

	Volume 27	Number 7	1 April 2007	ISSN 0278-4343
CONTINENTAL SHELF RESEARCH				
Editors: Michael Collins Southampton, UK Richard W. Sternberg Seattle, WA, USA				
Review				
O. Nikiema, J.-L. Devenon and M. Baklouti	873	Numerical modeling of the Amazon River plume		
Research Papers				
W.-C. Liu, W.-B. Chen, R.T. Cheng, M.-H. Hsu and A.Y. Kuo	900	Modeling the influence of river discharge on salt intrusion and residual circulation in Danshuei River estuary, Taiwan		
A. Ullmann, P.A. Pirazzoli and A. Tomasin	922	Sea surges in Camargue: Trends over the 20th century		
P.L. Woodworth, R.A. Flather, J.A. Williams, S.L. Wakelin and S. Jevrejeva	935	The dependence of UK extreme sea levels and storm surges on the North Atlantic Oscillation		
C.N. Rooper and M. Zimmermann	947	A bottom-up methodology for integrating underwater video and acoustic mapping for seafloor substrate classification		
M. Furnas	958	Intra-seasonal and inter-annual variations in phytoplankton biomass, primary production and bacterial production at North West Cape, Western Australia: Links to the 1997–1998 El Niño event		
P.-M. Poulain and E. Zambianchi	981	Surface circulation in the central Mediterranean Sea as deduced from Lagrangian drifters in the 1990s		
J. Sellanes, E. Quiroga, C. Neira and D. Gutiérrez	1002	Changes of macrobenthos composition under different ENSO cycle conditions on the continental shelf off central Chile		
www.elsevier.com/locate/csr				

This article was originally published in a journal published by Elsevier, and the attached copy is provided by Elsevier for the author's benefit and for the benefit of the author's institution, for non-commercial research and educational use including without limitation use in instruction at your institution, sending it to specific colleagues that you know, and providing a copy to your institution's administrator.

All other uses, reproduction and distribution, including without limitation commercial reprints, selling or licensing copies or access, or posting on open internet sites, your personal or institution's website or repository, are prohibited. For exceptions, permission may be sought for such use through Elsevier's permissions site at:

<http://www.elsevier.com/locate/permissionusematerial>



ELSEVIER

Available online at www.sciencedirect.com

ScienceDirect

Continental Shelf Research 27 (2007) 1002–1016

CONTINENTAL SHELF
RESEARCH

www.elsevier.com/locate/csr

Changes of macrobenthos composition under different ENSO cycle conditions on the continental shelf off central Chile

Javier Sellanes^{a,b,*}, Eduardo Quiroga^c, Carlos Neira^d, Dimitri Gutiérrez^e

^aUniversidad Católica del Norte, Facultad de Ciencias del Mar, Larrondo 1281, Coquimbo, Chile

^bCentro de Investigación Oceanográfica en el Pacífico Sur Oriental (COPAS), Universidad de Concepción, Chile

^cCentro de Investigación en Ecosistemas de la Patagonia (CIEP), Bilbao 449, Coyhaique, Chile

^dIntegrative Oceanography Division, Scripps Institution of Oceanography, 9500 Gilman Drive, La Jolla, CA 92093-0218, USA

^eDirección de Investigaciones Oceanográficas, Instituto del Mar del Perú, P.O. Box 22, Callao, Perú

Received 14 December 2005; received in revised form 23 November 2006; accepted 3 January 2007

Available online 16 January 2007

Abstract

The course of environmental conditions and shelf macrobenthic communities off Central Chile (~36°S) during the strong 1997–98 El Niño (EN) event is compared with a subsequent and basically “normal” period (2002–2003). Changes in macrofaunal community, feeding mode structure, and biomass size spectra are contrasted over time with changes in oceanographic and sediment settings, in order to assess intra- and inter-annual changes in faunal composition during both ENSO periods.

During EN, there was a decrease in biomass and abundance of species known to be well adapted to organic-rich, oxygen-deficient environments, such as the interface-feeding polychaete *Paraprionospio pinnata*. On the other hand the abundance of highly mobile, burrowing polychaetes remained unaffected, or even increased in biomass. The decline of *P. pinnata* lasted several years after the demise of warm conditions, possibly due to negative interactions with those more mobile burrowing polychaetes. The percent contribution of subsurface-deposit feeders to total biomass increased during EN ($49.3 \pm 12.4\%$ during summer) and declined only in the summer-fall period of 2002–03 ($11.1 \pm 4.1\%$). An opposite trend was observed for interface and surface-deposit feeders. From EN to summer-fall 2002–03 (i.e., normal to low oxygen conditions) the size-structure of the macrobenthos switched from a larger to a smaller-sized assemblage. However, biomass was maintained due to successful recruitment and high abundance of both *P. pinnata* and the squat lobster, *Pleuroncodes monodon*.

Our results suggest that the shelf macrofaunal community structure exhibit fluctuations at various time scales, and that these changes are more pronounced during and after a strong EN event. In such cases, the effects of such an event may be recorded at latitudes as far south as 36°S, with consequences in the biota lasting for many years after the demise of warm conditions.

© 2007 Elsevier Ltd. All rights reserved.

Keywords: Macrobenthos; Feeding modes; Deposit-feeders; Biomass size spectra; ENSO; Central Chile

*Corresponding author. Universidad Católica del Norte, Facultad de Ciencias del Mar, Larrondo 1281, Coquimbo, Chile.
Tel.: +56 51 209802.

E-mail address: sellanes@ucn.cl (J. Sellanes).

1. Introduction

The coastal zone off central Chile ($\sim 36^\circ\text{S}$), strongly influenced by seasonal wind-driven upwelling, is one of the areas with the highest known primary production rates worldwide (Fossing et al., 1995; Daneri et al., 2000). Furthermore, a pronounced oxygen minimum zone (OMZ), located at depths between 50 and 250 m and associated with the Equatorial Subsurface Water (ESSW), partially covers the continental shelf. When upwelling prevails during summer, the OMZ can be found only a few meters from the surface within Concepción Bay (Ahumada et al., 1983). As a result, high accumulation rates of undegraded organic carbon occur (Muñoz et al., 2004a).

A peculiarity of the biota thriving in these organic-rich sediments is indicated by the presence of an important prokaryotic community, mostly composed of the filamentous, gliding bacteria *Thioploca* spp., which sometimes has greater biomass than the eukaryotic fauna (Gallardo, 1977; Schulz et al., 2000). The metazoan fauna is small (body sizes < 1.0 mm); dominated both in biomass and abundance by polychaetes, while other groups like mollusks, crustaceans and cnidarians are unusual (Gallardo, 1985; Gallardo et al., 1995). Meiofauna is abundant and dominated by nematodes (Sellanes et al., 2003). It has been also reported that during non-El Niño years, the benthic fauna attains their maximum abundance and biomass during fall and winter, probably due to favorable environmental conditions (i.e., absence of hypoxic bottom waters, less reduced sediments) (Carrasco and Arcos, 1984).

Studies indicate that most of the more abundant polychaete species are well adapted to cope with oxygen-deficient conditions, by having enzymatic mechanisms related with anaerobic pathways (González and Quiñones, 2000); among them, *Paraprionospio pinnata* and *Nephtys ferruginea* are the best adapted. These two species displayed high activities of four pyruvate oxidoreductases, suggesting a high metabolic plasticity to thrive even in anoxic conditions. Consistently, *P. pinnata* is the dominant species among the eukaryotic benthos in the study area (Gallardo et al., 1972, 1995; Carrasco and Carbajal, 1998; Gutiérrez et al., 2000).

Continental shelf benthic communities are often strongly influenced by El Niño (EN), the warm phase of the ENSO cycle, in the Eastern Pacific (Tomicic, 1985; Arntz and Fahrbach, 1996). Off

central Chile, seasonal and inter-annual changes in upwelling intensity can lead to changes in bottom-water dissolved oxygen (DO) concentration, in the amount of organic matter reaching the bottom (Gutiérrez et al., 2000), in the quality and lability of deposited organic matter (Neira et al., 2001a; Sellanes and Neira, 2006), and in the sediment nitrogen fluxes (Muñoz et al., 2004b). It is known that the impacts of EN on environmental conditions may last from a few months to several years (Gallardo, 1985; Tarazona et al., 1996). However, very little is known about its effects on benthic communities beyond 23°S (i.e., Antofagasta, Chile), which usually has been considered the southern limit of the most impacted area by strong EN events (Arntz et al., 1991).

During the last strong EN event (1997–98), we learned that at the shelf the most noticeable effects of EN on the macroinfauna were a switch in their composition, the deepening of its distribution within the sediment and an increase in their bioturbation potential, associated with a decrease of the sediment organic matter reactivity (Gutiérrez, 2000; Gutiérrez et al., 2000). However, these studies were carried out during the event, and no comparison was made with non-EN conditions. In the present paper, we fill this gap by comparing macrofaunal community response to changing environmental conditions during two key phases of the ENSO cycle: a warm (EN) phase and a subsequent non-EN phase. The EN phase is the period May 1997–March 1998, one of the strongest warm events of the last decades (Mc Phaden, 1999), and the non-EN phase was the period April 2002–June 2003. In both phases, we examine the structure of the benthic macrofauna, in terms of composition, density, biomass size-spectra, and feeding modes, with the aim to link it with seasonal- and ENSO-related variability of the water column and sediment habitat conditions. Sampling was carried out at a site representing typical shelf conditions for central Chile (i.e., a site where under “normal” conditions, higher fluxes of phytodetritus from the water column to the seafloor occur during summer, and hypoxic bottom water occurs year round). We also identified key species structuring the macrobenthic community, which in turn, may serve as indicators of the prevalent ENSO cycle phase.

We test the hypotheses that (i) EN conditions trigger community changes due to disturbances in the annual oxygen and organic matter flux regime, favoring the dominance of larger-bodied, burrowing organisms instead of smaller-bodied, tube-dwelling

interface feeding organisms (e.g., the polychaete *P. pinnata*), and (ii) time responses of key species and/or ecological interactions retard the return to a pre-EN community for a period longer than the event itself.

2. Material and methods

2.1. Field sampling

The study site is located on the continental shelf (88 m depth) off Concepción, central Chile ($36^{\circ}30.8' S$; $73^{\circ}07.7' W$; Fig. 1). Sampling was conducted aboard the R.V. *Kay Kay* (University of Concepción), during two periods: (a) from May 1997 to February 2000, and (b) from May 2002 to June 2003. The first sampling (May 1997) took place shortly after the onset of the 1997–98 EN, and after the initial sampling, samples were taken, in general, on a seasonal basis.

Water column temperature, salinity and DO were measured using a CTDO. In addition, DO measurements were made by a modified, semi-automatic Winkler method using a photometric end-point detector, a Dosimat 665 (Metrohm), and a chart

recorder (Williams and Jenkinson, 1982). The analytical procedures were conducted as suggested by Knap et al. (1993).

2.2. Sediment parameters

Sediment cores were retrieved using a mini multiple-corer (tube i.d. 95 mm) (Barnett et al., 1984). Concurrently with the biological sampling, a set of sediment environmental parameters was measured during the August 1997–May 1998 (strong EN conditions) and the September 2002–June 2003 (non-EN conditions) sub-periods (Table 1, Fig. 2 dotted-line rectangles). From the original cores, sub-samples for chemical analysis were taken using plexiglas liners (i.d. 36 mm). Sub-samples were kept cool and in the dark until further processing in the laboratory (in general within 12 h). Sediment (top 0–1 cm) for Chlorophyll-*a* (Chl-*a*) and phaeopigments (Phaeop) as well as total organic carbon (TOC) and total nitrogen (TN) content was kept frozen ($-20^{\circ}C$) until analysis. Two additional cores were sub-sampled for dissolved sulfide at each opportunity. Pore water was extracted under N_2 atmosphere with a pneumatic

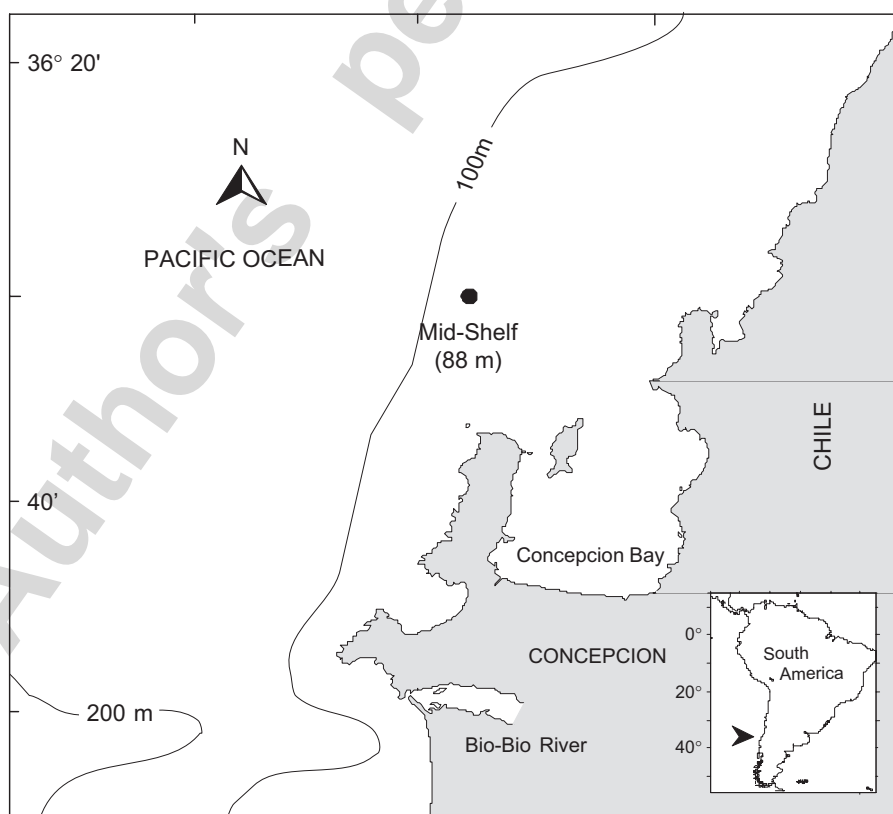


Fig. 1. Study site, located at the mid-shelf (88 m) off Concepción, central Chile.

Table 1
Sediment environmental conditions during the 1997–98 and 2002–03 sampling periods

Variables	1997–98				2002–03			
	August	November	March	May	September	November	March	June
TOC (mg g^{-1})	27.9	33.5	37.5	36.1	45.9	30.7	51.8	42.6
TN (mg g^{-1})	3.9	4.5	5.5	4.9	4.7	3.9	7.2	5.3
C:N (molar)	8.43	8.68	7.95	8.60	11.30	9.21	8.48	9.49
TOM (%)	16.57	16.58	14.38	14.83	14.24	14.91	14.27	16.26
CPE ($\mu\text{g g}^{-1}$)	309.5	293.0	264.6	195.8	225.7	231.6	794.6	460.6
RPD (cm)	2	3	9	7	20	20	10	11.5
DO (mL L^{-1})	0.85	0.52	0.31	1.11	0.68	0.35	0.08	1.22
$\Sigma\text{H}_2\text{S}$ (mmol m^{-2})	nd	1.00	2.70	3.15	nd	nd	23.11	1.21

TOC = total organic carbon, TN = total nitrogen, C:N = carbon to nitrogen ratio, TOM = total organic matter, CPE = chloroplastic pigment equivalent (i.e., sum of Chl*a* and phaeopigments), RPD = redox potential discontinuity depth, DO = bottom-water dissolved oxygen, $\Sigma\text{H}_2\text{S}$ = sulphide inventories integrated for the upper 15 cm.

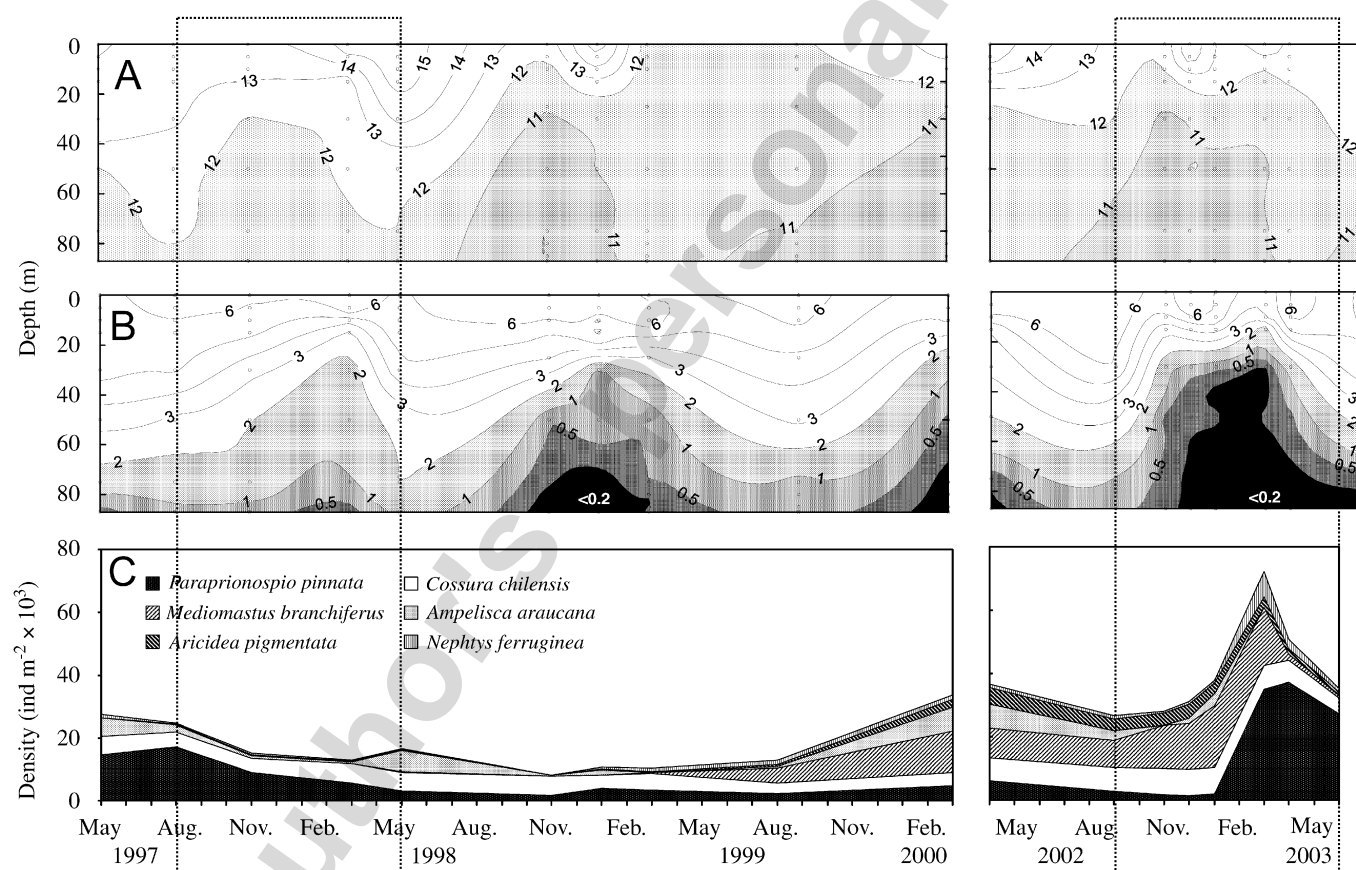


Fig. 2. Contour graphs showing the time course of: (A) Water column temperature ($^{\circ}\text{C}$), (B) Dissolved oxygen (mL L^{-1}) and (C) Abundance of the six most representative species of the macrobenthos. The study period covers a strong El Niño (May 1997–May 1998) and post-El Niño conditions (May 1998–March 2000/April 2002–July 2003) at the mid-shelf site off Concepción. The superimposed dotted-line rectangles indicate the periods used to compare environmental conditions during EN and a subsequent non-EN period.

squeezer at 1 and 2 cm sections down to 15 cm sediment. Water content and porosity were determined at 1 cm intervals down to 15 cm in order to estimate sulfide inventories.

Chloroplastic pigments (Chl-*a* and Phaeop) were determined fluorometrically according to the method of Lorenzen and Jeffrey (1980). Pigments were extracted from ca. 0.3 g of sediment with 90%

acetone on a vortex stirrer, sonicated for 10 min and then centrifuged (at 1500g), for 5 min. This extraction was done twice. The supernatant was used to determine the Chl-*a* concentration, and then, acidified with 0.1 N HCl to estimate Phaeop using a Turner AU-10 fluorometer. The sum of Chl-*a* and phaeop was operationally defined as chloroplastic pigments equivalent (CPE) and was used as a measure of the input of phytodetrital material to the sediments (Pfannkuche and Soltwedel, 1998). TOC and TN were determined after acidification with 1 N HCl (to remove carbonates) using a Heraeus-CHN elemental analyzer. Porewater sulfide was determined colorimetrically at 670 nm using the methylene blue technique (Cline, 1969). Sediment redox potential was measured at intervals of 1 cm using a platinum standard combination electrode with a calomel internal reference. The depth at which the transition of positive to negative redox values occurred was considered the redox potential discontinuity depth (RPD).

2.3. Macrofauna

For macrofaunal analysis, four independent replicates (each replicate consisting of two pooled cores from independent multicore drops; total area 0.0142 m²) were taken at each sampling date. In order to examine the vertical distribution of the fauna, cores were sliced at 0–2, 2–5, 5–10, 10–15, and 15–20 cm. Each section was preserved unsieved in 10% buffered formalin until further analysis. In the laboratory, macrobenthic animals (>0.5 mm) were sorted and identified to the lowest taxon possible under a dissecting microscope (up to 50× magnification). Biomass was determined for each taxon in terms of wet weight with a precision of 0.1 mg.

Taxa were assigned to feeding modes based on the literature (Fauchald and Jumars, 1979) and previous work in the area (Carrasco and Carbajal, 1998; Gutiérrez et al., 2000). The feeding modes considered here were: interface feeders (IF), surface deposit-feeders (SDF), subsurface deposit-feeders (SSDF), suspension-feeders (SF), and omnivores/predators (OP). Here we should note that IF includes those species that are able to switch from suspension-feeding to surface deposit-feeding, as explained in Gutiérrez et al. (2000).

2.4. Data analysis

Density and biomass data from each replicate were first standardized by area (m²) and then used to determine the means and standard deviations per month. To assess temporal changes during contrasting ENSO cycle phases (i.e., the 1997–98 and the 2002–03 periods), changes in abundance and in biomass of the total assemblage and of the most representative species were assessed by a one-way Analysis of Variance (ANOVA; $\alpha = 0.05$). The raw data were fourth-root transformed and the homoscedasticity (Bartlett's test), as well as the normality of residuals were checked (Zar, 1974). When significant differences were observed, contrasts were performed by *a posteriori* Tukey's HSD test (Zar, 1974). To compare the community structure of the 1997–98 versus the 2002–03 periods, multivariable analyses of macrofaunal communities were conducted using PRIMER software (PRIMER version 5; Clarke and Gorley, 2001). The species density data matrix was transformed according to $Y = \sqrt{\sqrt{X}}$ (Clarke and Warwick, 1994). The ordination method used was non-metric multidimensional scaling (NMDS) analysis (Field et al., 1982), and the significance of differences between sampling dates was examined by the randomization test ANOSIM (Clarke, 1993). Canonical correspondence analysis (CCA) was performed with the software MVSP (version 3.13). CCA was applied to relate the set of environmental parameters to both (i) species and (ii) feeding mode composition among sampling dates, as suggested by Jongman et al. (1987).

In order to explore seasonal and EN effects on the size structure of the macrobenthic communities, normalized biomass size-spectra (NBSS) were constructed as described by Platt and Denman (1977, 1978). The intercept of NBSS is an indicator of total biomass of the system (Sprules and Munawar, 1986; Quiroga et al., 2005). Mean individual wet weight (*W*) was estimated as total macrofauna community biomass divided by total macrofauna community density. The parameters of the NBSS were determined by regressing the log₂ (normalized biomass) against log₂ (individual weight). Differences among the slopes of NBSS were assessed by an analysis of covariance according to Zar (1974). The spectra were constructed using a maximum of 11 size classes, and pooling data in order to cover the following periods: (i) winter/spring and (ii) summer/fall of 1997–98 and (iii) winter/spring and (iv) summer/fall of 2002–03.

3. Results

3.1. Water column temperature and DO

A notable deepening of the 12 °C isotherm occurred from May 1997 to November 1998, which was located beyond 80 m depth during August 1997 and May 1998. In contrast, the 12 °C isotherm remained above 40 m from November 1998 to June 2003 (Fig. 2A). The highest bottom water DO concentration was recorded in May 1997 (1.11 ml L⁻¹). During following non-EN summers, DO was very low (<0.2 ml L⁻¹). Remarkably strong oxygen-deficient conditions were observed during 2003, with hypoxic waters ascending up to 30 m depth (Fig. 2B).

3.2. Sediment conditions

TOC ranged from 27.9 mg g⁻¹ in August 1997 to 51.8 mg g⁻¹ in March 2003 (Table 1). TN ranged from 3.9 mg g⁻¹ in August 1997 to 7.2 mg g⁻¹, in March 2003. The C/N molar ratio did not show major changes, varying between 8.43 and 11.30. The CPE content in sediments of the study site was more variable, ranging from 195.84 µg g⁻¹ in May 1998 to 794.63 µg g⁻¹ in March 2003. A major increase in CPE was observed in March and June 2003. The redox RPD ranged from 2 cm (August 1997) to 3 cm (November 1997), while the thickest layers of oxidized sediments were observed in September and November 2002. Inventories of sulfide (upper 15 cm) were low in November 1997 and in May 1998, ranging from 1.00 to 3.15 mM m⁻², respectively. High pore water sulfide concentrations were found only in March 2003, with 23.11 mM m⁻², coinciding with the severe hypoxia and organically enriched sediments.

3.3. Macrofaunal community structure, feeding modes and vertical distribution

A total of 45 species of macrofauna were recorded during the whole period of study (Table 2). Polychaetes were the dominant group (30 species), followed by crustaceans (11 species including two larval stages) and mollusks (three species, including two bivalves and one gastropod). One species of nemertean and one species of sipunculid were also found in some samples.

On average for the whole study period, five species of polychaetes (*P. pinnata*, *Mediomastus*

Table 2

Pooled data of species composition, mean density, standard deviation (SD), and percent of total macrofauna for the whole study period

Species	Mean density (ind. m ⁻²)	SD	%
Annelida (Polychaeta)			
<i>Paraprionospio pinnata</i>	9580.9	11,162.2	33.77
<i>Mediomastus branchiferus</i>	6154.8	6879.9	21.7
<i>Cossura chilensis</i>	5905.2	1576.1	20.82
<i>Aricidea pigmentata</i>	1740.0	1704.9	6.13
<i>Nephtys ferruginea</i>	1317.2	1735.2	4.64
<i>Magelona phyllisae</i>	368.9	197.3	1.3
<i>Sigambra bassi</i>	229.1	319.3	0.81
<i>Isolda viridis</i>	183.2	508.7	0.65
<i>Polydora</i> sp.	87.3	370.2	0.31
<i>Protodorvillea</i> sp.	81.4	134.3	0.29
Spionid sp.	72.4	298.9	0.26
<i>Megalomma monoculata</i>	66.8	129.5	0.24
<i>Ninoe chilensis</i>	37.1	56.6	0.13
<i>Nereis dorsolobata</i>	18.8	53.4	0.07
<i>Glycera americana</i>	12.9	23.5	0.05
Lumbrinerid sp.	12.4	19.9	0.04
<i>Harmothoe brevipalpa</i>	6.1	25.9	0.02
<i>Pectinaria chilensis</i>	6.1	25.9	0.02
<i>Typosyllis</i> sp.	5.3	13.1	0.02
Cirratulid sp.	4.6	11.8	0.02
Orbinid sp.	4.0	9.7	0.01
Hesionid sp.	3.7	12.2	0.01
Syllid sp.	3.7	15.7	0.01
<i>Podarke</i> sp.	3.7	15.7	0.01
<i>Haploscoloplos kerguelensis chilensis</i>	2.8	8.6	0.01
Maldanid sp.	1.2	5.2	^a
Oweniid sp.	1.2	5.2	^a
<i>Exogone</i> sp.	1.2	5.2	^a
<i>Prionospio peruana</i>	0.9	3.9	^a
<i>Goniada uncinigera</i>	0.9	3.9	^a
Crustacea			
<i>Ampelisca araucana</i>	2329.5	2575.6	8.21
<i>Pleuroncodes monodon</i>	41.4	115.3	0.15
Cumacea	29.7	65.0	0.1
<i>Pimmixia</i> sp.	4.6	11.2	0.02
Oedicerotid sp.	3.7	10.8	0.01
Zoea n.i.	3.7	15.7	0.01
Gammarid sp.	1.8	7.8	0.01
<i>Heterocarpus reedi</i>	1.8	7.8	0.01
Megalopa n.i.	1.8	7.8	0.01
Ostracoda	0.9	3.9	^a
Mollusca			
<i>Nuculana cuneata</i>	30.0	54.8	0.11
<i>Vitrinella kaykayae</i>	2.8	8.6	0.01
<i>Thyasira tomeana</i>	0.9	3.9	^a
Others			
Nemertea	1.8	7.9	0.01
Sipunculida	0.9	3.9	0.00

n.i. = not identified.

^aPercentage less than 0.01.

branchiferus, *Cossura chilensis*, *Aricidea pigmentata* and *N. ferruginea*), along with the amphipod *Ampelisca araucana* accounted for more than 95% of the overall total abundance (Table 2). The time course of macrofaunal density for the whole period is shown in Fig. 2C. The same trend in density was observed for biomass (Table 3), with these same species accounting for 79–100% of total biomass during the study period.

Comparing the 1997–98 EN and the 2002–03 period, macrofaunal density was lowest in March 1998 ($14,249 \pm 1452 \text{ ind m}^{-2}$) and highest in March 2003 ($73,943 \pm 6863 \text{ ind m}^{-2}$) (ANOVA, $F_{7,23} = 80.63$; $p < 0.001$, and *a posteriori* contrasts). The lowest total biomass was observed in November 1997 ($26.51 \pm 11.09 \text{ g wet weight m}^{-2}$), and the highest in June 2003 ($68.42 \pm 18.47 \text{ g wet weight m}^{-2}$); however, they were not significant (ANOVA $F_{7,23} = 1.47$; $p = 0.55$). The changes of the six dominant species over time, both in terms of abundance and biomass, and feeding modes, are shown in Table 3. Most of these species showed temporal changes in biomass and density. Exceptions were *C. chilensis* and *N. ferruginea* whose abundances did not change significantly (ANOVA $p = 0.39$ and 0.54 , respectively) during the two sampling periods considered. The density of *P. pinnata*, one of the most conspicuous species of

the Chilean margin, was lowest in May 1998 ($3033 \pm 1175 \text{ ind m}^{-2}$) and highest in March 2003 ($34,917 \pm 3675 \text{ ind m}^{-2}$). The capitellid *M. branchiferus* was absent during August and November 1997, but present on later sampling dates. Its densities ranged from $35 \pm 70 \text{ ind m}^{-2}$ (March 1998) to a peak of $18,199 \pm 2917 \text{ ind m}^{-2}$ (March 2003). A similar increasing pattern was observed in the abundance of the paraonid *A. pigmentata*, with low densities during the first sampling period (EN) and higher values during the second (non-EN). The amphipod *A. araucana* disappeared during spring–summer of 2002–03, which was coincident with the low concentration of bottom water DO and high abundances of the polychaetes *P. pinnata*, *M. branchiferus*, *A. pigmentata* and *N. ferruginea*.

Despite the absence of significant changes in total biomass during both periods, there were significant changes in the relative contribution of the different species to the total biomass. Significant biomass increases (ANOVA $p < 0.001$) were observed in *P. pinnata* (from 5.64 ± 3.00 to $35.82 \pm 6.81 \text{ g wet weight m}^{-2}$) from March 1998 to June 2003, in *M. branchiferus* (from 0 to $3.47 \pm 1.46 \text{ g wet weight m}^{-2}$) from August/November 1997 to March 2003, and in *A. pigmentata* (from 0.01 ± 0.01 to $0.86 \pm 0.19 \text{ g wet weight m}^{-2}$) from August 1997 to March 2003. In contrast, a

Table 3

Mean biomass (g wet weight m^{-2}) of the dominant six species and of the total macrofaunal assemblage, and contribution of each feeding mode to total biomass at each sampling

Feeding mode	1997–98				2002–03												
	August		March		November		May		September		November		March		June		
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
(A) Biomass (g wet wm^{-2})																	
<i>Paraprionospio pinnata</i> IF	22.14	5.18	12.46	8.63	5.64	3.00	16.16	5.93	7.43	5.28	3.37	1.33	31.12	11.95	35.82	6.81	
<i>Cossura chilensis</i> SSDF	1.44	1.28	0.51	0.44	0.53	0.06	4.68	3.92	3.66	2.29	1.73	0.51	2.19	0.52	2.74	1.04	
<i>Mediomastus branchiferus</i> SDF	—	—	—	—	0.01	0.01	0.01	0.01	0.01	1.93	0.40	3.05	0.34	3.47	1.46	0.07	0.09
<i>Ampelisca araucana</i> IF	1.23	1.32	1.15	0.94	0.44	0.33	6.54	4.92	2.54	1.20	—	—	—	—	0.42	0.32	
<i>Nephtys ferruginea</i> OP	5.70	6.79	5.68	4.39	2.71	1.69	11.85	11.69	23.90	12.51	7.00	0.94	11.57	2.24	10.86	6.19	
<i>Aricidea pigmentata</i> SDF	0.01	0.01	0.02	0.01	0.02	0.03	0.16	0.13	0.64	0.12	0.78	0.29	0.86	0.19	0.22	0.19	
Total	33.93	10.59	26.51	11.09	51.65	74.82	41.90	13.07	40.90	23.03	48.67	58.00	56.53	20.85	68.42	18.47	
(B) Contribution by feeding mode (%)																	
IF	78.6	7.0	55.8	17.7	42.7	12.8	55.5	21.4	21.3	2.6	6.2	1.2	47.2	2.8	76.9	9.2	
SDF	0.8	1.2	1.9	1.7	1.6	1.5	3.1	1.7	45.9	7.3	66.1	9.1	29.5	2.9	4.3	1.9	
SSDF	18.0	6.7	36.8	17.4	49.3	12.4	39.2	18.5	27.9	5.7	30.8	10.0	11.1	4.1	14.1	5.6	
OP	2.5	1.6	5.5	2.7	6.1	3.3	1.8	1.8	4.6	1.4	2.6	1.3	11.6	7.7	4.4	3.5	
Others	0.0	0.0	0.0	0.0	0.2	0.4	0.4	0.5	0.2	0.3	0.6	0.4	0.5	0.4	0.4	0.1	

IF = interface feeders, SDF = surface deposit-feeders, SSDF = subsurface deposit-feeders, OP = omnivores/predators.

significant decrease in biomass (ANOVA $p < 0.001$) of the amphipod *A. araucana* (from 6.53 ± 4.92 to $0 \text{ g wet weight m}^{-2}$) was observed from May 1998 to March 2003.

Regarding the feeding modes, IF and subsurface deposit feeders were the most common feeding habits observed among shelf macrofauna, followed, on average, by surface deposit feeders (Table 3). The proportional representation of each feeding mode varied between periods. The proportional representation of IF was higher prior to EN conditions and at the end of the summer 2003 (~70%), while lower contributions were observed at the end of EN and at the beginning of the 2002–03 period (~21%, Table 3). The proportional representation of subsurface deposit feeders decreased from 50% to 10.4% (March 1998 to March 2003). The contribution of surface deposit feeders was low during the EN phase. The contribution of opportunistic and predator species did not show a clear pattern during the study period.

The vertical distribution of the macrofauna species (i.e., depth at which 50% and 95% of total number occurred) is shown in Fig. 3. In the EN phase (1997–98) a larger proportion of the macrofauna (mostly polychaetes) was found at the deeper layers of the sediment during the whole period, whereas there was an upward migration (> 50% of macrofauna thriving in the upper 2 cm) during the summer/fall 2002–2003 (non-EN).

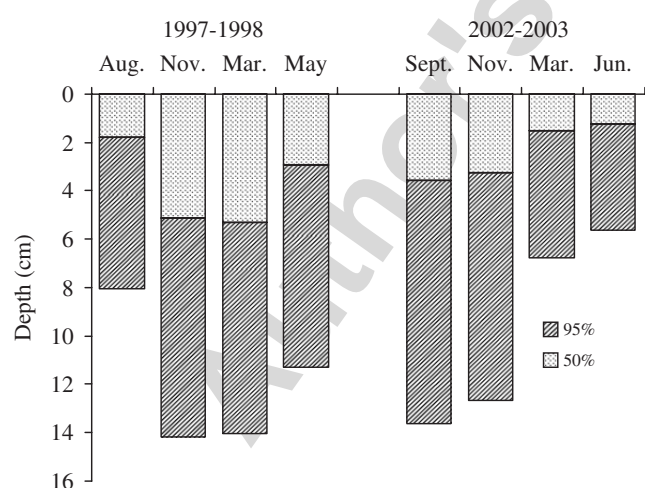


Fig. 3. Vertical distribution of macrofaunal biomass in the upper 20 cm of the sediment during winter/spring and summer/fall 1997–1998 and winter/spring and summer/fall 2002–2003. Bars indicate the location of the accumulative 50% and 95% of total biomass.

3.4. Normalized biomass size spectra

The slopes of the normalized biomass size spectra (NBSS) significantly differed from 0 ($p < 0.05$), with slopes ranging from -0.633 (summer/fall 1997–98) to -1.066 (summer/fall 2002–03) (Fig. 4). A less negative slope at the end of EN suggests a higher contribution of larger-sized organisms. However, when comparing different periods (i.e., winter/spring and summer/fall 1997–98 (Fig. 4A and B), and winter/spring and summer/fall 2002–03 (Fig. 4C and D) the differences were not significant ($p > 0.05$). However, the intercepts of the NBSS, an indicator of total biomass of the system, ranged between 3.304 (summer/fall 1997–98) and 4.975 (summer/fall 2003–03), showing significant differences between them ($p < 0.05$), pointing to higher biomass during non-EN conditions.

3.5. Ordination analyses

The results of the CCA are shown in Fig. 5. Only the five environmental variables that explained most of the variance were included in the analysis (i.e., CPE, RPD, TOC, DO and bottom water temperature). When the abundance of the dominant macrofaunal species is related to the environmental variables (Fig. 5A) the first two CCA axis eigenvalues accounted for 83.3% of the total variance. When feeding mode composition was used (Fig. 5B), the first two CCA axis accounted for 85.2% of the explained variance. This suggests a relatively good dispersal of the biological data along the different axis in both analyses (Kröncke and Türkay, 2003; Narayanaswamy et al., 2003). For the macrofauna specific composition, the first axis reveals gradients influenced by temperature ($r = -0.85$), RPD ($r = 0.79$) and DO ($r = -0.58$), while the second axis reflects a gradient influenced by TOC ($r = 0.73$) and CPE ($r = -0.60$) (Fig. 5A). For the functional composition (i.e., feeding modes), the first axis indicates that temperature ($r = -0.78$) and RPD ($r = 0.89$) were the most important variables, while CPE ($r = 0.88$) and TOC ($r = 0.57$) best explained the variance along the second axis.

Multivariate analyses (NMDS) based on all density data collected in each sampling date, showed distinct assemblages, forming a clockwise temporal gradient (Fig. 6). The ANOSIM test revealed five different period-groups ($p < 0.05$), (i) August 1997, November 1997 and March 1998,

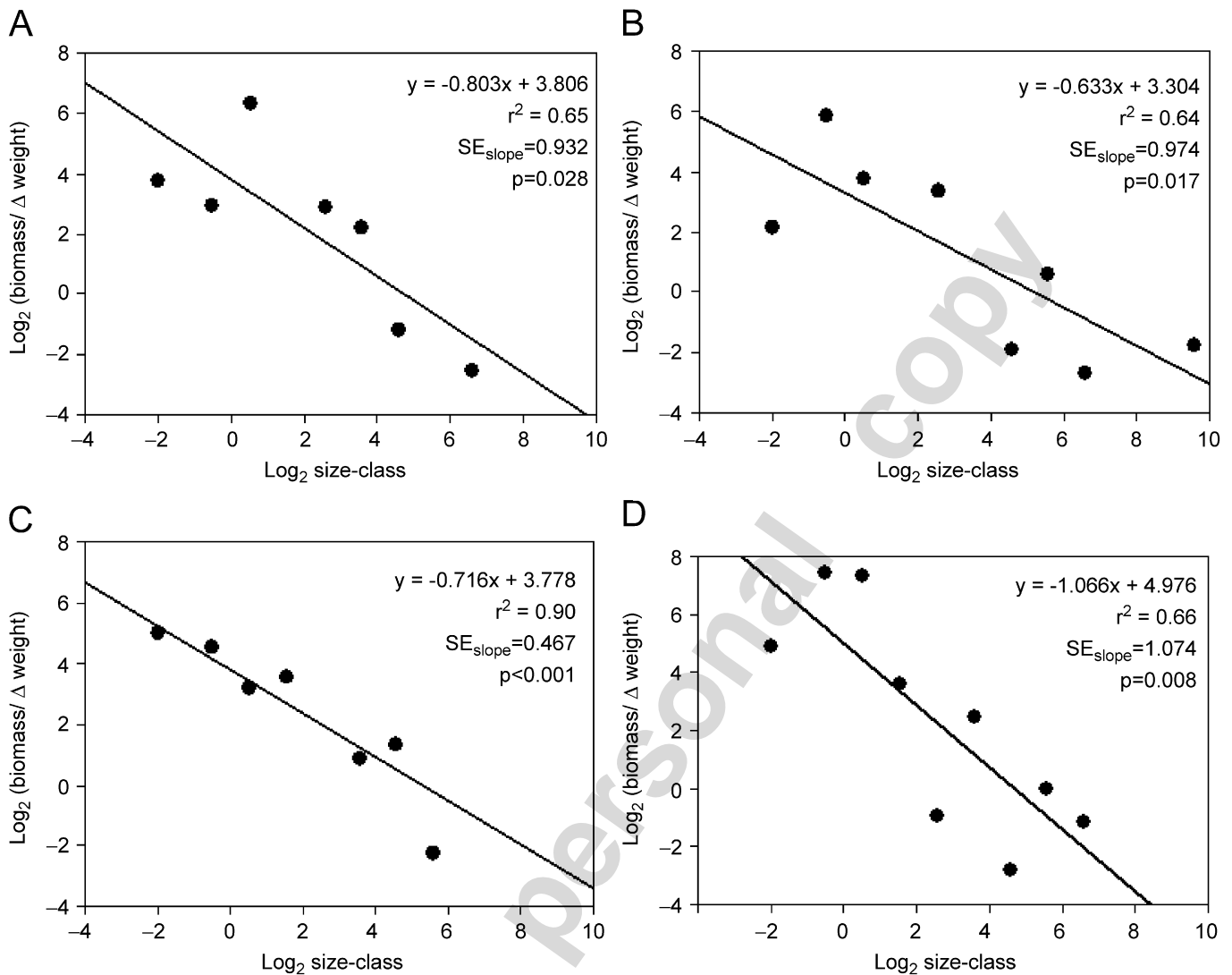


Fig. 4. Normalized biomass size-spectra of the macrofauna in: (A) winter/spring and (B) summer/fall, of the 1997–98 period; and (C) winter/spring and (D) summer/fall of the 2002–03 periods. The squared correlation coefficient (r^2), the Standard Error of the slope (SE_{slope}) and the p -values are indicated for each regression.

- (ii) May 1998, (iii) September and November 2002, (iv) March 2003, and (v) June 2003.

4. Discussion

4.1. Water column and sediment conditions, intra- and inter-annual variability

During the 1997–98 EN phase, the water column was, in general, warmer ($>12^\circ\text{C}$) and more oxygenated (bottom water oxygen $>0.5 \text{ ml L}^{-1}$) than the following summers. In contrast, an extended hypoxia during late summer 2002–03 was observed (bottom water oxygen $\sim 0.08 \text{ ml L}^{-1}$). In fact, under normal spring and summer conditions, upwelled Equatorial Sub-surface Water, rich in

nutrients and low in oxygen, covers large areas of the continental shelf. In contrast, during winter or EN conditions, upwelling is unusual or non-existent, and the shelf is covered by Sub-Antarctic Water rich in oxygen (Strub et al., 1998). In this way, during an EN period, most important seasonal effects over shelf hydrographic conditions, like the ascent of colder, nutrient-rich and oxygen deficient water during summer, are suppressed or at least, smoothed. The overall result is that winter-like conditions (i.e., absence of bottom water oxygen deficiency and low organic input) persist for a whole year over the shelf. Indeed, a recent study showed that although seasonal timing of the upwelling period was similar for both periods (1997–98 EN vs. 2002–03 non-EN), the strength of the upwelling

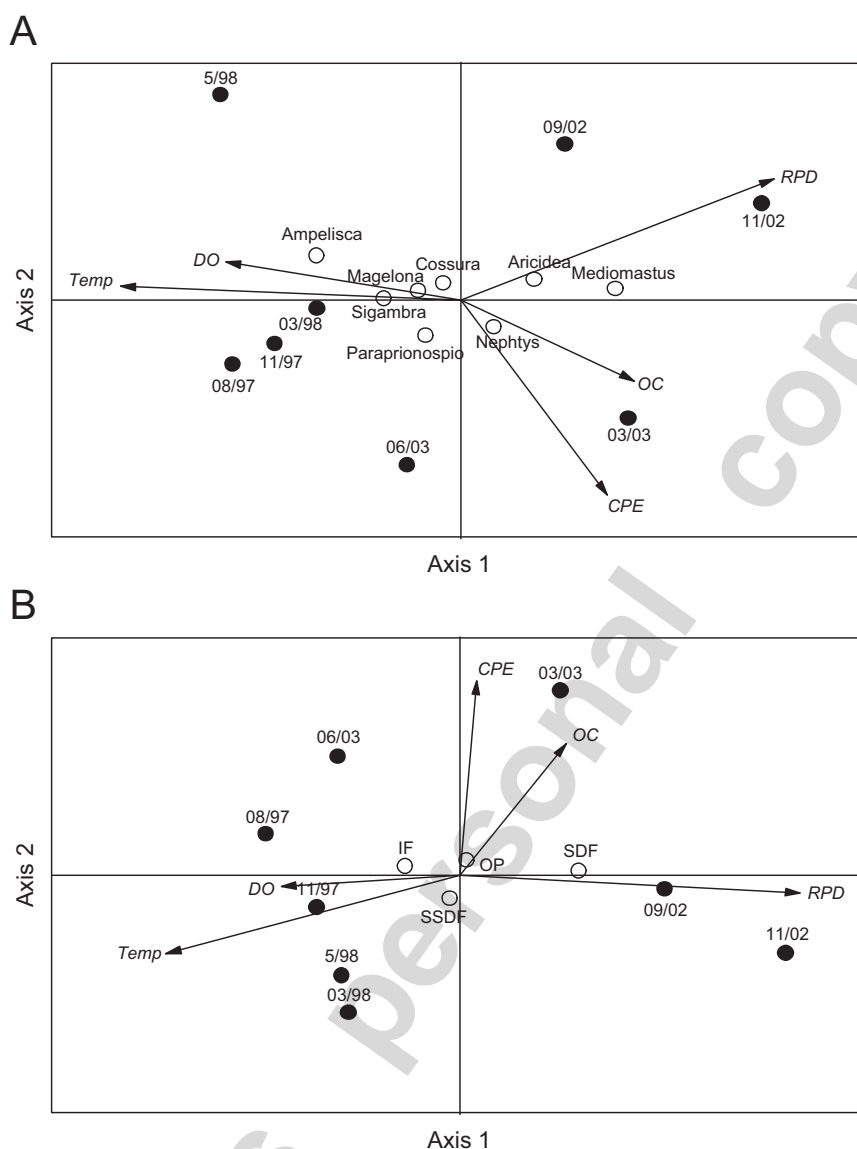


Fig. 5. Canonical correspondence analyses (CCA) ordination plot of the macrofaunal species (A) and the feeding mode groups (B), including sampling periods and environmental variables. The feeding modes were: IF = interface feeders, SDF = surface deposit-feeders, SSDF = sub-surface deposit feeders, OP = omnivores-predators. Abbreviations for environmental variables as in Table 1, Temp = bottom water temperature.

during EN was about three times lower. This was attributed to the effects of EN on the thermocline depth (S. Contreras, unpublished data).

Differences in sediment settings between both periods were also evident. The year after EN, cold or “La Niña” conditions developed (Sellanes, 2002; Escribano et al., 2004), and in subsequent years normal or non-EN conditions prevailed, i.e., environmental settings returned to the condition of oxygen-depleted bottom water, high content of TOC and fresh phytodetritus (CPE) in the sediments, with high concentrations of porewater sulfide. These characteristics were most evident in

March 2003 (Fig. 2, Table 1). As an example, TOC values at this month were 52 mg g^{-1} , while during the whole EN year values never surpassed 38 mg g^{-1} (Table 1). Typical values TOC for non-EN years for this site are always over 40 mg g^{-1} , as reported by previous studies (e.g., Thamdrup and Canfield, 1996; Gutiérrez, 2000).

The apparent discordance between the oxidation state of the sediment (deeper RPD) and the returning of oxygen-deficient conditions after EN (Table 1), could be explained by the associated return of bottom waters rich in nitrate, an important electron acceptor whose concentrations

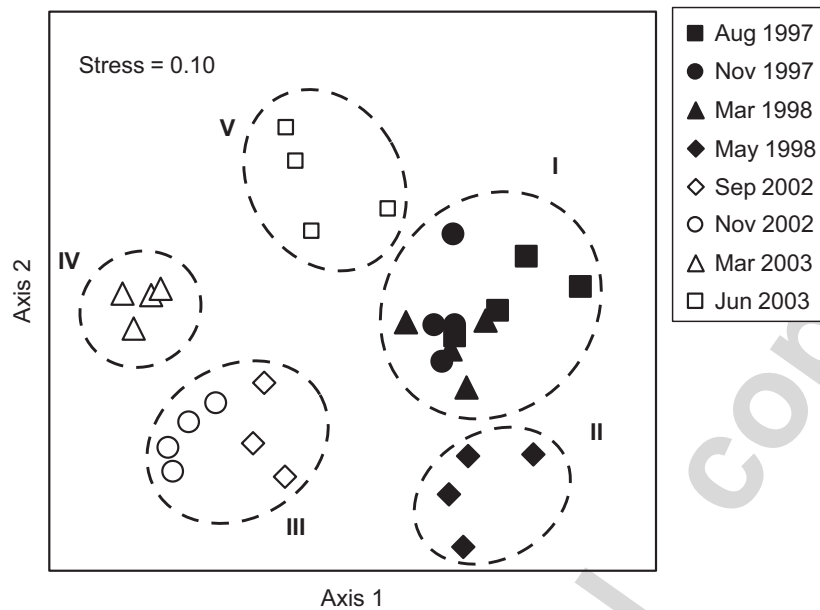


Fig. 6. Non-metric multidimensional scaling (NMDS) ordination plot based on macrofaunal species density, at the different sampling dates and during the study period. The ellipses indicate the five groups formed by the ANOSIM test ($p < 0.05$).

usually exceed $25 \mu\text{M}$ during non-EN periods (e.g., [Thamdrup and Canfield, 1996](#)). Alternatively, the deepening of the RPD layer during the 2002–03 winter/spring could be the result of the high abundances of the burrowing polychaete *M. branchiferus*, which dominated the community prior to the following summer/fall period. Burrowing activity can enhance the sediment oxidation by mixing and subducting oxidized solutes and Fe^{+3} -rich particles that remove free sulfide ([Díaz et al., 1994](#)).

4.2. Response of the fauna to environmental changes

A decreasing trend in macrofaunal density and deepening into the sediment evolved towards the end of the 1997–98 EN, mainly due to the decrease of the interface-feeder polychaete *P. pinnata* ([Gutiérrez et al., 2000](#)), an opportunistic polychaete that has metabolic adaptations to cope with hypoxic conditions ([González and Quiñones, 2000](#)). Several observations indicated that *P. pinnata* was the dominant macrofaunal organism in these sediments, at least until the previous 2 years before the 1997–98 EN ([Gallardo et al., 1995](#); [Huettel et al., 1996](#); [Vásquez, 1999](#)). It appears that more oxygenated bottom water and oxidized sediment during EN caused *P. pinnata* to fail in its summer recruitment. In addition, it is probable that increased competition and predation by other species have contributed to its decline. Indeed, it has been reported that

during EN, many subtropical predators invade the coastal areas, or even local predators change their depth zonation ([Arntz et al., 1991](#)), negatively affecting the surface-feeding polychaetes ([Tarazona et al., 1996](#)). Off Peru, during EN 1992–93, these predators consisted mainly in highly motile megafaunal species such as decapod crabs and shrimps, and fishes ([Arntz et al., 1991](#)). Since no data on megafaunal or demersal fishes assemblages exist for our benthic study, this factor still remains speculative for the shelf off Concepción. On the other hand, [Levin and Gage \(1998\)](#) suggested that while the dominance patterns of polychaete communities correlate with the organic matter content, the species richness was modulated by oxygen availability. This model fits well with what we observed for the whole polychaetes assemblage. During EN the decrease in abundance of *P. pinnata* related well with the lower organic matter quality (mainly in terms of CPE) and higher oxygen. However, *P. pinnata* recovered its numerical dominance only in summer 2003, i.e., 5 years after the end of EN. Following the 1997–98 EN, a rapid switch to La Niña conditions occurred, and high fluxes of organic matter and strong reducing conditions were detected in summer 1999 ([Gutiérrez, 2000](#); [Graco et al., 2006](#)). Notwithstanding with these conditions, *P. pinnata* failed to recruit in the shelf and in the bay of Concepción ([Gutiérrez, 2000](#)). This lack of population response suggests that the recruitment failure was not due to habitat selectivity but was

more likely due to reduced larvae supply by the weakened adult population. The following succession of dominant burrowing deposit-feeders (*M. branchiferus*; Fig. 2C) and the delayed post EN recovery of *P. pinnata* can be explained by the combination of the prevailing environmental conditions and the negative mobility-mode interactions between burrowing and tube-dwelling infauna (Posey, 1990; Hall, 1994). In this sense, the successful recruitment of surface and subsurface-deposit feeders in 1999 coincided with the absence of tube mats in the sediment surface. Once established, the predominantly burrowing community could have precluded the successful recruitment of *P. pinnata* until severe hypoxic and sulfidic conditions were developed during summer 2003. It is possible that the large organic fluxes to the bottom (Muñoz et al., 2004b) contributed to a rapid return to reducing conditions in the sediment/water interface. Under these conditions dominant burrowing polychaetes (*M. branchiferus*, *C. chilensis*, *A. pigmentata*) were inhibited or displaced. Free of these burrowing competitors, *P. pinnata* recruited successfully, and the population increased explosively.

The results of the multivariate analyses revealed significant effects of changing temperature, DO and sediment-related parameters on macrofaunal community structure. Effects were also reflected in changes in feeding modes, in the vertical distribution of animals in the sediment and in the size spectra. Two clear groupings were formed (CCA analysis), one related to the 1997–98 period, associated with higher bottom oxygen and temperature, and the other (2002–03) related to higher TOC and CPE loadings, in particular during March 2003. It is remarkable that at species- and feeding-mode level the first two axes (Fig. 5) explained most of the variance, suggesting with a high degree of confidence that the selected variables (temperature, RPD, oxygen, CPE and TOC) were responsible for the observed patterns of macrofaunal community structure and feeding modes. The NMDS analysis, based on macrofaunal species densities at each sampling date, agreed with the separation of two distinct groups, each related to the different seasons/ENSO phases.

An important consequence of the deepening of the OMZ during EN is the contact of oxygenated waters with sub-oxic sediments on the shelf (Gutiérrez et al., 2000). This led to changes in the sediment biogeochemistry influencing the commu-

nity structure, distribution, and the relative contribution of functional groups (Gutiérrez et al., 2000; Neira et al., 2001a,b). Higher rates of reworking and extensive irrigation of surface sediments were observed during the EN period compared with the 2002–03 non-EN period (Muñoz et al., in press), consistent with the observed patterns of macrofaunal vertical distribution and density. Particle-mixing coefficients (D_b) estimated for the study site by Gutiérrez (2000) using excess ^{234}Th concentrations, ranged from 47 to 188 $\text{cm}^2\text{yr}^{-1}$ during EN. Moreover, excess ^{234}Th (half-life = 24.1 d), which tracks particles input to the seabed, penetrated as deep as 10 cm. Similar estimates made from Chl-*a* distribution in the sediments ranged from 11 to 286 $\text{cm}^2\text{yr}^{-1}$, indicating higher bioturbation rates at the end of EN (Gutiérrez, 2000). Although no excess ^{234}Th measurements in the study site were available for the 2002–03 period, the presence of more macroinfauna living near the sediment surface (Fig. 3) and low bioturbation coefficients estimated by Chl-*a* profiles suggest that re-working was considerably diminished (4 $\text{cm}^2\text{yr}^{-1}$) in March 2003 (Muñoz et al., in press).

4.3. Normalized biomass-size spectra

The results suggest that the body size of the macrobenthic community tended to be larger during the EN period, compared with the subsequent period when low oxygen concentrations prevailed. NBSS have been used to describe and compare benthic communities (e.g., Drgas et al., 1998; Saiz-Salinas and Ramos, 1999). In the study area, low oxygen conditions greatly influence the size structure of macrobenthic communities (Quiroga et al., 2005). Although not significantly different, the slope of the NBSS for macrofauna was less negative during the 1997–98 EN (slope = -0.633) (Fig. 4B) compared with the same period under non-EN conditions (-1066) (Fig. 4D). This evidence, together with the measured biomass values, suggests the occurrence of a higher biomass during non-EN conditions, particularly during summer–fall 2002–03. The biomass decrease during EN could be explained by the population crash of *P. pinnata*, which alone was able to represent more than 50% of the total density prior to the 1997–98 EN (Vásquez, 1999; Gutiérrez, 2000). This is also consistent with the macrofaunal biomass drop reported by Gallardo (1985) during the previous EN (1982–83) for the

shelf off Concepción, who found values 4.4 times lower than previous measurements in 1975 (a non-EN year). However, off Peru, during the 1982–83 EN a significant increase in macrofaunal biomass was reported at a shallow (34 m) shelf site in the Bay of Ancón (Tarazona et al., 1996), but at deeper sites (40–110 m), these changes were not evident (Arntz et al., 1991).

5. Concluding remarks

Based on oceanographic and sediment parameters, we conclude that the environmental conditions at the study site are highly variable, at both seasonal and inter-annual scales. However, supported also by the limited data available for the study area, we attribute these changes to different phases of the ENSO cycle. The primary effect induced by its warm phase seems to be an attenuation in seasonal differences (i.e., inter-annual variability), between the winter/spring and summer/fall periods. Indeed, winter-like conditions prevailed the whole 1997–98 EN period (i.e., higher bottom temperature, oxygenated bottom water, lower organic matter, and oxidized sediments). The biota responded to this apparent lack of seasonal variation during EN period with an absence of major changes in size spectra as well as in vertical distribution of the fauna. In contrast, during the 2002–03 period, smaller, more abundant and near-surface living animals tended to dominate towards the end of the austral summer. This was most likely caused by a successful recruitment of *P. pinnata*. To our knowledge the present study is the first to suggest an inter-annual variability in size structure of macrobenthic communities in the region, which we relate with changes in environmental conditions during the two contrasting phases of the ENSO cycle.

The environmental and biological data also suggest that a strong EN can trigger a complex cascade of biogeochemical and ecological processes in the surface sediment, that begin with a decrease of sediment organic loading of the shelf area during the event. However, the effects on the benthic community last longer than the period of the oceanographic disturbance, most probably due to the response lag of the populations (e.g., *P. pinnata*), as well as other ecological interactions. In this case, it took 5 years before *P. pinnata*, an opportunistic polychaete well fit to cope with anoxic or sulphidic conditions, recovered its dominance in the

macrofauna (Fig. 2). However, to assert how many of these observed changes repeat, and how much variation could be effectively attributed to the ENSO cycle, we need longer-term studies following several cycles.

Acknowledgments

We specially thank the captain and crew of the R.V. *Kay Kay*, as well as the technical staff of the Marine Biology Station of the University of Concepción at Dichato. We also thank T. Höpner (ICBM, University of Oldenburg) for support and laboratory facilities. Special thanks to L. Levin, C. Whitcraft and two external anonymous reviewers for helpful comments on earlier versions of this manuscript. This research was funded by CONICYT, Chile (FONDECYT project #1971336 and FONDAF program) and the Center for Oceanographic Research in the Eastern South Pacific (COPAS). Additional support was provided to J.S. by the Deutscher Akademischer Austauschdienst (DAAD).

References

- Ahumada, R., Rudolph, A., Martinez, V., 1983. Circulation and fertility of waters in Concepción Bay. *Estuarine, Coastal and Shelf Science* 16, 95–105.
- Arntz, W.E., Fahrback, E., 1996. El Niño: experimento climático de la naturaleza. Causas físicas y efectos biológicos. Fondo de Cultura Económica, México DF.
- Arntz, W., Tarazona, J., Gallardo, V.A., Flores, L.A., Salzwedel, H., 1991. Benthos communities in oxygen deficient shelf and upper slope areas of the Peruvian and Chilean Pacific coast, and changes caused by El Niño. In: Tyson, R.V., Pearson, T.H. (Eds.), *Modern and Ancient Continental Shelf Anoxia*, Geological Society Special Publications, vol. 58, 1991, pp. 131–154.
- Barnett, P.R., Watson, J., Connelly, D., 1984. A multiple corer for taking virtually undisturbed samples from shelf, bathyal and abyssal sediments. *Oceanologica Acta* 7, 399–408.
- Carrasco, F., Arcos, D., 1984. Life history and production of a cold-temperate population of the sublittoral amphipod *Ampelisca araucana*. *Marine Ecology Progress Series* 14, 245–252.
- Carrasco, F., Carbajal, W., 1998. The distribution of polychaetes feeding guilds in organics enriched sediments of San Vicente bay, Central Chile. *International Review of Hydrobiologia* 83, 233–249.
- Clarke, K., 1993. Non-parametric multivariable analysis of changes in community structure. *Australian Journal of Ecology* 18, 117–143.
- Clarke, K., Gorley, R., 2001. User Manual/Tutorial, Primer version 5. Primer-E, Plymouth.

- Clarke, K., Warwick, R., 1994. Changes in marine communities: an approach to statistical analysis and interpretation. Bourne Press Ltd, Plymouth.
- Cline, J.D., 1969. Spectrophotometric determination of hydrogen sulfide in natural waters. *Limnology and Oceanography* 14, 454–458.
- Daneri, G., Dellarossa, V., Quiñones, R., Jacob, B., Montero, P., Ulloa, O., 2000. Primary production and community respiration in the Humboldt Current System off Chile and associated oceanic areas. *Marine Ecology Progress Series* 197, 41–49.
- Díaz, R.J., Cutter, G.R., Rhoads, D.C., 1994. The importance of bioturbation to continental slope sediment structure and benthic processes off Cape Hatteras, North Carolina. *Deep-Sea Research II* 41, 719–734.
- Drgas, A., Radziejewska, T., Warzocha, J., 1998. Biomass size spectra of near-shore shallow-water benthic communities in the Gulf of Gdansk (Southern Baltic Sea). *Marine Ecology* 19, 209–228.
- Escribano, R., Daneri, G., Farías, L., Gallardo, V.A., González, H., Gutiérrez, D., Lange, C., Morales, C., Pizarro, O., Ulloa, O., Braun, M., 2004. Biological and chemical consequences of the 1997–1998 El Niño in the Chilean coastal upwelling system: a synthesis. *Deep-Sea Research II* 51, 2389–2411.
- Fauchald, K., Jumars, P.A., 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology: An Annual Review* 17, 191–284.
- Field, J., Clarke, K., Warwick, R., 1982. A practical strategy for analyzing multispecies distribution patterns. *Marine Ecology Progress Series* 8, 37–52.
- Fossing, H., Gallardo, V.A., Jørgensen, B.B., Hüttel, M., Nielsen, L.P., Schulz, H.N., Canfield, D.E., Forster, S.E., Glud, R.N., Gundersen, J.K., Küver, J., Ramsing, N.B., Teske, A., Thamdrup, B., Ulloa, O., 1995. Concentration and transport of nitrate by the mat-forming sulfur bacterium *Thioploca*. *Nature* 374, 713–715.
- Gallardo, V.A., 1977. Large benthic microbial communities in sulphide biota under the Peru–Chile subsurface counter-current. *Nature* 268, 331–332.
- Gallardo, V.A., 1985. Efectos del fenómeno de “el Niño” sobre el bentos sublitoral frente a Concepción, Chile. In: Arntz, W.A., Landa, A., Tarazona, J. (Eds.), “El Niño”: su Impacto en la Fauna Marina. Boletín Instituto del Mar del Perú (edición especial) Callao, Perú, pp. 79–85.
- Gallardo, V.A., Castillo, J.G., Yañez, L.A., 1972. Algunas consideraciones preliminares sobre ecología bentónica de los fondos sublitorales blandos en la Bahía Concepción. *Boletín de la Sociedad de Biología de Concepción, Chile* 44, 169–190.
- Gallardo, V.A., Carrasco, F.D., Roa, R., Cañete, J.I., 1995. Ecological patterns in the benthic macrobiota across the continental shelf off central Chile. *Ophelia* 40, 167–188.
- González, R.R., Quiñones, R.A., 2000. Pyruvate oxidoreductase involved in glycolytic anaerobic metabolism on polychaetes from the continental shelf off central-south Chile. *Estuarine Coastal and Shelf Science* 51, 507–519.
- Graco, M., Gutiérrez, D., Farías, L., 2006. Inter-annual variability of the pelagic–benthic coupling in the upwelling system off central Chile. *Advances in Geosciences* 6, 127–132.
- Gutiérrez, D., 2000. Bioperturbación y macrofauna en fondos sublitorales de un área de Surgencias frente a Chile central (36° 30' S): variación espacial y temporal en el período 1997–1999. Ph.D. Thesis, Universidad de Concepción, Chile, unpublished.
- Gutiérrez, D., Gallardo, V.A., Mayor, S., Neira, C., Vásquez, C., Sellanes, J., Rivas, M., Soto, A., Carrasco, F.D., Baltazar, M., 2000. Effects of dissolved oxygen and fresh organic matter on macrofaunal bioturbation potential in sublittoral bottoms off central Chile, during the 1997–1998 El Niño. *Marine Ecology Progress Series* 202, 81–99.
- Hall, S.J., 1994. Physical disturbance and marine benthic communities: life in unconsolidated sediments. *Oceanography and Marine Biology: An Annual Review* 32, 179–239.
- Huettel, M., Forster, S., Klösser, S., Fossing, H., 1995. Vertical migration in the sediment-dwelling sulfur bacteria *Thioploca* spp. in overcoming diffusion limitations. *Applied and Environmental Microbiology* 62, 1863–1872.
- Jongman, R., Ter Braak, C., van Tongeren, O., 1987. *Data Analysis in Community and Landscape Ecology*. PUDOC, Wageningen, 299pp.
- Knap, A., Michaels, A., Dow, R., Johnson, R., Gundersen, K., Sorensen, J., Close, A., Howse, A., Hammer, F., Bates, N., Doyle, A., Waterhouse, T., 1993. *Bermuda Atlantic Time Series Study Methods Manual (Version 3)*. Bermuda Biological Station for Research, Inc., US JGOFS.
- Kröncke, I., Türkay, M., 2003. Structural and functional aspects of the benthic communities in the deep Angola Basin. *Marine Ecology Progress Series* 260, 43–53.
- Levin, L., Gage, J., 1998. Relationships between oxygen, organic matter and diversity of bathyal macrofauna. *Deep-sea Research II* 45, 129–163.
- Lorenzen, C., Jeffrey, J., 1980. Determination of chlorophyll in sea water. *UNESCO Technical Papers in Marine Sciences* 35, 1–20.
- Mc Phaden, M.J., 1999. Genesis and evolution of the 1997–1998 El Niño. *Science* 283, 950–954.
- Muñoz, P., Lange, C., Gutiérrez, D., Hebbeln, D., Salamanca, M., Dezileau, L., Reyss, J., Benninger, L., 2004a. Recent sedimentation and mass accumulation rates based on ²¹⁰Pb along the Peru–Chile continental margin. *Deep-Sea Research II* 51, 2523–2541.
- Muñoz, P., Salamanca, M., Neira, C., Sellanes, J., 2004b. Nitrogen sediment fluxes in an upwelling system off central Chile (Concepción bay and adjacent shelf) during the 1997–98 El Niño. *Revista Chilena de Historia Natural* 77, 305–318.
- Muñoz, P., Sellanes, J., Lange, C., Palma, M., Salamanca, M.A. Temporal variability of ²¹⁰Pb fluxes in shelf sediments beneath a high primary production area of central southern Chile (36°S). *Progress in Oceanography*, in press.
- Narayanaswamy, B., Nickell, T., Gage, J., 2003. Appropriate levels of taxonomic discrimination in deep-sea studies: species vs. family. *Marine Ecology Progress Series* 257, 59–69.
- Neira, C., Sellanes, J., Soto, A., Gutiérrez, D., Gallardo, V.A., 2001a. Meiofauna and sedimentary organic matter off central Chile: response to changes caused by the 1997–1998 El Niño. *Oceanologica Acta* 24, 313–328.
- Neira, C., Sellanes, J., Levin, L.A., Arntz, W.E., 2001b. Meiofaunal distributions on the Peru margin: relationship to oxygen and organic matter availability. *Deep-Sea Research I* 48, 2453–2472.
- Pfannkuche, O., Soltwedel, T., 1998. Small benthic size classes along the N.W. European continental margin: spatial and temporal variability in activity and biomass. *Progress in Oceanography* 42, 189–207.

- Platt, T., Denman, K., 1977. Organization in the pelagic ecosystem. *Helgolaender Wissenschaftliche Meeresuntersuchungen* 30, 575–581.
- Platt, T., Denman, K., 1978. The structure of pelagic ecosystems. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer* 173, 60–65.
- Posey, M.H., 1990. Functional approaches to soft-substrate communities: how useful are they? *Aquatic Sciences* 2 (3–4), 343–356.
- Quiroga, E., Quiñones, R., Palma, M., Sellanes, J., Gallardo, V.A., Gerdes, D., Rowe, G., 2005. Biomass size-spectra of macrobenthic communities in the oxygen minimum zone off Chile. *Estuarine, Coastal and Shelf Science* 62, 217–231.
- Saiz-Salinas, J., Ramos, A., 1999. Biomass size-spectra of macrobenthic assemblages along water depth in Antarctic. *Marine Ecology Progress Series* 178, 221–227.
- Schulz, H.N., Strotmann, B., Gallardo, V.A., Jørgensen, B.B., 2000. Population study of the filamentous sulfur bacteria *Thioploca* spp. off the bay of Concepción. *Marine Ecology Progress Series* 200, 117–126.
- Sellanes, J., 2002. Efectos de El Niño 1997-1998 sobre los indicadores bioquímicos de la calidad de la material orgánica sedimentaria y la meiofauna en un área de surgencia costera de Chile central. Ph. D. Thesis, Department of Oceanography, University of Concepción, Chile, unpublished.
- Sellanes, J., Neira, C., 2006. ENSO as a natural experiment to understand environmental control of meiofaunal community structure. *Marine Ecology* 27, 31–43.
- Sellanes, J., Neira, C., Quiroga, E., 2003. Composition, structure and energy flux of the meiobenthos off central Chile. *Revista Chilena de Historia Natural* 76, 401–415.
- Sprules, W., Munawar, M., 1986. Plankton size spectra in relation to ecosystem productivity, size, and perturbation. *Canadian Journal of Fisheries and Aquatics Sciences* 43, 1789–1794.
- Strub, P.T., Mesías, J.M., Montecinos, V., Rutllant, J., Salinas, S., 1998. Coastal ocean circulation off western South America. In: Robinson, A.R., Brink, K.H. (Eds.), *The Sea*, vol. 11, pp. 273–313.
- 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.
- Thamdrup, B., Canfield, D.E., 1996. Pathways of carbon oxidation in the continental margin off central Chile. *Limnology and Oceanography* 41, 1629–1650.
- Tomicic, J., 1985. Efectos del fenómeno El Niño 1982–83 en las comunidades litorales de la península de Mejillones. *Investigaciones Pesqueras* 32, 209–213.
- Vásquez, C., 1999. Variación temporal y espacial de la macroinfauna bentónica de Bahía Concepción y plataforma continental adyacente (36°40'S, 73°02'W). Undergraduate Thesis, Department of Oceanography, University of Concepción, Chile, unpublished.
- Williams, P., Jenkinson, N.W., 1982. A transportable micro-processor controlled precise Winkler titration suitable for field station and shipboard use. *Limnology and Oceanography* 27, 576–584.
- Zar, J., 1974. *Biostatistical Analysis*, second ed. Prentice-Hall, Englewood Cliffs, NJ.