetes, rotifers, kinorhynchs, tardigrades, amphipods, cumaceans, gastropods, and bivalves). The meiofaunal community was dominated by nematodes, which comprised >95% of total meiofauna at all sampling sites. Polychaetes and cope-

Table 2. Mean values of bottom water dissolved oxygen, sediment parameters and faunal abundance and biomass at the five sites sampled off Concepción during El Niño 1997–1998.

		May 1997					August 1997					November 1997					March 1998					May 1998				
parameters	units	MB	BM	IS	MS	OS	MB	BM	IS	MS	OS	MB	BM	IS	MS	OS	MB	BM	IS	MS	OS	MB	BM	IS	MS	OS
bottom water																										
dissolved oxygen	$ml\cdot l^{-1}$	3.62	5.20	5.05	0.28	0.19	4.17	4.50	3.69	0.84	1.21	2.16	3.18	2.02	0.52	0.88	0.28	1.56	1.00	0.31	0.46	4.06	5.00	2.66	1.11	1.39
sediment																										
Chl *a*	$\mu g\cdot g^{-1}$ DW	20.3	2.6	1.6	3.5	1.7	2.7	2.8	1.3	1.4	1.3	3.7	3.4	1.2	2.0	2.0	17.4	5.2	1.1	2.3	1.4	5.7	2.9	1.7	1.7	0.9
phaeopigments	$\mu g\cdot g^{-1}$ DW	134.3	57.9	50.5	147.7	68.3	51.0	44.6	33.7	59.0	89.4	42.6	28.8	21.7	50.0	52.4	74.7	34.4	21.7	58.8	56.3	64.4	41.9	31.5	72.6	70.1
CPE	$\mu g\cdot g^{-1}$ DW	154.6	60.5	52.1	151.2	70.0	53.7	47.4	35.0	60.4	90.7	46.3	32.2	22.9	52.0	54.4	92.1	39.6	22.8	61.1	57.7	70.1	44.8	33.2	74.3	71.0
%Chl *a* in CPE	%Chl-*a*	13.1	4.3	3.1	2.3	2.4	5.1	5.8	3.8	2.2	1.4	8.0	10.6	5.0	3.8	3.8	18.9	13.0	5.0	3.7	2.5	8.2	6.4	5.2	2.3	1.2
Chl *a*:TOC ratio	$\mu g\ mg\cdot C^{-1}$	17.3	3.5	2.3	4.0	1.4	3.5	3.7	2.6	2.1	1.1	4.5	4.0	1.6	2.5	1.8	15.0	5.9	1.8	2.6	1.1	7.0	3.9	2.9	2.0	0.8
RPD	cm	0	9.0	8.0	12.0	-	0	4.5	3.5	2.0	5.0	0	1.5	6.5	2.5	10.0	2.5	5.5	4.5	6.5	12.0	2.5	6.0	4.5	6.5	12.0
$\sum H_2S$	$mmol\cdot m^{-2}$	192.4	1.9	1.1	3.6	0.8	16.9	2.1	1.4	-	1.1	23.2	1.1	0.8	1.0	0.8	15.1	2.2	2.1	2.7	2.2	11.4	3.2	2.5	3.1	2.8
TOC	$mg\cdot g^{-1}$ DW	49.9	31.9	29.9	37.6	50.0	33.4	32.1	21.5	27.9	50.9	35.2	35.8	30.1	33.5	47.0	49.3	36.9	26.7	37.5	55.5	34.6	31.5	25.3	36.1	46.9
TN	$mg\cdot g^{-1}$ DW	8.2	4.5	3.8	5.4	7.0	4.4	4.9	2.9	3.9	8.2	5.0	5.0	3.5	4.5	6.6	7.7	5.5	3.6	5.5	8.1	5.5	4.4	2.9	4.9	6.5
TOC/TN ratio	–	7.1	8.3	9.2	8.1	8.3	8.8	7.6	8.6	8.4	7.2	8.2	8.4	10.0	8.7	8.3	7.5	7.8	8.7	8.0	8.0	7.3	8.4	10.2	8.6	8.4
PRT	$mg\ C\cdot g^{-1}$ DW	4.3	2.7	1.8	4.8	7.5	2.8	2.7	2.0	3.5	5.5	2.6	3.5	2.9	4.4	6.8	4.8	3.1	2.6	3.4	6.3	2.7	2.5	2.2	3.8	4.5
CHO	$mg\ C\cdot g^{-1}$ DW	3.0	1.7	1.4	2.0	2.4	2.0	2.0	0.9	0.9	2.3	3.0	2.1	1.5	2.2	2.9	4.6	1.1	0.5	1.5	1.6	2.3	1.1	0.5	1.0	1.5
LIP	$mg\ C\cdot g^{-1}$ DW	15.4	2.0	1.7	4.0	4.6	3.1	7.1	5.3	5.6	8.5	5.2	2.8	3.5	4.6	5.3	7.5	3.2	2.6	3.9	9.0	4.5	2.5	1.4	3.0	3.8
LC	$mg\ C\cdot g^{-1}$ DW	22.7	6.4	4.9	10.8	14.5	7.9	11.8	8.2	10.0	16.3	10.8	8.4	7.9	11.2	15.0	16.9	7.4	5.7	8.8	16.9	9.5	6.1	4.1	7.8	9.8
%LC in TOC	% LC	45.3	19.9	16.4	28.8	28.9	23.8	36.9	38.0	35.9	32.1	30.4	23.4	26.5	33.3	31.8	34.4	20.1	21.6	23.2	30.4	27.4	19.5	16.2	21.7	20.7
Meiofauna																										
Nematodes	$ind.\cdot 10\ cm^{-2}$	1463	10361	2567	2257	1310	4214	6145	2793	1194	907	4312	6937	4711	1664	1047	4310	8692	5896	2418	1268	4964	8479	5160	1839	739
Copepods	$ind.\cdot 10\ cm^{-2}$	3	138	16	0	1	13	40	28	2	2	54	34	22	17	12	10	28	52	8	26	14	53	29	17	12
Nauplii	$ind.\cdot 10\ cm^{-2}$	2	145	7	0	1	19	6	16	0	1	12	6	3	3	3	0	20	18	1	5	31	63	41	3	6
Polychaetes	$ind.\cdot 10\ cm^{-2}$	5	114	26	8	1	30	42	70	5	6	19	17	14	5	3	66	11	18	5	1	27	21	10	7	0
'Others'	$ind.\cdot 10\ cm^{-2}$	1	38	3	1	6	6	4	3	1	2	6	10	1	3	2	0	8	5	1	0	1	5	0	1	0
total biomass	$mg\cdot 10\ cm^{-2}$ DW	0.67	5.09	1.24	1.03	0.59	2.01	2.89	1.48	0.55	0.41	2.03	3.50	2.16	0.78	0.52	2.10	4.77	2.73	1.11	0.59	2.31	4.70	2.37	0.86	0.34

'Others' includes: Turbellaria, Gastrotricha, Rotifera, Kinoryncha, Oligochaeta, Tardigrada, Ostracoda, Amphipoda, Cumacea, Halacarida, Gastropoda, and Bivalvia.

Study sites: MB, mid-bay; BM, bay mouth; IS, inner shelf; MS, mid-shelf; OS, outer shelf.

Other abbreviations: CPE, chloroplastic pigments equivalent, *i.e.* sum of Chl *a* and phaeopigments; TOC, total organic carbon; RPD, redox potential discontinuity depth; $\sum H_2S$, sulphide inventories in the upper 15 cm; TN, total nitrogen; PRT, total proteins; CHO, total carbohydrates; LIP, total lipids; LC, labile carbon (sum of PRT, CHO, and LIP); DW, dry weight.

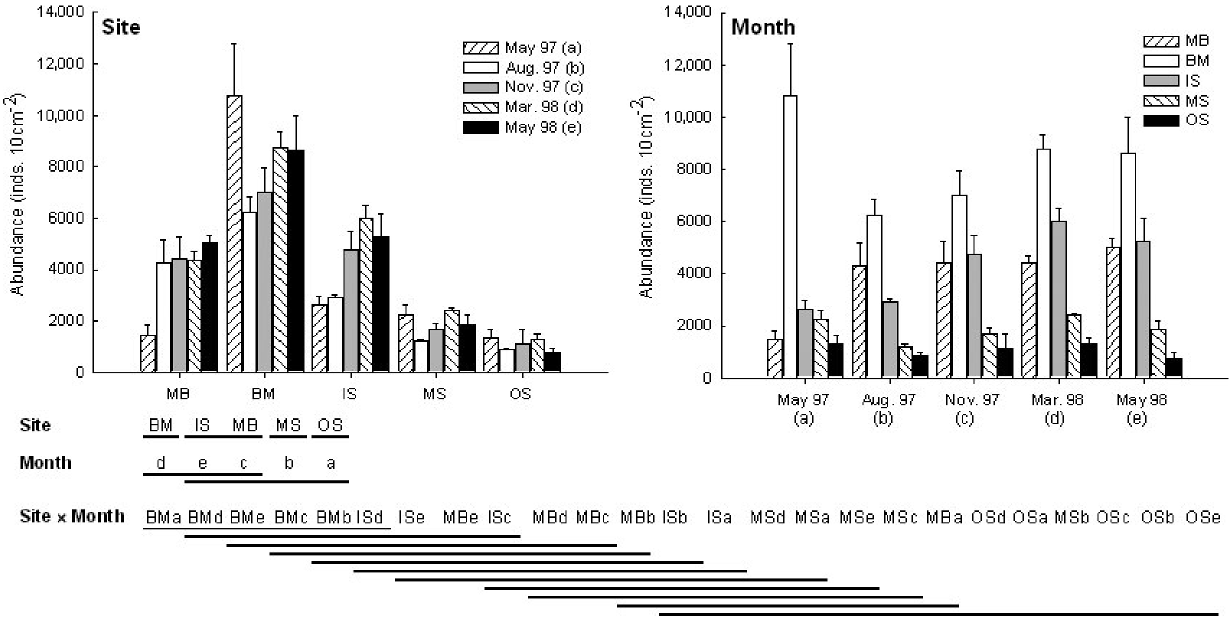

Fig. 2. Spatial (site) and temporal (month) variation of total meiofaunal abundance during the study period. Study sites: MB, mid-Bay; BM, bay mouth; IS, inner Shelf; MS, mid-shelf, OS, outer shelf. Contrasts made using *a posteriori* Tukey HSD tests, after a significant two-way ANOVA ($P < 0.05$) including sites and months as factors and their interaction (site × month), are shown in the lower panel. Horizontal bars indicate homogeneous groups. Lower-case letters indicate sampling month (a, May 1997; b, August 1997; c, November 1997; d, March 1998; and e, May 1998). Error bars indicate 1 SE.

pods + nauplii seldom represented >2% of total abundance whereas the remaining 12 taxa, in Table 2 grouped as 'others', never represented >0.5% of total abundance.

Nematodes, as the dominant group, dictated the general trend of meiofaunal abundance (total meiofaunal abundance *versus* nematode abundance, $r^2 = 0.99$, $P < 0.001$, $n = 25$). Nematode densities ranged from 739 to 10 361 ind. 10 cm^{-2}, always with the lower values at the outer shelf and the higher values at the bay mouth (Table 2).

Total meiofaunal densities, in general, were higher at the bay mouth, intermediate values were found at the mid-bay and inner shelf, and lower values at the mid- and outer shelf sites (two-way ANOVA, $F_{4,50} = 101.13$; $P < 0.001$), followed by *a posteriori* HSD Tukey comparisons (Fig. 2). Regarding temporal variations, pooling all sites, an overall total abundance increase was observed towards March 1998 ($F_{4,50} = 4.47$; $P = 0.003$) (Fig. 2). An interaction between sampling sites and months was detected ($F_{16,50} = 3.38$; $P < 0.01$), the most important change (at a single site) was the increase of total meiofaunal abundance at the mid-bay towards May 1998 (1474–5036 ind.·10 cm^{-2}). A similar temporal trend was observed at the inner shelf site (2618–5241 ind.·10 cm^{-2}, from May 1997 to May 1998, respectively); however, it was not significant, as indicated by Tukey's *a posteriori* contrasts (Fig. 2). At the other sites the total abundances remained fairly unchanged.

The highest abundance of copepods + nauplii and polychaetes were found in the bay mouth, and the lowest in the mid- and outer shelf sites. Copepods, a sensitive group to oxygen-deficient conditions, increased their densities towards the end of EN by about one order of magnitude at the mid-bay, mid-shelf and outer shelf (Table 2). A similar increase was observed for polychaetes at the mid-bay site, from May 1997 to March/May 1998 (Table 2).

The 'other' taxa, in general were represented by very few specimens, <10 ind.·cm^{-2}. Only the ostracods contributed with a higher number of individuals (38 ± 18 ind.·10 cm^{-2}) in the bay mouth in May 1997; however, at the end of El Niño (May 1998) their densities were reduced by one order of magnitude.

Total biomass exhibited the same general temporal and spatial pattern reported for the density, with the lowest and highest values at the outer shelf and at the bay mouth sites, respectively. Total biomass ranged from 0.34 to 5.09 mg·10 cm^{-2}, dry weight, found at the outer shelf and the bay mouth sites, respectively (Table 2).

Correlations between biotic and abiotic factors

Results of Spearman rank correlations between meiofaunal abundance and abiotic factors are presented in Table 3. In general, bottom-water dissolved oxygen (DO) and

Table 3. Spearman rank correlations between the abundance of major taxonomic groups and environmental parameters including all sites and sampling dates.

	Chl *a*	Pheop	CPE	%Chl *a* CPE	Chl *a*: TOC	RPD	$\sum H_2S$	TOC	TN	C:N	PRT	CHO	LIP	LC	%LC TOC	DO
NEM	0.41*	−0.61**	−0.57**	0.70**	0.58**	ns	ns	−0.52**	−0.45*	ns	−0.65**	ns	−0.55**	−0.59**	−0.44*	0.55**
COP	ns	−0.75**	−0.72**	0.45*	ns	ns	ns	−0.54**	−0.51**	ns	−0.69**	ns	−0.45*	−0.55**	ns	0.57**
NAU	ns	−0.60**	−0.57**	0.40*	ns	ns	ns	−0.54**	−0.45*	ns	−0.74**	ns	−0.58**	−0.70**	−0.56**	0.76**
POL	ns	ns	ns	0.51**	0.52**	ns	ns	−0.56**	−0.48*	ns	−0.69**	ns	ns	−0.42*	ns	0.63**
OTR	ns	−0.41*	−0.42*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
total	0.40*	−0.61**	−0.57**	0.70**	0.57**	ns	ns	−0.52**	−0.45*	ns	−0.65**	ns	−0.55**	−0.59**	−0.44*	0.55**

n = 25, except for RPD and $\sum H_2S$ that n = 24.

DO, dissolved oxygen, other abbreviations for environmental parameters as in Table 2. NEM, nematodes; COP, copepods; NAU, nauplii; POL, polychaetes; OTR, others (including ostracods, halacarids, gastrotrichs, turbellarians, oligochaetes, rotifers, kinorhynchs, tardigrades, amphipods, cumaceans, gastropods, and bivalves); total, total abundance.

*P < 0.05; **P < 0.01; ns, non significant.

Table 4. Suites of environmental variables, identified by the BIOENV procedure that best correlated with the multivariate community structure.

by site (all months)	mid-bay		bay mouth		inner shelf		mid-shelf		outer shelf	
	parameters	ρ_w	parameters	ρ_w	parameters	ρ_w	parameters	ρ_w	parameters	ρ_w
	RPD $\sum H_2S$ TOC PRT DO	0.95***	Pheop LC	0.57**	Chl*a*:TOC $\sum H_2S$ TOC C:N	0.72**	Chl*a* Chl*a*:TOC TOC N	0.87***	RPD $\sum H_2S$ CHO DO	0.54*
by month (all sites)	**May 1997**		**August 1997**		**November 1997**		**March 1998**		**May 1998**	
	parameters	ρ_w	parameters	ρ_w	parameters	ρ_w	parameters	ρ_w	parameters	ρ_w
	TOC	ns	Chl*a* LC:TOC DO	0.95***	%Chl*a* CPE PRT CHO LC DO	0.99***	RPD PRT LC:TOC DO	0.90***	%Chl*a* CPE RPD TOC PRT	0.82***
total					**all sites and months**					
					parameters					ρ_w
					% Chl*a* CPE Chl*a*:TOC DO					0.56**

Abbreviations for environmental parameters are the same that in Table 2.

The weighted Spearman correlation value (ρ_w) is reported. The significance level was obtained using the RELATE procedure.

*P < 0.05; **P < 0.01; ***P < 0.001; ns, non-significant.

parameters indicating freshness of the settled phytodetritus such as Chl *a*, its contribution to total pigments (% Chl *a* in CPE), and its ratio *versus* organic carbon (Chl *a*:TOC), correlated positively with total meiofauna abundance. Conversely, parameters indicating bulk organic content (Phaeop, TOC, and TN) as well as labile carbon content (PRT, LIP, LC, and LC:TOC) were negatively correlated with meiofaunal densities. No significant univariate correlations were found between meiofaunal density and RPD, $\sum H_2S$, C:N, and CHO.

The suites of environmental variables identified by the BIOENV procedure that best explained the observed faunal abundance patterns by site, by sampling date and by combining both, are given in Table 4. The contribution of Chl *a* in CPE, the Chl *a*:TOC ratio and DO was the set of variables that explained the most variance (weighted Spearman's correlation = 0.56, $P < 0.01$). To further corroborate this, the sampling sites at different months were ordered by means of a NMDS analysis according to (i) the whole set of environmental variables (Fig. 3A); (ii) the three variables identified by the BIOENV procedure that best explained faunal abundance pattern (Fig. 3B); and (iii) the abundance of the different taxa (Fig. 3C). In all cases stress remained equal or <0.08, indicating a good fit (Clarke & Ainsworth 1993). As seen in Fig. 3B and C, two groupings are evident corresponding mainly to the shelf and bay stations.

Discussion

Sediment settings

The sediment TOC content (~40 $mg \cdot g^{-1}$) was similar to values measured in other upwelling areas like the Arabian Sea (14.3–54.3 $mg \cdot g^{-1}$; Smallwood & Wolff 2000), SW Perú margin (32–75 $mg \cdot g^{-1}$; Henrichs & Farrington 1984), and off Namibia (~49 $mg \cdot g^{-1}$; Klok *et al.* 1984) but lower than values reported off NW Africa (up to 79 $mg \cdot g^{-1}$; Ten Haven *et al.* 1992) and off Callao, Perú (up to 205 $mg \cdot g^{-1}$; Neira *et al.* 2001b). Thamdrup & Canfield (1996) observed in 1994 values of the same order as the ones found at the beginning of the study at the inner bay (~70 $mg \cdot g^{-1}$) and over the shelf (30–40 $mg \cdot g^{-1}$).

The fraction of organic carbon generated by phytoplanktonic primary production that reaches the seafloor decreases with water depth (Berger *et al.* 1987). Considering that (i) based in a mass balance study of Pb within the bay, there is a negligible particulate matter transport from the bay to the shelf and vice versa (Muñoz 2002); (ii) since the shelf area is bordered by deep canyons that channel the sediments of the Bio Bio and Itata rivers to the trench, significant lateral transport is precluded (Muñoz 2002); and (iii) assuming that the difference in primary production over such a short transect (~37 km) is negligible, an overall decreasing organic content along the transect is expected. However, only Chl *a* followed this pattern. TOC and the different descriptors of organic matter (*i.e.* TN, C/N, CHO, LIP, PRT, and LC:OC) exhibited a parabolic distribution, decreasing from the bay to the inner shelf but increasing again towards the outer shelf. This is consistent with enhanced organic matter preservation under oxygen deficient conditions (Berner 1980; Dauwe *et al.* 2001). In non-El Niño years the mid-shelf and outer shelf sites (impinged by the OMZ) underlay the OMZ, while during El Niño, the OMZ deepens, releasing the mid-shelf completely and in part the outer shelf, from the influence of the OMZ. Although the outer shelf site bears an impoverished macrofauna (Gallardo *et al.* 1995; Gutiérrez *et al.* 2000) as well as meiofauna (Neira *et al.* 2001c) when compared with the shallower sites, slight increases in abundances during El Niño conditions have been observed (Gutiérrez *et al.* 2000; Neira *et al.* 2001c). At this outer shelf site, lower

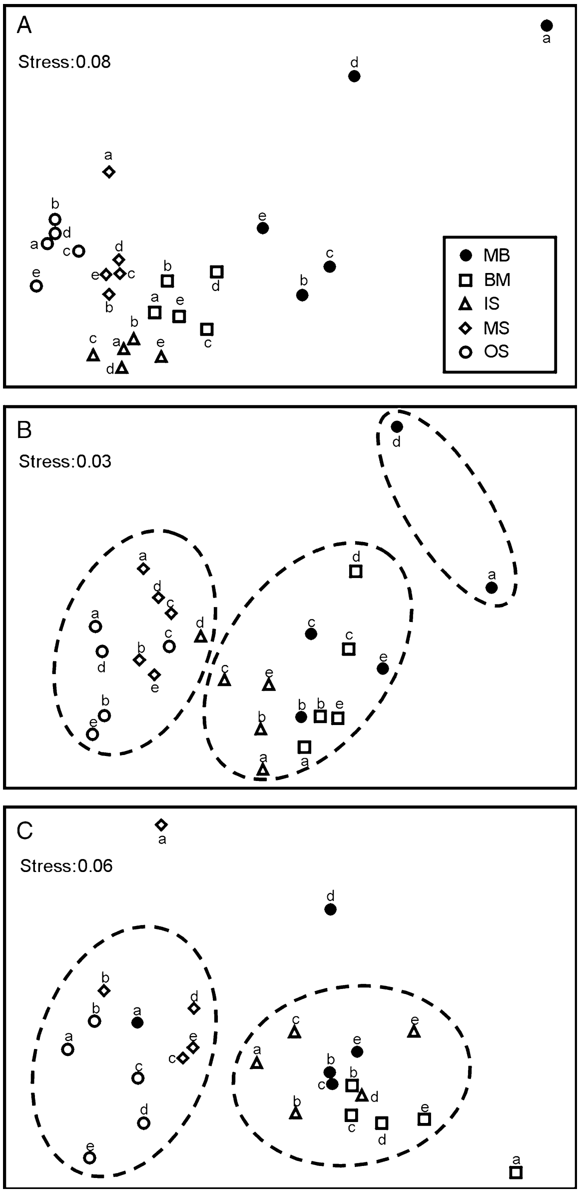

Fig. 3. Non-metric multidimensional scaling (NMDS) ordination of all the locations by sampling date using: (A) all the environmental variables registered (see Table 2); (B) just the three variables that best correlated with multivariate methods with the meiofaunal structure (% Chl *a* in CPE, Chl *a*:TOC and dissolved oxygen; $\rho_w = 0.56$, $P < 0.01$; see Table 3); and (C) the meiofaunal abundance by major taxonomic groups. Lower-case letters indicate sampling month (a, May 1997; b, August 1997; c, November 1997; d, March 1998; and e, May 1998). The ellipses group sites with similar characteristics identified by cluster analysis of respective similarity matrices. In (B) the ellipses correspond to an Euclidean distance of 1.4 and in (C) to a Bray–Curtis similarity of 85%.

rates of bioturbation and organic matter remineralization have been reported during El Niño (Gutiérrez 2000).

The mid-bay site presented the greatest temporal variations, where conditions differed most from the beginning to the end of the study. A 2.5 cm sediment oxidized layer was generated towards the end of EN (Table 2). Sulphidic conditions of the sediment and anoxic bottom water, typical of summer/early-fall at this site (Farías *et al.* 1996; Zopfi *et al.* 2001), occurred in May 1997. However, during El Niño these conditions did not develop, and a general decrease in all the indicators of organic matter quantity and quality occurred. Probably, this was due to the lower primary production reported for this area in this period (<0.17 gC·m^{-2}·day^{-1}; typically it is 1.5–5 gC·m^{-2}·day^{-1}, Farías *et al.* 2004) and consequent lower flux of phytodetritus. The decrease of LIP towards 1998 is consistent with this observation, since they are present in large quantity in phytoplankton cells, mainly in diatoms (Neira *et al.* 2001c).

At the shelf, the most important changes, in addition to the normal seasonal oscillation of most of the parameters, occurred at the mid- and outer shelf sites. A decreased supply of phytodetritus during austral summer (early 1998 or end of El Niño) was revealed by the lower values of the Chl *a*:TOC ratio compared with May 1997 (Table 2). This was consistent with the LC, which in spite of fluctuations during the course of El Niño, decreased ~30% (top 1 cm) at the end of the sampling period (May 1998). Higher degradation rates of biochemical components of organic matter under enhanced oxic conditions could have contributed to the reduction of LC. Degradation rates can be up to 40% higher under oxic- than under anoxic conditions (Harvey *et al.* 1995).

Factors structuring the meiofaunal community

Our results suggest that metazoan meiofaunal communities off Concepción, in general (pooling sites and months), are controlled primarily by the freshness of phytodetritus, best indicated by the Chl *a*:TOC ratio, the contribution of Chl *a* in CPE, and the oxygen availability. This can also be observed through the non-metric multidimensional ordination of sampling sites and months for these three parameters and by comparing them with the ordination obtained for biological attributes.

Regarding El Niño effects on meiofaunal abundance, the clearest positive response occurred at the mid-bay, a site characterized by its high content of organic matter of phytodetrital origin (Chl *a*:TOC >3.5 μg·mg·C^{-1}, C:N <8.8; Table 2). At this site, increased meiofaunal abundances towards May 1998 coincided with the absence of severe oxygen-deficient conditions and the deepening of the RPD during austral summer (early 1998).

The role of oxygen as a key factor for structuring meiofaunal communities is well documented for the shelf and slope off Perú (Thiel 1978; Neira *et al.* 2001c), for a seamount intersecting the OMZ off México at bathyal depths (Levin *et al.* 1991) and for the Arabian Sea (Cook *et al.* 2000; Gooday *et al.* 2000). For shallower areas research is scarce, occurring mainly in oxygen-deficient basins like the Black Sea (Rhoads & Morse 1971), southern California (Bernhard *et al.* 2000) and the fjord area of western Sweden (Josefson & Widbom 1988). Several authors have suggested that abundance of taxa like nematodes, known to be resistant to anoxic conditions, is inversely proportional to oxygen deficiency (Giere 1993). These taxa generally have enhanced abundances in organic-rich, oxygen-deficient sediments (Levin *et al.* 1991; Moodley *et al.* 1997; Cook *et al.* 2000; Neira *et al.* 2001b). However, the rapid increase in abundance (and biomass) observed at the mid-bay suggests that even the nematodes were relieved from the sulphidic stress. As shown in Table 4, sulphide inventory and redox conditions are among the factors that explain the multivariate structure of the mid-bay meiofaunal community, suggesting that the sulphidic environment in part maintains meiofaunal communities below their carrying capacity. On the other hand, it is known that crustaceans, in general, are not able to withstand hypoxic conditions for more than a few hours (Theede 1973; Jørgensen 1980; Josefson & Widbom 1988). All sites experienced increased copepod and nauplii abundances during the El Niño (Table 2), with the exception of the bay mouth, indicating enhanced oxygen availability along the transect.

Our results show that among primary factors controlling meiofaunal distribution off Concepción, oxygen-related parameters have greatest influence at the extreme sites (*i.e.* mid-bay and outer shelf; Table 4). Food quality, as indicated by LC, seems to have importance only when oxygen is not limiting (*i.e.* El Niño condition), in this case, August and November 1997, and March 1998 (Table 4). On the other hand, most indicators of labile organic content (*e.g.* PRT, LIP, LC, and LC:TOC; Table 3) correlated negatively with meiofaunal density.

As mentioned in the previous section (cf. Sediment settings), low primary production triggered by El Niño was recorded at the mid-shelf site in early 1998. Nevertheless, food did not appear to limit meiofaunal abundance, since indicators of labile organic matter content and food potential remained relatively high when compared with similar studies carried out in the OMZ off Peru (Neira *et al.* 2001b) and in oligotrophic systems such as the Mediterranean Sea (*e.g.* Danovaro *et al.* 1995a,b; Fabiano *et al.* 1995; Albertelli *et al.* 1999; Danovaro *et al.* 2000). In the absence of oxygen as a limiting factor and probably also related to favourable redox conditions within the sediment along the whole transect (*i.e.* during El Niño), meiofaunal abundance off Concepción tended to decrease with depth rather than exhibiting a parabolic pattern. Here it is interesting to note that it has been reported that meiofaunal abundance can be negatively correlated with oxygen concentration, with nematodes becoming dominant under oxygen deficient conditions, as occurred off Peru (Neira *et al.* 2001b). In our study, the opposite trend prevails, *i.e.* greater abundances associated to oxygenated conditions. It seems evident that the assemblages off Peru and Concepción probably bear different specific adaptations to the different oxygen regimes (while off Peru the OMZ is permanent, off Concepción it depicts a seasonal cycle). Consistently, off Peru one of the dominant species within the OMZ is the epsilonematid nematode *Glochinema bathyperuviensis* (Neira *et al.* 2001a). The presence of prokaryotic ectobionts, probably sulphide oxidizers, has been recently suggested for other species of epsilonematids (Neira *et al.* 2005). Although the species composition off Concepción is still unknown, we have not observed such highly adapted nematodes.

During El Niño, the indicators that best reflected changes in food quality with depth seemed to be the Chl *a*-related indices (Tables 3 and 4), which suggests that food quality acquired a more important role in modulating meiofaunal communities off Concepción. The decreasing pattern of abundance with depth is well documented in places such as the Mediterranean Sea, where oxygen is not limiting. There, the decrease of meiofaunal abundance has been related to food quality (Albertelli *et al.* 1999).

Among other factors that may be influencing meiofaunal distribution and community structure are bacteria. It has been hypothesized that the mat-forming bacteria *Thioploca*, by its sulphide-oxidizing capacity, could have a positive effect over metazoan communities (Gallardo *et al.* 1996a). Indeed, *Thioploca* and total meiofaunal densities are positively correlated (Neira *et al.* 2001c). But as these are observational studies and correlation does not necessarily mean causality, further studies involving experimental and manipulative approaches are needed to identify and clarify the role of the biotic and abiotic factors underlying meiobenthic faunal structure. On the other hand, the role of intra- and inter specific relations among meiofauna, interactions with macrofauna, as well as predation by larger organisms are also overlooked, in spite of their potential importance (*e.g.* Gregg & Fleeger 1998; Austen *et al.* 1999). During the 1997–1998 El Niño event, an increased penetration of the meiofauna in the sediment at the mid-bay and inner shelf sites relative to non-El Niño periods was observed (Neira *et al.* 2001c). The same pattern occurred with the macrofauna at the mid-bay and the outer shelf sites (Gutiérrez *et al.* 2000).

Conclusions

The variety of changes observed in environmental settings during the course of El Niño 1997–1998, and the different meiofaunal response to these changes among sites off Concepción, support the hypothesis that abiotic factors (bottom water oxygen concentration and 'freshness' of organic matter), probably interacting with some biotic factors (including competition and removal of predators), are modulating meiofaunal communities.

This study shows evident effects of an El Niño event on the different biotic and abiotic components in the benthic realm off central Chile, as do related studies (Gutiérrez *et al.* 2000; Neira *et al.* 2001b; Levin *et al.* 2002). Questions are raised regarding the carbon fluxes mediated by the fauna. It is envisaged that, during strong warm events, benthic organisms play an important role of in the remineralization of the carbon pool that the system accumulates during non-EN years. Indeed, it has been estimated that, at the mid-bay site (Concepción Bay), the role of the meiofauna in sediment carbon cycling (secondary production + respiration) from the beginning to the end of EN increased from 15.66–52.65 $\text{gC}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ (Sellanes *et al.* 2003).

Furthermore, biomimetic approaches (*i.e.* enzymatic digestion) regarding the bioavailability of organic matter (*e.g.* Fabiano & Pusceddu 1998; Grémare *et al.* 2002) would contribute to a more accurate assessment of the biopolymeric fraction of organic matter potentially available for consumers. This approach could further elucidate whether food quality (instead of oxygen) can be a limiting factor at the deeper shelf sites off Concepción, which only occasionally (*e.g.* during El Niño), are not influenced by the OMZ.

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