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The subtidal macrobenthic assemblages of Bahía San Sebastián (Tierra del Fuego, Argentina)

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Abstract Bahía San Sebastián (BSS), a shallow and protected environment on the eastern coast of Tierra del Fuego (Argentina), is a prime habitat for several species of nearctic migratory birds that visit the area during summer to feed in its huge intertidal mudflats. The area has also great economic value due to the extraction and transport of hydrocarbons. Twentythree dredge stations were analysed and presence/ absence data were used to classify stations and species by cluster analysis. Two algae and 113 taxa of macrobenthic invertebrates from 12 animal phyla were identified. Species richness was one order of magnitude higher (mean 29.0 sp st $^{-1}$) in stations located outside or in the southern unprotected section of BSS than in most muddy or sandy stations within the bay (mean 3.7 sp st^{-1}). Hard bottom stations outside BSS were dominated by a rich assemblage of sessile filter-feeders, mainly bryozoans, hydrozoans, ascidians, sponges, and the bivalve Aulacomya atra. Soft bottom areas inside BSS were mainly populated by relatively few species of deposit-feeders, such as the orbiniid polychaete Phylo felix, which was particularly frequent and widespread. Shells of the clam Mulinia edulis are very common, representing one of the few hard substrata available for sessile species on soft bottoms. Epibenthic assemblages within BSS were dominated by the detritivorous isopod Serolis paradoxa and the crab Eurypodius latreillei. The macrobenthic fauna of BSS

can be regarded as typical of the Magellan region, showing affinities with those of other localities around Tierra del Fuego, the Straits of Magellan and the southern Chilean fjords.

Keywords Bahía San Sebastián · Subtidal benthic assemblages · Magellan region · Tierra del Fuego · Argentina

Introduction

Bahía San Sebastián (BSS), a shallow and protected coastal environment on the eastern shore of Tierra del Fuego (Argentina), is a prime habitat for many species of birds, including several nearctic migratory shorebirds that visit the area during summer to feed in its huge intertidal mudflats (Yorio 1998). It is estimated that 43% of the population of Hudsonian godwits (Limosa haemastica), 40% of the white-rumped sandpipers (Calidris fuscicollis), and 14% of the redknots (Calidris canutus) reaching Argentina are found in northern Tierra del Fuego during summer, mainly in Bahía Lomas (Chile) and BSS (Goodall 1996). In 1995, the Ramsar Convention included BSS in an international list of wetlands in need of protection due to its value as a site of non-reproductive concentration of migratory birds. The bay is also included in the Tierra del Fuego Atlantic Reserve, part of the Western Hemisphere Shorebird Reserve Network (Yorio 1998).

As well as other Patagonian gulfs (Zaixso et al. 1998), BSS is a potential scenario for conflicts between the conservation of endangered or charismatic species and the exploitation of natural resources, since it lies in

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the heart of the most important hydrocarbon extraction area of Tierra del Fuego. BSS is surrounded by hundreds of oil wells and oil is loaded on tankers from a buoy in the southern part of the bay. As wind velocities over 60 km h⁻¹ occur for 200 days of the year (Isla et al. 1991), an oil spill is always a potential risk and can have persistent effects in this area (Colwell et al. 1978), where loading and transport of hydrocarbons often take place during rough seas.

Baseline information on benthic community structure is critical to avoid confounding the consequences of an impact, given the high level of variability in natural assemblages (Smith and Simpson 1995; Gelin et al. 2003). It has been stressed that pre-impact data are essential to understand the effects of an oil spill (Paine et al. 1996).

In spite of the ecological and economic importance of BSS, its macrobenthic assemblages are almost unknown, except for scattered records in the taxonomic literature [e.g. four species of amphipods recorded for El Páramo Peninsula (Schellenberg 1931), ten species of sponges collected in Cape San Sebastián (Sarà 1978)]. Therefore, the aim of this study is to present a first survey of the subtidal macrobenthic assemblages of BSS, to compare the assemblages occurring inside and outside the bay and to discuss possible abiotic factors influencing their distribution.

Materials and methods

Study area

Bahía San Sebastián (Fig. 1) lies in the Atlantic coast of Tierra del Fuego, just SE of the eastern entrance of the Straits of Magellan (53°02'S-53°19'S, 68°10'W-68°40'W). It is a large semicircular depression 55 km long by 40 km wide, open to the sea on the eastern side. The huge Bahía Inútil-BSS depression was formed by a great Pleistocene glacier which flowed NE. The northern part of the bay is closed by El Páramo Peninsula, a 17 km long spit formed by wave-induced southward transport of sand and gravel (Isla et al. 1991). The north and west coasts of BSS are characterized by extensive, almost horizontal tidal mudflats crossed by numerous drainage channels (Ferrero and Vilas 1988). The unprotected southern coast is steeper and narrower, with coarser sediments and boulders (Fig. 1). Tides are semidiurnal, with maximum amplitude of 10.4 m (Vilas et al. 1987). Depths of 9–13 m have been recorded in the middle of the bay. Maximum depths (up to 48 m) are found around the tip of El Páramo Peninsula. Strong tidal currents occur near the mouth of the bay. Water temperature ranges from 5-6°C in winter to 9–11°C in summer. Salinity ranges from 30 to 34 PSU. BSS has been regarded by some authors as a coastal lagoon (Piccolo and Perillo 1997) due to the presence of a partial barrier closing the mouth, but fresh-



Fig. 1 Left distribution of stations and substrata inside and outside Bahía San Sebastián. Pentagons stones and boulders. Circles muddy sand. Squares sandy mud. See Table 1 for the exact location of each station. Right station groups and species richness.

Circles Group A. *Squares* Group B (see Results). Stations 5, 7, 8, 14, 16, 21 and 24 were not included in this analysis (see Materials and methods)

water runoff from Río San Martín is scarce, because of relatively low precipitation. A considerable volume of water (up to 64% during spring tides) flows in and out of the bay with each tidal cycle. Therefore, water temperature and salinity of BSS are similar to those recorded on the shallow continental shelf off eastern Tierra del Fuego (see Guerrero and Piola 1997).

Sampling

A benthic survey of BSS was performed on November 12–13, 2002 onboard *Tango I*, a supply vessel rented by the oil company operating in the area. Thirty dredge stations were collected, 24 within BSS and 6 on neighbouring areas beyond the mouth of the bay (Fig. 1 and Table 1). Position of stations was determined by GPS. Depth was recorded by an echosound, except for seven stations (1–4, 6, 29, 30) whose depths were estimated using chart H-425 of Servicio de Hidrografía Naval. Qualitative samples of the biota were obtained in all stations with a rectangular (60 cm \times 20 cm) dredge with a mesh size of 15 mm. All biological samples were immediately washed on a 1-mm sieve and fixed in 10% formalin. Taxa were sorted and identified under

stereoscopic microscope. One sample for sediment particle size analysis was taken in each station with a Van Veen grab. However, grabs failed to retrieve sediment in all stations outside BSS. Observations of the material collected in the dredge samples showed that substrata in these stations were coarse, consisting of stones, boulders and shells. Sediment samples were oven-dried at 60°C until constant weight. Percentages of gravel, sand and mud were calculated by sieving the sediment through mesh sizes of 1 mm and 62 µm.

Qualitative observations on the epibenthic assemblages inside BSS are based on 12 hauls made with a $1.28 \text{ m} \times 4.16 \text{ m}$ otter trawl (mesh size: 32 mm) onboard the supply vessel *Laurel* on March 10–12, 2006. Epibenthic species collected with the otter trawl are not listed in Table 2. Bivalve and gastropod shells cast ashore during high tides were also examined on March 13–15, 2006 in the intertidal zone of BSS.

Data analysis

Two stations without macrobenthos (21, 24) and five stations with only one species (5, 7, 8, 14, 16; Table 1) were not included in the analysis. Similarities among

Station	Latitude (S)	Longitude (W)	Depth (m)	Gravel (%)	Sand (%)	Mud (%)	Number of species
1	53°22′	68°00′	8	_	_	_	55
2	53°20′	68°02′	6	_	_	-	39
3	53°15′	68°04′	7	_	_	-	24
4	53°12′	68°06′	20	_	_	-	36
5	53°07′	68°08′	26	_	-	-	1
6	53°05′	68°10′	12	_	-	-	31
7	53°09′	68°15′	31	18.82	23.23	57.95	1
8	53°09′	68°18′	16	0.25	36.79	62.95	1
9	53°09′	68°21′	7	0.00	43.31	56.69	3
10	53°11′	68°22′	8	0.00	46.12	53.88	2
11	53°11′	68°19′	13	0.00	53.60	46.40	5
12	53°11′	68°16′	17	1.84	58.69	39.47	6
13	53°11′	68°13′	24	0.34	38.19	61.46	2
14	53°13′	68°13′	20	1.66	68.40	29.94	1
15	53°13′	68°16′	18	0.02	58.42	41.56	3
16	53°13′	68°19′	16	0.00	43.55	56.45	1
17	53°13′	68°22′	18	0.00	19.77	80.23	3
18	53°13′	68°25′	8	0.42	28.00	71.57	6
19	53°15′	68°24′	9	0.00	79.52	20.48	3
20	53°15′	68°21′	12	0.00	43.15	56.85	4
21	53°15′	68°18′	16	1.50	50.55	47.94	_
22	53°15′	68°15′	19	0.35	65.57	34.08	12
23	53°15′	68°12′	22	0.52	88.27	11.21	3
24	53°17′18′′	68°18'48''	17	0.08	29.31	70.62	_
25	53°16′50′′	68°14′41′′	22	0.88	42.19	56.93	6
26	53°16′57′′	68°14'25''	22	0.00	37.27	62.73	2
27	53°16′30′′	68°14'09''	22	0.88	67.69	31.43	11
28	53°16′18′′	68°13'40''	23	6.49	74.74	18.77	3
29	53°16′17′′	68°13'37''	15	3.32	72.20	24.48	24
30	53°16′16′′	68°13'35''	15	0.88	74.26	24.86	4

Table 1Geographic location,
depth, percentage of gravel,
sand and mud, and number of
species of 30 benthic stations
inside and outside BSS

Depth of stations 1–4, 6, 29 and 30 was estimated using chart H-425 of Servicio de Hidrografía Naval. Sediment was not analysed in stations 1– 6, which were only sampled with dredge

Table 2	Assemblages of macrobenthic taxa found in Bahía San Sebastián and neighbouring areas, and number of stations of each group
in which	each species is present

Taxa	Phylum/class/order	Number of stations	
		Group A	Group B
Assemblage 1			
Joeropsis curvicornis (Nicolet 1849)	Isopoda	2	-
Munida subrugosa Henderson 1847	Decapoda	1	_
Campanularia sp.	Hydrozoa	1	_
Edotia tuberculata Guérin-Méneville 1843	Isopoda	3	_
Serolis paradoxa (Fabricius 1775)	Isopoda	2	_
Atylus cf. villosus Bate 1862	Amphipoda	1	_
Celleporina bicostata Hayward 1980	Brvozoa	1	_
Codonellina galeata (Busk 1881)	Bryozoa	1	_
Pseudosuberites sulcatus (Thiele 1905)	Porifera	1	_
Smittina jullieni Movano 1983	Brvozoa	1	_
Smittina smittiana (Busk 1884)	Bryozoa	1	_
Trochita pileus (Lamarck 1822)	Gastropoda	1	_
Allotanais hirsutus (Beddard 1886)	Tanaidacea	1	_
Andreella patagonica López Gappa 1981	Bryozoa	1	_
Plagioecia sp.	Bryozoa	1	_
Alcvonidium sp.	Bryozoa	1	_
Halosydna patagonica Kinberg 1867	Polychaeta	1	_
Pedicelling cernug (Pallas 1771)	Entoprocta	3	_
Podoceridae	Amphipoda	2	_
Magellania venosa (Solander 1786)	Brachiopoda	3	_
Philobrya sp	Bivalvia	2	_
Entodesma sp	Bivalvia	1	_
Undetermined hirudineen	Hirudinea	1	
Probalisca sp	Amphipoda	1	
Prohaminia antinoda Schellenberg 1935	Amphipoda	1	_
Symplectoscyphus milneanus (d'Orbigny 1846)	Hydrozoa	3	—
Anastarias sp	Asteroidea	2	-
Caharaa darwinii Busk 1884	Bryozoa	$\frac{2}{2}$	-
Dhumularia setacaa (Linnoous 1758)	Hudrozoa	5	-
A cholia narvula (Lomon 1023)	Pychogonida	2	-
Achema parvana (Loman 1925)		2	-
Smitting sp	Bruozon	3	-
Santularalla robusta Coughtron 1876	Hudrozoa	2	-
Duura laguman (Lesson 1830)	Assidiação	2	_
Cladostanhus sn	Phaeophyta	5	-
Sullidae sp. 1	Polychaeta	1	-
Symulaetoscuphus subdichotomus (Kirchonpouer 1884)	Hudrozoo	4 5	-
Clathriidae	Porifera	3	_
Clatifilidae	Polyabaata	4	_
America management (Michilosh 1863)	Polychaeta	5	_
Disponentia functional (Dusk 1054)	Bryozoa	5	_
Collaria maluinanaia (Busk 1873)	Bryozoa	5	_
A stee anguine (Linnesus 1759)	Bryozoa	0	_
Aereu anguina (Linnaeus 1758)	bryozoa	7	-
Ampnisbetia operculata (Linnaeus 1758) Mutilus shilawis Humó 1854	Hydrozoa Divelvie	7	1
<i>Mynuus chuensis</i> Hupe 1854	Bivalvia	/	-
<i>Triceuaria acuteata</i> (d'Orbigny 1847)	Bryozoa	8	-
Bicrisia biciliata (MacGillivray 1869)	Bryozoa	8	-
Celleporella tenuelcha Lopez Gappa 1985	Bryozoa	8	-
Celleporella patagonica (Busk 1852)	Bryozoa	2	-
<i>Fenestruina</i> sp.	Bryozoa	2	_
Austrodecus curtipes Stock 1957	Pycnogonida	3	-
Umbonula alvareziana d'Orbigny 1847	Bryozoa	4	-
Electra monostachys (Busk 1854)	Bryozoa	2	-
Alcyonium sp.	Alcyonida	3	_
Osthimosia eatonensis (Busk 1881)	Bryozoa	5	-
Tubulipora organisans d'Orbigny 1847	Bryozoa	4	-
<i>Lasaea</i> sp.	Bivalvia	1	-
Orchomenella (Orchomenopsis) cf. chilensis (Heller 1865)	Amphipoda	1	-

Table 2 continued

Taxa	Phylum/class/order	Number of stations	
		Group A	Group B
Celleporellla hvalina (Linnaeus 1767) sensu lato	Bryozoa	1	_
Ceramium cf. rubrum (Huds.) C.A. Ag.	Rodophyta	1	-
Didemnum sp.	Ascidiacea	1	-
Gammaropsis (Paranaenia) cf. typica (Chilton 1884)	Amphipoda	1	-
Tubulipora anderssoni Borg 1944	Bryozoa	2	-
Arabella protomutans Orensanz 1990	Polychaeta	2	-
Chaperiopsis galeata (Busk 1854)	Bryozoa	2	-
Exochella longirostris Jullien 1888	Bryozoa	2	-
Polyzoa opuntia Lesson 1830	Ascidiacea	2	-
Pseudocnus dubiosus leoninus (Semper 1868)	Holothuroidea	2	-
Penjeridae	Polychaeta	2	_
Parasmitting dubitata Hayward 1980	Bryozoa	$\frac{2}{3}$	_
Harmothoe spinosa Kipberg 1855	Polychaeta	3	
Osthimosia hicornis (Busk 1881)	Bryozoa	3	_
Seba saundersii Stebbing 1875	Amphipoda	1	_
Svllidae sp. 2	Polychaeta	1	_
Celleporella yagana Moyano and Gordon 1980	Bryozoa	1	_
Cirratulus cirratus (Müller 1776)	Polychaeta	1	_
Gammaropsis (Gammaropsis) sp.	Amphipoda	1	_
Goniada falklandica Pratt 1901	Polychaeta	1	-
Haplocheira barbimana robusta Barnard 1932	Amphipoda	1	-
Ianiridae	Isopoda	1	-
Idanthyrsus armatus Kinberg 1867	Polychaeta	1	-
Immergentia zelandica patagonica López Gappa 1981	Bryozoa	1	-
Lumbrineris magalhaensis Kinberg 1865	Polychaeta	1	-
Neastacilla sp.	Isopoda	1	-
Polynoidae	Polychaeta	1	-
Romancheina labiosa (Busk 1854)	Bryozoa	1	-
Autacomya atra (Molifia 1782)	Bivalvia	3	-
Lassa alonsoaa Conlan 1000	Amphipoda	3	_
Typosyllis proliva (Ehlers 1001)	Polychaeta	$\frac{2}{2}$	-
	Toryenacta	2	
Assemblage 2 Deltarian an in condume (White 1842)	Deserado		1
Travisia sp	Polychaeta	_	1
Colfingia margaritacea (Sars 1851)	Sipuncula	-	1
Abatus cavernosus (Philinii 1845)	Echinoidea	_	4
Aega sp	Isopoda	_	1
Kinbergonuphis dorsalis (Ehlers 1897)	Polychaeta	_	1
Lilieborgia cf. georgiana Schellenberg 1931	Amphipoda	_	1
Clymenella minor Arwidsson 1911	Polychaeta	_	3
Actinida	Anthozoa	_	1
Hemioedema spectabilis (Ludwig 1882)	Holothuroidea	1	1
Artacama proboscidea Malmgren 1866	Polychaeta	1	4
Nemertean	Nemertinea	3	3
Mulinia edulis (King and Broderip 1832)	Bivalvia	-	1
Ophioglycera eximia (Ehlers 1900)	Polychaeta	-	1
Nepthys sp.	Polychaeta	1	5
<i>Gymnonereis hartmannschroederae</i> Pettibone 19/0	Polychaeta	-	5
Phylo felix Kinberg 1866	Polychaeta	-	8
Alexanidium gustuale d'Handt and Mayana 1070	Polychaeta	-	2 1
Amphiura princaps Koehler 1007	Ophiuroidea	1	1
Ampharetinae	Polychaeta	_ 1	1
Ninoe falklandica Monro 1936	Polychaeta	1 	2
Indiated amonica	1 orgenuetu		2
Isolated species	Polychaeta		2
Cristaserolis gaudichaudi (Audonin et Milne Edwards 1840)	Isopoda	_	∠ 1
Cristuscions gunaichanna (Audouin et Minne Edwards 1840)	isopoua	_	1

For composition and distribution of station groups A and B, see Figs. 1 and 2. Species are ordered as in the dendrogram of Fig. 3

the remaining 23 stations were calculated applying the Sorensen index on presence/absence data (Crisci and López Armengol 1983). Dendrograms for hierarchical clustering of stations (Q-mode analysis) and species (R-mode analysis) were constructed by group-average linking (Clarke and Warwick 1994).

Results

Sediment

Sediment from the six stations outside BSS consisted of stones and boulders and could not be quantitatively analysed since it was collected with dredge. On the contrary, sediment from 24 grab samples located within the bay consisted of mud and sand in different proportions (Table 1). Sandy bottoms prevailed near the mouth of BSS, whereas muddy ones occurred mainly in more sheltered areas (Fig. 1). Station 7, the only one within BSS with a relatively high proportion of gravel (Table 1), was located near the tip of El Páramo Peninsula (Fig. 1).

Biota

Two algae and 113 taxa of macrobenthic invertebrates belonging to 12 animal phyla were identified (Table 2). The most specious groups were bryozoans, polychaetes and peracarid crustaceans. The dendrogram obtained by cluster analysis classified the stations into two main groups (Fig. 2). Group A consisted of eight stations, five of which were located outside the bay, and the other three in the southern, unprotected area of BSS. Group B comprised 15 stations, all located inside BSS (Figs. 1, 2).

Species richness (Table 1 and Fig. 1) was one order of magnitude higher in Group A than in Group B (Group A: mean 29.0 sp st⁻¹, Group B: mean 3.7 sp st⁻¹; Mann-Whitney U test, U = 120, $P = 4.5 \times 10^{-5}$).

Species were classified by cluster analysis into two main assemblages (Fig. 3). Assemblage 1 consisted of 91 species (Table 2), 90 (98.9%) of which were found exclusively in stations belonging to Group A. This assemblage was dominated by epifaunal filter-feeders, mainly bryozoans, hydrozoans, sponges and ascidians. The bivalve Aulacomya atra was found only in Stations 1-3, outside BSS. Its shells are used as substrate by colonial ascidians and many species of encrusting bryozoans. The tangled masses of A. atra, composed of living animals, shell fragments, byssal threads and sediment are also a favourable habitat for many polychaetes, amphipods and isopods. The densely ramified colonies of the hydrozoan Amphisbetia operculata serve as substrate and refuge for many species, mainly the bryozoans Tricellaria aculeata, Bicrisia biciliata, Aetea anguina and Celleporella tehuelcha, amphipods, pycnogonids and juveniles of the mussel, Mytilus chilensis. The massive bright orange colonies of the compound ascidia Polyzoa opuntia were very abundant in Stations 1 and 2, located outside BSS.

Assemblage 2 consisted of 22 species (Table 2), 16 (72.7%) of which were found exclusively in stations



Fig. 2 Cluster analysis of stations. Stations are numbered as in Table 1



Fig. 3 Cluster analysis of species. Species are ordered from left to right as in Table 2. The polychaete *Notocirrus virginis* and the isopod *Cristaserolis gaudichaudi* appear isolated on the right side of the dendrogram

belonging to Group B. Bryozoans, hydrozoans, ascidians and sponges were completely absent from this association, which was dominated by infaunal depositfeeders. The orbiniid polychaete *Phylo felix* was particularly frequent (Table 2) and widespread in muddy and sandy bottoms within BSS.

Just seven species (6.1%) were simultaneously present in both groups of stations (Table 2). The polychaete *Notocirrus virginis* and the isopod *Cristaserolis gaudichaudi*, which were found only in soft bottom stations of Group B, showed a very low level of similarity with all other species and remained isolated in the dendrogram (Fig. 3). Lower-order clusters within assemblages 1 and 2 were mainly determined by the number of samples in which each species was present (see Fig. 3 and Table 2).

Living specimens of the clam *Mulinia edulis* were found just in one muddy station inside BSS (St. 18), but the shells of this bivalve were very common, representing one of the few hard substrata available for epifaunal species on muddy and sandy bottoms inside the bay. Shells of *Mulinia edulis* and the clam *Darina solenoides* (King and Broderip 1832) cast ashore by high tides were frequently found in the intertidal zone of BSS perforated by circular boreholes made by naticid gastropods, probably *Natica limbata* d'Orbigny 1837.

Epibenthic assemblages inside BSS were dominated by the detritivorous isopod *Serolis paradoxa* and the spider crab *Eurypodius latreillei* Guérin 1928. Other species frequently found in epibenthic samples were *Cristaserolis gaudichaudi*, the crab *Peltarion spinosulum* and the gastropods *Natica limbata* and *Buccinanops paytense* (Kiener 1834).

Discussion

From the biogeographic point of view, the macrobenthic assemblage of BSS can be regarded as typical of the Magellan region, showing affinities with faunas of other localities around Tierra del Fuego, the Straits of Magellan, the southern Chilean fjords or even some Subantarctic islands of the Scotia Arc. Examples of species exhibiting this distribution are, among others, the sponge Pseudosuberites sulcatus (Pansini and Sarà 1999), the hydrozoans Symplectoscyphus milneanus and S. subdichotomus (Peña Cantero and García Carrascosa 1999), the bryozoans Cellaria malvinensis and Tricellaria aculeata (Moyano 2005), the sipunculan Golfingia margaritacea (Saiz-Salinas and Pagola-Carte 1999), the ascidians Paramolgula gregaria, Pyura legumen and Polyzoa opuntia (Ramos-Esplá et al. 2005), the molluscs Trochita pileus and Natica limbata (Linse 1999), the polychaetes Artacama proboscidea, Phylo felix, Ninoe falklandica and Kinbergonuphis dorsalis (Gambi and Mariani 1999), the tanaidacean Allotanais hirsutum (Schmidt and Brandt 2001), the isopod Joeropsis curvicornis (Doti et al. 2005), the amphipods Jassa alonsoae and Seba saundersii (Chiesa et al. 2005), and the decapods Munida subrugosa, Peltarion spinos*ulum* and *Eurypodius latreillei* (Gorny 1999).

Sediments with different proportions of mud and sand occupied most of BSS and were dominated by an association of deposit-feeders. Orbiniid, terebellid, opheliid, maldanid (such as *Phylo felix*, *Artacama proboscidea*, *Travisia* sp. and *Clymenella minor*, respectively) and ampharetid polychaetes are usually considered surface or sub-surface non-selective deposit-feeders (Fauchald and Jumars 1979). In San José Gulf (Patagonia), *Phylo felix, Artacama proboscidea* and *Clymenella minor* occur at 0–60 m depth in bottoms with fine and very fine sediments (Zaixso et al. 1998; Pastor de Ward 2000).

Little overlap was found in BSS between assemblages of deposit- and filter-feeders. Spatial segregation of these two feeding groups has been reported by many authors on a worldwide scale. The low proportion of filter-feeders on muddy bottoms is thought to be related to bioturbation and surface instability, which would clog their filtering structures (Rhoads and Young 1970; Rhoads 1974).

Loose shells of the clam *Mulinia edulis* are very frequent on soft bottoms inside BSS, where other hard substrata for encrusting species are extremely scarce. In southern Chile, this infaunal bivalve inhabits the low intertidal zone of mudflats (Jaramillo et al. 1985; Velasco and Navarro 2002). Living clams were rare in subtidal habitats, but might be abundant at low intertidal levels of the north and west sections of BSS, a very difficult zone for biological sampling.

This study shows a clear pattern of increasing species richness in bottoms populated by epifaunal filterfeeders as compared with soft bottoms inhabited mainly by infaunal deposit-feeders. San José Gulf, in northern Patagonia, is another example of this trend. In this gulf, the assemblage dominated by the ribbed mussel *Aulacomya atra* also shows high species richness (150 taxa) due to great structural complexity and spatial heterogeneity, whereas the soft bottom assemblage dominated by the crab *Peltarion spinosulum* and the holothuroid *Chiridota marenzelleri* is composed of just 34 species (Zaixso et al. 1998).

A. atra was not found inside BSS but is a key species in shallow areas outside the bay. Its presence creates a suitable habitat for a wide variety of sessile and colonial filter-feeders, as well as for mobile invertebrates such as polychaetes and peracarid crustaceans. Low tolerance of this bivalve to very fine sediments is thought to be related to its fixation mechanism by byssal threads and to its filter-feeding habit (Zaixso 1999).

High species richness observed in stations located outside as well as in unprotected areas within BSS (Group A) can also be partially explained by the presence of *Amphisbetia operculata*. Many bryozoans, peracarid crustaceans and juveniles of the mussel *Mytilus chilensis* were associated with dense mats of this hydrozoan. Clumps of *Amphisbetia operculata* serve as primary substrata for the settlement of mussels in shallow waters off Buenos Aires province (Argentina) (Genzano et al. 2003), where a wide variety of associated epizoites has been described (Genzano 1994). A similar association between sertulariid hydrozoans and bryozoans dominates gravelly and sandy bottoms of San Jorge Gulf, in southern Patagonia (Roux et al. 1995).

The classification of three sandy stations from the southern part of BSS in the same cluster as five stations from outside BSS due to the presence of suspension-feeding invertebrates suggests that hard and sandy bottoms may coexist in the southern half of the bay, which is affected by east-west oriented flood currents and oceanic waves (Isla et al. 1991).

Similar studies performed in other Patagonian gulfs have also reported a close relationship between the composition of their macrobenthic assemblages and the sedimentary characteristics of the bottom. In San Jorge Gulf, Roux et al. (1995) found two clearly defined communities. Muds and sandy muds occupying most of the gulf were populated by deposit-feeding bivalves and echinoids, while gravelly and sandy bottoms at the entrance of the gulf were dominated by an association of colonial filter-feeders.

As a considerable amount of water is renewed with each tidal cycle in this macrotidal bay, water temperature and salinity do not appear as important environmental factors explaining differences in composition of macrobenthic assemblages. Results of this study indicate that the hydrodynamic characteristics of the bay (i.e. wave action and tidal currents), and consequently the distribution of different sediment fractions, are fundamental factors determining the composition of the benthos. The presence of extensive areas of fine and very fine sediments dominated by an assemblage of deposit-feeders depends on the existence of El Páramo Peninsula, a spit just 50 m wide between storm berms in its central section, which can be passed over by sea waves during episodic high tides (Isla et al. 1991).

This study presents the first data on the composition and distribution of macrobenthic assemblages in BSS. Further research is needed to provide a quantitative description of community structure and to gain a more detailed understanding of the relationships between benthic biodiversity and environmental factors.

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