

## ORIGINAL PAPER

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## Quantitative analysis of macrobenthic soft-bottom assemblages in South Shetland waters (Antarctica)

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**Abstract** Macrobenthic assemblages were investigated at 26 stations located around Livingston Island, Deception Island and the Bransfield Strait at depths ranging from 42 to 671 m. Representatives of 30 major taxa were found. The maximal density was 5,260 specimens · m<sup>-2</sup> at Livingston Island; the mean abundance per station ranged from 160 to 4,380 specimens · m<sup>-2</sup>. The total biomass of the macrozoobenthos declined with depth, with mean values of 3,201 g · m<sup>-2</sup> at shallower depths (< 100 m) and 210 g · m<sup>-2</sup> further down (> 100 m). After multivariate analysis (cluster analysis, MDS) based on Bray-Curtis dissimilarities, most stations could be assigned to one of three groups on the basis of distinct biomass differences between sites. The first cluster with a rich Ascidiacea biomass is

common on shallower bottoms. The second, with Ophiuroidea as a characteristic group, is common on deeper bottoms. The absence of an 'indicator' taxon is characteristic of the remaining cluster of those stations with the lowest biomass values. No significant correlations were detected between macrobenthic biomass and any sediment parameters measured, probably because part of the benthos (i.e. the epifauna) could be better explained by the coupling with a highly productive water column. The role of the epi-infauna sensu Gallardo as the main factor structuring benthic assemblages in the investigated area is discussed.

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### Introduction

Research over the past few decades has established that the Antarctic benthos, especially on the shelf, is characterized by high biomass levels (Knox 1994). However, according to Gutt (1991), biomass exhibits extreme variation and thus wide variation rather than high biomass is to be regarded as characteristic of the Antarctic benthos. Suspension-feeding epifauna in Antarctic waters appear to have a biomass one or two orders of magnitude larger than that of deposit-feeding infauna (Gallardo 1987). A third benthic component, 'epi-infauna', was proposed by Gallardo (1987). This term was coined for the Antarctic epifaunal sessile suspension feeders occurring on soft substrata. This soft-bottom epi-infauna shares many attributes with the epifauna living on hard substrates, such as large biomass and a similar feeding mode.

The South Shetland Islands are one of the principal Antarctic investigation areas (Arntz et al. 1994), where two Sites of Special Scientific Interest have been designated. Studies were mainly carried out in more or less closed bays of Greenwich Island (Gallardo and Castillo 1969; Gallardo et al. 1977), Deception Island (Retamal et al. 1982), King George Island (Jazdzewski et al. 1986) and Anvers Island (Lowry 1975; Richardson and Hedgpeth

1977). Gallardo (1992) has summarized all benthic field studies carried out to date at the South Shetland Islands. The results of Mühlenhardt-Siegel (1988, 1989) were based on dredge hauls around the South Shetland, Elephant and South Orkney Islands in both summer and winter.

Spain as a member state of the SCAR, has managed different Antarctic scientific programmes close to its Antarctic station (Base Juan Carlos I) on Livingston Island. Two projects, BENTART-94 (Olaso 1994) and BENTART-95 (Ramos 1995), were devoted to studying the fauna of the seabed around Livingston and Deception Islands and the Bransfield Strait. The aims of the present paper are (1) to distinguish faunal assemblages

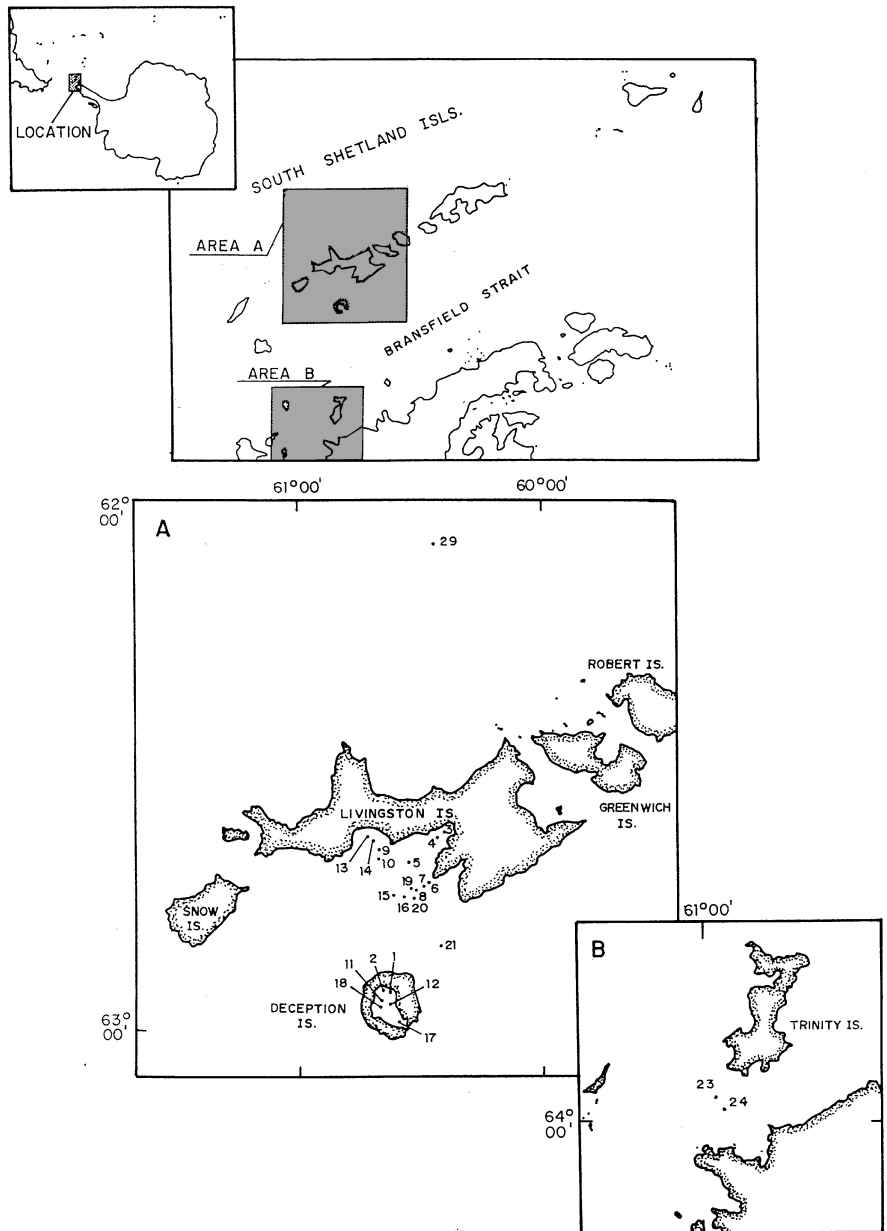
and (2) to identify environmental variables probably responsible for the distribution of the benthic assemblages.

### Materials and methods

#### Field sampling

The research programme of the BENTART-95 cruise aboard RV Hespérides was carried out from 16 January to 4 February 1995, during the austral night. Twenty-six stations located around Livingston Island, Deception Island and in the Bransfield Strait in water 42–671 m deep (Fig. 1, Table 1) were sampled using a quantitative van Veen (VV) grab of 0.1 m<sup>2</sup> sampling area and a boxcorer (BC)

**Fig. 1** Position of the sampling stations during the BENTART-95 cruise



**Table 1** Station list with location and environmental parameters. All sediment parameters refer to the surface of the seabed. (D Deception Island, L Livingston Island, B Bransfield Strait, nd not determined)

Station	D1	D2	L3	L4	L5	L6	L7	L8	L9	L10	D11	D12	L13
Latitude S	62°55'	62°56'	62°37'	62°38'	62°41'	62°43'	62°44'	62°44'	62°39'	62°40'	62°57'	62°57'	62°38'
Longitude W	60°36'	60°38'	60°23'	60°25'	60°31'	60°27'	60°28'	60°30'	60°39'	60°38'	60°39'	60°36'	60°41'
Depth (m)	46.1	153.4	68.5	182.5	263.8	121.4	76.2	114	170.4	216.3	162.8	162.8	45.1
pH (at seabed surface)	7.29	6.98	7.06	7.28	7.17	7.1	7.27	7.01	7.14	7.2	6.34	6.05	7.15
Redox potential at seabed surface (mV)	248	-40	-24	-19	-16	-100	-75	nd	-83	72	-97	219	62.8
Carbonates (%)	3.125	3.125	3.125	3.906	39.06	3.125	3.906	4.688	39.06	39.06	4.688	3.125	39.06
Sediment organic matter (%)	4.669	4.212	7.458	9.861	9.177	8.198	7.184	5.59	7.398	9.73	5.754	9.062	8.667
Median particle size (µm)	45.77	22.94	13.85	9.395	9.898	7.278	9.867	6.872	27.44	13.71	10.18	12.29	24.22
Sorting coefficient	2.59	2.77	2.79	2.27	2.26	2.217	2.63	2.04	3.22	2.73	2.41	2.25	3.14

Station	L14	L15	L16	D17	D18	L19	L20	L21	D22	B23	B24	B25	L29
Latitude S	62°38'	62°45'	62°45'	62°59'	62°57'	62°44'	62°45'	62°50'	63°03'	63°57'	63°58'	63°56'	62°05'
Longitude W	60°40'	60°35'	60°34'	60°35'	60°39'	60°31'	60°31'	60°24'	60°39'	60°57'	60°52'	60°45'	60°25'
Depth (m)	72.4	352.2	416	107.8	162.4	240	393.9	649.3	178.8	103	286	440	239.5
pH (at seabed surface)	7.12	7.3	7.17	6.41	5.72	7.63	7.33	7.56	7.58	7.44	nd	7.12	7.11
Redox potential at seabed surface (mV)	-54	182	127	87.9	169	5	nd	273	nd	112.7	nd	nd	101
Carbonates (%)	54.69	3.906	39.06	3.125	3.906	3.125	nd	3.906	3.906	18.75	nd	4.688	3.125
Sediment organic matter (%)	9.469	8.106	8.077	4.325	5.222	9.188	nd	2.828	1.976	11.31	nd	5.143	3.585
Median particle size (µm)	18.99	12.9	13.68	24.52	10.54	12.28	nd	539.6	180.7	10.02	nd	38.26	38.89
Sorting coefficient	2.89	2.49	2.66	2.38	2.27	2.6	nd	1.31	1.3	2.57	nd	4.1	3.69

with a maximum 60-cm breakthrough and an effective sampling area of  $30 \times 20$  cm. Four VV grabs plus 1 BC were accomplished at each station. The first VV grab was used immediately after sampling for measures of temperature and pH at the surface with a Hanna HI 9025c pH meter, and later subsampled for sediment grain size distributions, organic content and carbonates. The BC was used to obtain vertical profiles of redox (Eh) values, measured with an Orion ORP 9678 electrode coupled to a Hanna model HI 9025c mV meter, and for subsequent meiobenthic studies. Readings of Eh were taken after an arbitrary 60-s period (Pearson and Stanley 1979). A standard redox solution (Hanna HI 7020) was used as reference. The three remaining replicate VV grabs were used to obtain means and standard deviations of the quantified biotic variables. The content of each replicate was sieved using three mesh sizes (5, 1 and 0.5 mm) and later separated into major taxonomic groups (Table 2). Only specimens retained on a 1.0-mm screen were counted on board the ship and their wet weight (WW) biomass was determined according to the recommendations of Jazdzewski et al. (1986) and Mühlenhardt-Siegel (1988). Finally, the biological material was preserved and distributed to taxonomists in Spain for further identification. Analyses of sediment particle size distribution, organic content (loss-on-ignition method) and carbonates were performed following Buchanan (1984).

#### Data analyses

Data analysis followed the scheme proposed by Field et al. (1982). 'Root-root' transformed biomass values were used to construct a Bray-Curtis dissimilarity matrix. Classification was performed using the complete linkage clustering technique, whereas ordination (multidimensional scaling, MDS) was used to evaluate the group separation derived by cluster analysis. 'Indicator' taxa separating each station group were identified by the magnitude of the Kruskal-Wallis test.  $H$  values were calculated for each taxon and listed in order of the magnitude of its contribution to the different station groups. Spearman's rank correlation coefficients were used to assess the strength and direction of the relationship between macrobenthic biomass and environmental variables (pH, Eh, organic matter, carbonates, median particle size, sorting coefficient of sediments and water depth).

## Results

### Number of taxa, abundance and biomass

Figure 2 presents the number of taxa as well as the mean abundance and biomass at each sampling station. The stations at Deception Island, all taken inside Port Foster, were characterized by relatively low values for all three parameters (6–10 taxa, 160–876 specimens  $\cdot$  m $^{-2}$ , 50–220 g  $\cdot$  m $^{-2}$ ), except for the relatively shallow station D1 (45 m depth) where the highest biomass was found (6,673 g  $\cdot$  m $^{-2}$ ). The stations of Livingston Island exhibited large variations in the number of taxa, abundances and biomass. The highest biomass value was recorded at L13 (5,205 g  $\cdot$  m $^{-2}$ ), the lowest (23.3 g  $\cdot$  m $^{-2}$ ) at the deep offshore station L21 (653 m). Abundances varied between 4,380 specimens  $\cdot$  m $^{-2}$  (L19) and 240 specimens  $\cdot$  m $^{-2}$  (L21), the number of taxa between 32 (L7) and 9 (L10).

Overall, the average macrobenthic biomass was 1,169 g  $\cdot$  m $^{-2}$ . Ascidiaceans accounted for almost half of it

(46.7%), followed by sponges (19.9%) and polychaetes (13.4%); the rest (20%) was distributed among several groups such as bryozoans, bivalves and echinoderms. In terms of abundance, polychaetes were the most important group (about 50%), followed by bivalves. Crustaceans, echinoderms, ascidians, sponges and other groups had much lower densities.

### Benthic assemblages

Three main groups could be discriminated both in the cluster dendrogram (Fig. 3) and the MDS plot (Fig. 4). The first cluster, 'Ascidiaceae dominance' (A), consisted of shallower stations (mostly < 100 m) strongly dominated in biomass by epifaunal Ascidiaceae (Fig. 5, Table 2). Together with other filter-feeding taxa, such as sponges and bryozoans, they accounted for over 85% of the mean WW biomass (3,201 g  $\cdot$  m $^{-2}$ ).

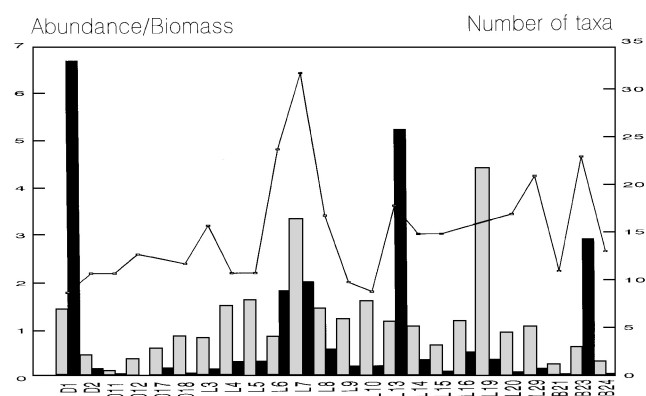


Fig. 2 Mean biomass (solid bars, kg WW  $\cdot$  m $^{-2}$ ), densities (light bars, specimens  $\cdot$  m $^{-2}$   $\times$  1,000) and number of taxa (line) at the sampling stations

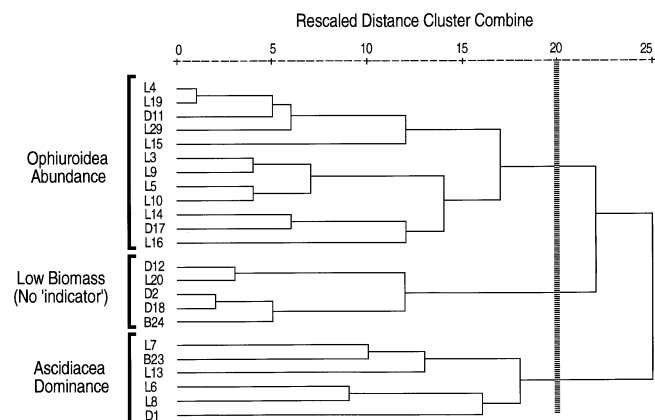


Fig. 3 Dendrogram using complete linkage. Three main clusters are delineated, characterized by Ascidiaceae, Ophiuroidea and low biomass values

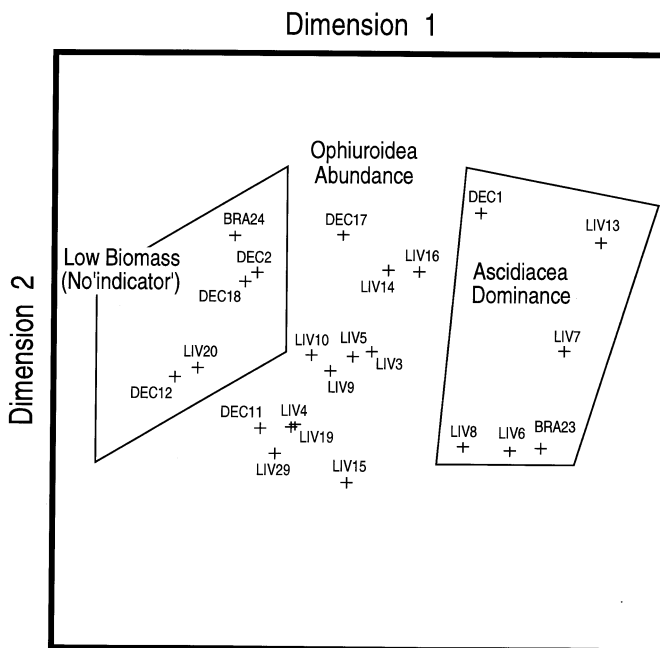


Fig. 4 MDS plot. Stress is 0.16. Station groups delineated in the dendrogram in Fig. 3 are also present here

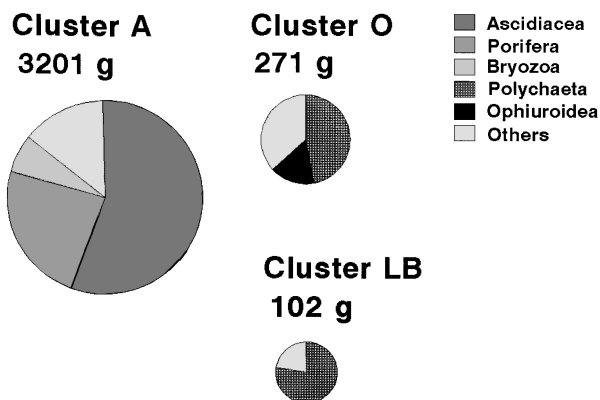


Fig. 5 Biomass proportions of major taxonomic components in the station clusters distinguished in the study area. Pie area is proportional to the mean biomass ( $\text{g wet weight} \cdot \text{m}^{-2}$ ). A Ascidiacea dominance, O Ophiuroidea abundance, LB low biomass (no 'indicator')

The second cluster 'Ophiuroidea abundance' (O) and the third cluster 'low biomass' (LB) were formed by deeper stations (mostly  $> 100 \text{ m}$ ), characterized by the presence of epibenthic Ophiuroidea and the absence of a distinctive epifauna, respectively. The biomass in the two last clusters was dominated by polychaetes (Fig. 5). The third cluster (LB) included stations with the lowest mean biomass ( $102 \text{ g} \cdot \text{m}^{-2}$ ), while that of cluster O was slightly higher ( $271 \text{ g} \cdot \text{m}^{-2}$ ).

Ordination based on MDS was used to evaluate the group separation derived by the cluster analysis. The two-dimensional plot (Fig. 4) corroborated the results

of the classification. Two major groups (A and LB) are segregated along dimension 1, which can be identified as an 'increasing biomass gradient'. Group O with intermediate biomass values and populated distinctively by an Ophiuroidea epifauna remains in the centre of the plot.

Non-parametric Kruskal-Wallis tests of biomass differences among the clusters, performed for each taxon, confirmed the importance of epifaunal Ascidiacea ( $H = 21.4$ ;  $P < 0.0001$ ) and Ophiuroidea ( $H = 11.1$ ;  $P = 0.0038$ ) as the core taxa defining cluster groups A and O, respectively. However, no 'indicator' taxon was found for the remaining group LB. Using major taxonomic categories, a particular infaunal taxon could not be found to explain the existence of this third group.

#### Relationship between biotic and environmental variables

The sediments at the stations investigated consisted mainly of poorly sorted silty clays, with relatively high contents of organic matter (Table 1). Carbonate contents were low, probably due to strong terrestrial influences; higher values were found close to Walker Bay. The superficial sediments appeared to be oxidized, as shown by Eh values greater than  $-100 \text{ mV}$ . The pH values in surface sediments were below 7.0 at stations located inside Port Foster (Deception Island). It remains to be demonstrated these values indicate the prevalence of acidic conditions induced by episodes of volcanic activity within this sea-breached caldera. Spearman's rank correlations between biomass data and abiotic environmental variables (Table 1) showed the absence of significant values, with the exception of depth ( $r_s = -0.57$ ).

#### Discussion

WW biomass values from the Antarctic peninsula and adjacent islands range from  $\geq 1$  to  $\leq 6,000 \text{ g} \cdot \text{m}^{-2}$ , with a grand mean of about  $1,000 \text{ g} \cdot \text{m}^{-2}$  (Gutt 1991). According to Knox (1994), epifaunal biomass is generally much greater than infaunal biomass (up to  $4,200 \text{ g} \cdot \text{m}^{-2}$  and up to  $700 \text{ g} \cdot \text{m}^{-2}$ , respectively). The average biomass in our study ( $1,169 \text{ g} \cdot \text{m}^{-2}$ ) is in the ranges of those previously compiled in the literature by Jazdzewski et al. (1986), Mühlenhardt-Siegel (1988), Gerdes et al. (1992) and Knox (1994) from different Antarctic locations.

The absence of significant correlations between macrobenthic biomass and any of the sediment parameters examined suggests that water depth (or depth-related factors) plays the most important role in structuring the macrobenthic biomass along a vertical gradient of

**Table 2** Macrozoobenthic taxa in the waters of the investigated area. Means ( $\pm$  standard deviations) of abundance (specimens  $\cdot$  m<sup>-2</sup>) and biomass (g wet weight  $\cdot$  m<sup>-2</sup>) are given for all the stations combined as well as for each of the three benthic assemblages distinguished

	Total						Assemblage "A"			Assemblage "LB"			Assemblage "O"			
	Biomass		Abundance		Biomass		Abundance		Biomass		Abundance		Biomass		Abundance	
Porifera	199.058	( $\pm$ 818.236)	1.596	( $\pm$ 4.384)	762.5	( $\pm$ 1461.829)	4.450	( $\pm$ 7.372)	0	( $\pm$ 0)	0.278	( $\pm$ 0.622)	0.833	( $\pm$ 1.988)		
Actinaria	0.145	( $\pm$ 0.471)	0.435	( $\pm$ 1.495)	0.278	( $\pm$ 0.622)	1.117	( $\pm$ 2.497)	0	( $\pm$ 0)	0.139	( $\pm$ 0.462)	0.275	( $\pm$ 0.912)		
Hydroidea	0.218	( $\pm$ 0.562)	0.578	( $\pm$ 1.601)	0.278	( $\pm$ 0.622)	1.117	( $\pm$ 2.497)	0	( $\pm$ 0)	0.278	( $\pm$ 0.622)	0.550	( $\pm$ 1.230)		
Gorgonaria	0.507	( $\pm$ 2.052)	0.287	( $\pm$ 0.930)	1.945	( $\pm$ 3.654)	1.100	( $\pm$ 1.556)	0	( $\pm$ 0)	0	( $\pm$ 0)	0	( $\pm$ 0)		
Bryozoa	53.317	( $\pm$ 164.658)	5.217	( $\pm$ 12.819)	199.945	( $\pm$ 273.499)	18.900	( $\pm$ 19.323)	0.666	( $\pm$ 1.332)	1.942	( $\pm$ 4.394)	0.275	( $\pm$ 0.912)		
Nemertini	3.985	( $\pm$ 13.796)	5.504	( $\pm$ 11.651)	11.938	( $\pm$ 25.235)	12.217	( $\pm$ 19.771)	0.334	( $\pm$ 0.668)	1.340	( $\pm$ 1.729)	3.883	( $\pm$ 5.419)		
Nematoda	0.507	( $\pm$ 1.035)	2.026	( $\pm$ 5.180)	1.110	( $\pm$ 1.570)	6.117	( $\pm$ 8.703)	0.668	( $\pm$ 0.818)	1.320	( $\pm$ 0.462)	0.275	( $\pm$ 0.912)		
Echiura	6.217	( $\pm$ 29.162)	0.143	( $\pm$ 0.673)	0	( $\pm$ 0)	0	( $\pm$ 0)	0	( $\pm$ 0)	11.917	( $\pm$ 39.523)	0.275	( $\pm$ 0.912)		
Priapulida	0.870	( $\pm$ 1.379)	2.313	( $\pm$ 3.858)	0.557	( $\pm$ 0.787)	1.100	( $\pm$ 1.556)	1.332	( $\pm$ 1.631)	4.660	( $\pm$ 1.444)	1.942	( $\pm$ 3.181)		
Sipuncula	1.740	( $\pm$ 2.113)	14.491	( $\pm$ 30.336)	4.167	( $\pm$ 2.098)	25.550	( $\pm$ 18.609)	1.002	( $\pm$ 0.818)	6.020	( $\pm$ 6.123)	12.492	( $\pm$ 38.471)		
Polychaeta	133.670	( $\pm$ 110.112)	794.900	( $\pm$ 837.021)	190.333	( $\pm$ 142.729)	575.500	( $\pm$ 317.628)	80.080	( $\pm$ 59.026)	458.660	( $\pm$ 93.613)	1,044.700	( $\pm$ 1,065.140)		
Oligochaeta	0.145	( $\pm$ 0.471)	5.070	( $\pm$ 21.117)	0	( $\pm$ 0)	0	( $\pm$ 0)	0.334	( $\pm$ 0.668)	20.660	( $\pm$ 41.320)	1.108	( $\pm$ 3.676)		
Hirudinea	0.073	( $\pm$ 0.341)	0.143	( $\pm$ 0.673)	0	( $\pm$ 0)	0	( $\pm$ 0)	0	( $\pm$ 0)	0.139	( $\pm$ 0.462)	0.275	( $\pm$ 0.912)		
Solenogastrea	0.435	( $\pm$ 0.882)	1.304	( $\pm$ 3.650)	0.835	( $\pm$ 0.835)	3.333	( $\pm$ 6.098)	0.334	( $\pm$ 0.668)	0.660	( $\pm$ 0.920)	0.558	( $\pm$ 1.852)		
Gastropoda	4.057	( $\pm$ 7.684)	7.678	( $\pm$ 11.400)	6.667	( $\pm$ 6.597)	21.667	( $\pm$ 13.297)	0.334	( $\pm$ 0.668)	0.660	( $\pm$ 0.920)	3.608	( $\pm$ 5.002)		
Scaphopoda	1.377	( $\pm$ 2.123)	6.059	( $\pm$ 10.127)	0	( $\pm$ 0)	0	( $\pm$ 0)	1.000	( $\pm$ 1.333)	6.000	( $\pm$ 9.031)	8.608	( $\pm$ 11.500)		
Bivalvia	14.057	( $\pm$ 14.305)	163.187	( $\pm$ 212.671)	13.055	( $\pm$ 7.287)	255.000	( $\pm$ 322.692)	9.980	( $\pm$ 4.066)	67.340	( $\pm$ 42.340)	157.217	( $\pm$ 160.619)		
Pycnogonida	1.305	( $\pm$ 1.901)	4.922	( $\pm$ 8.832)	2.223	( $\pm$ 2.078)	11.667	( $\pm$ 12.416)	0.334	( $\pm$ 0.668)	0.660	( $\pm$ 1.320)	3.325	( $\pm$ 6.232)		
Cumacea	1.667	( $\pm$ 2.823)	6.083	( $\pm$ 10.340)	4.443	( $\pm$ 4.158)	16.667	( $\pm$ 14.658)	0	( $\pm$ 0)	0.973	( $\pm$ 1.067)	3.325	( $\pm$ 4.299)		
Isopoda	2.028	( $\pm$ 3.862)	2.752	( $\pm$ 3.361)	4.718	( $\pm$ 6.473)	3.883	( $\pm$ 3.563)	0.666	( $\pm$ 1.332)	1.340	( $\pm$ 1.381)	2.775	( $\pm$ 3.292)		
Amphipoda	6.017	( $\pm$ 5.268)	53.917	( $\pm$ 98.656)	11.400	( $\pm$ 6.696)	141.117	( $\pm$ 160.445)	2.334	( $\pm$ 1.669)	7.320	( $\pm$ 4.896)	29.733	( $\pm$ 21.963)		
Ostracoda	0.218	( $\pm$ 0.562)	0.430	( $\pm$ 1.111)	0.278	( $\pm$ 0.622)	0.550	( $\pm$ 1.230)	0.334	( $\pm$ 0.668)	0.660	( $\pm$ 1.320)	0.275	( $\pm$ 0.912)		
Tanaidacea	0.290	( $\pm$ 0.800)	0.865	( $\pm$ 2.809)	1.112	( $\pm$ 1.242)	3.317	( $\pm$ 4.702)	0	( $\pm$ 0)	0	( $\pm$ 0)	0	( $\pm$ 0)		
Asteroida	7.448	( $\pm$ 23.041)	2.609	( $\pm$ 4.173)	26.607	( $\pm$ 39.175)	5.000	( $\pm$ 5.709)	0	( $\pm$ 0)	0	( $\pm$ 0)	2.5	( $\pm$ 3.373)		
Ophiuroidea	31.578	( $\pm$ 33.502)	56.904	( $\pm$ 60.640)	31.943	( $\pm$ 29.226)	108.317	( $\pm$ 82.694)	1.668	( $\pm$ 1.053)	17.980	( $\pm$ 5.571)	41.667	( $\pm$ 36.878)		
Echinoidea	21.939	( $\pm$ 55.171)	3.913	( $\pm$ 5.797)	21.662	( $\pm$ 28.732)	7.783	( $\pm$ 7.132)	0.666	( $\pm$ 1.332)	1.340	( $\pm$ 2.680)	3.050	( $\pm$ 4.999)		
Holothuroidea	30.696	( $\pm$ 71.572)	4.787	( $\pm$ 9.215)	84.112	( $\pm$ 107.868)	12.783	( $\pm$ 13.664)	0	( $\pm$ 0)	0	( $\pm$ 0)	2.783	( $\pm$ 4.887)		
Enteropneusta	0.290	( $\pm$ 0.800)	1.161	( $\pm$ 3.050)	0.555	( $\pm$ 1.241)	1.667	( $\pm$ 3.727)	0	( $\pm$ 0)	0	( $\pm$ 0)	1.392	( $\pm$ 3.184)		
Ascidiacea	466.841	( $\pm$ 1,293.461)	61.013	( $\pm$ 169.588)	1,788.167	( $\pm$ 2,012.763)	231.667	( $\pm$ 266.150)	0.334	( $\pm$ 0.668)	0.660	( $\pm$ 1.320)	0.833	( $\pm$ 1.988)		
Osteichthyes	7.826	( $\pm$ 36.708)	0.291	( $\pm$ 1.366)	30.000	( $\pm$ 67.082)	1.117	( $\pm$ 2.497)	0	( $\pm$ 0)	0	( $\pm$ 0)	0	( $\pm$ 0)		

increasing depth. Since benthic assemblages depend heavily on the supply of food from the water column, the vertical pattern of biomass in the investigated area suggests a possible response to the degree of plankton/benthos interaction.

As has been recently noted (Dayton et al. 1994), the Antarctic seas show two contrasting situations: a highly productive plankton system capable of supporting large populations of tetrapod vertebrates and cephalopods, but benthic assemblages characterized by low growth rates and secondary production. Since the epifaunal filter-feeders obtain their food from sedimenting phytoplankton and resuspension from the sediments (Knox 1994), they are most prevalent at shallower depths (Barnes and Hughes 1988) where they can achieve large biomasses provided that sufficient concentrations of suspended particulate organic matter are available in the water column. However, deposit-feeding infauna will be successful on sediments regardless of their bathymetric position, although large quantities of sediment may have to be sorted and/or consumed (Barnes and Hughes 1988) to concentrate a comparable quantity of food. It is always more rewarding to wipe off particles retained on passive filters placed in the water column than to swallow large quantities of soft organic-rich sediments with their large percentage of inorganic ash. In fact, Gallardo (1987) suggested that the relatively small biomasses of infaunal organisms on Antarctic soft bottoms were caused by filter-feeders reducing the food material reaching the sediments. The group of shallow-stations (A), delimited in the classification and ordination methods, is defined by the dominance of suspension-feeders (Ascidacea, Porifera and Bryozoa) and delineates the most eutrophic environments in the investigated area. Three stations (L6, L7 and L8) are close to a cape (Miers Bluff), suggesting the existence of an area of relatively rapid water flow off Livingston Island, which promotes a high biomass of suspension-feeders.

Both deeper station clusters O and LB showed a deposit-feeding polychaete biomass dominance. The main difference between them lies in the presence in cluster O of a rich epifauna of ophiuroids, some of which are important predators in the Antarctic (Sieg and Wägele 1990; Dayton 1990; Arntz et al. 1994). In fact, a prey-predator dependence can be suggested, since ophiuroids are absent at those stations with the lowest biomass values (corresponding to station cluster LB). Stomach content analysis of aggregated ophiuroids on deep bottoms of the Scotia and Weddell Seas (Sokolova 1993) demonstrated that they used a continuous 'rain of planktonic corpses' as a food source. Thus, large aggregations of ophiuroids may indicate that aphotic conditions on deeper bottoms (> 100 m) are strongly affected by the large productivity of the euphotic water masses above. On the other hand, low endobenthic biomass (as shown by the LB cluster

group) can be used to detect oligotrophic areas with low levels of pelagic production (Ahn and Kang 1991).

The differences in faunal composition between stations are probably due to different trophic dynamics. The relationship between pelagic productivity and benthic biomass was studied by Dayton and Oliver (1977). They related the existence of a high benthic biomass to eutrophic water columns, whereas lower benthic biomasses resulted from oligotrophic, nutrient-poor water flowing above the benthos. Shallow waters close to the coast of the investigated area probably develop high productivity in the euphotic zone, promoting the dominance of a suspension-feeding epifauna to such an extent that infaunal assemblages appear smothered by it (Gallardo 1987). In fact, the high concentrations of particles measured in the Weddell Sea were limited to a depth of about 80 m (Rabitti et al. 1990). On the other hand, deep aphotic water masses cannot sustain a rich epifauna, promoting the dominance of a deposit-feeding infauna unable to attain the large biomasses of the epifauna, since the food quality of soft organic-rich sediments is always lower due to their inherently higher percentage of inorganic ash (Valiela 1984).

In conclusion, our results show (1) a trophic zonation of the Antarctic benthos based on water depth and (2) the displacement of the deposit-feeding infauna to deeper bottoms when competing for food and space with the suspension-feeding epifauna in the shallower waters of nutrient-enriched environments, as suggested previously by Gallardo (1987).

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## References

- Ahn IY, Kang YC (1991) Preliminary study on the macrobenthic community of Maxwell Bay, South Shetland Islands, Antarctica. *Korean J Polar Res* 2: 61-71
- Arntz WE, Brey T, Gallardo VA (1994) Antarctic zoobenthos. In: Ansell AD, Gibson RN, Barnes M (eds) *Oceanography and marine biology: an annual review*, vol. 32. UCL Press, London, pp 241-304
- Barnes RSK, Hughes RN (1988) *An introduction to marine ecology*, 2nd edn. Blackwell Scientific, Oxford
- Buchanan JB (1984) Sediment analysis. In: Holme NA, McIntyre AD (eds) *Methods for the study of marine benthos*. Blackwell Scientific, Oxford, pp 41-65

- Dayton PK (1990) Polar benthos. In: Smith WO (ed) Polar oceanography. Part B: chemistry, biology and geology. Academic Press, London, pp 631–685
- Dayton PK, Oliver JS (1977) Antarctic soft-bottom benthos in oligotrophic and eutrophic environments. *Science* 197: 55–58
- Dayton PK, Mordida BJ, Bacon F (1994) Polar marine communities. *Am Zool* 34: 90–99
- Field JG, Clarke KR, Warwick RM (1982) A practical strategy for analysing multispecies distribution patterns. *Mar Ecol Prog Ser* 46: 7–12
- Gallardo VA (1987) The sublittoral macrofaunal benthos of the Antarctic shelf. *Environ Int* 13: 71–87
- Gallardo VA (1992) Estudios bentónicos en bahías someras antárticas de Archipiélago de las Islas Shetland del Sur. In: Gallardo VA, Ferretti O, Moyano HI (eds) *Oceanografía en Antártica*. ENEA – Proyecto Antártica, pp 383–393
- Gallardo VA, Castillo JC (1969) Quantitative benthic survey of the infauna of Chile Bay (Greenwich Island, South Shetland Islands). *Gayana Zool* 16: 3–17
- Gallardo VA, Castillo JG, Retamal MA, Yañez A, Moyano HI, Hermosilla JG (1977) Quantitative studies on the soft-bottom macrobenthic animal communities of shallow Antarctic Bays. In: Llano GA (ed) *Adaptations within Antarctic ecosystems*. Proc 3rd SCAR Symp Antarct Biol. Smithsonian Institution, Washington DC, pp 361–387
- Gerdes D, Klages M, Arntz WE, Herman RL, Galéron J, Hain S (1992) Quantitative investigations on macrobenthos communities of the southeastern Weddell Sea shelf based on multibox corer samples. *Polar Biol* 12: 291–301
- Gutt J (1991) Are Weddell Sea holothurians typical representatives of the Antarctic benthos? A comparative study with new results. *Meeresforschung* 33: 312–329
- Jazdzewski K, Jurasz W, Kittel W, Presler P, Sicinski J (1986) Abundance and biomass estimates of the benthic fauna in Admiralty Bay, King George Island. *Polar Biol* 6: 5–16
- Knox GA (1994) Benthic communities. In: *The biology of the Southern Ocean*. Cambridge University Press, New York, pp 193–220
- Lowry JK (1975) Soft-bottom macrobenthic community of Arthur Harbor, Antarctica. *Antarct Res* 23: 1–19
- Mühlenhardt-Siegel U (1988) Some results on quantitative investigations of macrozoobenthos in the Scotia Arc (Antarctica). *Polar Biol* 8: 241–248
- Mühlenhardt-Siegel U (1989) Quantitative investigations of Antarctic zoobenthos communities in winter (May/June) 1986 with special reference to the sediment structure. *Arch Fischereiwiss* 39: 123–141
- Olaso I (1994) Campaña Bentart 94 en el B.I.O. Hespérides en febrero de 1994. Instituto Español de Oceanografía, Santander (Final Report for the Spanish CICYT)
- Pearson TH, Stanley SO (1979) Comparative measurement of the redox potential of marine sediments as a rapid means of assessing the effect of organic pollution. *Mar Biol* 53: 371–379
- Rabitti S, Gouleau D, Boldrin A (1990) Suspended matter, phytoplankton and nutrients. In: Arntz W, Ernst W, Hempel I (eds) *The Expedition Antarktis VII/4 (Epos leg 3) and VII/5 of RV "Polarstern" in 1989*. *Ber Polarforsch* 68: 50–66
- Ramos A (1995) Informe de la Campaña Bentart-95. Instituto Español de Oceanografía, Fuengirola (Málaga) (Final Report for the Spanish CICYT)
- Retamal MA, Quintana R, Neira F (1982) Análisis cuali y cuantitativo de las comunidades bentónicas en Bahía Foster (Isla Decepción) (XXXV Expedición Antártica Chilena, enero 1981). *Publ Inst Antart Chil Ser Cient* 29: 5–15
- Richardson MD, Hedgpeth JW (1977) Antarctic soft-bottom macrobenthic community adaptations to a cold, stable, highly productive, glacially affected environment. In: Llano GA (ed) *Adaptations within Antarctic ecosystems*. Gulf Publishing, Houston, pp 181–196
- Sieg J, Wägele JW (eds) (1990) *Fauna der Antarktis*. Parey, Berlin.
- Sokolova MN (1993) New data on the trophic structure of macrobenthos in the abyss of the Atlantic Ocean. In: Vinogradova NG (ed) *The deep-sea bottom fauna in the southern part of the Atlantic Ocean*. Trans P.P. Shirshov Inst Oceanol, vol 127. Russian Academy of Sciences, "Nauka", Moscow, pp 50–64 (in Russian with English summary)
- Valiela I (1984) *Marine ecological processes*. Springer, Berlin Heidelberg, New York