



SPECIAL TOPIC

Diversity patterns along and across the Chilean margin: a continental slope encompassing oxygen gradients and methane seep benthic habitats

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Abstract

In the present study we review datasets available for the Chilean margin to assess the relationship between environmental (or habitat) heterogeneity and benthic diversity. Several factors, such as the presence of different water masses, including the oxygen-deficient Equatorial Sub-surface Waters (ESSW) at the continental shelf and upper slope, and the Antarctic Intermediate Waters (AIW) at mid slope depths appear to control the bathymetric distribution of benthic communities. The presence of methane seeps and an extended oxygen minimum zone (OMZ) add complexity to the benthic distribution patterns observed. All these factors generate environmental heterogeneity, which is predicted to affect the diversity patterns both along and across the Chilean continental margin. The response to these factors differs among different faunal size groups: meio-, macro-, and megafauna. Physiological adaptations to oxygen deficiency and constraints related to body size of each group seem to explain the larger-scale patterns observed, while sediment/habitat heterogeneity (e.g. at water mass boundaries, hardgrounds, biogeochemical patchiness, sediment organic content, grain size) may influence the local fauna diversity patterns.

Problem

The SE Pacific coast off South America harbors one of the largest and most productive marine ecosystems worldwide, the Humboldt Current Large Marine Ecosystem (Alheit & Bernal 1993). Wind-driven upwelling sustains a high primary production and pelagic biomass (e.g. Walsh 1981; Bernal *et al.* 1989). Associated with the poleward Equatorial Sub-surface Water (ESSW), an intense Oxygen Minimum Zone (OMZ) develops within the main thermocline (100–600 m) over the continental shelf and slope along the coast (Alheit & Bernal 1993). This OMZ develops due to the high oxygen demand of decomposing organic matter and slow rates of water renewal by ventila-

tion (Wyrтки 1962). Below the OMZ, the well-oxygenated Antarctic Intermediate Water (AIW, located from ~500 to 1200 m) flows northward, with the Pacific Deep Water (PDW, >1200 m depth) lying below it (Silva & Konow 1975).

Latitudinal patterns of benthic communities along the Chilean coast have been studied intensively, but it is still not clear whether these patterns also persist when deeper assemblages are considered. One of the first attempts to investigate the zoogeographic patterns of the sublittoral benthic fauna off Chile resulted from the ‘The Lund University Chile Expedition 1948–1949’ and ‘The Royal Society Expedition to Southern Chile’, reviewed in Brattström & Johanssen (1983). These expeditions achieved a good

geographic coverage, including almost the entire coast of Chile, but with most of the sampling effort centered in the southern areas, and encompassing a fair bathymetric resolution (in general shallower than 500 m water depth). These studies concluded that the predominance of the Humboldt Current from about 42°S and flowing northwards strongly modulates the variability of hydrographic conditions, and thus the observed assemblages. Consistently, most studies indicate that within this vast latitudinal range (42°–20°S, *i.e.* ~2450 km), there is only a transition zone in coastal benthic communities, *i.e.* from a southern cold-temperate region to a northern warm-temperate region located between 33° and 30°S (Bratström & Johannsen 1983). However, although these studies took into account climatic conditions and some hydrographic aspects, the classification of faunal assemblages was mostly based on a biological perspective (presence/absence).

When deeper assemblages are considered the story becomes more intricate, as many water masses with different characteristics occur in a 3-dimensional perspective, *i.e.* horizontal (latitudinal gradient), perpendicular to the coast (longitudinal gradient) and vertical (bathymetric range), adding further heterogeneity to the more or less static picture envisaged for the coastal zone. Most important for benthic organisms is the effect of the OMZ associated with the ESSW, which is permanently present at shelf and upper bathyal depths in the north, but diminishes southwards, until it disappears at about 42°S (Silva & Konow 1975). The effect of OMZs over the different components of the benthic community is evident, but differs among different taxa (reviewed in Levin 2003).

Aspects such as benthic pelagic-coupling, patterns of benthic community structure, and role of habitat heterogeneity (including, in addition to water masses, habitat types such as seeps, OMZ) in modulating benthic faunal communities, are issues still poorly addressed for the Chilean margin beyond its shelf break.

In this context, environmental gradients present in the bathyal zone (*i.e.* from the shelf break, about 150 m depth, to the lower slope, about 4000 m depth), as well as local spots of heterogeneity may influence geographic patterns of diversity by affecting habitat characteristics and biogeochemical processes, as well as larval transport and recruitment. At methane seeps, aggregation of ecosystem engineers such as tube builders, burrowers and cold-water coral communities are usually referred to as generators of habitat heterogeneity. As an example, the first precisely located methane seep site off Chile was reported only a few years ago (Sellanes *et al.* 2004), and recent investigations in the area have resulted in the discovery of a faunal aggregation 'hot spot' (including commercial species and many new taxa), adding substantial knowledge to the

ecology and ecosystem functioning of the deep sea off south-central Chile (Sellanes *et al.* 2008).

The aim of this paper is to review recent research for the Chilean slope fauna (meio-, macro- and megafauna) on structural patterns within the benthic community and its diversity in relation to habitat heterogeneity along (~22°–42°S) and across (~100–2000 m) a portion of the Chilean margin. This is the first time that these data are assembled to provide holistic insight into the different adaptations and strategies exhibited by the different size groups of benthic fauna (*i.e.* meio-, macro- and megafauna). We will consider bottom-water dissolved oxygen, organic loading of the sediment, type of substratum, and the presence of particular habitats (*e.g.* methane seeps) as the main generators of habitat heterogeneity at the study area. The main questions that will be addressed are: (i) Which environmental factors change with depth and latitude on the Chilean margin, and how do these changes relate to community composition and body-size patterns of benthic organisms? (ii) Is there a relationship between margin benthic habitat heterogeneity (*e.g.* depth, bottom water dissolved oxygen, sediment organic matter content, grain size) and meio- and macrofaunal biodiversity on a local scale? (iii) How does the presence of methane seep hardgrounds affect megafaunal diversity patterns? and (iv) How does the relationship between environmental changes and diversity vary across the different size groups of organisms?

Material and Methods

Data used in the present study were compiled from our own datasets, or manuscripts derived from different cruises off Chile. These covered either a substantial latitudinal and bathymetric range, and had biotic and/or abiotic data recorded. These cruises were the *Thioploca* '99 expedition (1999), the R/V *Sonne* SO-156 expedition (2001), the SeepOx cruise to the Concepción Methane Seep Area (CMSA) (2006) and the R/V *Vidal Gormáz* 07 cruise (2007). The SO-156 cruise was the most extensive of all both in spatial and bathymetric coverage. This cruise included three transects (~100–2000 m water depth): off Antofagasta (~22°S), Concepción (~36°S) and Chiloé (~42°S) (Fig. 1). Results were published independently for meio-, macro- and megafauna (Palma *et al.* 2005; Quiroga *et al.* 2009; Veit-Köhler *et al.* 2009; respectively). For the stations covered during the SO-156 cruise, abiotic data include: sediment chlorophyll (Chl-*a*), phaeopigment (Phaeo) and chloroplastic pigment equivalent (CPE), total organic carbon of surface sediments (TOC), grain size and bottom water dissolved oxygen (DO) (Table 1). For details of the methodology see the corresponding articles. Briefly, sediments were collected using

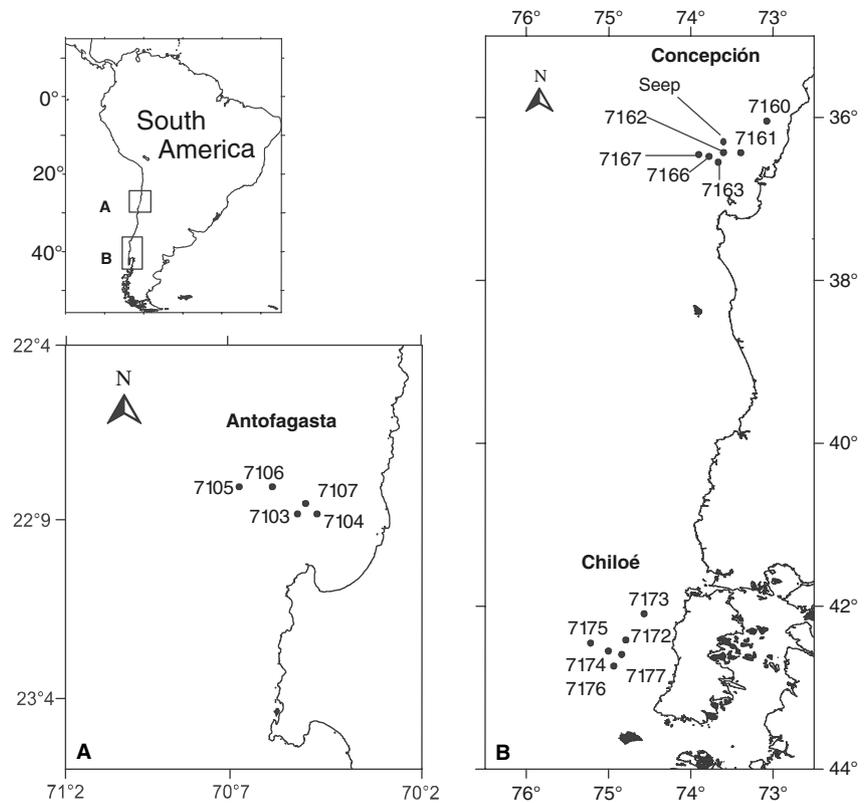


Fig. 1. Map showing the sampling stations used for this study. Except for the seep site, the stations were visited during the SO-156 cruise. Modified from Quiroga *et al.* (2009).

Table 1 Station information (location, depth and date sampled).

Location	Station	Bathymetric zone	Lat. S	Long. W	Date	Depth (m)	Sample	DO (ml l ⁻¹)	Sand (%)	Chl-a (µg g ⁻¹)	CPE (µg g ⁻¹)	TOC (%)
Antofagasta	7110	Shelf	22°48'68	70°25'73	04.05.01	98	Ma	0.02	n.d	n.d	n.d	n.d
	7102	Shelf	22°49'59	70°28'29	04.01.01	142	Ma	0.05	99.47	4.83	35.66	n.d.
	7104	Upper bathyal	22°51'96	70°29'39	04.02.01	294–319	Me, Ma, Mf	0.06	26.22	4.61	38.26	4.8
	7107	Middle bathyal	22°50'50	70°30'93	04.04.01	502–632	Ma, Mf	0.90	94.47	7.35	56.44	nd
	7103	Middle bathyal	22°51'99	70°32'58	04.02.01	864–895	Ma, Mf	1.28	25.89	3.40	31.53	4.99
	7106	Lower bathyal	22°47'98	70°32'58	04.04.01	1347–1380	Ma, Mf	1.70	97.97	2.58	23.28	3.14
	7105	Lower bathyal	22°48'07	70°42'29	04.03.01	1649–1900	Ma, Mf	n.d	n.d	n.d	n.d	n.d
Concepción	7161	Shelf	36°25'52	73°23'36	04.23.01	120–124	Me, Ma, Mf	0.45	1.25	10.33	85.29	4.28
	7160	Upper bathyal	36°02'35	73°04'40	04.23.01	365	Me, Ma, Mf	0.79	2.24	3.56	29.91	2.97
	7163	Middle bathyal	36°25'49	73°35'72	04.24.01	538–550	Ma, Mf	2.92	27.48	2.31	20.5	2.06
	7162	Middle bathyal	36°32'54	73°40'05	04.24.01	798–850	Ma, Mf	2.30	4.31	4.08	25.61	2.61
	Seep	Middle bathyal	36°21'90	73°43'21	09.02.06	710–870	Mf	2.60	n.d	n.d	n.d	n.d
	7166	Lower bathyal	36°27'99	73°46'47	04.25.01	1294–1424	Ma, Mf	1.48	3.07	2.83	27.16	3.08
	7167	Lower bathyal	36°27'17	73°54'18	04.26.01	2060–2201	Ma, Mf	1.82	1.67	3.48	31.85	3.04
Chiloé	7173	Shelf	42°05'36	74°33'55	04.30.01	160–185	Ma, Mf	1.28	58.86	1.5	14.03	1.34
	7172	Upper bathyal	42°24'61	74°47'26	04.30.01	286–297	Me, Ma, Mf	1.52	45.43	1.23	14.06	1.56
	7176	Upper bathyal	42°35'35	74°48'35	05.02.01	480–502	Ma, Mf	2.79	nd	nd	nd	nd
	7177	Middle bathyal	42°34'96	74°50'22	05.03.01	971–1016	Ma, Mf	2.31	1.78	2.5	24.4	3.53
	7174	Lower bathyal	42°32'66	75°01'10	05.01.01	1445–1776	Ma, Mf	1.87	1.19	2.07	21.2	3.4
7175	Lower bathyal	42°27'13	75°12'61	05.01.01	1876–2010	Ma, Mf	1.93	1.95	1.65	17.81	3.12	

Sample indicates which size groups have been sampled (Me = meiofauna, Ma = macrofauna and Mf = megafauna). DO = dissolved oxygen, CPE = chloroplastic pigment equivalents, TOC = total organic carbon. Modified from Palma *et al.* (2005), Quiroga *et al.* (2009).

a multiple corer (tube inner diameter = 95 mm). Chl-*a* and Phaeo contents were analyzed photometrically according to Lorenzen & Jeffrey (1980) after acetone extraction. The sum of Chl-*a* and Phaeo is referred as the CPE and is used as an indicator of the phytodetrital material input to the sediments (Pfannkuche & Soltwedel 1998). Sediment TOC was obtained using a Heraeus-CHN-analyzer of HCl-decalcified samples. Grain size analysis was performed using geological sieves, and particle size data were analyzed following Folk (1974). Water column temperature, salinity, and dissolved oxygen were measured at each station using a Seabird CTDO 25 probe mounted on a rosette. The output of the oxygen sensor was calibrated using measurements from water samples taken at appropriate depths. Dissolved oxygen was then measured according to the modified Winkler method (Knap *et al.* 1993), using a semiautomatic version of the photometric end-point detector, Dosimat 665 (Metrohm), and a chart recorder for the titration.

Meiofauna (metazoans from 0.040 to 0.5 mm body size) were collected using a multicorer. Three replicate 10-cm² sub-samples were analyzed from each site, samples were preserved onboard in 4% seawater-buffered formaldehyde, and then identified in the laboratory to major taxa under low power stereomicroscope (Veit-Köhler *et al.* 2009). The macrofauna samples were collected with a deep-sea multiple box-corer with nine separate box-cores each measuring 0.024 m² in area (Gerdes 1990). The sediment samples were sieved on deck through 500- μ m mesh size and the retained macrofauna preserved in 10% seawater-buffered formaldehyde. In the laboratory, the fauna was sorted, transferred to a 70% ethanol solution and then identified to the lowest possible taxonomic level (Palma *et al.* 2005). The distribution of the body size [normalized biomass size-spectra (NBSS)] of the macrofauna is also discussed from empirical model data from Quiroga *et al.* (2005), to analyze the effects of low oxygen on the body-size of the macrofauna.

Megafaunal specimens (>1 cm) were collected by means of a modified Agassiz trawl (AGT) with a beam width of 1.5 m and 10 mm mesh size at the cod-end operated in 20-min hauls. Specimens were preserved onboard ship in 10% buffered formaldehyde. The megafaunal SO-156 data were complemented with seep data, available from Sellanes *et al.* (2008). A photo sledge, consisting of a vertically oriented camera combined with two strobes, provided high resolution images of the seafloor at the three studied transects (SO-156 cruise) and at three discrete depths (100, 300 and 500 m). At each station a series of 50 pictures were taken, imaging approximately 1 m² of seafloor each, and distributed along a transect of ~500 m length (Hebbeln 2001). These images provided *in situ* views of the benthic habitat and were used to

study the epibenthic communities, their marks over the sediment (*lebensspuren*) and the general characteristics of the seafloor at each site.

A principal component analysis (PCA) was used to identify the relationships between stations and the environmental variables TOC, grain size, Chl-*a*, Phaeo, CPE, DO and depth. Data for macrofauna and megafauna are available mostly at the species level, while for meiofauna, data are at a higher taxonomic level. Data analysis (except for meiofauna) included two diversity indices: Shannon's H' (base 2) and Pielou's evenness J'. In addition, the rarefaction (ESn) method, as modified by Hurlbert (1971), was used to compare the diversity of samples of unequal sizes for megafauna (Magurran 1988). Spearman Rank correlation analysis was used to evaluate relationships between environmental parameters and biological diversity measurements for macrofauna and megafauna for the combined dataset (*i.e.* Antofagasta, Concepción and Chiloé).

Results

Environmental characteristics

Low oxygen conditions (<1.42 ml·l⁻¹) were recorded at stations located on the continental shelf and upper slope off Antofagasta (98–895 m) and Concepción (120–365 m), and in the uppermost station off Chiloé (160–185 m) (Table 1). OMZ conditions (<0.5 ml·l⁻¹) were present on the shelf and upper slope off Antofagasta (98–319 m), and on the shelf off Concepción (120–124 m), typically associated with ESSW. Oxygen concentrations begin to increase below 500 m off Antofagasta and below 365 m off Concepción, in association with the presence of the AIW. No OMZ is reported off Chiloé (Table 1). The grain-size of the sediments collected off Antofagasta and off Chiloé appeared to be more heterogeneous than off Concepción (Table 1). High percentages of sand (>25%, and up to 99%) were observed at all stations off Antofagasta and at the shelf and upper bathyal stations off Chiloé (58% and 45%, respectively). In contrast, sediments off Concepción were predominantly muddy (% sand <5%), with the exception of the site located at 538–550 m (% sand ~27%). At the seep site, sampling of the sediment for grain size and other environmental variables was precluded due to the presence of carbonate hardgrounds. The highest organic enrichment (TOC > 4.2%) of the sediments was observed in the upper bathyal and shelf zones off Antofagasta and Concepción, respectively (Table 1). Principal component analysis of normalized environmental data (depth, DO, TOC, Chl-*a*, and CPE, and percentages of sand) is shown in Fig. 2. The first two PCA axes accounted for 75% of the total variance. The environmental variables that most influenced the gradient

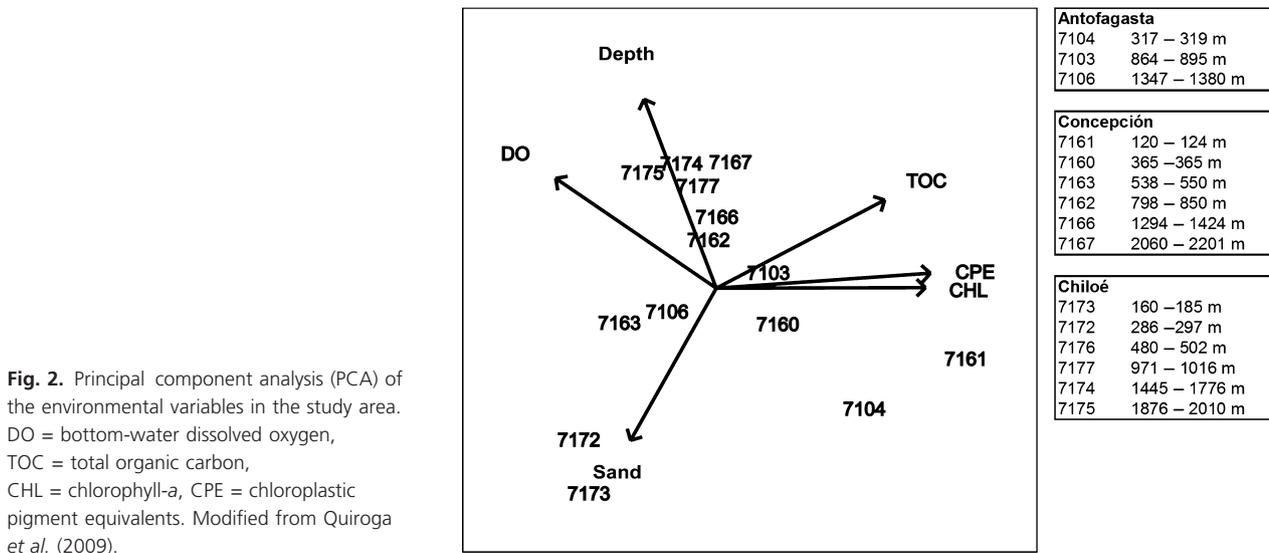


Fig. 2. Principal component analysis (PCA) of the environmental variables in the study area. DO = bottom-water dissolved oxygen, TOC = total organic carbon, CHL = chlorophyll-*a*, CPE = chloroplast pigment equivalents. Modified from Quiroga *et al.* (2009).

in PC 1 (51%) were those related to organic loading (TOC, CPE and Chl-*a*) and oxygen content (DO). Water depth and sand content were the variables that better related to PC 2 (24%). In general this reflects: (i) the high organic carbon and pigment content associated with low dissolved oxygen at the shelf and upper slope off Antofagasta and Concepción, (ii) the finer sediments at most of the deeper water stations associated with higher oxygen (iii) the occurrence of coarser-grain sediments at upper bathyal depths off Chiloé and Antofagasta.

Representative images of the benthic habitat at ~100, ~300 and ~500 m depth, at the three transects, are presented in Fig. 3. At the upper boundary of the OMZ off Antofagasta (Fig. 3A) sparse patches of filamentous bacteria were present, whereas no megafauna or animal traces (*lebensspuren*) were observed. The seafloor appearance at ~300 m, within the core of the OMZ (DO = 0.06 ml·l⁻¹), with authigenic crusts (probably phosphoritic) with no visible megafauna or traces (Fig. 3B), contrasts with the enhanced presence of organisms beyond the OMZ at ~500 m (Fig. 3C). The fine sediments within the OMZ off Concepción (Fig. 3D) also showed little evidence of animal activity, although galatheid crabs (*Pleuroncodes monodon*) were present. At ~300 m (DO = 0.79 ml·l⁻¹) fine sediments with presence of infauna (indicated by burrows) and surface animal traces dominate (Fig. 3E), while at ~500 m (Fig. 3F) the presence of *lebensspuren* noticeably increases, together with the diversity of the epibenthic megafauna. Finally, off Chiloé, where no OMZ was detected (DO always > 1 ml·l⁻¹), the images of the shallower site show coarse-grained sediments and scarce *lebensspuren* (Fig. 3G), while traces of majid crabs, polychaete burrows and gastropods on fine sediments are characteristic at ~300 m (Fig. 3H). At ~500 m the

seafloor environment is formed by patches of hardgrounds with sessile organisms, mobile megafauna such as spider crabs and starfish (as well as their traces) present over a fine veneer of sediment overlying the harder substrate (Fig. 3I).

Benthic fauna

Information for meiofauna is only available for four stations ranging in DO from 0.06 to 1.52 ml·l⁻¹. The highest meiofauna abundance ($n = 7713 \text{ ind} \cdot 10 \text{ cm}^{-2}$) was found at the station with DO = 0.79 ml·l⁻¹, whereas the most oxygenated site yielded the lowest densities ($n = 1428 \text{ ind} \cdot 10 \text{ cm}^{-2}$) (Table 2). However, with increasing bottom-water oxygenation, meiofauna became more diverse at a higher taxon level ($S = 16$ different classes/suborders off Chiloé *versus* $S = 4$ within the OMZ off Antofagasta and Concepción). The nematode/copepod (nem/cop) ratio, calculated from abundance data given in Veit-Köhler *et al.* (2009), decreased consistently from north (nem/cop = 1765) to south (nem/cop = 775 and 521 off Concepción), being lowest off Chiloé (nem/cop = 12.8) where the OMZ is absent and sandy sediments dominate. Nematodes were the most abundant meiofauna taxon at every station, followed by annelids, copepods, and nauplii. Copepods, nauplii and fauna other than nematodes and annelids, correlated positively with DO (Spearman r coefficient = 0.83, 0.94, and 0.92, respectively) and negatively with organic carbon (Spearman r coefficient = -0.90, -0.98, and -0.95, respectively) (Table 3).

In general a sharp increase in macrofaunal species diversity (S , H' and rarefied species number) was observed at the OMZ/AIW boundary, whereas within the

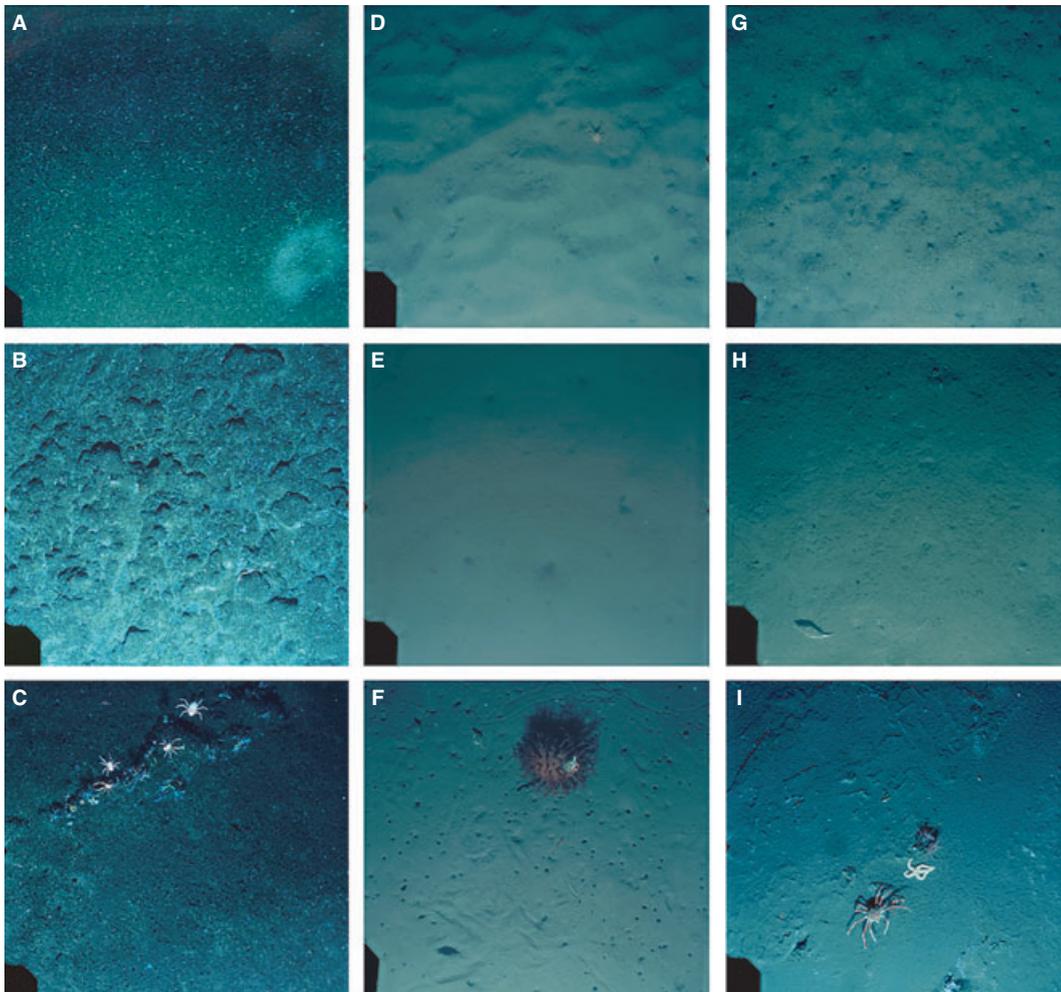


Fig. 3. Images of the seafloor taken at the three transects off Chile: (A) off Antofagasta at 142 m, bottom-water dissolved oxygen (DO) = 0.05 ml·l⁻¹, coarse sediment, with shell debris and a patch of filamentous bacteria at the lower right; (B) off Antofagasta, 319 m, DO = 0.06 ml·l⁻¹, authigenic crusts, probably phosphoritic with no visible megafauna or traces; (C) off Antofagasta, 502 m, DO = 0.90 ml·l⁻¹, patches of hard substratum covered with cnidarians and galatheid crabs; (D) off Concepción, 120 m, DO = 0.45 ml·l⁻¹, fine fluffy mud of greenish color, with some ripple marks and few *lebensspuren*, a couple of squat lobsters (*Pleuroncodes monodon*) in the center; (E) off Concepción 365 m, DO = 0.79 ml·l⁻¹, fine sediment with burrows and surface animal traces; (F) off Concepción 538 m, DO = 2.92 ml·l⁻¹, fine sediment with abundant *lebensspuren*, an alcyonarian with a commensal hermit crab and buccinid gastropods; (G) off Chiloé, 160 m, DO = 1.28 ml·l⁻¹, coarse sediment with some shell debris and *lebensspuren*; (H) off Chiloé 286 m, DO = 1.52 ml·l⁻¹, traces of majid crabs, polychaete burrows and a volutid gastropod (*Miomelon philippiana*) on fine sediments; and (I) off Chiloé, 480 m, BWDO = 2.79 ml·l⁻¹, patches of hard bottom with gorgonians, a spider crab (*Libidoctaea granaria*) and a starfish. The image field is ~1 m each side.

OMZ there were higher abundances ($n = 3500 \pm 3408$, mean ± 1 SD) and a dominance of small-size-bodied organisms (e.g. $H' = 1.07$ and $J' = 0.52$ at 294–319 m off Antofagasta, with DO = 0.06 ml·l⁻¹). Latitudinally, the number of species and diversity increased toward the southernmost stations (e.g. species richness ranged from 4 to 15, 14 to 31 and 26 to 43 off Antofagasta, Concepción and Chiloé, respectively, Table 2).

Similar to the meiofauna, macrofaunal patterns were also influenced by oxygen and organic carbon. Species richness, diversity and body size (NBSS slope) were posi-

tively correlated with DO, but negatively correlated with organic content (Chl-*a* and CPE) (Table 3). Rarefaction richness (ES_{100}) indicates depressed diversity at the OMZ core (295 m) off Antofagasta ($ES_{100} = 4$) and at its lower boundary ($ES_{100} = 5$ at 528 m) (Fig. 4A). However, higher values were observed at the shallowest stations ($ES_{100} = 14$ and 10 at 98 and 142 m, respectively), which had DO < 0.05 ml·l⁻¹. Rarefaction richness peaked at 890 m ($ES_{100} = 15$). Off Concepción, rarefaction richness was lowest at 124 m ($ES_{100} = 11$), and was followed by an unimodal pattern with depth, with a maximum at

Table 2. Summary of available quantitative information and diversity data for meio-, macro- and megafauna at the three depth transects along the Chilean margin.

	Depth (m)	Meiofauna		Macrofauna						Megafauna				
		S	N (ind·10 cm ⁻²)	S	N (ind·m ⁻²)	S.D.	H' (base 2)	J'	ES ₁₀₀	S	N	H' (base 2)	J'	ES ₁₀₀
Antofagasta	98*	n.d.	n.d.	15	4025	2576	2.13	0.51	14	n.d.	n.d.	n.d.	n.d.	n.d.
	142*	n.d.	n.d.	8	283	184	2.77	0.71	10	n.d.	n.d.	n.d.	n.d.	n.d.
	294–319*	4	1829	4	3500	3408	1.07	0.52	4	2	123	0.05	0.05	2
	502–632*	n.d.	n.d.	7	97	90	3.49	0.91	5	9	23	2.63	0.83	9
	864–895	n.d.	n.d.	15	491	207	3.54	0.82	15	13	62	0.83	0.22	9
	1347–1380	n.d.	n.d.	8	138	207	3.43	0.93	9	21	702	0.65	0.15	6
	1649–1900	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	15	27	3.17	0.81	15
Concepción	120–124	4	2071	20	13525	3914	2.27	0.76	11	3	16	0.87	0.55	3
	365	10	7713	14	441	158	3.55	0.88	14	14	621	2.71	0.71	12
	538–550	n.d.	n.d.	18	1741	481	3.71	0.73	14	24	201	3.57	0.78	21
	798–850	n.d.	n.d.	16	941	307	3.07	0.71	15	16	742	1.49	0.37	10
	710–870 (seep)*	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	47	778	2.29	0.59	24
	1294–1424	n.d.	n.d.	31	2450	265	3.52	0.67	19	31	226	3.87	0.78	25
	2060–2201	n.d.	n.d.	20	1533	409	3.19	0.69	14	14	315	2.05	0.54	10
Chiloé	160–185*	16	1428	33	3506	1135	3.89	0.75	20	5	25	1.88	0.81	5
	286–297*	n.d.	n.d.	32	2500	949	3.28	0.65	24	9	83	2.07	0.65	9
	480–502	n.d.	n.d.	39	1018	284	4.41	0.81	26	39	280	3.97	0.75	26
	971–1016	n.d.	n.d.	42	1423	404	4.83	0.84	29	34	708	1.92	0.38	11
	1445–1776	n.d.	n.d.	43	1631	228	4.57	0.80	29	23	1182	1.45	0.32	7
	1876–2010	n.d.	n.d.	26	722	367	3.96	0.78	22	17	196	2.73	0.67	15

■ OD < 0.5 ml l⁻¹.■ 0.5 ml l⁻¹ < OD < 1 ml l⁻¹.

Shaded areas indicate those stations within the OMZ. An asterisk after the depth range indicates the presence of hardgrounds. For meiofauna, S indicates higher taxa numbers (class/order).

Table 3. Spearman Rank correlations between environmental variables and available quantitative and diversity parameters for the three faunal size groups studied.

		Depth	DO	Sand	CHL	CPE	TOC
Meiofauna	Nematode density	0.52	-0.01	-0.61	-0.12	-0.15	-0.09
	Copepod density	0.62	0.83	0.24	-0.73	-0.73	-0.90
	Nauplii density	0.53	0.94	0.49	-0.8	-0.78	-0.98
	Annelid density	0.77	0.24	-0.27	-0.49	-0.51	-0.37
	Others	0.46	0.92	0.75	-0.84	-0.81	-0.95
Macrofauna	No. of species S	0.24	0.58	-0.53	-0.69	-0.61	-0.24
	Total density N	-0.41	-0.16	-0.37	-0.29	-0.24	-0.08
	Diversity H' (base 2)	0.48	0.53	-0.29	-0.60	-0.51	0.01
	Evenness J'	0.31	0.25	0.00	0.04	0.03	0.28
	Exp. species ES ₁₀₀	0.33	0.45	-0.37	-0.48	-0.42	0.14
	NBSS (slope)	0.41	0.57	0.12	-0.28	-0.23	-0.20
	NBSS (intercept)	-0.49	-0.54	0.51	0.51	0.45	0.23
Megafauna	No. of species S	0.75	0.82	-0.25	-0.44	-0.40	-0.11
	Total density N	0.71	0.42	-0.12	-0.22	-0.21	0.27
	Diversity H' (base 2)	0.25	0.62	-0.31	-0.45	-0.43	-0.55
	Evenness J'	-0.18	0.31	-0.21	-0.29	-0.29	-0.66
	Exp. species ES ₁₀₀	0.53	0.74	-0.24	-0.44	-0.42	-0.32

Significant correlations are given in bold (P < 0.05).

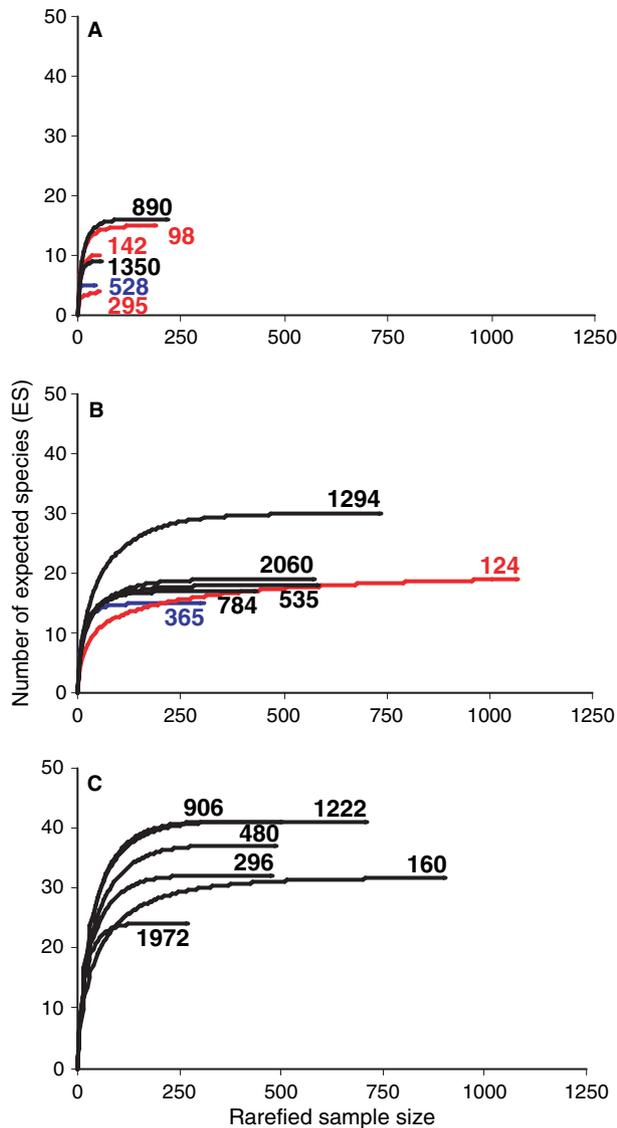


Fig. 4. Rarefaction (ES) plots for the macrofauna observed: (A) off Antofagasta, (B) off Concepción, including the CMSA, and (C) off Chiloé. The depths are shown for each curve. Black lines indicate sites with bottom water $\text{DO} > 1 \text{ ml}^{-1}$, blue lines $1 \text{ ml}^{-1} > \text{DO} > 0.5 \text{ ml}^{-1}$, and red lines $\text{DO} < 0.5 \text{ ml}^{-1}$.

1294 m ($\text{ES}_{100} = 19$) (Fig. 4B). Off Chiloé, where the OMZ is absent, rarefaction richness was lowest at both extremes of the transect ($\text{ES}_{100} = 20$ at 160 m and $\text{ES}_{100} = 22$ at 1972 m), and peaked ($\text{ES}_{100} = 29$) at 902 and 1222 m (Fig. 4C).

Empirical model data from Quiroga *et al.* (2005) regarding the effects of low oxygen on the distribution of body size of the macrobenthos indicate distinct, consistent patterns in the normalized biomass size-spectra (NBSS) in the communities located within the OMZ

(slope = -0.84) and in those located outside the OMZ (slope = -0.46). The more negative slope observed within the OMZ indicates a higher contribution of smaller-size fauna to total biomass in these oxygen-deficient environments. Consistently, the NBSS slope was positively correlated with DO (Table 3). Polychaete species with small body size, such as *Aricidea pigmentata* and *Mediomastus branchiferus*, are in general the ones that contribute most to total biomass. However, off northern Chile, the contribution of oligochaetes (probably *Olavius* sp.) and other polychaetes such as *Magelona phyllisae*, *Cirratulus cirratus* and *Levensenia gracilis* are significant. In central Chile, the OMZ stations were dominated by the small-bodied polychaetes *Cossura chilensis* and *Paraprionospio pinnata*.

For the megafauna, rarefaction curves indicate a sharp increase in species number off Antofagasta and Concepción just below the OMZ (528 and 365 m, respectively) (Fig. 5). Indeed, rarefaction richness for the Antofagasta samples was lowest at 300 m ($\text{ES}_{100} = 2$) and in general increased with depth (Fig. 5A). Off Concepción, as for the macrofauna, rarefaction richness was lowest at 120 m ($\text{ES}_{100} = 3$), and then followed a unimodal pattern with depth, with a maximum at 1294 m ($\text{ES}_{100} = 25$) (Fig. 5B). Notable is the enhanced diversity at the seep site ($\text{ES}_{100} = 24$) compared with the non-seep site at a similar depth ($\text{ES}_{100} = 10$) (Table 2). Off Chiloé, rarefaction richness was lowest at 160 m ($\text{ES}_{100} = 5$), increased with depth to 500 m ($\text{ES}_{100} = 26$), and then declined at 2000 m ($\text{ES}_{100} = 15$). Diversity patterns (H') followed this trend, but in general a second peak was observed at the deepest stations. The maximum number of megafaunal species at a single station was observed at the CMSA ($S = 47$), but diversity was moderate (H' base 2 = 2.29) (Table 3).

The number of species (S) and density (N) of the megafauna was significantly positively correlated with depth, while bottom water DO was positively correlated with S , H' and ES_{100} . Total organic carbon was negatively correlated with H' and J' (Table 3).

Discussion

Faunal response to different sources of heterogeneity on the Chilean margin

Meiofauna assemblages became more diverse (in terms of higher taxa) with increasing DO and decreasing organic carbon, due to increased abundances of fauna other than nematodes. The highest taxon diversity was observed at an upper slope site, with relatively high sand content off Chiloé, beyond the OMZ influence. This is also supported by the lower nematode/copepod ratio at this site. The

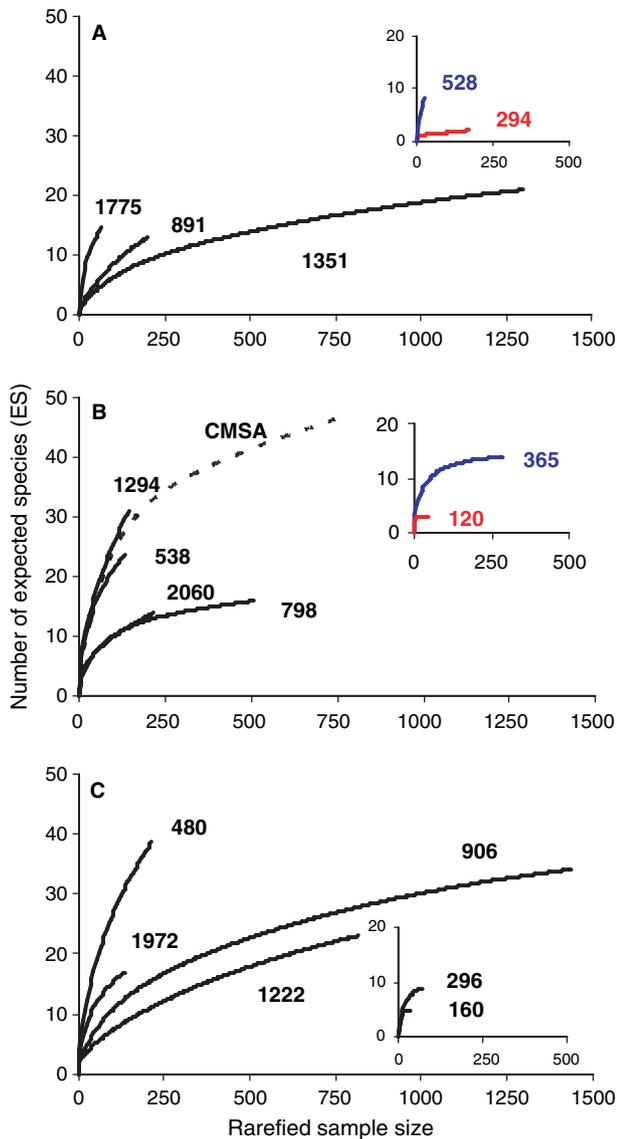


Fig. 5. Rarefaction (ES) plots for the megafauna observed: (A) off Antofagasta, (B) off Concepción, including the CMSA, and (C) off Chiloé. The depths are shown for each curve, and the insets show curves that are not easily visualized if put together with the others. Black lines indicate sites with bottom water DO $> 1 \text{ ml l}^{-1}$, blue lines $1 \text{ ml l}^{-1} > \text{DO} > 0.5 \text{ ml l}^{-1}$, red lines $\text{DO} < 0.5 \text{ ml l}^{-1}$ and the dotted line corresponds to the seep site.

reduction or absence of forms unable to tolerate low oxygen concentration in the OMZ, such as harpacticoid copepods, is well documented (Hicks & Coull 1983; Murrell & Fleeger 1989; Neira *et al.* 2001a). For this indicator of alpha diversity (taxon number), there is a positive effect of either sand content or release of negative effects of oxygen deficiency. However, no species data are available, and we still do not know how OMZ habitats

add to beta or even gamma diversity for this group (*i.e.* are those OMZ-endemic species? if so, then they must be added to the regional species pool). Examples of OMZ endemics are *Glochinema bathyperuviensis* and *Glochinema spinithorni*, species apparently endemic to the OMZ bathyal sediments off Peru and Baja California, respectively (Neira *et al.* 2001b, 2005).

Studies off Peru indicate that beyond the OMZ habitat, sediment heterogeneity has more relevance in shaping meiofaunal higher taxa diversity compared to the OMZ core, where oxygen is the limiting factor. Different oxygen requirements of some species may explain vertical partitioning in the sediment by nematodes (Neira *et al.* 2001b; Neira & Decraemer 2009). In the deep sea, small-scale, biogenic relief generates heterogeneity that persists longer and contributes more to niche diversification than in shallow water, where water turbulence and rapid obliteration by sedimentation occur (Jumars 1975, 1976). Regarding the larger size classes, there were no correlations between the diversity attributes of macrofauna (S, N, H', J' and ES) and those of megafauna (*e.g.* S of macrofauna versus S of megafauna for the same stations), suggesting different response patterns to habitat characteristics. Megafaunal abundances were usually lowest at shallower stations; megafauna are almost excluded within the OMZ, in contrast with the abundant macrofauna dominated by a few species.

However, for both macro- and megafauna, the highest diversity was observed in general at the OMZ/AIW boundary or at deepest sites. A depth-related grouping of assemblages was reported by Palma *et al.* (2005) for the macrofauna. This in turn was explained by the different environments generated by the water masses involved, including dissolved oxygen as a main variable. The boundaries of the three important deep water masses in the region, the ESSW (down to about 400 m), the AAIW (500–1200 m depth), and the PDW ($>1200 \text{ m}$ depth), coincided quite well with the depth ranges of station groups and with specific species inventories in the study area (Palma *et al.* 2005). However, the causes for the change in species composition with depth are complex and several factors might act to produce the observed pattern. Indeed, zonation patterns in the deep sea have been attributed to physical and/or biological factors such as temperature (Rowe & Menzies 1969), pressure (Young *et al.* 1996), hydrographic conditions and topography (Lampitt *et al.* 1986; Rice *et al.* 1990), nutrient input (Rex 1981; Rice *et al.* 1990), larval dispersal (Rowe & Menzies 1969; Billett 1991), competition, predation and trophic level (Rex 1981; Cartes & Sardà 1992). Although many of these factors, if not all, could be acting off Chile to generate the observed patterns, the effect of the OMZ on macrobenthic communities is evident, with a commu-

Table 4. Metazoan benthic species that have been collected only within the OMZ core along the SE Pacific margin.

Size group	Class: Family	Species	Locality	Depth (m)	DO (ml ⁻¹)	References
Meiofauna	Nematoda: Epsilonematidae	<i>Glochinema bathyperuensis</i>	off Callao, Peru (~12°S)	305	0.017	Neira <i>et al.</i> (2001a,b)
	Nematoda: Selachinematidae	<i>Desmotersia levinae</i>	off Callao, Peru (~12°S)	305	0.017	Neira & Decraemer (2009)
Macrofauna	Oligochaeta: Tubificidae	<i>Olavius crassitunicatus</i>	off Concepcion, Chile (~36°S)	124	0.45	Levin (2003)
	Polychaeta: Cirratulidae	<i>Aphelochaeta multifilis</i>	off Quique, Chile (~20°S)	313	<0.5	Palma <i>et al.</i> (2005)
	Polychaeta: Dorvilleidae	<i>Diaphorosoma</i> sp.	off Antofagasta, Chile (~22°S)	98	0.02	Levin (2003)
	Polychaeta: Sabellidae	<i>Chone chilensis</i>	off Antofagasta, Chile (~22°S)	98	0.02	Palma <i>et al.</i> (2005)
	Polychaeta: Syllidae	<i>Sphaerosyllis</i> sp.	Callao, Peru to Antofagasta, Chile (12°–22°S)	305–319	0.017–0.06	Palma <i>et al.</i> (2005)
	Mollusca: Columbellidae	<i>Astyris</i> sp.	off Concepcion, Chile (~36°S)	240	<0.5	Levin <i>et al.</i> (2002); Quiroga <i>et al.</i> (2009)
Megafauna	Mollusca: ischnochitonidae	<i>Tripoplax balaenophila</i>	off Antofagasta, Chile (~22°S)	319	0.06	Schwabe & Sellanes (2004)
	Mollusca: Leptochitonidae	<i>Leptochiton</i> sp.	off Antofagasta, Chile (~22°S)	319	0.06	Schwabe and Sellanes (in press)

nity characterized by a low number of taxa, low species richness and diversity, and high dominance of a few species (Table 2). This was also reported by Levin *et al.* (2002) and Gallardo *et al.* (2004) for OMZ communities off Peru and central Chile, respectively, and during the onset of dysoxic conditions (*i.e.* bottom water dissolved oxygen <1 ml·l⁻¹) at the shelf off Concepción (Sellanes *et al.* 2007). Indeed, only a few polychaete species were in general responsible for total biomass within the OMZ; among them, the polychaetes *Aricidea pigmentata* and *Mediomastus branchiferus* were the dominant ones (Quiroga *et al.* 2005). These species have been previously described as highly abundant in habitats associated with low-oxygen environments and high concentrations of organic matter (Gallardo *et al.* 1995; Carrasco *et al.* 1999). In terms of abundance, off northern Chile, the OMZ stations were dominated by polychaetes and oligochaetes, constituting about 90–100% of the macrofauna. The polychaete *Magelona phyllisae* and *Oligochaeta* sp. A (probably *Olavius* sp.) were the most abundant organisms in this area, followed by *Cirratulus cirratus* and *Levensenia gracilis*, although the latter also occurred outside the OMZ (Palma *et al.* 2005). In central Chile, the OMZ stations were dominated by the small-bodied polychaetes *Cossura chilensis* and *Paraprionospio pinnata* (Palma *et al.* 2005). Studies indicate that most of the more abundant polychaete species in this area are well adapted to cope with oxygen-deficient conditions by having enzymatic mechanisms associated with anaerobic pathways (González & Quiñones, 2000); *P. pinnata* is among the best adapted, displaying high activities of four pyruvate oxidoreductases, suggesting a high metabolic plasticity conferring the ability to thrive even in anoxic conditions. At stations beneath the OMZ, the larger polychaetes *Paramphinome australis*, Fauvelopsidae sp. A and *Maldane sarsi*, and the amphipod Ampeliscidae sp. A, showed higher densities (Palma *et al.* 2005; Quiroga *et al.* 2005).

Although indicators of alpha diversity are lower within the OMZ when compared with more oxygenated down-slope habitats, the number of OMZ endemic species probably increases the regional inventory, thus adding to beta diversity. A review of beta diversity patterns (cumulative species turnover with depth) within different OMZs, including the same three transects off Chile discussed in this article, is presented by Gooday *et al.* (2010). In general, on margins with an OMZ, species turnover is marked above the OMZ, is depressed within it and then increases again as DO levels begin to rise across the lower boundary. Off Chile, this depressed turnover within the OMZ is often caused by species that have been only reported for the OMZ core, and could thus be considered OMZ-endemics (an exception is *P. pinnata*, which is an opportunistic species that often proliferates in

dysoxic conditions but is not an OMZ-endemic). An example of some of OMZ-endemic species is provided in Table 4. The relatively low number of these species reported so far for this margin does not necessarily mean that there are few OMZ-endemics, but is probably an effect of the paucity of taxonomic studies on deep-water benthic assemblages in the SE Pacific.

Enhanced species richness and diversity of macrofauna and megafauna was observed at the sites just beneath the OMZ (e.g. >500 m off Antofagasta and >365 m off Concepción, Table 2). Consistent with this, another characteristic reported for the benthic assemblages within and beyond the OMZ at many sites, is a sharp zonation within the lower OMZ transition zone (e.g. Volcano 7 off Mexico – Levin *et al.* 1991; Wishner *et al.* 1995; Oman – Levin *et al.* 2000; Chile – Gallardo *et al.* 2004; Pakistan margin – Levin *et al.* 2009). This feature has been explained by the different tolerance thresholds to low oxygen concentrations by different groups (Gooday *et al.* 2009). In general, annelids are more tolerant than mollusks, followed by crustaceans and the echinoderms, with the last being the least tolerant (Díaz & Rosenberg 1995; Vaquer-Sunyer & Duarte 2008). All these observations strongly suggest that the OMZ boundaries constitute highly heterogeneous sub-zones in terms of environmental conditions with, in general, abrupt shifts in animal communities, sometimes at vertical scales of tens of meters (e.g. at the Pakistan margin – Levin *et al.* 2009).

Local heterogeneity influence on regional-scale diversity

The macrofauna of the Chile margin seeps have yet to be studied, but may include additional species not characteristic of the other habitats. Levin *et al.* (2010) found that nearly half of the seep macrofauna present on the Oregon and California margin (500–800 m depth) were seep endemics, not present in OMZ or other slope settings.

The maximum megafaunal species number and rarefied species richness were always observed below the OMZ, but a little bit deeper than the maximum observed for the macrofauna, at mid slope depths (e.g. below 1347 m off Antofagasta and at 1294 m off Concepción). However, for the megafauna, the maximum number of species (considering all sites) was observed at the seep site (CMSA), although local diversity (H') and rarefied species richness was moderate. At the CMSA the overall increase in abundance, biomass, and diversity of the heterotrophic megafaunal communities, including top predatory fishes, is not a function of increased local primary production, because stable isotope analysis indicates that there is no reliance on *in situ* (chemosynthetic) production (Sellanes *et al.* 2008). However, methane-derived authigenic carbonates provide a suitable habitat for sessile organisms

and associated fauna, and this hard substratum may in turn provide a rich feeding ground for other mobile species. This has been also suggested for the Gorda Escarpment off northern California, where multispecies aggregations of octopus (*Benthoctopus* sp. and *Graneledone* sp.) and blob sculpins (*Psychrolutes phrictus*) brood at seep sites. This preference has been ascribed to the interaction of local topography, physical, and geological settings (Drzen *et al.* 2003).

As indicated by rarefaction analysis (Fig. 5), in general, species number and diversity increase toward higher latitudes, with the diversity peak tending to be found at shallower depths in the same direction. Off Chiloé, where the OMZ was absent, a high diversity and number of species were recorded at 480 m. This coincided with the presence of hardgrounds, evidenced by underwater images and trawled rocks at this site (Fig. 4I, Hebbeln 2001). Megafauna is the only group that has been studied off Chile for regular slope, OMZ and seep habitats. In spite of the low diversity, megafaunal assemblages within the OMZ have some endemic species (Table 4), such as the columbellid gastropod *Astyris* sp. (Quiroga *et al.* 2009) and a new species of polyplacophoran, *Leptochiton* sp., with an enhanced number of branchial structures (Schwabe & Sellanes submitted). On the other hand, seep sites with a high local diversity also contribute to regional diversity, with many endemic species. For instance, at the CMSA off Concepción, 112 megafaunal species have been reported by Sellanes *et al.* (2008); 11 of them are seep endemics (chemosymbiotic clams and polychaetes, and their commensal fauna) and at least 10 other species are new to science, *i.e.* so far only known from this site. Thus, both habitats, seeps and OMZ sediments, increase the regional pool of species, although to different degrees. It has been postulated that at a regional scale, OMZs can act as a barrier to gene-flow between allopatric populations, creating strong vertical gradients in physical and biological parameters (White 1987; Rogers 2000). Along with a limited utilization of sinking organic matter in the OMZ water column, which results in an abundant supply of food for organisms immediately below it, this may lead to strong vertical gradients in selective pressure for optimal rates of growth, modes of reproduction and development, interaction with other species. These selective agents, combined with increased habitat specialization in the lower boundaries of OMZs, may translate into enhanced regional biodiversity.

The results suggest that the bathymetric distribution of sublittoral benthic organisms of the Chilean margin are controlled largely by the water masses occurring in the region, which modulate bottom-water oxygen conditions and sediment organic loading, whereas hardgrounds, when present, constitute faunal attractors primarily for

larger organisms. However, as indicated in the previous section, different taxa, and even different size groups, have a distinct response to these environmental factors, including the still poorly studied small fauna associated to carbonates. Physiological adaptations to oxygen deficiency and constraints related to body size of each group would be responsible for the large-scale patterns (e.g. zonation and latitudinal trends), whereas habitat heterogeneity (e.g. at water mass boundaries, heterogeneous sediments, seeps) would explain the local fauna diversity patterns and the occurrence of many endemic species.

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