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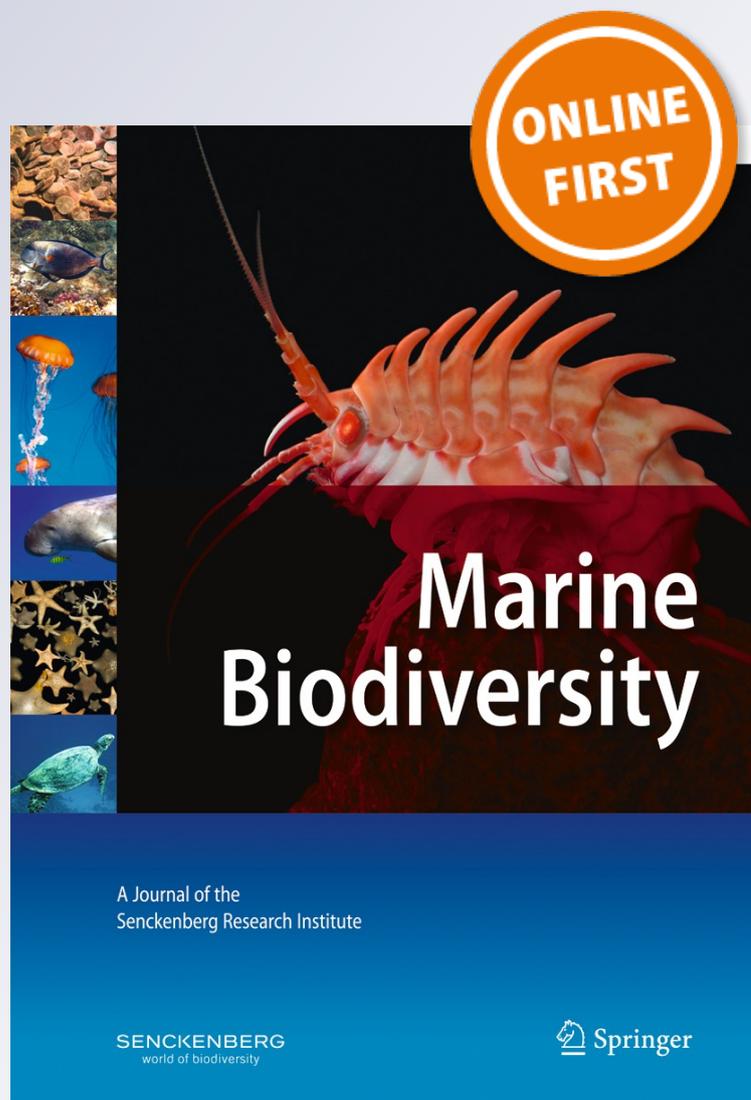
**Eulogio Soto, Eduardo Quiroga,
Benjamín Ganga & Guillermo Alarcón**

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Influence of organic matter inputs and grain size on soft-bottom macrobenthic biodiversity in the upwelling ecosystem of central Chile

Eulogio Soto¹ · Eduardo Quiroga² · Benjamín Ganga¹ · Guillermo Alarcón¹

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Abstract Soft-bottom macrobenthic communities on the continental shelf of central Chile were characterised, in number, by polychaetes, followed by amphipods, bivalves and cumaceans, while biomass was dominated by *Amphioplus magellanicus* (Ophiuroidea). The standing stocks followed a parabolic pattern relative to depth (highest at mid-shelf) but the species were divided into inshore (22 to 50 m) and offshore (80 to 140 m) assemblages, based on the similarity in species composition. Diversity (E_s) was highest in the shallow assemblage and lowest at the deeper locations, suggesting that the decline in oxygen offshore was impacting the numbers of species. Dominance followed the opposite pattern, with greatest dominance at the deepest two stations. The distribution of sizes at each site, measured as normalised biomass size spectra (NBSS), was not different among the sites, although total biomass was concentrated in the single large ophiuroid at the deepest location. Significant correlations ($p < 0.05$) indicated that diversity and number of species were mainly related to the organic content (i.e. total organic carbon) and sediment composition (grain size). Therefore, food supply from primary production and the physical properties of the seafloor are thought to be the main forces structuring the macrobenthos biodiversity and distribution.

Keywords Benthic diversity · Community structure · Organic content · Spatial distribution · Terrigenous inputs · Southeast Pacific

Introduction

Macrobenthic communities are diverse and an important constituents of soft-bottom marine ecosystems, exhibiting a high adaptability to different habitats (Díaz-Castañeda and Valenzuela-Solano 2009). They inhabit a wide range of environments from intertidal to hadal systems, in which the sediment conditions play a key factor in controlling the structure and functioning of ecosystems (Olsgard et al. 2003; Gray and Elliot 2009). Despite substantial effort expended on environmental impact studies, there is a considerable uncertainty about the detection and estimation of ecological impacts due to anthropogenic activity or natural spatial and temporal variability (Osenberg and Schmitt 1994). Coastal and continental shelf benthic communities exhibit defined spatial and temporal patterns which are, in turn, associated with natural environmental forces, such as the oxygen minimum zones (OMZ), terrigenous run-off or warm phase of the El Niño–Southern Oscillation (ENSO) cycle (e.g. Tarazona et al. 1996; Sumida et al. 2005; Arntz et al. 2006; Levin et al. 2009a, b; Zalmon et al. 2013). In addition, macrobenthic communities appear to be particularly sensitive to anthropogenic activities, such as sewage outfalls (Elías et al. 2005; Smith and Shackley 2006), oil spills (Gray et al. 1990), dredging (Boyd et al. 2003) and trawling (Thrush and Dayton 2002). These perturbations produce important changes in the environmental conditions that can modify the biogeochemical properties of the water column and sediments, shaping the macrobenthic community biodiversity (Pearson and Rosenberg 1978; Dauer and Conner 1980; Dauvin et al. 2003).

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✉ Eulogio Soto
eulogio.soto@uv.cl

¹ Facultad de Ciencias del Mar y de Recursos Naturales, Universidad de Valparaíso, P.O. Box 5080 Reñaca, Avenida Borgoño 16344, Viña del Mar, Chile

² Escuela de Ciencias del Mar, Pontificia Universidad Católica de Valparaíso (PUCV), Av. Altamirano 1480, P.O. Box 1020, Valparaíso, Chile

The environmental conditions appear to be a main factor controlling the benthic diversity patterns in soft-bottom systems. Sediment composition or grain size (Seiderer and Newell 1999; Van Dalfsen et al. 2000; Etter and Grassle 1992; Moreira et al. 2006), salinity (Mannino and Montagna 1997; Gray 2002), organic matter (e.g. Gutiérrez et al. 2000; Quiroga et al. 2012) and dissolved oxygen levels (Cooksey and Hyland 2007) are the most important variables that determine the abundance, diversity and distribution patterns of macrobenthic communities (Snelgrove and Butman 1994; Gray and Elliot 2009). In addition, Levin and Gage (1998) pointed out that dissolved oxygen and organic matter content are key environmental factors that may be influencing the diversity and species compositions distributions.

Macrobenthic communities inhabiting the continental shelf off north (23°S) and central-south (36°S) Chile are influenced by several oceanographic features, such as OMZ (Gallardo et al. 2004; Sellanes et al. 2007, 2010), coastal upwelling (Fossing et al. 1995; Gutiérrez et al. 2006) and the ENSO cycle (Neira et al. 2001; Sellanes et al. 2007; Moreno et al. 2008). Studies on these communities along the continental margin off Chile are restricted mostly to the continental shelf and upper slope (e.g. Gallardo et al. 2004; Palma et al. 2005; Sellanes et al. 2007). However, there are no detailed ecological and biodiversity studies on the macrobenthic communities of central Chile (33°S), in particular Valparaiso Bay, which is one the largest bays in central Chile, with a wide variety of oceanographic processes and human activities that influence its coastal waters. In this bay, previous records indicated that the presence of low oxygen concentrations (Silva et al. 2009), sewage outfalls (Andrade et al. 1986) and terrigenous inputs could be influencing the coastal hydrodynamics and the nature of sediment conditions in shallow waters (Sievers and Vega 2000). These factors suggest changes of sediment properties and, therefore, the benthic communities would be highly heterogeneous in space and time. Nevertheless, the knowledge of the temporal and spatial variability and the response of macrobenthic communities inhabiting the soft-bottom sediments of Valparaiso Bay to natural and anthropogenic conditions have not been well studied.

It has been suggested that climate change will reinforce the negative consequences of man-made eutrophication (Rabalais et al. 2010). In fact, recent studies have demonstrated that hypoxia and OMZ are expanding to the coastal regions (Riebesell et al. 2007) as a consequence of climate change (Stramma et al. 2008; Pierce et al. 2012), with negative effects on marine biodiversity (Boesch 2008). There is also evidence for a higher proportion of declining oxygen trends near coastlines than in the open ocean, most probably due to run-off of nutrients in the coastal region (Gilbert et al. 2009). Therefore, a loss or decreasing pattern on marine community diversity or absence of fauna could be observed (De Jonge and Elliot 2001; Stramma et al. 2010; Gewin 2010). It is important to

note that OMZ macrofaunal communities exhibit reduced densities, low species richness and high dominance of annelids (Levin 2003). In coastal areas, a decrease of marine diversity should also be reflected due to increased sewage outfalls and terrigenous input, which result in increases of organic supply and hypoxia of sediments and bottom waters (Diaz and Rosenberg 2008). Therefore, we hypothesise that, along the environmental gradient, coastal macrobenthic communities affected by these conditions could be considered as localised extensions of the OMZ benthos, observing similarities in their ecological descriptors as response. This paper aims to: (1) assess the species composition, diversity, community structure, biomass and body size distribution of the macrofauna and (2) determine the spatial patterns of macrobenthic communities in response to upwelling conditions (i.e. high total organic carbon [TOC] flux and low oxygen levels), terrigenous inputs and sewage outfalls at Valparaiso Bay, central Chile. The assessment of macrobenthos temporal variability was not considered in the current paper waiting for ENSO conditions forecasted for 2015 and its influence on benthic communities.

Materials and methods

Study site

Valparaiso Bay (32°9'S, 71°6'W) is located on the continental shelf of central Chile in the southeast Pacific Ocean (Fig. 1). This bay is characterised by the influence of several environmental conditions, such as upwelling, winds and currents regularly from S-SW, which are marked OMZ and ENSO events (Rutllant et al. 2004; Fuenzalida et al. 2009), and the presence of subantarctic and subsurface equatorial water masses (Silva et al. 2009). In addition, sewage outfalls (Andrade et al. 1986) and terrigenous inputs from Aconcagua River (Sievers and Vega 2000) contribute to the organic supply in coastal areas. Species sensitivity levels are thus influenced by complex local hydrographic conditions (Teixeira et al. 2012). In this context, the sampling stations were categorised as station 1, located close to the Aconcagua River mouth and the discharge of submarine sewage outfall. Stations 2, 3 and 4 were located in a transitional area between the sewage outfall site and the OMZ. Station 5 is located in the middle shelf, which is associated to the OMZ (Fig. 1, Table 1).

Sampling

Four seasonal sampling cruises (December 2012, March, June and September 2013) were carried out along a depth transect across the continental shelf (Table 1). At each station, water column temperature, salinity and dissolved oxygen concentration (DO) were measured using a CTDO seabird 19 Plus. In

Fig. 1 Study area showing the sampling oceanographic stations. Depths are indicated by the numbers. The star below station 1 indicates the position of sewage outfall discharge. Modified from Google Earth



In addition, discrete water samples at different depths were collected with Niskin bottles for DO, chlorophyll *a* (Chl_a) and particulate organic carbon (POC). Sediment samples for macrofaunal studies were collected using a modified van Veen grab (0.04 m²). Three replicate sediment samples were taken for macrofaunal analysis. The sediment samples were sieved through a 500- μ m mesh size screen and the biological material was fixed in a 10 % buffered formaldehyde–seawater solution. A fourth sample was collected for grain size characterisation. In addition, non-disturbed 4–5 sediment samples were collected using a gravity corer (internal diameter of 50 mm) for sediment variables. Sediment redox potential (Eh_{NHE}) and pH was measured for the 0–2=cm surface sediment layer using a platinum standard combination electrode with a calomel internal reference (SGTM, Mettler Toledo). Samples were kept frozen (–20 °C) prior to analyses of total organic matter (TOM), carbon stable isotope ratio ($\delta^{13}\text{C}$), chloroplast pigments (Chl_a and phaeopigments), TOC and the total organic carbon/total organic nitrogen ratio (C/N).

Water column analysis

The samples for DO were analysed by the Winkler method as modified from Carpenter's technique (Knap et al. 1993), and microtitrated with a DOSIMAT. Chl_a samples were filtered in duplicate (GF/F glass fibre filters) and frozen (–20 °C) until analysis by fluorometry (Turner Design), according to the standard procedure described by Holm-Hansen et al. (1965). Determination of POC was carried out using the method of Parsons et al. (1984).

Fauna and sediment treatment

In the laboratory, the fauna was identified to the lowest taxonomic level possible using a NIKON SMZ 800 stereomicroscope and light microscope NIKON eclipse E200. Biomass was determined as wet weight with a precision of 0.1 mg using an analytical scale. Macrofauna species were preserved in 70 % ethanol and stored for future comparative studies.

Sediment samples for chemical analysis were kept immediately after recovery, labelled with date, depth and station number information, and then stored frozen at –20 °C prior to analysis. TOM in marine sediments was determined by loss of weight on ignition at 475–500 °C for 4 h (Byers et al. 1978). Carbon stable isotope content ($\delta^{13}\text{C}$) was analysed by mass spectrometry (VG Micromass 602C equipment) at the Environment Isotopes Laboratory of the CCHEN (Chile). The $\delta^{13}\text{C}$ (‰) values are relative to the Pee Dee Belemnite (PDB) Standard (Silva et al. 2011). The contribution of the allochthonous (i.e. of terrestrial source) organic matter (AOM) to the sediments was evaluated by applying a two-source mixing model suggested by Bianchi (2007):

$$\% \text{AOM} = \left[\frac{(\delta^{13}\text{C}_{\text{sample}} - \delta^{13}\text{C}_{\text{marine}})}{(\delta^{13}\text{C}_{\text{terrestrial}} - \delta^{13}\text{C}_{\text{marine}})} \right] * 100.$$

We used –26.9‰ as the terrestrial reference value (Silva et al. 2011) and –21.7‰ for marine sediment as the average value obtained from samples in the study area.

Chl_a and phytopigment (Phaeop) degradation products (i.e. phaeopigments) were extracted from duplicate subsamples of wet sediment (ca. 1 g) using 90 % acetone. After 24 h of darkness at 4 °C, the samples were sonicated for 5 min,

Table 1 Station data and environmental variables

| Station | 1 | 2 | 3 | 4 | 5 |
|--|---------------|---------------|---------------|---------------|---------------|
| Latitude (°S) | 32°54'31 | 32°54'31 | 32°54'31 | 32°54'31 | 32°54'31 |
| Longitude (°W) | 71°32'47 | 71°34'49 | 71°35'44 | 71°36'48 | 71°38'57 |
| Depth (m) | 22 | 50 | 80 | 100 | 140 |
| Bottom water | | | | | |
| Dissolved oxygen (ml L ⁻¹) | 4.18 (0.57) | 3.31 (1.08) | 2.35 (0.75) | 1.83 (1.20) | 1.66 (1.22) |
| Particulate organic carbon (mg L ⁻¹) | 3.50 (2.45) | 3.82 (2.36) | 3.73 (2.14) | 4.0 (2.56) | 3.6 (2.57) |
| Chlorophyll <i>a</i> (mg m ⁻³) | 10.0 (9.74) | 2.70 (2.71) | 2.66 (1.72) | 1.67 (1.14) | 1.8 (1.30) |
| Temperature (°C) | 12.52 (0.57) | 11.58 (0.09) | 11.30 (0.19) | 11.25 (0.23) | 11.18 (0.22) |
| Salinity | 34.30 (0.08) | 34.4 (0.07) | 34.47 (0.05) | 34.47 (0.07) | 34.55 (0.04) |
| pH | 8.56 (0) | 8.44 (0) | 7.92 (0.61) | 8.12 (0.34) | 8.12 (0.16) |
| Surface sediments | | | | | |
| Mud (%) | 67.87 (10.0) | 60.3 (3.34) | 77.67 (11.56) | 79.15 (10.83) | 91.33 (2.47) |
| Sand (%) | 32.12 (10.0) | 34.7 (9.19) | 22.32 (11.56) | 20.85 (10.83) | 8.63 (2.51) |
| Graphic mean (Mz) | 5.03 (0.19) | 5.58 (0.5) | 5.3 (0.46) | 4.69 (0.91) | 4.98 (0.66) |
| Sorting (σ ₁) | 1.71 (0.07) | 1.53 (0.09) | 1.81 (0.32) | 2.11 (0.45) | 1.89 (0.36) |
| Eh _{NHE} (mV) 0–1 cm | 146 (0) | 331 (4.9) | 132 (65.5) | 130 (57.2) | 173 (83.0) |
| pH | 8.40 (0.2) | 8.29 (0) | 7.97 (0.47) | 8.07 (0.33) | 8.16 (0.20) |
| δ ¹³ C (‰) | -22.6 (0.87) | -24.0 (0.94) | -24.4 (0.58) | -24.0 (0.51) | -22.9 (1.44) |
| Allochthonous material (%) | 17.31 (16.76) | 45.51 (18.17) | 53.36 (11.25) | 44.71 (9.85) | 23.07 (27.73) |
| Total organic matter (%) | 1.79 (0.54) | 1.80 (0.29) | 5.26 (0.71) | 7.01 (2.58) | 4.96 (2.36) |
| Chlorophyll <i>a</i> (μg g ⁻¹) | 7.32 (5.54) | 8.27 (3.89) | 6.79 (3.66) | 7.44 (3.68) | 13.18 (8.92) |
| CPE (μg g ⁻¹) | 30.27 (21.17) | 41.43 (13.72) | 31.54 (9.9) | 32.57 (16.32) | 60.77 (49.81) |
| TOC (μg g ⁻¹) | 1.43 (0.52) | 2.50 (7.55) | 14.29 (1.93) | 16.36 (6.11) | 10.51 (2.62) |
| C/N (molar) | 9.85 (0.44) | 11.42 (1.44) | 13.05 (0.62) | 12.65 (0.97) | 10.55 (0.43) |
| Chla/TOC | 6.28 (6.22) | 4.42 (4.79) | 0.50 (0.32) | 0.48 (0.17) | 1.26 (0.80) |

Mean values and standard deviations in brackets are shown

CPE: chloroplast pigment equivalents; Eh_{NHE}: redox potential; δ¹³C: carbon stable isotope content; TOC: total organic carbon; C/N: carbon–nitrogen ratio; Chla/TOC: chlorophyll *a*–carbon ratio

centrifuged at 3000 rpm (1000×g) for 10 min and extracts were fluorometrically analysed for Chla and Phaeop content. Chla and Phaeop values were obtained before and after acidification with 1 N HCl, respectively, according to the method of Lorenzen (1967), as described by Parsons et al. (1984), where the volume of water is substituted by the dry weight (DW) of the sediment expressed in grammes. Values were expressed, corrected for porosity as measured by the water content, as μg Chla g⁻¹ DW. This was obtained after drying duplicate sediment subsamples (ca. 1 g) at 105 °C for 20 h. Chloroplast pigment equivalents (CPE) were obtained from Chla and Phaeop.

Particle grain size data were analysed following the Folk & Ward scale (Folk 1980; Blott and Pye 2001). The median particle diameter (MPD), sorting coefficient (σ) and graphic standard deviation (σ₁) were obtained using GRADISTAT software (Blott and Pye 2001). The total sulphides content was determined colourimetrically according to method of Cline (1969). TOC and total nitrogen (TN) content samples were freeze-dried and then ground and homogenised in an

agate mortar before processing. About 50 mg of sediment were weighed in tin cups, the carbonate was removed by acidifying with 25 % v/v HCL and the sediment sample measured in a CHN Elemental Analyzer (Delta V Advantage with Flash EA 2000 and Conflo IV) (Tung and Tanner 2003).

Data analysis

Abundance and biomass data were standardised to individuals per m² before analysis to determine means and standard deviations. To describe and compare the community structure, Margalef species richness (S), Shannon–Wiener (H'), evenness (J'), Simpson dominance (D) and Sanders–Hurlbert expected species number (ES₁₀) indices were used. In addition, K-dominance curves were also calculated to demonstrate diversity structure. Multivariable analyses were carried out using PRIMER v6 statistical software (Clarke and Gorley 2006). Spatial differences in the abundance were determined with a non-metric multidimensional scaling (NMDS) ordination analysis (Clarke and Green 1988; Clarke 1993), using the

Bray–Curtis index (Ludwig and Reynolds 1988) as the similarity measure. The significance of differences between stations was examined by the randomisation test analysis of similarities (ANOSIM). A non-parametric one-way analysis of variance (ANOVA, Kruskal–Wallis) was used to test for significant differences ($p < 0.05$) among stations (Zar 1996).

Normalised biomass size spectra (NBSS) were constructed to test for spatial differences in the size structure of the macrobenthic communities as described by Platt and Denman (1977, 1978). In addition, Spearman rank correlation analysis was used to calculate correlations between biological diversity variables (i.e. abundance, biomass, community parameters) and environmental variables (i.e. depth, BWDO, TOM, chloroplast pigments, total organic carbon, grain size).

The NBSS coefficients (slope and intercept) have been proposed as quantitative indices of aquatic ecosystem structure (Sprules and Munawar 1986; Quiroga et al. 2005; 2014). Mean individual wet weight was estimated as total macrofauna community biomass divided by total macrofauna community density. The parameters of the NBSS were determined by regressing the \log_2 (normalised biomass) against \log_2 (individual weight). Differences among the slopes of NBSS were assessed by an analysis of covariance according to Zar (1996). The mean individual body size (mg wet mass) is also calculated.

Results

Bottom water and sediment conditions

The environmental parameters are summarised in Table 1. DO concentrations were higher at shallow stations and decreased to the deepest stations, where hypoxic conditions were observed. DO concentrations varied from $4.18 \pm 0.57 \text{ ml L}^{-1}$ at station 1 (25 m) to $1.66 \pm 1.22 \text{ ml L}^{-1}$ at station 5 (140 m). POC and salinity exhibited low variability between sites, with mean values of $3.7 \pm 0.19 \text{ mg L}^{-1}$ and 34.4 ± 0.09 , respectively. High concentrations of Chla were recorded at station 1 ($10.03 \pm 9.74 \text{ mg m}^{-3}$) in comparison with the rest of the stations, which did not exceed 2.7 mg m^{-3} . Bottom water temperature decreased with depth; a mean value of $11.56 \text{ }^\circ\text{C}$ was recorded for the study site. Salinity showed little variability between stations. A mean value of 8.23 was recorded for pH.

The surficial sediments were a grain size poorly sorted with higher proportion of mud fractions (75 %) and minor fine sandy fractions (24 %). Mud content increased with depth, reaching a maximum mean of $91 \pm 2.47 \%$ at station 5, while higher fine sandy fractions were recorded at shallow stations (mean values of 34.7 ± 9.2 and $32.1 \pm 10 \%$ at stations 2 and 1, respectively). TOM contents as well as Chla and CPE concentrations were highest at deepest stations, showing wide variations between them. TOM ranged from 1.79 % at station 1 to 7.02 % at station 4, Chla varied from $6.79 \text{ } \mu\text{g g}^{-1}$ at station 3

to $13.18 \text{ } \mu\text{g g}^{-1}$ at station 5, and CPE ranged from $30.27 \text{ } \mu\text{g g}^{-1}$ at station 1 to $60.78 \text{ } \mu\text{g g}^{-1}$ at station 5. A similar spatial pattern was observed for TOC and C/N, with maximum mean values at stations 4 and 3. Allochthonous material percentage and $\delta^{13}\text{C}$ stable isotopes recorded mean maximum values at station 3 and the lowest values at station 1. The overall averages for these variables were $36.8 \pm 15.6 \%$ and $-23.6 \pm 0.8 \text{ } \delta^{13}\text{C} \text{ } \text{‰}$. The redox potential (Eh) recorded a mean of $182.6 \pm 84.9 \text{ mV}$ (Table 1).

Faunal composition, abundance and biomass

A total of 138 taxa were recognised as distinct species in the study site. Macrobenthos composition was dominated by polychaetes, which comprised 45.9 % of the total individuals collected. The second and third most abundant groups were mollusks and crustaceans (i.e. bivalves and amphipods). Both groups accounted for 25.2 % and 22.4 % of the total number of individuals, respectively. The remaining faunal groups, such as ophiuroids, cnidarians, nemerteans, picnogonids and sipunculids, contributed about 6.5 % to the overall total (Fig. 2).

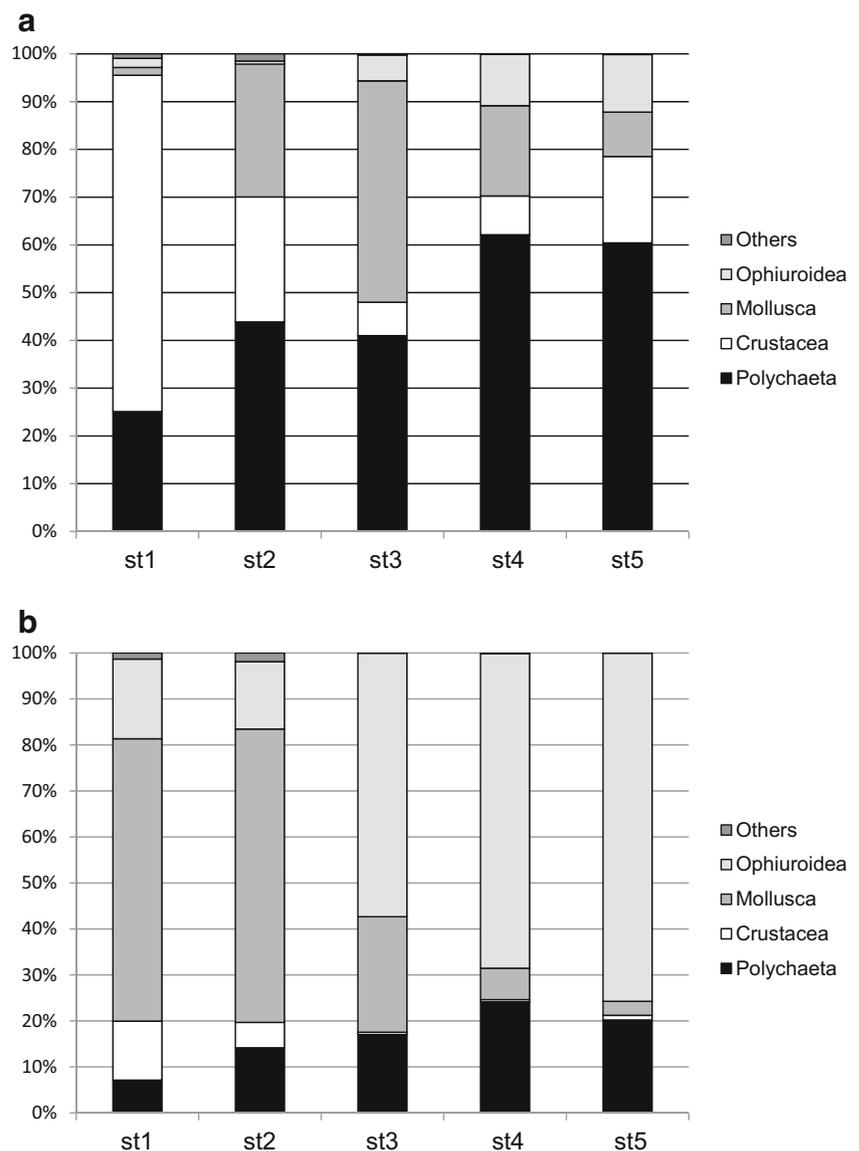
Sixty-three species of polychaetes belonging to 20 families were identified. The families having the most species were Spionidae and Cirratulidae with nine and eight species, respectively, Nephythidae and Lumbrineridae with seven species, Paraonidae with five species and the Capitellidae, Syllidae, Sabellidae and Ampharetidae with three species (Table 2).

Among the Crustacea, the most taxonomically diverse group was the gammarid amphipods with 22 species, with the cumaceans (10 spp.), ostracods (7 spp.) and isopods (5 spp.). Decapods, copepods and mysidaceans were also recorded. Mollusca was represented by 16 species, with bivalves and gastropods being the most diverse, with ten and five species, respectively. One species of aplacophoran (*Chaetoderma araucanae*) was also recorded. Other taxa, such as nemerteans, sipunculans, pycnogonids, cnidarians and ophiuroids, were also present. From this last group, just the ophiuroid *Amphioplus magellanicus* was important in terms of density and occurrence in the study area (Table 2).

Species composition exhibited differences among stations. Polychaetes were dominant at deeper stations (Fig. 2a), where low DO concentrations were recorded. *Cossura chilensis* (Cossuridae) was dominant at these stations, reaching the second highest macrofaunal density for the study, with a mean of $2416 \pm 429 \text{ ind. m}^{-2}$. *Levinsenia gracilis*, *Aricidea pigmentata* and cirratulid polychaetes were also recorded with high densities (Table 2).

Crustaceans showed high relative abundance at shallow stations, being dominant at station 1 (25 m) with 70 % (Fig. 2a). Gammarid amphipods such as *Ampelisca gracilicauda* ($400 \pm 159 \text{ ind. m}^{-2}$), *Metharpinia longirostris* ($333 \pm 110 \text{ ind. m}^{-2}$) and *Microphoxus cornutus* ($304 \pm 80 \text{ ind. m}^{-2}$), together with the cumacean *Anchistylis watlingi* ($475 \pm 109 \text{ ind. m}^{-2}$), had the

Fig. 2 Taxonomic composition (%) of relative abundance (a) and biomass (b) at the study site. Made using Excel (MS Office)



highest mean densities. Mollusca exhibited the highest relative abundance at station 3 (80 m) with 46 %, followed by polychaetes with 41 %. At this station, the highest density was recorded by the bivalve *Nucula pisum*, with 1544 ± 1515 ind. m^{-2} . This species had the highest macrofaunal density for the study site (2440 ± 549 ind. m^{-2}). There was no clear faunal dominance pattern at station 2. At this station, the relative abundance was characterised by polychaetes (43 %), mollusks (28 %) and crustaceans (26 %) (Fig. 2a). The total macrofaunal density was $42,905$ ind. m^{-2} . Mean densities varied from 1416 ± 1596 at station 5 to 3440 ± 2833 ind. m^{-2} at station 3 (Table 3), with significant differences between stations (Kruskal–Wallis test $p < 0.05$).

Mean biomass varied from 21 ± 13 gm^{-2} at station 2 to 48 ± 39 gm^{-2} at station 3, with an overall mean of 31.65 ± 11.75 gm^{-2} and recording significant differences among stations at

the study site (Kruskal–Wallis test $p < 0.05$). A higher number of small soft-bodied polychaetes would explain the low biomass values recorded. Biomass was mainly dominated by ophiuroids (51 %) and in a lower proportion by mollusks (28 %). Polychaetes and crustaceans contributed together in a minor proportion, with 20 %. The contribution of each macrofaunal group showed differences among stations (Fig. 2). Shallow stations (1 and 2) were dominated by mollusks (mainly *Oliva peruviana*, *Nassarius dentifer* and *Nucula pisum*), with a relative biomass above 61 %. The deepest stations were characterised by the high presence of *Amphiopus magellanicus* (Ophiuroidea, Echinodermata), with relative biomass higher than 57 % (Fig. 2b). The contribution of polychaetes to the total biomass never exceeds 25 %, with a slight increase at the deepest stations.

Table 2 Species composition, density, biomass, standard deviation (SD) and percentage of total macrofauna

| | Mean density (ind. m ⁻²) | SD | % | Mean biomass (g m ⁻²) | SD | % |
|--|---|-------|-------|--------------------------------------|---------|---------|
| Polychaeta | | | | | | |
| <i>Cossura chilensis</i> | 2416.7 | 429.1 | 20.29 | 0.07096 | 0.0682 | 0.2242 |
| <i>Chaetozone</i> sp1 | 397.9 | 100.9 | 3.34 | 0.01839 | 0.0301 | 0.0581 |
| <i>Levinsenia gracilis</i> | 300.0 | 57.4 | 2.52 | 0.01229 | 0.0190 | 0.0388 |
| <i>Aricidea pigmentata</i> | 270.8 | 74.7 | 2.27 | 0.00713 | 0.0107 | 0.0225 |
| <i>Monticellina</i> sp. | 193.8 | 34.3 | 1.63 | 0.00631 | 0.0015 | 0.0199 |
| <i>Aphelochaeta</i> sp. | 193.8 | 16.2 | 1.63 | 0.01405 | 0.0225 | 0.0444 |
| <i>Nephtys magellanica</i> | 145.8 | 37.1 | 1.22 | 0.05400 | 0.0746 | 0.1706 |
| <i>Nephtys ferruginea</i> | 137.5 | 42.5 | 1.15 | 0.11985 | 0.1639 | 0.3786 |
| Lumbrineridae sp2 | 116.7 | 18.0 | 0.98 | 0.31877 | 0.3850 | 1.0069 |
| Lumbrineridae sp5 | 104.2 | 23.0 | 0.87 | 0.19736 | 0.1800 | 0.6234 |
| <i>Aglaophamus</i> sp4 | 91.7 | 17.4 | 0.77 | 0.07261 | 0.0892 | 0.2294 |
| <i>Aricidea</i> sp2 | 87.5 | 8.6 | 0.73 | 0.00543 | 0.0098 | 0.0171 |
| <i>Paraprionospio pinnata</i> | 85.4 | 27.3 | 0.72 | 0.11588 | 0.2360 | 0.3660 |
| <i>Lumbrineris</i> sp1 | 85.4 | 25.2 | 0.72 | 0.40070 | 0.5433 | 1.2657 |
| <i>Spiophanes duplex</i> | 75.0 | 29.0 | 0.63 | 0.04600 | 0.1008 | 0.1453 |
| <i>Cirratulus</i> sp. | 70.8 | 27.3 | 0.59 | 0.05308 | 0.1000 | 0.1677 |
| Ampharetidae sp1 | 68.8 | 17.1 | 0.58 | 0.01724 | 0.0175 | 0.0545 |
| <i>Aricidea</i> sp3 | 56.3 | 13.0 | 0.47 | 0.00048 | 0.0006 | 0.0015 |
| <i>Prionospio peruana</i> | 52.1 | 14.0 | 0.44 | 0.01627 | 0.0284 | 0.0514 |
| <i>Goniada</i> sp1 | 37.5 | 13.0 | 0.31 | 0.01968 | 0.0267 | 0.0622 |
| <i>Aglaophamus</i> sp3 | 31.3 | 6.5 | 0.26 | 0.15406 | 0.1852 | 0.4866 |
| Lumbrineridae sp3 | 31.3 | 8.4 | 0.26 | 0.02065 | 0.0182 | 0.0652 |
| <i>Nephtys</i> sp2 | 27.1 | 5.0 | 0.23 | 0.12356 | 0.1700 | 0.3903 |
| <i>Cirrophorus</i> sp. | 22.9 | 5.5 | 0.19 | 0.00119 | 0.0026 | 0.0038 |
| <i>Ampharete</i> sp1 | 20.8 | 6.5 | 0.17 | 0.00658 | 0.0120 | 0.0208 |
| <i>Perkinsyllis longisetosa</i> | 18.8 | 7.5 | 0.16 | 0.00088 | 0.0020 | 0.0028 |
| <i>Sphaerodoropsis</i> sp. | 16.7 | 5.7 | 0.14 | 0.00001 | <0.0001 | <0.0001 |
| <i>Kinbergonuphis</i> sp1 | 14.6 | 4.9 | 0.12 | 0.00471 | 0.0065 | 0.0149 |
| <i>Hemipodus simplex</i> | 14.6 | 4.9 | 0.12 | 0.00583 | 0.0083 | 0.0184 |
| <i>Scolecopsis chilensis</i> | 14.6 | 5.8 | 0.12 | 0.00492 | 0.0110 | 0.0155 |
| <i>Paraprionospio</i> sp1 | 12.5 | 5.0 | 0.10 | 0.01550 | 0.0347 | 0.0490 |
| Cirratulidae sp4 | 12.5 | 5.0 | 0.10 | 0.01200 | 0.0268 | 0.0379 |
| Sabellidae sp1 | 10.4 | 4.2 | 0.09 | 0.01018 | 0.0228 | 0.0322 |
| <i>Aglaophamus peruana</i> | 10.4 | 3.2 | 0.09 | 0.06085 | 0.1092 | 0.1922 |
| <i>Mediomastus</i> sp. | 10.4 | 1.9 | 0.09 | 0.96733 | 2.1609 | 3.0557 |
| <i>Nicomache</i> sp. | 10.4 | 1.9 | 0.09 | 0.62333 | 1.1342 | 1.9690 |
| Maldanidae sp1 | 8.3 | 1.6 | 0.07 | 0.11767 | 0.1420 | 0.3717 |
| Spionidae sp1 | 8.3 | 0.8 | 0.07 | 0.00133 | 0.0009 | 0.0042 |
| <i>Artacama valparisiensis</i> | 8.3 | 2.4 | 0.07 | 0.01800 | 0.0262 | 0.0569 |
| <i>Syllis pectinans</i> | 6.3 | 1.7 | 0.05 | 0.00030 | 0.0006 | 0.0009 |
| <i>Laonice</i> sp. | 6.3 | 2.5 | 0.05 | 0.00500 | 0.0112 | 0.0158 |
| Lumbrineridae sp4 | 6.3 | 1.7 | 0.05 | 0.08763 | 0.1944 | 0.2768 |
| <i>Lumbrineris</i> cf. <i>tetraura</i> | 6.3 | 2.5 | 0.05 | 0.00246 | 0.0055 | 0.0078 |
| <i>Aglaophamus</i> sp2 | 4.2 | 1.0 | 0.03 | 0.04679 | 0.0726 | 0.1478 |
| Cirratulidae sp5 | 4.2 | 1.7 | 0.03 | 0.00775 | 0.0173 | 0.0245 |
| Onuphidae sp2 | 4.2 | 1.0 | 0.03 | 0.06383 | 0.1188 | 0.2016 |
| Phyllococe sp1 | 4.2 | 1.7 | 0.03 | 0.00042 | 0.0009 | 0.0013 |
| <i>Syllides</i> sp. | 4.2 | 1.0 | 0.03 | 0.00005 | 0.0016 | 0.0002 |

Table 2 (continued)

| | Mean density (ind. m ⁻²) | SD | % | Mean biomass (g m ⁻²) | SD | % |
|---------------------------------|---|-------|------|--------------------------------------|---------|---------|
| Pilargidae sp. | 4.2 | 1.0 | 0.03 | 0.00103 | 0.0022 | 0.0032 |
| Phyllodocidae sp. | 3.1 | 1.3 | 0.03 | 0.00017 | 0.0004 | 0.0005 |
| <i>Sosane</i> sp1 | 2.1 | 0.8 | 0.02 | 0.00053 | 0.0012 | 0.0017 |
| <i>Notomastus</i> sp. | 2.1 | 0.8 | 0.02 | 1.41550 | 3.0747 | 4.4714 |
| Capitellidae sp1 | 2.1 | 0.8 | 0.02 | 0.00001 | <0.0001 | <0.0001 |
| <i>Chaetozone</i> sp2 | 2.1 | 0.8 | 0.02 | <0.00001 | <0.0001 | <0.0001 |
| <i>Brada</i> sp. | 2.1 | 0.8 | 0.02 | 0.01488 | 0.0333 | 0.0470 |
| <i>Glycera</i> sp. | 2.1 | 0.8 | 0.02 | 0.06600 | 0.1476 | 0.2085 |
| <i>Lumbrineris</i> sp. | 2.1 | 0.8 | 0.02 | 0.05442 | 0.1217 | 0.1719 |
| <i>Naineris</i> sp1 | 2.1 | 0.8 | 0.02 | 0.00771 | 0.0172 | 0.0243 |
| Sabellidae sp2 | 2.1 | 0.8 | 0.02 | 0.00146 | 0.0033 | 0.0046 |
| <i>Chone</i> sp. | 2.1 | 0.8 | 0.02 | 0.00031 | 0.0007 | 0.0010 |
| Spionidae sp2 | 2.1 | 0.8 | 0.02 | 0.00038 | 0.0008 | 0.0012 |
| <i>Spiophanes bombyx</i> | 2.1 | 0.8 | 0.02 | 0.00167 | 0.0037 | 0.0053 |
| Crustacea | | | | | | |
| <i>Anchistylis watlingi</i> | 475.0 | 109.6 | 3.99 | 0.02985 | 0.0468 | 0.0943 |
| <i>Ampelisca gracilicauda</i> | 400.0 | 159.0 | 3.36 | 0.36899 | 0.8251 | 1.1656 |
| <i>Metharpinia longirostris</i> | 333.3 | 110.9 | 2.80 | 0.01006 | 0.0181 | 0.0318 |
| <i>Microphoxus cornutus</i> | 304.2 | 80.1 | 2.55 | 0.03553 | 0.0530 | 0.1122 |
| <i>Heterophoxus oculatus</i> | 187.5 | 31.0 | 1.57 | 0.05688 | 0.0459 | 0.1797 |
| <i>Ampelisca</i> sp. | 158.3 | 36.3 | 1.33 | 0.09074 | 0.1105 | 0.2866 |
| <i>Anchistylis</i> sp. | 154.2 | 36.4 | 1.29 | 0.01490 | 0.0250 | 0.0471 |
| Ostracoda sp1 | 106.3 | 26.7 | 0.89 | 0.00012 | 0.0002 | 0.0004 |
| <i>Eudorella</i> sp. | 97.9 | 27.2 | 0.82 | 0.00451 | 0.0071 | 0.0143 |
| <i>Ampelisca</i> sp2 | 95.8 | 25.9 | 0.80 | 0.06118 | 0.0602 | 0.1933 |
| Ostracoda sp5 | 95.8 | 18.6 | 0.80 | 0.00102 | 0.0017 | 0.0032 |
| <i>Diastylis tongoyensis</i> | 75.0 | 11.0 | 0.63 | 0.00576 | 0.0059 | 0.0182 |
| <i>Leucon</i> sp. | 58.3 | 11.8 | 0.49 | 0.00288 | 0.0020 | 0.0091 |
| <i>Eudorella</i> sp1 | 45.8 | 14.3 | 0.38 | 0.00150 | 0.0029 | 0.0047 |
| <i>Liljeborgia</i> sp. | 39.6 | 3.6 | 0.33 | 0.01446 | 0.0127 | 0.0457 |
| <i>Paramonoculopsis</i> sp. | 37.5 | 7.0 | 0.31 | 0.00956 | 0.0180 | 0.0302 |
| Metharpiniinae sp. | 35.4 | 9.8 | 0.30 | 0.01137 | 0.0197 | 0.0359 |
| <i>Edotea</i> sp. | 31.3 | 11.5 | 0.26 | 0.00090 | 0.0016 | 0.0028 |
| <i>Metharpinia</i> sp. | 22.9 | 8.2 | 0.19 | 0.00333 | 0.0066 | 0.0105 |
| <i>Macrochiridotea</i> sp. | 18.8 | 5.7 | 0.16 | 0.00542 | 0.0121 | 0.0171 |
| <i>Eudevenopus gracilipes</i> | 16.7 | 6.7 | 0.14 | 0.00067 | 0.0015 | 0.0021 |
| Ostracoda sp2 | 16.7 | 6.7 | 0.14 | 0.00001 | <0.0001 | <0.0001 |
| Ostracoda sp4 | 16.7 | 5.7 | 0.14 | 0.00004 | 0.0001 | 0.0001 |
| <i>Gomezia serrata</i> | 12.5 | 5.0 | 0.10 | 0.13371 | 0.2990 | 0.4224 |
| Dastylidae sp. | 12.5 | 3.1 | 0.10 | 0.00249 | 0.0035 | 0.0079 |
| <i>Diastylis</i> sp. | 12.5 | 3.1 | 0.10 | 0.00030 | 0.0006 | 0.0009 |
| <i>Leptostylis</i> sp. | 10.4 | 4.2 | 0.09 | 0.00117 | 0.0026 | 0.0037 |
| <i>Serolis</i> sp. | 8.3 | 2.4 | 0.07 | 0.00310 | 0.0061 | 0.0098 |
| <i>Munna</i> sp. | 8.3 | 2.4 | 0.07 | 0.00017 | 0.0004 | 0.0005 |
| <i>Pinnixa</i> sp. | 8.3 | 2.4 | 0.07 | 0.01367 | 0.0272 | 0.0432 |
| Decapoda indet. 1 | 8.3 | 2.0 | 0.07 | 0.00525 | 0.0072 | 0.0166 |
| Oedicerotidae sp. | 6.3 | 2.5 | 0.05 | 0.00030 | 0.0007 | 0.0009 |
| Ostracoda sp3 | 6.3 | 2.5 | 0.05 | 0.00002 | <0.0001 | 0.0001 |
| <i>Photis</i> sp. | 4.2 | 1.7 | 0.03 | 0.00013 | 0.0003 | 0.0004 |

Table 2 (continued)

| | Mean density (ind. m ⁻²) | SD | % | Mean biomass (g m ⁻²) | SD | % |
|---------------------------------|---|-------|-------|--------------------------------------|---------|---------|
| <i>Phoxocephalopsis zimmeri</i> | 4.2 | 1.7 | 0.03 | 0.00021 | 0.0005 | 0.0007 |
| <i>Bathymedon</i> sp. | 4.2 | 1.7 | 0.03 | 0.00055 | 0.0012 | 0.0017 |
| <i>Heterophoxus</i> sp. | 4.2 | 1.7 | 0.03 | 0.00346 | 0.0077 | 0.0109 |
| Amphipoda indet 2 | 4.2 | 1.7 | 0.03 | <0.00001 | 0.0000 | <0.0001 |
| Amphipoda indet. 3 | 4.2 | 1.0 | 0.03 | 0.00245 | 0.0047 | 0.0078 |
| Copepoda sp. | 4.2 | 1.0 | 0.03 | <0.00001 | <0.0001 | <0.0001 |
| Leuconidae sp. | 4.2 | 1.0 | 0.03 | 0.00021 | 0.0005 | 0.0007 |
| <i>Pagurus villosus</i> | 4.2 | 1.0 | 0.03 | 0.00292 | 0.0058 | 0.0092 |
| Lysianassidae sp. | 2.1 | 0.8 | 0.02 | 0.00083 | 0.0019 | 0.0026 |
| Metharpiniinae sp1 | 2.1 | 0.8 | 0.02 | 0.00079 | 0.0018 | 0.0025 |
| <i>Atyloella</i> sp. | 2.1 | 0.8 | 0.02 | 0.00379 | 0.0085 | 0.0120 |
| Amphipoda indet. 4 | 2.1 | 0.8 | 0.02 | 0.00046 | 0.0010 | 0.0014 |
| Cirolanidae sp. | 2.1 | 0.8 | 0.02 | 0.00003 | 0.0006 | 0.0001 |
| Mysidacea sp. | 2.1 | 0.8 | 0.02 | 0.05108 | 0.1142 | 0.1614 |
| Ostracoda sp6 | 2.1 | 0.8 | 0.02 | 0.00003 | 0.0003 | 0.0001 |
| Ostracoda sp7 | 2.1 | 0.8 | 0.02 | 0.00007 | 0.0006 | 0.0002 |
| Mollusca | | | | | | |
| <i>Nucula pisum</i> | 2439.6 | 548.7 | 20.48 | 2.44621 | 3.3412 | 7.7272 |
| <i>Nuculana cuneata</i> | 175.0 | 28.4 | 1.47 | 0.33308 | 0.3382 | 1.0521 |
| <i>Nassarius dentifer</i> | 83.3 | 27.2 | 0.70 | 2.36195 | 4.5476 | 7.4611 |
| <i>Chaetoderma araucanae</i> | 79.2 | 11.4 | 0.66 | 0.07243 | 0.0540 | 0.2288 |
| <i>Mysella molinae</i> | 14.6 | 4.9 | 0.12 | 0.00504 | 0.0109 | 0.0159 |
| <i>Mysella</i> sp2 | 14.6 | 4.9 | 0.12 | 0.00007 | 0.0002 | 0.0002 |
| Gastropoda sp2 | 12.5 | 2.4 | 0.10 | 0.00287 | 0.0051 | 0.0091 |
| <i>Pandora cistula</i> | 10.4 | 2.3 | 0.09 | 0.07883 | 0.1659 | 0.2490 |
| <i>Retrotapes</i> sp. | 8.3 | 2.0 | 0.07 | 0.05758 | 0.1014 | 0.1819 |
| <i>Ennucula grayi</i> | 6.3 | 2.5 | 0.05 | 0.63500 | 1.4199 | 2.0059 |
| <i>Malletia chilensis</i> | 6.3 | 1.7 | 0.05 | 0.00092 | 0.0013 | 0.0029 |
| <i>Oliva peruviana</i> | 4.2 | 1.7 | 0.03 | 2.76583 | 6.1846 | 8.7369 |
| <i>Thyasira tomeana</i> | 4.2 | 1.7 | 0.03 | 0.05550 | 0.1241 | 0.1753 |
| <i>Cyclocardia compressa</i> | 4.2 | 1.7 | 0.03 | 0.00333 | 0.0075 | 0.0105 |
| Gastropoda sp1 | 2.1 | 0.8 | 0.02 | 0.00007 | 0.0002 | 0.0002 |
| Buccinidae sp. | 2.1 | 0.8 | 0.02 | 0.00083 | 0.0019 | 0.0026 |
| Others | | | | | | |
| <i>Amphioplus magellanicus</i> | 647.9 | 90.6 | 5.44 | 16.23443 | 12.4488 | 51.2823 |
| Nemertea sp1 | 10.4 | 1.9 | 0.09 | 0.00530 | 0.0101 | 0.0167 |
| Nemertea sp2 | 10.4 | 3.2 | 0.09 | 0.00552 | 0.0105 | 0.0174 |
| Nemertea sp3 | 10.4 | 2.3 | 0.09 | 0.00483 | 0.0070 | 0.0153 |
| Pycnogonida sp. | 8.3 | 3.3 | 0.07 | 0.00062 | 0.0004 | 0.0020 |
| <i>Parborlasia</i> sp. | 6.3 | 1.7 | 0.05 | 0.09333 | 0.1326 | 0.2948 |
| Sipunculida sp1 | 4.2 | 1.7 | 0.03 | 0.00033 | 0.0007 | 0.0011 |
| <i>Renilla chilensis</i> | 2.1 | 0.8 | 0.02 | 0.00821 | 0.0184 | 0.0259 |
| Sipunculida 2 | 2.1 | 0.8 | 0.02 | 0.02954 | 0.0661 | 0.0933 |
| Sipunculida 3 | 2.1 | 1.0 | 0.02 | 0.00583 | 0.0130 | 0.0184 |

Macrofaunal diversity and community structure

The number of species varied widely between stations. A mean of 17 ± 6 species was recorded at the deepest station (station 5), while the highest mean number of species was at station 2, with 35 species. Species richness estimated by rarefaction was highest at shallow stations ($E[S_{10}] = 6.9\text{--}6.2$) and the lowest was recorded at station 3 ($E[S_{10}] = 4.8$), coinciding with the diversity (H') values (Fig. 3 and Table 3). Margalef species richness ranged from 43 species (station 5) to 77 species (station 2).

The macrofaunal community structure recorded spatial variability on diversity indexes with a moderate abundance distribution pattern among stations. The highest diversity (H') and evenness (J') values were recorded at shallow stations, where the dominance (D) had the lowest values in the same way as that indicated by K-dominance curves. Overall, a low dominance (D) was observed with moderate variation between stations (Table 3 and Fig. 3). The Kruskal–Wallis test performed for all diversity descriptors indicated that there were no significant differences between stations ($p > 0.05$).

Faunal community and multivariate analysis

The macrofaunal composition and density examined by MDS analysis showed a clear spatial pattern. Two main assemblages were observed: the shallow stations (1 and 2) and the deeper stations (3 and 4). The MDS ordination analysis based on abundance data revealed significant differences between these groupings (ANOSIM, $R = 0.515$, $p < 0.05$). Similar results were observed in the cluster analysis, characterised with two major groups of stations at a similarity level of 20 %. However, station 5 did not cluster neatly with either of these two groups, reflecting differences in abundance recorded at this station (Fig. 4a, b).

Normalised biomass size spectra

The NBSS of the macrobenthic communities obtained at all stations are presented in Fig. 5. All NBSS were statistically

significant ($p < 0.05$), with slopes ranging from -0.323 to -0.598 . No significant differences were found between the slopes of the NBSS ($p > 0.05$). The slopes indicate that smaller organisms are present at station 5 and bigger organisms were recorded at station 2. The intercept of the NBSS ranged between 0.310 and 1.408 for stations 4 and 1, respectively, reflecting the differences in biomass. Mean animal body size (MBS) varied from 58.5 to 226.7 mg wet mass, showing a bell-shaped distribution pattern across the transect (Table 3).

Faunal relationship with environmental parameters

Diversity (H') was positively correlated with the Chla/TOC ratio and negatively correlated with clay content, TOM and TOC ($p < 0.05$). The Simpson's dominance (D') was correlated positively with TOC and negatively with Chla/TOC ($p < 0.05$). Species richness (S) was positively correlated with sorting coefficient and negatively correlated with organic matter content (TOM) ($p < 0.05$). The slope (b) of the NBSS was negatively correlated with clay and positively correlated with sand contents ($p < 0.05$). The intercept (a) of the NBSS was positively correlated with Chla/TOC, while it was negatively correlated with the organic content (TOM, C/N and TOC) ($p < 0.05$) (Table 4).

Discussion

Environmental setting

DO concentrations decreased with depth, exhibiting a mean value of 1.74 ml L^{-1} at the deepest stations (100 m and 140 m). Nevertheless, the record of concentrations below 1 ml L^{-1} at these stations (0.7 and 0.6 ml L^{-1}) at the end of study period would indicate the presence of hypoxic conditions in the bay at 100 m depth, probably associated to the intrusion of OMZ in the inner continental shelf (Silva et al. 2009). Palma et al. (2005) recorded lower concentrations ($0.02\text{--}1.28 \text{ ml L}^{-1}$) than those reported in our study area at similar depths for Antofagasta (22° S) and Concepción (36° S)

Table 3 Macrofaunal community parameters at Valparaiso Bay

| Stations | N (ind. m^{-2}) | B (g m^{-2}) | MBS (mg) | S | H' (\log_2) | E (S_{10}) | J' | D' |
|----------|---------------------------|-------------------------|------------------|-------------|-------------------|-----------------|-----------------|-----------------|
| 1 | 1754 ± 1213 | 23 ± 23 | 81.8 ± 350 | 30 ± 6 | 3.52 ± 0.63 | 6.48 ± 1.27 | 0.72 ± 0.11 | 0.16 ± 0.09 |
| 2 | 1880 ± 1095 | 21 ± 13 | 58.5 ± 116 | 35 ± 1 | 4.00 ± 0.61 | 7.32 ± 1.27 | 0.77 ± 0.12 | 0.12 ± 0.08 |
| 3 | 3440 ± 2833 | 48 ± 39 | 226.7 ± 1125 | 32 ± 11 | 2.83 ± 0.25 | 4.83 ± 0.46 | 0.58 ± 0.07 | 0.28 ± 0.05 |
| 4 | 2238 ± 1930 | 37 ± 31 | 77.5 ± 345 | 24 ± 10 | 2.88 ± 0.23 | 5.22 ± 0.54 | 0.66 ± 0.10 | 0.23 ± 0.07 |
| 5 | 1416 ± 1596 | 24 ± 31 | 161.2 ± 760 | 17 ± 6 | 2.95 ± 0.40 | 5.51 ± 0.95 | 0.74 ± 0.07 | 0.20 ± 0.06 |

Mean values and standard deviation are shown

N: abundance; B: biomass; MBS: mean body size (mg wet mass); S: species richness; H' : Shannon diversity; E (S_{10}): rarefaction richness; J' : Pielou evenness; D' : Simpson dominance

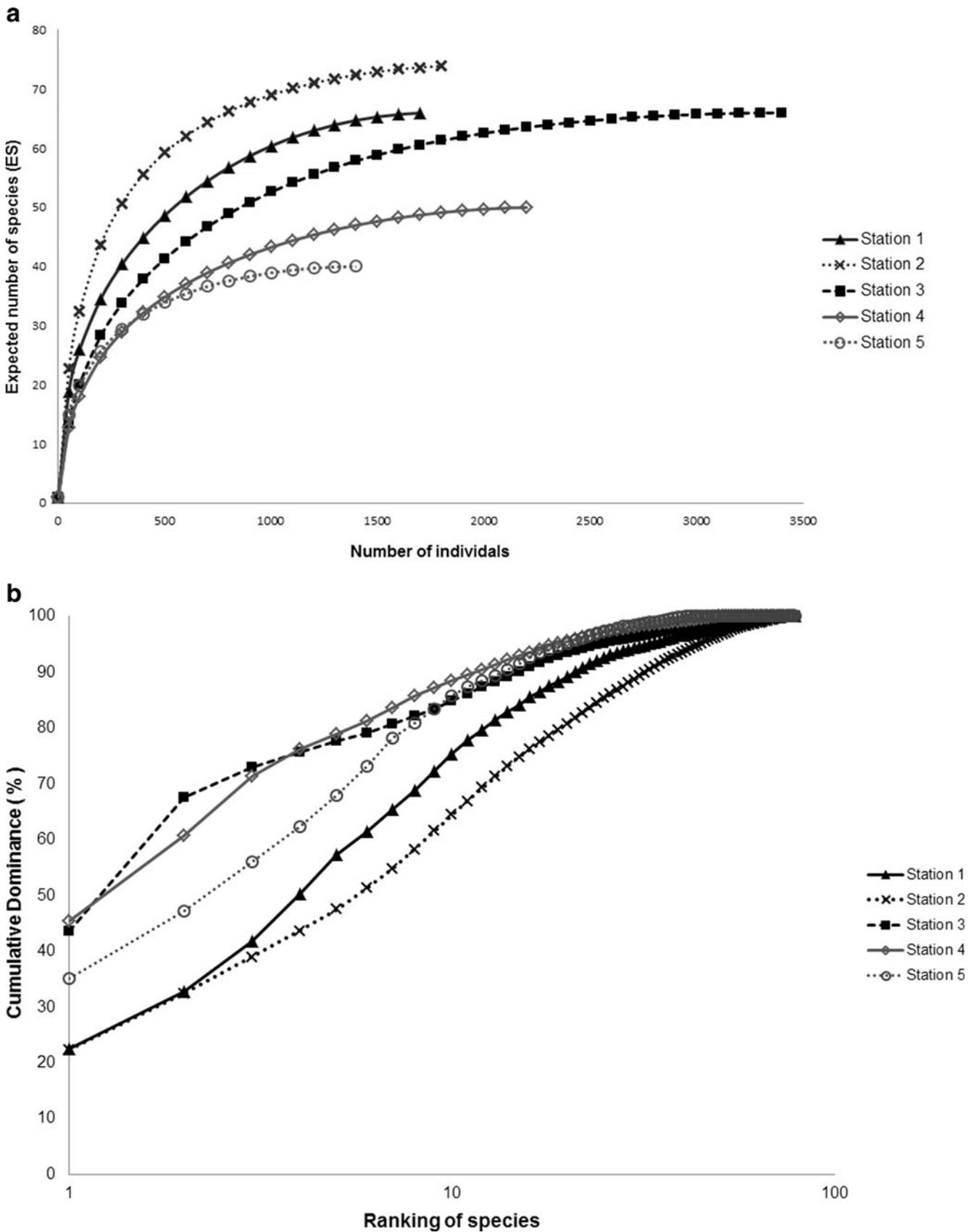
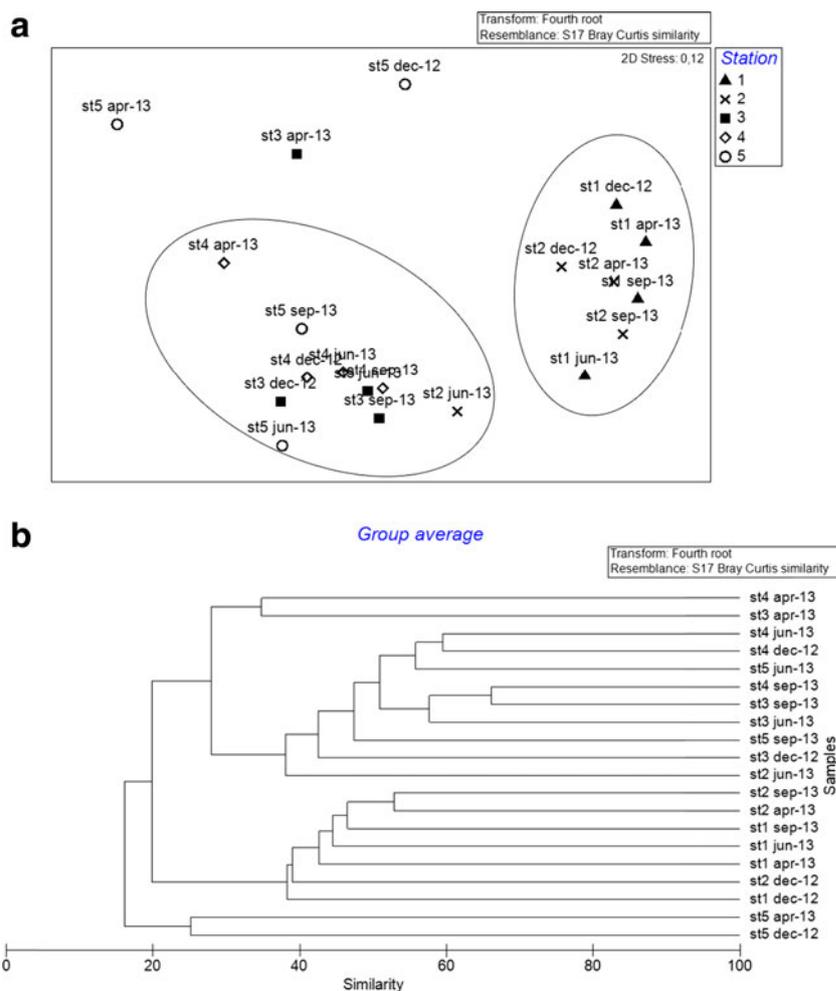


Fig. 3 Sanders–Hurlbert rarefaction diversity (a) and K-dominance curves (b) for the sampled macrofauna at each station. Graphs drawn using PRIMER v6 statistical software

Fig. 4 Non-metric multidimensional scaling (NMDS) ordination plot (a) and cluster analysis (b) based on macrofaunal species density at the different sampling sites during the study period. Drawn using PRIMER v6 statistical software



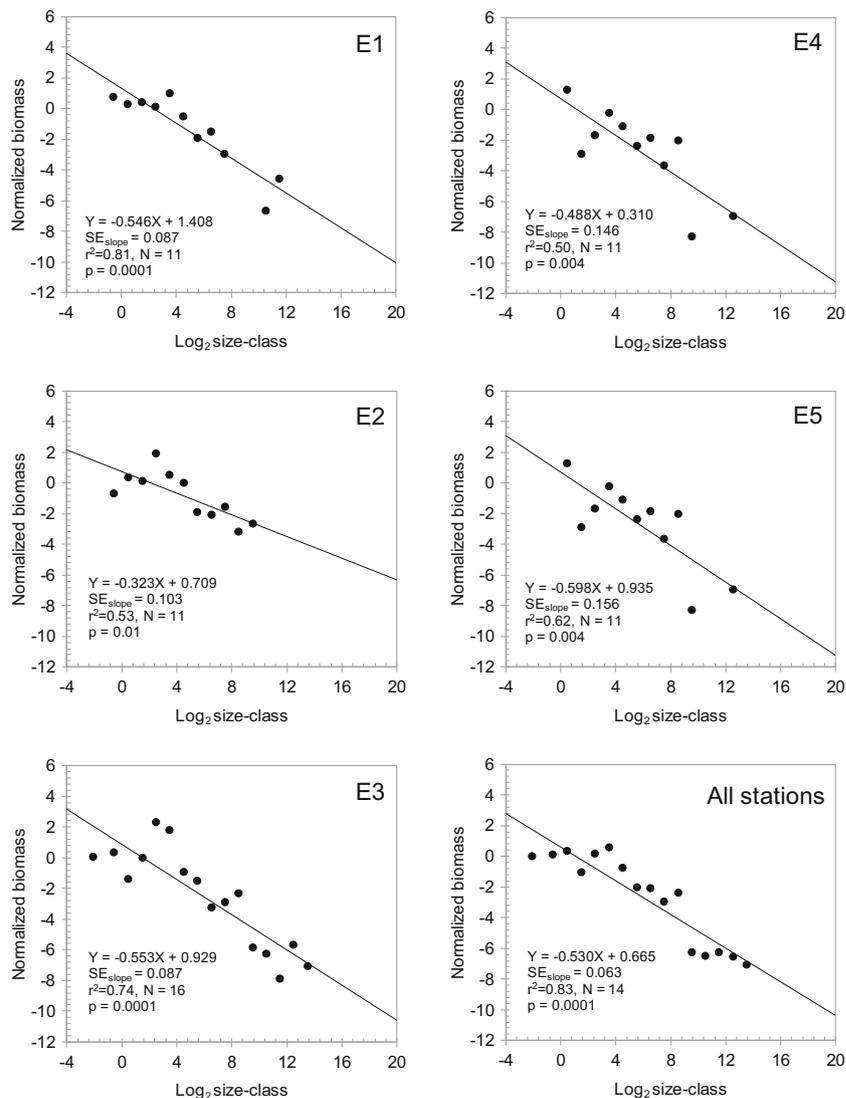
on the continental shelf. The DO levels measured in this study appeared to be similar to those reported in the same bathymetric rank for the West and East Indian margin (Ingole et al. 2010; Raman et al. 2014). For shallow waters below 80 m depth off the Peru coast, DO values ranged from $>1 \text{ ml L}^{-1}$ to 2.5 ml L^{-1} (Gutiérrez et al. 2008; Yupanqui et al. 2007), being lower than those in this study. After ENSO conditions, Laudien et al. (2007) recorded concentrations between 0.7 and 3.5 ml L^{-1} at 20 m for Mejillones Bay in the north of Chile, while Moreno et al. (2008) found an average of 2.57 ml L^{-1} at Iquique Bay at depths of 22–33 m. However, a mean value of 0.58 ml L^{-1} recorded off Concepción, central Chile by Sellanes et al. (2007) would be lower than the values recorded in this study (Table 5).

In our study area, sediment properties exhibited a high variability among stations, with a higher proportion of mud in all stations ($>60\%$). The high content of sand ($\sim 33\%$) at stations 1 and 2 could be associated with aperiodic discharges from the Aconcagua River. A higher proportion of sand ($>63\%$) at the deepest stations in June 2013 after a strong rain suggests that the volume of the river in May 2013 increased sand deposition at deeper stations. Aconcagua River

discharges measured at the Romeral station increased suddenly during that period from $1.48 \text{ m}^3/\text{s}$ to $34.14 \text{ m}^3/\text{s}$ in only 11 days (Dirección de General de Aguas: Ministerio de Obras Públicas de Chile; <http://www.dga.cl>).

Stable carbon and nitrogen isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively), the organic allochthonous material and the elemental ratio of TOC to TN, expressed as C/N, have been widely used as proxies of the sources of organic matter in coastal sediments (Ramaswamy et al. 2008; Rumolo et al. 2011; Gao et al. 2012; Silva et al. 2011; Ruiz-Fernández et al. 2002). At station 1, the TOM, TOC and C/N ratio were lower than deeper stations, suggesting that there was no organic enrichment in coastal sediments associated with sewage outfalls as was previously thought. This may be due to bottom currents and sediment resuspension related to shallow depths and the Aconcagua River inputs, resulting in the transport of the sediment and organic matter. In fact, values of $\delta^{13}\text{C}$ appear to be slightly less negative (-22.6‰) compared to those reported for sediment influenced by untreated sewages (-22.8 to -28.5‰) (see Rumolo et al. 2011 and references cited therein). Rabalais et al. (2014) have noted shifts in the stable isotopes ratio in relation to hypoxia and increased nutrients

Fig. 5 Normalised biomass size spectra (NBSS) plots of the macrofauna obtained at five stations in the study area (E1, E2, E3, E4 and E5). Equation parameters, squared correlation coefficient (r^2), standard error of the slopes (SE_{slope}) and p -values are indicated for all data sets in each regression. Graphs drawn using Excel (MS Office)



loads in coastal zones. From our results, a similar response was detected, with a parabolic distribution being recorded for $\delta^{13}C$ and allochthonous material.

Chla, TOC and CPE are tracers of fresh organic carbon and food quality in deep-sea sediments (Stephens et al. 1979) and

in sublittoral environments (e.g. Boon and Duineveld 1998; Radziejewska et al. 1996; Boon et al. 1998). Temporal and spatial variations observed from TOC and chloroplast pigments for the study area would indicate different regimes of productivity, resulting in an overall lower food supply in

Table 4 Spearman rank correlations between environmental variables and macrofaunal community parameters at the study site. Parameter derived from the normalised biomass size spectra (NBSS, slope = b, intercept = a)

| | H' | D' | Density | Biomass | S | b | a |
|--------------------------|---------------|---------------|---------|---------|---------------|---------------|---------------|
| Clay (%) | -0.54* | 0.44 | -0.01 | -0.01 | -0.32 | -0.59* | 0.07 |
| Sand (%) | 0.39 | -0.28 | 0.02 | 0.05 | 0.24 | 0.46* | 0.01 |
| Sorting (Mz) | 0.33 | -0.16 | 0.16 | -0.01 | 0.48* | 0.36 | -0.14 |
| TOM (%) | -0.48* | 0.30 | -0.35 | -0.19 | -0.60* | -0.12 | -0.49* |
| C/N molar | -0.25 | 0.25 | 0.04 | 0.09 | -0.04 | 0.21 | -0.64* |
| TOC $\mu\text{g g}^{-1}$ | -0.62* | 0.54* | 0.01 | 0.02 | -0.29 | -0.12 | -0.50* |
| Chla/TOC | 0.55* | -0.54* | -0.13 | -0.14 | 0.14 | 0.00 | 0.52* |

Significant correlations are shown in **bold** and indicated with an asterisk (*)

Table 5 Comparison of ecological and environmental data from previous works conducted at various locations off Chile and Perú

| Location | Bottom oxygen (ml L ⁻¹) | Mean biomass (g m ⁻²) | Mean abundance (ind. m ⁻²) | H'(log ₂) | J' | Latitude (°S) and depth (m) | Reference |
|----------------------|-------------------------------------|-----------------------------------|--|-----------------------|-----------|-----------------------------|------------------------|
| Antofagasta | 0.02 | 13.8 ⁺ | 4025 | 2.13 [#] | 0.51 | 22° 98 | Palma et al. (2005) |
| Concepción | 0.10 | 60.9 | 16,478 | 2.07 | 0.58 | 35° 122 | Gallardo et al. (2004) |
| Concepción | 1.28 | 32 | 13,808 | 2.27 [#] | 0.76 | 36° 124 | Palma et al. (2005) |
| Concepción | 0.58 | 26–42 | 14,249 | Nd | Nd | 36° 88 | Sellanes et al. (2007) |
| Mejillones | 0.7–3.5 | 496 | 1601 | 0.94–1.95 | 0.54–0.71 | 23° 20 | Laudien et al. (2007) |
| Iquique [§] | 3.4–2.7 | Nd | 1151–985 | ~2.8–2.2 | Nd | 20° 32 | Moreno et al. (2008) |
| Iquique | 0.24 | 12 | <2000 | Nd | Nd | 20° 111 | Quiroga et al. (2005) |
| Chiloé | 1.28 | 7.83 ⁺ | 3506 | 3.89 | 0.75 | 42° 160 | Sellanes et al. (2010) |
| Piura Perú | 1.7–2.5 | 35 | 1727 | 3.5 | 0.74 | 5° 60 | Yupanqui et al. (2007) |
| Callao Perú | 0.02 | 8.6 | 16,233 | 2.3 | 0.22 | 12° 305 | Levin et al. (2002) |
| Valparaiso* | 1.8–1.6 | 37–24 | 2238–1416 | 2.8–2.9 | 0.66–0.74 | 32° 120 ¹ | This study |

Nd: no data

*Data range for stations 4 and 5

¹ Average depth between stations 4 and 5⁺ Quiroga et al. (2005)[#] Jack-knifed Shannon diversity index[§] During and after El Niño 1997–98

comparison to southern Chile (36° S). In fact, TOC values reported by Gutiérrez et al. (2000) and Sellanes et al. (2007) for Concepción Bay were largely higher than those reported in our study. In addition, CPE ranged from 30.3 µg g⁻¹ at 22 m to 60.8 µg g⁻¹ at 140 m for the study sites. These values were lower than those reported by Gutiérrez et al. (2000), Sellanes et al. (2007) and Palma et al. (2005) for the continental shelf during non-ENSO conditions. Our results suggest that the study area would be influenced by a minor input of fresh organic supply to the sediments from primary production. The high variability of chemical seafloor parameters could be explained by the seasonal food supply during upwelling conditions and the aperiodic organic matter continental inputs.

Macrofaunal standing stock and biodiversity

In terms of species composition, abundance and biomass, the macrobenthos communities studied were typical of muddy and sandy coastal habitat of the continental margin off Chile (e.g. Gutiérrez et al. 2000; Sellanes et al. 2007; Palma et al. 2005). Macrobenthic communities exhibited marked changes in the standing stock and diversity patterns in relation to depth. The mean abundance recorded at station 3 was higher than that reported by Yupanqui et al. (2007) for Peru, but largely lower than recorded by Sellanes et al. (2007) for Concepción during the 1998 ENSO conditions. In addition, shallow standing stock appeared to be similar to those reported by Laudien et al. (2007) for Mejillones Bay (northern Chile). Polychaetes

were the main group, followed by peracarid crustaceans (i.e. amphipods and cumaceans) and bivalves. The faunal composition observed at Valparaiso Bay share some faunal components reported by Gallardo et al. (2004) and Palma et al. (2005) for Concepción at similar depths, e.g. high densities of some species like *Cossura chilensis* and *Aricidea pigmentata*, as well as spionid and cirratulid polychaetes. However, some dominant species in the current study, such as *Nucula pisum*, *Amphioplus magellanicus* and *Anchistylis watlingi* (Cumacea), were not ever recorded in Concepción. Levin et al. (2009a, b) suggested that cumaceans would be highly tolerant to hypoxia, but they were not found in high densities at stations under hypoxic conditions in our study area. On the other hand, Lancelotti and Stotz (2004) recorded high abundance and occurrence of the cumaceans *Diastylis tongoyensis* in northern Chile in sediments associated to discharges of iron mine tailings. Similar composition and dominance of the fauna by a few species have also been recorded for hypoxic systems from Northeast Indian margin (Raman et al. 2014; Levin 2003; Hughes et al. 2009). In terms of biomass, it is important to note that 51 % of total biomass in this study was represented only by *Amphioplus magellanicus*, which is a large suspension-feeding ophiuroid, dominant in muddy sediments and not previously recorded at the continental shelf of central and south Chile. Sellanes et al. (2007) recorded higher and similar biomasses during non-ENSO and ENSO conditions, respectively, off Concepción, with polychaetes and crustaceans as dominant groups.

The spatial diversity patterns were different to those observed for abundance and biomass. Diversity recorded its highest values at the shallowest stations, where some indicators of the organic content in sediments were low and a higher proportion of sand was recorded. The Simpson dominance (D'), evenness (J') and the majority of diversity variables showed scarce variation between stations, with no significant differences being recorded (Kruskal–Wallis $p > 0.05$). Shannon diversity (H') ranged from 2.83 to 4.0 bits, exhibiting the highest mean values at shallow stations in the same way as data provided by Sanders–Hurlbert rarefaction curves (ES_{10}), which appear to be higher than those reported by Sellanes et al. (2010). These diversity values were higher than those reported for the OMZ station on the continental shelf off central Chile (Palma et al. 2005) and similar to those reported for the Pakistan margin (Hughes et al. 2009). By contrast, Shannon diversity values were higher in the Indian margin, where hypoxic conditions have been recorded (3.0–6.8 bits; Ingole et al. 2010). It is known that hypoxic conditions affect benthic communities off Peru and central Chile, influencing community structure, characterised by loss of species, low diversity and high dominance (Gallardo et al. 2004; Levin et al. 2002; Sellanes et al. 2007). In fact, in our study area, *C. chilensis* and *N. pisum* accounted for more than 40 % of total abundance; however, dominance (D') exhibited low values. Overall, the higher diversity values recorded in the current study appeared to be characterised by the higher number of polychaetes and peracarid crustacean species.

The presence of two assemblages consisting of a shallow (stations 1 and 2) and a deeper benthic community (ANOSIM $R = 0.515$, $p < 0.05$) may be related to the abundance of polychaetes increasing with depth, while crustaceans (mainly amphipods and cumaceans) were in greatest abundance at shallow stations and the mollusks were the most abundant group at station 3 (Fig. 2).

Macrofaunal abundances showed a parabolic pattern, with decreased densities at stations 1 and 5 and maximum density at station 3. Biomasses also showed a similar spatial distribution, with a clear dominance of mollusks in the shallower stations and a higher contribution of ophiuroids represented solely by *Amphioplus magellanicus* in the deepest stations. The abundance and biomass values of the deepest station (station 5) were similar to those shallowest stations which could be related to food supply from primary production and the influence of terrigenous inputs from the Aconcagua River, respectively, despite differences in faunal composition. Ingole et al. (2010) found a similar ‘parabolic’ distribution, but did not observe changes in composition between sites. Raman et al. (2014) recorded a similar pattern with depth regarding polychaetes and crustaceans.

Macrofaunal response and biotic and abiotic relationships

In upwelling systems, pulses of fresh organic matter from the column water to the seabed have important consequences for the abundance (Gooday and Turley 1990), biomass (Duineveld et al. 2000; Brown et al. 2001) and biodiversity patterns (e.g. Levin and Gage 1998; Gutiérrez et al. 2000; Levin et al. 2002; Moreno et al. 2008). It is known that sediment habitat heterogeneity can be generated by hydrodynamic features such as terrigenous run-off, bottom currents or biological components, such as megafauna bioturbation (Gooday et al. 2010). Such habitat heterogeneity creates high variability of composition, distribution and diversity (Levin 2003; Zalmon et al. 2013). From NMDS ordination, two assemblages were identified (i.e. shallow and deep, see Fig. 4a). However, station 5 seems to be influenced by hypoxia and it would be forming a different group, characterised by lower standing stock. Therefore, the shallow assemblage could not be considered as an OMZ extension, despite some ecological parameters being similar to station 5. In this sense, the hypothesis set up could not be accepted, although some ecological descriptors, such as density and biomass, recorded a parabolic distribution, with the highest in the middle, and the species richness and dominance also recorded a similar distribution pattern. The diversity is highest close to shore and declines offshore, that is, it does not follow the density gradient. K-dominance is the inverse of the expected species diversity, illustrating that dominance controls the diversity calculation. However, is the dominance at each site the same or different species among the sites? In terms of density, *Ampelisca gracilicauda* and *Nucula pisum* were dominants at the shallow assemblage, while *Nucula pisum* and *Cossura chilensis* were dominants at the deep assemblage.

The lowest values of density and species richness were recorded at station 5, with the lowest DO concentrations. The Spearman correlation analysis showed that diversity and species richness appeared to be related to sediment characteristics (i.e. clay percentage and grain size) and total organic matter. In fact, low diversity values and species number in the study area were found at stations with a high content of TOM; the dominance measure (J') was positively associated with high concentrations but with a low quality of TOC. Our values of the Chla and CPE in the study area confirm this situation, probably related to high environmental variability at shallow and deep stations.

It is important to note that the NBSS did not differ among stations in our study area. The slope of the NBSS is widely used as an ecological indicator in benthic systems (e.g. Akoumianaki et al. 2006; Hua et al. 2013; Quiroga et al. 2005, 2014). This value of the slope in our study was less negative than those

reported for the OMZ (Quiroga et al. 2005) and Concepción Bay (Sellanes et al. 2007), suggesting that community structure was controlled by sediment characteristics (see Table 4). It is known that the slope of the NBSS is affected by the physical habitats afforded by the sediment (Drgas et al. 1998); however, oxygen levels and organic matter may also be influencing the community size structure of the macrofauna (Drgas et al. 1998; Akoumianaki et al. 2006; Quiroga et al. 2012). The mean animals' body size varied widely between sites, observing that the highest value (226.7 at station 3) is not directly related to the highest values of organic sources. Sites with organic inputs and hypoxia usually exhibit an overall pattern with smaller body size animals. This pattern may be explained by physiological constraints, where small organisms are better able to satisfy their metabolic demands because they have a higher surface area to body volume ratio (Forbes and Lopez 1990; Quiroga et al. 2005). In this study, *Cossura chilensis*, a small deposit-feeding polychaete, was dominant, where the lower oxygen levels and the highest organic values were recorded. However medium-sized animals with large branchiae like *Paraprionospio pinnata* were also recorded at deep sites, demonstrating the influence of hypoxia on body size spectra, as reported by Qu et al. (2015).

In our study area, the Shannon diversity (H') was negatively correlated with clay, TOM and TOC, and positively correlated with Chla/TOC. By contrast, dominance was positively related to TOC content and negatively related to clay. Our results confirm that the grain size distribution seems to be influencing the spatial distribution of macrofauna. Peracarid crustaceans such as amphipods and cumaceans were frequently found in shallow sediments with a higher proportion of sand and with low organic content, while small soft-bodied polychaetes were demonstrated to mostly inhabit deeper muddy sediments with higher organic supply. In addition, ophiuroids were only important in biomass from station 3, where sand was less than 23 % and the organic content was higher.

Finally, soft-bottom macrobenthic communities in the study area exhibited a clear on- to offshore spatial pattern that may reflect the relevant influence of the grain size and organic matter. The causes of this response could be explained by the food supply from the column water to the seabed that generated evident changes on the chemical properties of the sediments that are influenced by regular upwelling conditions and the changes on physical variables of the sediment that determine habitat heterogeneity as a result of a coastal hydrodynamic, where terrigenous inputs could also be influencing the diversity patterns of benthic communities, as demonstrated by carbon stable isotopes and chloroplast pigments measurements. Long time series studies will elucidate the real expansion of hypoxic zones to the coastal zones in upwelling systems and enable a better understanding of its influence on benthic biodiversity.

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