Cah. Biol. Mar. (1999) 40 : 195-202

The structure of the benthic macrofauna collected across a transect at the central chile shelf and relationships with giant sulfur bacteria *Thioploca* spp. mats.

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Abstract: The analysis of the community structure of macrobenthic (>0.25 mm) assemblages collected from a transect in the Central Chile shelf and the relationships with sulphur bacteria *Thioploca* spp. was performed. Samples were obtained in April 1982 (southern Autumn) with a 0.1 m^2 Smith-McIntyre grab at three cross-shelf stations off Concepción Bay, central Chile. Sediments consisted of fine muds (>95% silt-clay) with high (>15%) total organic matter. Here bottom waters showed the typical characteristics of the pole-ward flowing Sub-Surface Equatorial Waters, i.e., higher salinity than those at surface (>34.5‰) and low oxygen (<1.0 ml O_2 l^{-1}). Filaments of the giant bacteria *Thioploca* spp. were moderately collected at station E1 (31.9 g m^{-2} wet weight at 75 m depth), were scarce at station E2 (2.3 g m^{-2} w.wt. at 100 m), and absent at station E3 (121 m). In all sites macrofaunal composition was comparable, with a low total species richness, a low species diversity (27 species), and a high dominance. Average figures for abundance ranged from 77,880 ind m^{-2} at E1 to 14,770 ind m^{-2} at E3. Faunal biomass (w. wt.) ranged from 110 g m^{-2} at E1 to 32 g m^{-2} at E3. Polychaeta was the most abundant taxon (78% of the total), with *Paraprionospio pinnata* as the dominant species in all stations. Statistical analyses indicated significant differences among all sites, but in particular between E1, with a larger population of *Thioploca* spp., and the deeper E2 and E3 sites where *Thioploca* was scarse and absent, respectively.

Résumé: *Structure des communautés macrobenthiques du plateau continental du Chili central et étude de leurs rapports avec les bactéries géantes* Thioploca *spp*. Des échantillons de communautés macrobenthiques ont été prélevés en avril 1982 avec une benne Smith-McIntyre (0,1 m^2) dans trois stations situées le long d'un transect au large de la Baie de Concepción. Les sédiments étaient fins (>95% limon-argile) avec un pourcentage de matière organique totale supérieur à 15 %. Les eaux du fond montrent des caractéristiques typiques des Eaux Équatoriales de subsurface, avec une salinité plus elevée qu'à la surface (>34.5 ‰) et une concentration en oxygène plus faible (<1 ml O_2 l^{-1}). Les bactéries (*Thioploca* spp.) ont été récoltées en quantité moyenne à la station E1 (31.9 g m^{-2} poids humide à 75 m de profondeur), elles étaient rares à la station E2 (2.3 g m^{-2} à 100 m de profondeur), et absentes à la station E3 (121 m). La composition de la macrofaune était comparable dans toutes les stations avec une faible richesse spécifique (27 espèces), une faible diversité et de fortes dominances. Les abondances moyennes étaient de 77.880 ind m^{-2} à la station E1 contre 14.770 ind m^{-2} à E3. La biomasse de la faune (poids humide) était comprise entre 110 g m^{-2} à la station E1 et 32 gm^{-2} à E3. Les polychètes étaient les organismes les plus abondants (78 % du total), avec *Paraprionospio pinnata* comme espèce dominante dans toutes les stations. Les analyses statistiques indiquent des différences importantes entre les stations, mais en particulier entre la station E1, caractérisée par une grande population de *Thioploca* spp., et les stations E2 et E3, plus profondes où *Thioploca* était rare (E2) et absente (E3).

Keywords: Shelf macrobenthos, *Thioploca* bacteria, community structure, dominance, diversity, Chile.

Reçu le 10 décembre 1998; accepté après révision le 30 mai 1999
Received 10 December 1998; accepted in revised form 30 May 1999

Introduction

The presence of a large and abundant filamentous material in the sublittoral benthos off northern Chile was first noticed in 1962 (Gallardo, 1963). These mats were later described as made up of sulphur bacteria (*Thioploca* spp.) (Gallardo, 1977). Later contributions aimed at relating their presence and the structure of the macro- and megafauna to hydrographical conditions, in particular to dissolved oxygen throughout annual cycles and bathymetry (Gallardo et al., 1995). It was also suggested that mats of *Thioploca* will play a refugial role in the settlement of the squat lobster *Pleuroncodes monodon* (H. Milne Edwards) (see Gallardo et al. 1994). Of particular interest to benthic community ecology was the finding that *Thioploca* appeared to withdraw large amounts of hydrogen sulphide (Fossing et al., 1995; Huettel et al., 1996 & Ferdelman et al. 1997). This seemed to provide an explanation to the fact that macro- and megabenthos could occur in a time (spring-summer) and area (shelf depths) where the high rates of organic matter deposition from the seasonally highly productive surface waters off central Chile (Fossing et al., 1995) had the potential of creating strongly unfavourable conditions for their development. Thus, in the absence of *Thioploca*, the expected high rates of hydrogen sulphide production in the sediments could be lethal to the benthic macroinfauna. Under these stressful and varying circumstances we hypothesized that the infaunal macrobenthos would show, besides the differences expected from the different depths of the stations, sharper clinal differences in structure between stations according to *Thioploca* mats abundance.

Materials and methods

Samples of macrofauna (> 0.25 mm) were taken off Concepción Bay in central Chile (Fig. 1) in April 15, 1982 with a 0.1 m^2 Smith-McIntyre grab at three cross-shelf stations (E1 at 75 m, E2 at 100 m and E3 at 121 m depth) (Table 1). At each station three replicate samples were taken. Sediment samples were collected for grain and total organic matter analyses and the macroinfauna separated through a 0.25 mm mesh sieve. Menthol–relaxed specimens were fixed in a 10% buffered seawater solution of formaldehyde. Sorting of Bengal Rose-stained material was done under a dissecting microscope. Specimens were then transferred to a 70% ethanol solution, counted and weighed (wet weight). Water column temperature, salinity and dissolved oxygen were obtained by using a CTDO probe. Total organic matter was estimated by loss of weight by ignition of dried material in a furnace after two hours at 550ºC (Crisp, 1971). Sediment grain analysis was performed by sieving the larger grain fraction and by

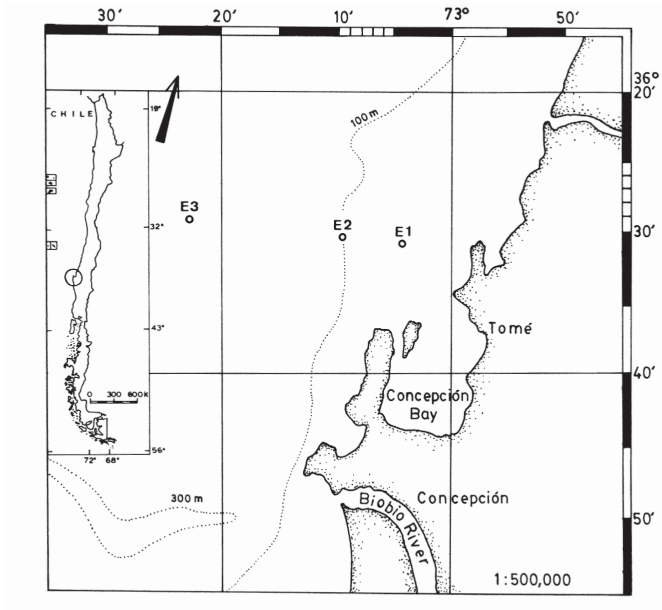

Figure 1. Map of the study area showing the three sampling benthic stations.

Figure 1. Carte de la région étudiée et localisation des trois stations benthiques échantillonnées.

pipetting the silt-clay fraction (Buchanan, 1971). Particle size data was analysed following Folk (1974).

Community structure parameters selected were the number of species or species richness (S), species diversity, estimated from Shannon-Wiener's information index ($H' = -\Sigma p_i \ln p_i$), where $p_i = n_i/N$, and evenness ($J' = H'/H'_{max} = H' / \ln S$) (Magurran, 1988).

The Shannon-Wiener H' was subjected to the jack-knifing analytical procedure to obtain bias and variance (Sokal & Rohlf, 1981). This allowed to test differences of H' among stations. Furthermore, Sanders-Hurlbert expected number of species (Sanders, 1968; Hurlbert, 1971) was also computed, with an expression which involves combination terms, as:

$$E(S_n) = \Sigma \left[1 - \frac{\binom{N - n_i}{m}}{\binom{N}{m}} \right]$$

where N = total number of individuals in the sample; n_i = number of individuals of the i-th species; and m = standardized sample size (Magurran, 1988). This information allowed to plot rarefaction curves (Sanders, 1968; Hurlbert, 1971), a method widely used in marine ecology, especially when comparing samples with different sizes (Rygg, 1985). To compare community parameters among stations a nonparametric analysis of variance (Kruskal-Wallis test) and pairwise stations comparisons with Mann-Whitney U test (Sokal & Rolf, 1981) were used. Dependency among faunistic collections was examined through Kendall's coefficient of rank correlation, τ (Conover, 1980). Faunal affinities among station samples were explored through a Non Metric Multidimensional Scaling (NMDS) analysis (Field *et al.*, 1982) on $Y = \sqrt{\sqrt{X}}$ transformed abundance data and using the Bray–Curtis coefficient. The above statistical computations were performed using the SYSTAT package (Wilkinson, 1990).

The ANOSIM nonparametric permutation test (Clarke, 1993), was used to test the null hypothesis, i.e. no difference between sites. Finally, also ABC (abundance, biomass comparisons) curves were plotted (Warwick, 1986). These are k–dominance curves for numerical abundance and biomass which combined display the ranking of species on the X axis, in a logarithmic scale, and the cumulative dominance (%) on the Y axis, using an arithmetic scale.

Table 1. Geographical coordinates and depth of the bottom for the three benthic stations studied off Concepción Bay. Sediment granulometric parameters and total organic matter content (TOM) of superficial (<2 cm depth) and subsuperficial (>2 cm depth) sediments are given.

Tableau 1. Coordonnées géographiques et profondeurs des trois stations benthiques étudiées au large de la Baie de Concepción. Les paramètres granulométriques du sédiment et le contenu total en matière organique (TOM) des sédiments de surface (<2 cm) et de subsurface (>2 cm) sont indiqués.

	Station E1	Station E2	Station E3
Latitude	36°31'00"S	36°30'30"S	36°29'30"S
Longitude	73°03'45"W	73°09'30"W	73°22'30"W
Depth	75 m	100 m	121 m
Graphic mean (ϕ)	7.13	7.23	6.97
Sorting (ϕ)	1.52	1.40	1.75
Silt-clay (%)	98.40	95.00	95.20
TOM surface (%)	15.20	17.40	17.00
TOM subsurface (%)	**14.60**	**16.50**	**16.40**

Results

1. Environment

Temperature profiles indicated the presence of a well defined end of summer thermocline in the area. Salinity curves (except for the most coastal sta. E1) were consistent with the presence of a surface layer with waters presumably affected by riverine and terrestrial run off. Below these, salinities (>34.5%o) and dissolved oxygen (<1 ml l^{-1}) in all stations were typical of Sub-Surface Equatorial Waters (SSEW). Sediments were homogeneous in all three stations (>95% silt-clay) with high total organic matter (TOM) content both in surface (< 2 cm depth) and sub-surface (> 2 cm depth) layers; mean grain size and sorting coefficients corroborated this similarity (Table 1).

2. Biotic composition

35,147 individuals belonging to 27 species and four

Table 2. Pooled numerical abundance (N 0.3m^{-2}) and biomass (B g wet weight 0.3 m^{-2}) and their contribution (%) to the total of macrobenthic infauna taxa collected off Concepción Bay. Total abundance and total biomass for fauna (Total (F)), and total biomass, for fauna and *Thioploca* spp. (Total (B)) are also indicated.

Tableau 2. Abondance (N 0.3 m^{-2}), biomasse (B g poids humide 0.3 m^{-2}) et contributions relatives (%) des différents taxons de la macrofaune benthique au large de la Baie de Concepción. L'abondance et la biomasse totales de la macrofaune (Total (F)) et la biomasse totale de la faune et de *Thioploca* spp. (Total (B)) sont aussi indiquées.

Taxa	Station E1				Station E2				Station E3			
	N	%	B	%	N	%	B	%	N	%	B	%
Polychaeta	18,233	78.2	16.90	39.6	7,235	97.7	8.44	82.0	4,412	99.6	11.89	98.6
Crustacea	4,992	21.4	10.22	24.0	141	1.9	0.34	3.3	11	0.2	0.14	1.2
Mollusca	0,079	0.3	3.35	7.9	26	0.4	0.83	8.1	8	0.2	0.03	0.2
Anthozoa	0,010	0.0	2.64	6.2	-	-	-	-	-	-	-	-
Total (F)	**23,314**	**100**	**33.11**	**77.6**	**7,402**	**100**	**9.61**	**93.4**	**4,431**	**100**	**12.06**	**100**
(Mean)	7,771		11.06		2,467		3.21		1,477		*	
(Std. dev.)	1,035		1.41		854		1.18		585		*	
Thioploca spp.			9.56	22.4			0.68	6.6			-	-
(Mean)			3.19				0.23				-	-
(Std. dev.)			1.93				0.32				-	-
Total (B)			**42.67**	**100.0**			**10.29**	**100.0**			**12.06**	**100.0**

*Not available

phyla were collected during this survey. Species richness, abundance and biomass decreased with depth. Polychaeta was the most species-rich and abundant group in all three stations, with a high dominance which increases with depth (Table 2). Total biomass decreased substantially with depth from station E1 to E3. *Thioploca* biomass exhibited a substantial decrease from station E1 to E2 and was absent in the deepest E3 station. The polychaete *Paraprionospio pinnata* (Ehlers) was the most abundant species throughout (Table 3), followed by a short list of lesser abundant species where the polychaetes *Aricidea pigmentata* Carrasco, *Mediomastus branchiferus* Hartmann-Schroeder, *Cossura chilensis* Hartmann-Schroeder, *Magelona phyllisae* Jones, and *Nephtys ferruginea* Hartman, and the amphipod *Ampelisca araucana* Gallardo, are the main species of this faunistic assemblage. Except for *Cossura chilensis*, all other species in the above list decreased in abundance with water depth. Noticeable differences are observed, however, in their percentage contributions to the correspondent station (Table 3): thus, while *Paraprionospio pinnata* is the dominant species in all stations, *Aricidea pigmentata*, *Ampelisca araucana* and *Mediomastus branchiferus* are numerically more important in the shallow station, *C. chilensis* and *M. branchiferus* in the intermediate and *C. chilensis in* the deeper collection. In terms of biomass the pattern is almost identical.

From the trophic point of view (Table 3) the surface deposit feeders rank first, followed by sub-surface deposit feeders. This pattern is observed in all three stations, but at the deeper station E3 *Cossura chilensis*, a sub-surface deposit feeder, reached the same abundance as *Paraprionospio pinnata*, a surface deposit feeder, being both

Table 3. Pooled numerical abundance (N, 0.3m^{-2}) and biomass (B, g wet weight 0.3m^{-2}) by stations of the benthic macrofauna from continental shelf off Concepción Bay; (Weights below 0.01 g are not shown, but were measured). The first 8 major species are also ranked for each station (R). For most abundant species the feeding guild are also presented (SD: deposit-feeder; SS: sub-surface deposit feeder; CM: motile carnivore). Taxonomic determination followed mainly Hartmann-Schroeder (1962, 1965) and Wesenberg-Lund (1962).

Tableau 3. Abondance (N, 0,3m^{-2}) et biomasse (B, g poids humide 0,3m^{-2}) de la macrofaune benthique du plateau continental au large de la Baie de Concepción aux 3 stations; les poids inférieurs à 0,01 g ne sont pas donnés bien qu'ayant été mesurés. Les 8 premières espèces les plus abondantes par station sont aussi classées par rang (R). La stratégie trophique de la plupart des espèces abondantes est également fournie (SD : déposivore de surface ; SS : déposivore de subsurface; CM : carnivore mobile). Les déterminations d'espèces ont été faites d'après Hartmann-Schroeder (1962, 1965) et Wesenberg-Lund (1962).

	Station E1					Station E2					Station E3				
	(R)	N	%	B	%	(R)	N	%	B	%	(R)	N	%	B	%
Paraprionospio pinnata (SD)	(1)	9843	42.0	10.23	30.9	(1)	5450	73.6	4.11	42.6	(1)	2018	45.5	3.56	29.6
Aricidea pigmentata (SD)	(3)	3829	16.4	1.94	5.9	(3)	343	4.6	0.08	0.8	(6)	42	1.0	0.01	0.1
Ampelisca araucana (SD)	(2)	4989	21.4	10.15	30.7	(5)	139	1.9	0.32	3.3	(7)	11	0.3	0.00	0.0
Mediomastus branchiferus (SS)	(4)	3169	13.6	0.62	1.9	(4)	205	2.8	0.02	0.2	(4)	155	3.5	0.02	0.2
Cossura chilensis (SS)	(5)	639	2.7	0.19	0.6	(2)	968	13.1	0.28	2.9	(2)	1952	44.1	0.52	4.3
Magelona phyllisae (SD)	(6)	263	1.1	0.26	0.8	(7)	75	1.0	0.05	0.5	(3)	115	2.6	0.11	0.9
Nephtys ferruginea (CM)	(7)	232	1.0	1.00	3.0	(6)	109	1.5	2.47	25.5	(5)	98	2.2	3.86	32.1
Nereis dorsolobata (CM)	(8)	98	0.4	0.51	1.5		1	0.0	0.00	0.0		1	0.0	0.00	0.0
Sigambra bassi (CM)		92	0.4	0.38	1.2	(8)	35	0.5	0.13	1.3	(8)	10	0.2	0.01	0.1
Nassarius gayi (SD)		67	0.3	2.11	6.4		25	0.3	0.79	8.2		4	0.1	0.10	0.8
Podarke sp. (CM)		36	0.2	0.03	0.1		16	0.2	0.02	0.2		8	0.2	0.08	0.7
Hesionid A (CM)		26	0.1	0.18	0.5		13	0.2	0.15	1.6		0	0.0	0.00	0.0
Lumbrineris bifilaris (CM)		16	0.1	1.17	3.5		1	0.0	0.12	1.2		1	0.0	0.26	2.2
Harmothoe brevipalpa (CM)		23	0.1	0.18	0.5		6	0.1	0.23	2.4		2	0.0	0.01	0.1
Phyllochaetopterus monroi		5	0.0	0.05	0.2		9	0.1	0.23	2.4		7	0.2	0.19	1.6
Saccactis coliumensis		10	0.0	2.64	8.0		0	0.0	0.00	0.0		0	0.0	0.00	0.0
Macoma sp.		8	0.0	0.36	1.1		1	0.0	0.04	0.9		1	0.0	0.03	0.3
Megalomma monoculata		6	0.0	0.00	0.0		0	0.0	0.00	0.0		0	0.0	0.00	0.0
Sthenelais helenae		0	0.0	0.00	0.0		3	0.0	0.07	0.7		2	0.0	0.00	0.0
Pinnixa sp.		3	0.0	0.07	0.2		2	0.0	0.02	0.2		0	0.0	0.00	0.0
Euromalea ?rufa		4	0.0	0.88	2.7		0	0.0	0.00	0.0		0	0.0	0.00	0.0
Nuculana sp.		0	0.0	0.00	0.0		0	0.0	0.00	0.0		3	0.0	0.01	0.1
Dodecaceria sp.		2	0.0	0.00	0.0		0	0.0	0.00	0.0		0	0.0	0.00	0.0
Glycera americana		1	0.0	0.01	0.0		0	0.0	0.00	0.0		1	0.0	3.26	27.1
Pectinaria chilensis		1	0.0	0.15	0.5		1	0.0	0.48	5.0		0	0.0	0.00	0.0
Scolelepis carrascoi		1	0.0	0.00	0.0		0	0.0	0.00	0.0		0	0.0	0.00	0.0
Tharyx sp.		1	0.0	0.00	0.0		0	0.0	0.00	0.0		0	0.0	0.00	0.0

dominant species. Filter feeders are quite rare, which is consistent with the fact that deposits in the area were of the poorly sorted type, indicating a low energy environment, unfavourable for filter feeders.

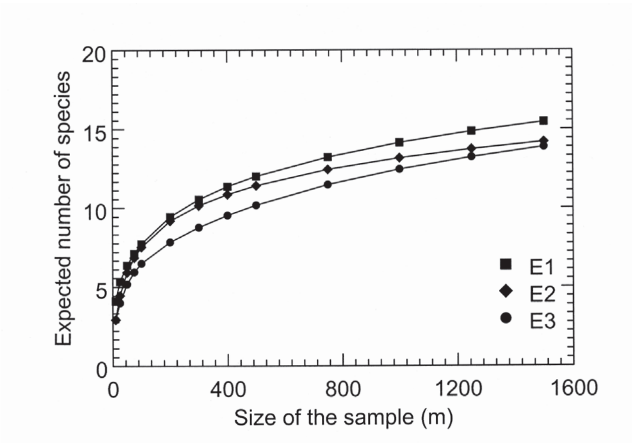

Figure 2. Rarefaction curves of Sanders-Hurlbert for the expected number of species corresponding to the 3 benthic stations analysed off Concepción Bay. In the abscissa the sample size (m of the Sanders-Hurlbert model) and in the ordinate the expected number of species.

Figure 2. Courbes de raréfaction de Sanders-Hurlbert pour les 3 stations benthiques étudiées au large de la Baie de Concepción. La taille de l'échantillon est indiquée en abscisse et le nombre attendu d'espèces en ordonnée.

Table 4. Community parameters calculated for the faunal collections of the three macrobenthic stations studied off Concepción Bay: pooled number of species (S), the mean number of species and standard deviations (s), Shannon species diversity index (H'), its jack-knifing statistic (H'(jk)), with variance (s2) and standard error (SE), evenness (J'), and the expected number of species of Sanders-Hurlbert ($E(S_n)$).

Tableau 4. Paramètres de la communauté calculés pour la macrofaune des trois stations étudiées au large de la Baie de Concepción : nombre d'espèces (S), nombre moyen d'espèces et écart type (s), indice de diversité de Shannon (H'), sa statistique "jack-knifed" (H'(jk)), avec la variance (s2) et l'erreur standard (SE), la regularité (J'), et le nombre attendu d'espèces de Sanders-Hurlbert ($E(S_n)$).

	Station E1	Station E2	Station E3
S	25	19	18
S (mean)	20.7	15.0	13.7
S (s)	1.53	1.73	0.58
H'	1.562	1.009	1.136
H' (jk)	1.571	0.998	1.136
s2	0.005	0.095	0.056
SE	0.003	0.054	0.033
J'	0.485	0.343	0.393
$E(S_n)$	4.121	2.934	2.932

3. The community

Results from the Kendall's τ test allow to reject the independence null hypothesis among the collections from stations (E1 vs E2, n=26, τ=0.662, T=215, P<<0.001; E1 vs E3, n=27, τ=0.524, T=184, P<<0.001; and E2 vs E3, n=21, τ=0.667, T=140, P<<0.001), reflecting the comparable faunistic composition of stations. Community parameters calculated from the pooled station data are shown in Table 4. The shallowest (E1) station shows the highest diversity (H') and the intermediate (E2) station the lowest, this being consistent with the values of evenness (J'). Rarefaction curves (Fig. 2), likewise drawn using pooled data, show the same geometry with low expected number of species, reflecting a very low species diversity in general.

A comparison of community parameters through Kruskal-Wallis test showed significant differences (P <0.05) in all parameters (abundance, number of species), among all stations, except for evenness (J'). The differences were more clear among station E1 vs. E2+E3 (Table 5).

The NMDS analysis for all samples collected reveals two main groups (Fig. 3): one conformed by station E1 and another including E2 and E3 stations. ANOSIM test indicated highly significant overall differences (R = 1; P < 0.004).

Table 5. Results of Kruskal-Wallis test for overall station comparisons and Mann-Whitney U tests for paired comparisons for differences between means of numerical abundance (N), number of species (S), H' diversity species index, and evenness (J'), of macroinvertebrates amongst the three benthic stations studied off Concepción Bay.

Tableau 5. Test de Kruskal-Wallis et test U de Mann-Whitney montrant les différences moyennes d'abondance (N), du nombre d'espèces (S), de l'indice de diversité H' et de la régularité (J'), pour la macrofaune des trois stations benthiques étudiées au large de la Baie de Concepción.

Parameter	Kruskal-Wallis statistic	Prob.	Paired station significant comparison (Mann-Whitney U-test)
N	6.49	P <0.039 (d.f.=2)	E1 vs E2: P < 0.05 (U test=9.0, χ^2 =3.86) E1 vs E3: P < 0.05 (U test=9.0, χ^2 =3.86)
S	5.90	P < 0.050 (d.f.=2)	E1 vs E2: P < 0.046 (U test=9.0, χ^2 =3.97) E1 vs E3: P < 0.046 (U test=9.0, χ^2 =3.97)
H'	5.60	P < 0.020 (d.f.=2)	E1 vs E2: P < 0.050 (U test=9.0, χ^2 =3.86) E1 vs E3: P < 0.034 (U test=9.0, χ^2 =3.86)
J'	5.60	P > 0.061 (d.f.=2)	E1 vs E2: P < 0.050 (U test=9.0, χ^2 =3.86) E1 vs E3: P < 0.050 (U test=9.0, χ^2 =3.86)

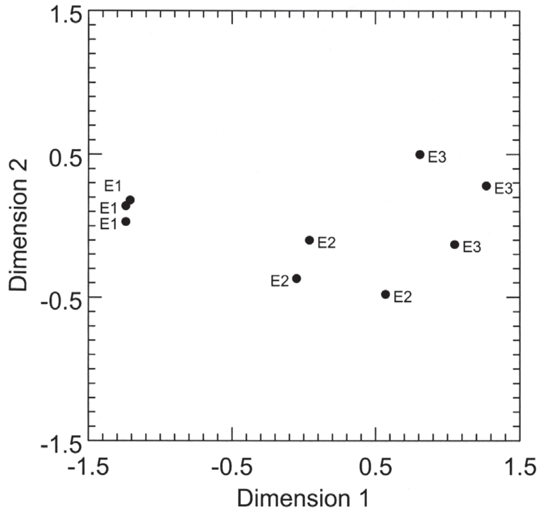

Figure 3. Multidimensional scaling analysis (NMDS) ordination of the 9 replicate samples of the 3 benthic stations analysed off Concepción Bay (stress = 0.0025).

Figure 3. Cadrage multidimensionnel non-métrique (NMDS) représentant les 9 échantillons prélevés en 3 stations benthiques au large de la Baie de Concepción (stress = 0,0025).

Dominance ABC curves are plotted in Fig. 4a, b, c. These, according to Warwick (1986), and unexpectedly, will represent grossly perturbed assemblages because the abundance curves are on the top of the biomass curves.

Discussion

Hydrographic conditions were typical for a late summer season in the area, with prevalence of hypoxic SSEW waters over the shelf. The substrate, consisting mainly of poorly sorted silt-clay fraction, reflects a relatively low energy sedimentary environment. The high TOM content values are in the range of those previously published for the sublittoral zone of the region (Carrasco *et al*., 1988; Gallardo *et al*., 1995) and appear to be typical of this seasonally highly productive coastal upwelling ecosystem. Some of the known highest levels of carbon (C) assimilation, with a primary production of 9.6 g C day^{-1} m^{-2}, have been measured in the area (Fossing *et al*., 1995). In Central Chile shelf *Thioploca* biomass has been found to vary from negligible to more than 1000 g (w.wt.) m^{-2} (Gallardo, 1977; Schulz *et al*., 1996), thus the highest value measured during this survey is in the low range. The macroinfauna appears comparable to that reported for the area (Carrasco & Gallardo, 1983; Gallardo *et al*., 1995), with a low number of major taxa, low species richness and species diversity, and elevated numerical densities and dominances. The fauna is dominated by the polychaete *Paraprionospio pinnata*, the amphipod *Ampelisca araucana*, and also by the small-bodied polychaetes *Aricidea pigmentata*, *Mediomastus branchiferus* and *Cossura chilensis*. These forms have been reported with similar ecological significance (Carrasco *et al*., 1988; Gallardo *et al*., 1995). *Nephtys ferruginea* is an important species because it contributes substantially to the total biomass. As expected, all these forms are deposit-feeders except *N. ferruginea* which is carnivorous.

The faunistic composition of the three sites appears comparable as evidenced by the significant results of the Kendall's τ test. The levels and ranges of community parameters and the rarefaction curves document a low species diversity and an high ecological dominance for these assemblages, especially in the deeper stations E2 and E3. Notwithstanding these considerations, clear and significant differences in community parameters can be established among the three stations. These were evidenced by paired comparison tests, between station E1 vs E2 vs E3

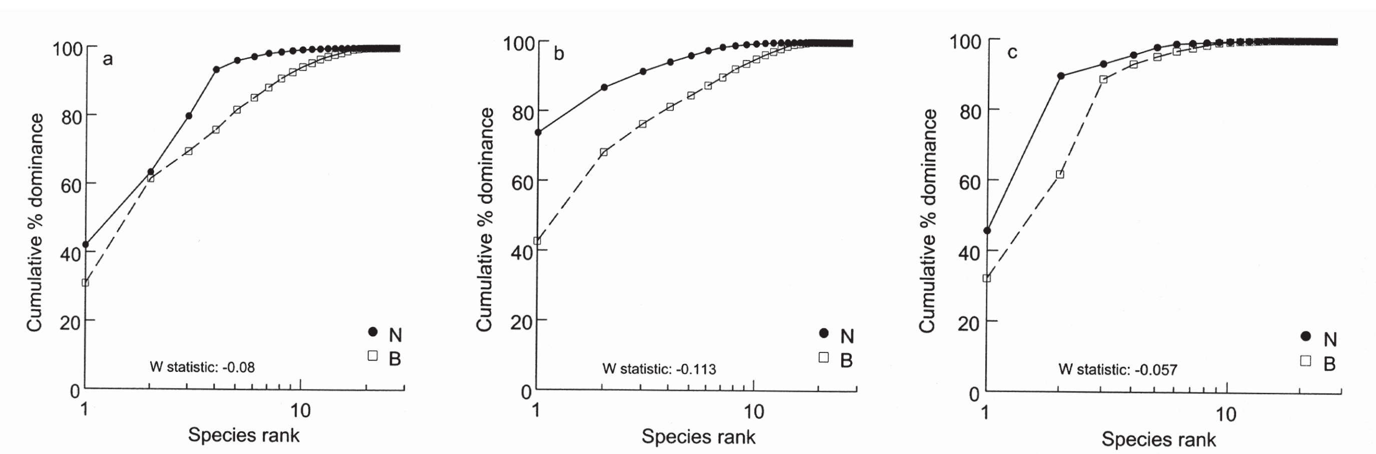

Figure 4. K-dominance curves for species biomass and abundance (ABC plots for the benthic stations studied off Concepción Bay (N: abundance; B: biomass). a) Station E1, b) Station E2, c) Station E3.

Figure 4. Courbes de k-dominance pour la biomasse et l'abondance (graphiques ABC) pour les stations benthiques étudiées au large de la Baie de Concepción (N : abondance; B : biomasse). a) Station E1; b) Station E2 ; c) Station E3.

for numerical abundance (N), number of species (S) and species diversity (H'), and also for station E1 vs station E2 for ecological dominance (1-J').

The NMDS analysis suggests the presence of two site-groups (station E1 and stations E2-E3). Results of ANOSIM test indicate significant differences between all the stations, although not when the infaunal data in a station-paired way, reflecting the transect array of stations, is analysed. Thus, from the above analytical approach, mainly involving analysis of community parameters, and also from classification and ordination strategies, significant differences between station E1 and stations E2 - E3 emerged.

Taking into consideration the depth and distance from the coast of the localities under study, the application of the ABC curves approach to the analysis of these benthic assemblages gave results that may be considered very inconsistent. The inconsistency has already been stressed, mainly by Beukema (1988) and Burd *et al*. (1990). Criticisms indicate that the method fails when a marked ecological dominance by small-bodied individuals, or species with short life-cycles, and also by recruits, are present.

In this study, the use of a 0.25 mm sieve could induce dominance but it explains only in part the noted inconsistency, because other studies in the area using a 0.5 mm sieve also produce these unexpected ABC curves (Carrasco & Gallardo, 1989). On the other hand it is assumed that the faunistic assemblage is initially in a steady-state or in equilibrium condition, a characteristic rarely achieved in 'physically-controlled communities' (Sanders, 1968). Other criticisms point out that moderately polluted sites bring about the most ambiguous results. However, this is a common problem with most of the pollution indexes. We suggest here that the inconsistency of the method in this survey originates from the fact that the benthic fauna under study sustains severe natural environmental perturbations, particularly with regard to dissolved oxygen, both in interannual (Gallardo, 1985, Arntz *et al*., 1991) and intrannual time scales (Gallardo *et al*., 1995). This is a seasonally highly productive coastal upwelling ecosystem under the aperiodic influence of ENSO (El Niño Southern Oscillation) phenomena. While the ENSO phenomena and winter conditions in the area mean high oxygen and low productivity, the spring and summer seasons are normally conducive to high productivity, by persistent wind-driven upwelling events fed by the nutrient-rich, hypoxic (sometimes anoxic) waters of the Sub-Surface Equatorial Water mass. We now know that these are the same conditions that favour the development of *Thioploca* mats (Fossing et al., 1995).

According to the above results, which are seasonally limited and originate from sites which are allocated conforming a depth gradient, and considering that the bulk of the bacteria *Thioploca* spp., albeit modest, is clearly associated with station E1 in particular, it appears that its eukaryotic assemblage exhibits differential characteristics which might be tentatively attributed to the presence of the prokaryotic component. Taking into account *Thioploca*'s high rate of sulphide utilization (Fossing *et al*., 1995), we have hypothesized that its influence on the health of the benthic community is through community habitat detoxification (Gallardo *et al*., pers. obs.), complementing other geochemical processes occurring in the sediments (Ferdelman *et al*., 1997). In this particular case, the macrofauna present on the bottom together with *Thioploca* (station E1 at 75 m depth) is characterized by a higher diversity and a higher numerical abundance, dominated by four species i.e.: i) the polychaete *Paraprionospio pinnata* (42% of the total numbers), ii) the amphipod *Ampelisca araucana* (21%), iii) the polychaete *Aricidea pigmentata* (16%), and iv) the polychaete *Mediomastus branchiferus* (14%). Those bottoms with negligible or without *Thioploca* show instead a lower diversity and lower abundance, and are characterized only by two species of Polychaeta, i.e. *P. pinnata* and *Cossura chilensis* (46% and 44%, respectively).

Acknowledgements

We wish to thank Ms. María A. Peña for collecting and processing samples and data. Also Mr. Luis Aburto for his field and laboratory assistance and the crew of the University of Concepción former research vessel *L/C Lund*. We thank the FONDAP-HUMBOLDT Program for financing. We are also grateful to Mr. Rubén Roa and two anonymous reviewers for extensive criticisms of manuscript.

References

Arntz W.E., Tarazona J., Gallardo V.A., Flores L. & Salzwedel H. 1991. Benthos communities in oxygen deficient shelf and upper slope areas of the Peruvian and Chilean Pacific coast, and changes caused by El Niño. In: *Modern and Ancient Continental Shelf Anoxia*. (Tyson, R.V. & T.H. Pearson, eds.). pp. 131-154. Geological Society Special Publication , 58.

Beukema J.J. 1988. An evaluation of the ABC-method (abundance/biomass comparison) as applied to macrozoobenthic communities living on tidal flats in the Dutch Wadden Sea. *Marine Biology,* **99**: 425-433.

Buchanan J.B. 1971. Measurement of the physical and chemical environment. In: *Methods for the Study of the Marine Benthos* (Holme, N.A. & A.D. McIntyre, eds.), pp. 30-58. Blackwell: Oxford.

Burd B.J., Nemec A. & Brinkhurst R.O. 1990. The development and application of analytical methods in benthic marine infaunal studies. *Advances in Marine Biology*, **26**: 169-247.

Carrasco F.D. & Gallardo V.A. 1983. Abundance and distribution of the macrobenthic infauna of the Gulf of Arauco, Chile. *Internationale Revue der Gesamten Hydrobiologie*, **68**: 825-838.

Carrasco F.D. & Gallardo V.A. 1989. La contaminación y el valor de la macroinfauna en su evaluación y vigilancia: casos de estudio en el litoral de Concepción, Chile. *Biología Pesquera*, **18**: 15-27.

Carrasco F.D., Gallardo V.A. & Medrano S. 1988. Sublittoral macrobenthic infaunal assemblages of two nearby embayments from Central Chile. *Internationale Revue der Gesamten Hydrobiologie*, **73**: 441-455.

Clarke K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, **18**: 117-143.

Conover W.J. 1980. *Practical Nonparametric Statistics*. 2nd Edition. J. Wiley & Sons: New York. 493 p.

Crisp D.J. 1971. Energy flow measurement. In: *Methods for the Study of the Marine Benthos* (N.A Holme & A.D. McIntyre, eds), pp. 197-279. Blackwell: Oxford.

Ferdelman T.G., Lee C., Pantoja S., Harder H., Bebout B.M. & Fossing H. 1997. Sulfate reduction and methanogenesis in a *Thioploca*-dominated sediment off the coast of Chile. *Geochimica & Cosmochimica Acta*, **61**: 3065-3079.

Field J.G., Clarke K.R. & Warwick R.M. 1982. A practical strategy for analyzing multispecies distribution patterns. *Marine Ecology Progress Series*, **8**: 37-52.

Folk R.L. 1974. *Petrology of Sedimentary Rocks*. Hemphill: Texas. 170 p.

Fossing H., Gallardo V.A., Jørgensen B.B., Hüttel M., Nielsen L.P., Schulz H., Canfield D.E., Forster S., Glud R.N., Gundersen J.K., Küver J., Ramsing N.B., Teske A., Thamdrup B. & Ulloa O. 1995. Concentration and transport of nitrate by the mat-forming sulphur bacterium *Thioploca*. *Nature*, **374**: 713-715.

Gallardo V.A. 1963. Notas sobre la densidad de la fauna bentónica en el sublitoral del norte de Chile. *Gayana* (*Zoología*), **10**: 3-15.

Gallardo V.A. 1977. Large benthic microbial communities in sulphide biota under Perú-Chile subsurface countercurrent. *Nature*, **268**: 331-332.

Gallardo V.A. 1985. Efectos del fenómeno de El Niño sobre el bentos sublitoral frente a Concepción, Chile. In: *El Niño y su impacto en la fauna marina* (W. Arntz, Landa, A. & J. Tarazona). Instituto del Mar del Perú, Boletín Extraordinario, p. 79-85.

Gallardo V.A., Cañete J.I., Enríquez-Briones S., Baltazar M. & Roa R. 1994. Preliminary notes on the recruitment of *Pleuroncodes monodon* (H. Milne Edwards, 1837) (Decapoda, Galatheidae) on the continental shelf off central Chile. *Journal of Crustacean Biology*, **44**: 665-669.

Gallardo V.A., Carrasco F.D., Roa R. & Cañete J.I. 1995. Ecological patterns in the benthic macrobiota across the continental shelf off Central Chile. *Ophelia*, **40**: 167-188.

Hartmann-Schroeder G. 1962. Zur Kenntnis des Eulitorals der chilensichen Pazifikkuste und der argentinischen Kuste Sudpatagoniensunter besonderer Berucksichtigung der Polychaeten und Ostracoden. Tl. II. Die Polychaeten des Eulitorals. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* **60** (Suppl.): 57-167.

Hartmann-Schroeder G. 1965. Zur Kenntnis des Sublitorals der chilenischen Kuste unter besonderer Berucksichtigung der Polychaeten und Ostracoden. Tl. II. Die Polychaeten des Sublitorals. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* **62** (Suppl.): 59-305.

Huettel M., Forster S., Klöser S. & Fossing H. 1996. Vertical migration in the sediment-dwelling sulfur bacteria *Thioploca* spp. in overcoming diffusion limitations. *Applied Environmental Microbiology*, **62**: 1863-1872.

Hurlbert S.H. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, **52**: 577-586.

Magurran A.E. 1988. *Ecological diversity and its measurement*. Chapman and Hall: London. 179 p.

Rygg B. 1985. Distribution of species along pollution-induced diversity gradients in benthic communities in Norwegian fjords. *Marine Pollution Bulletin*, **16**: 469-474.

Sanders H.L. 1968. Marine benthic diversity: a comparative study. *American Naturalist*, **102**: 243-282.

Schulz H.L., Jørgensen B.B., Fossing H.A. & Ramsing N.B. 1996. Community structure of filamentous sheath-building sulfur bacteria, *Thioploca* spp., off the coast of Chile. *Applied Environmental Microbiology*, **62**: 1855-1862.

Sokal R.R. & Rohlf J. 1981. *Biometry*. Freeman: San Francisco. 859 p.

Warwick R.M. 1986. A new method for detecting pollution effects on marine macrobenthic communities. *Marine Biology*, **92**: 557-562.

Wesenberg-Lund E. 1962. Polychaeta Errantia. Rep. Lund Univ. Chile Exped. (43). *Acta Universitatis Lundensis* **57**: 1-139.

Wilkinson, L. 1990. *SYSTAT: The System for Statistics*. SYSTAT Inc.: Evanston. 676 p.