Bacterial abundance, production and ectoproteolytic activity in the Strait of Magellan

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ABSTRACT· Bacterial abundance, bacterial secondary production (BSP) and potential ectoproteolytic activity (PEA) were measured at 6 stations along the Strait of Magellan, South America, toward the end of summer 1995. Because of hydrological and climatic factors, 3 main areas could be identified in which the bacterial component displayed specific characteristics. In the Pacific Ocean side, subjected to freshwater inputs from rainfalls and melting of glaciers, the bacterial activities showed the highest values (BSP: 228.2 ng C l^{-1} h^{-1}; PEA: 12.2 nmol l^{-1} h^{-1}). The bacterial biomass was greater than the phytoplanktonic biomass, probably due to organic inputs from land stimulating the bacterial growth. The central part of the Strait demonstrated the lowest values (BSP: 32.6 ng C l^{-1} h^{-1}, PEA: 4.6 nmol l^{-1} h^{-1}), although the ratio of bacterial biomass to phytoplanktonic biomass was greater than 1. In the third area, the Atlantic Ocean opening, subjected to strong tidal currents, BSP and PEA displayed high values, 80 to 88.7 ng C l^{-1} h^{-1} and 11.7 nmol l^{-1} h^{-1} respectively. Nevertheless, the ratio of bacterial to phytoplanktonic biomass was less than 1, like in eutrophic areas. On the other hand, no impact of the tide was noted on bacterial parameters. Considering all samples measured in the 0 to 50 m layer, although BSP and PEA were positively correlated with bacterial abundance, the PEA to BSP ratio was negatively correlated with the bacterial biomass (r = −0.72, p < 0.001, n = 22). This ratio could be an indicator of trophic conditions in the 3 subsystems of the Strait.

KEY WORDS: Bacteria · Strait of Magellan · Ectoproteolytic activity · Environmental factors

INTRODUCTION

The Strait of Magellan is a 550 km long channel located in the South American subantarctic region (52° 30' S, 69° to 74° W), between Patagonia and Terra del Fuego, connecting the Pacific and Atlantic Oceans. The Strait displays a complex topography including 2 sub-basins, an abundance of bays, capes, islands, openings of channels and fjords. Moreover, there are irregular freshwater inputs due to precipitation and melting of glaciers, and strong tidal currents in the eastern part. Knowledge of processes in the Strait of Magellan is mainly limited to hydrological studies (Pickard 1971, Medeiros & Kjerfve 1988, Michelato et al. 1991, Panella et al. 1991) A Pacific origin of the Strait of Magellan waters was observed by Glorioso

(1987) and Saggiomo et al. (1994), whereas Pickard (1971) suggested an Atlantic origin at least for waters of the eastern parts of the Strait. High amplitudes of tide, up to 8.4 m, recorded near the Atlantic entrance suggest a strong influence of water from the Atlantic Ocean (Medeiros & Kjerfve 1988, Michelato et al. 1991). Concerning the biology, most studies investigate the phytoplanktonic communities (Lembeye et al. 1978, Cabrini & Fonda Umani 1991, Uribe 1991, Saggiomo et al. 1994); regarding the bacterial component, to our knowledge, only 1 study reports on bacterial abundance (Bruni et al. 1993).

For their growth, bacteria can uptake only low molecular weight compounds able to cross the bacterial cytoplasmic membrane. This process requires the hydrolysis of large molecules that constitute the natural bulk of the dissolved organic matter (DOM). The preliminary hydrolysis of these molecules is known to
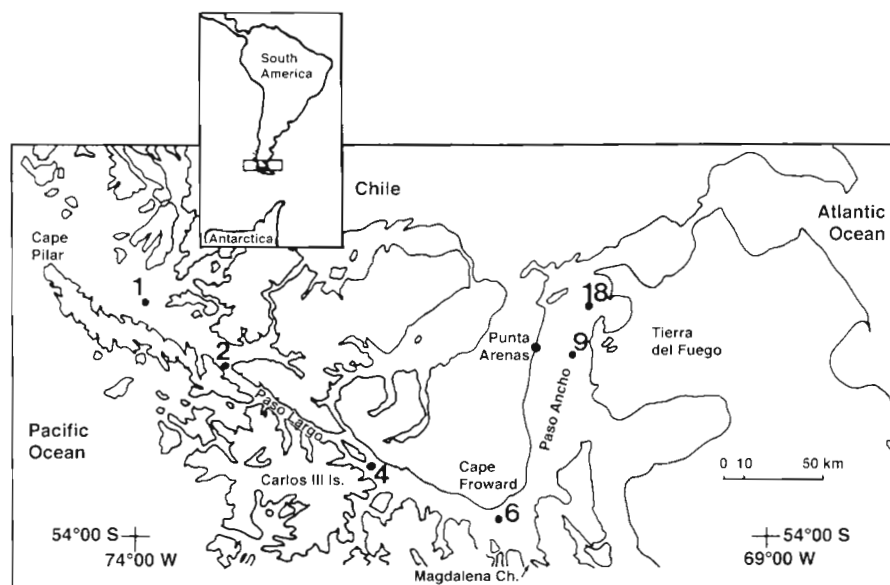
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Fig. 1. Location of the sampling stations in the Strait of Magellan

be a rate-limiting step for the growth of environmental bacteria (Chróst 1991a). Thus, studies of bacterial processes should include both bacterial production and hydrolytic activities in addition to the biomass determination (Hoppe et al. 1988). These 2 processes are under environmental control and, in return, can influence the functioning of the ecosystem (Chróst 1991b). Taking into account the 'bacterial paradox' described by Chróst (1991a), the relative fluctuation of bacterial secondary production, bacterial biomass and potential ectoproteolytic activity can provide informations on the environment under consideration.

A cruise was carried out in the Strait of Magellan on the RV 'Italica' toward the end of summer (25 March to 6 April 1995) within the framework of the Italian National Research Program in Antarctica (PNRA). The study was conducted along the Strait of Magellan from west to east in order to identify the possible influence of each ocean on the physical and biological characteristics of the investigated areas. In the present study we investigated the zone-specific relationships between bacterial parameters (i.e. bacterial abundance, production and ectoproteolytic activity) and physical and chemical features, at 6 sampling stations characterized by strong hydrological differences (Fig. 1). Moreover, to estimate the possible effect of tide on bacterial dynamics, repeated measurements were carried out at a station subject to strong tidal currents from the Atlantic Ocean.

MATERIAL AND METHODS

Location of stations and sampling. The western station (Stn 1) was located in the Pacific opening (Fig. 1).

Still on the Pacific Ocean side of the Strait, Stn 2 and Stn 4 were respectively located at the 2 extremities of the Paso Largo area, a narrow channel implying strong surface currents. Stn 6, located off Cape Froward (central part of the Strait of Magellan), was influenced by the Pacific waters reaching this area through the Magdalena Channel. Both Stns 9 and 18 were located in the Paso Ancho basin, the widest part of the Strait. Stn 9 was located in the central part of the Paso Ancho basin while Stn 18 was close to the exit of a channel connected to the Atlantic Ocean and characterized by strong tidal currents (Medeiros & Kjerfve 1988). Daily samplings over a period of 3 d were carried out at Stn 9 for the study of the tidal effects.

Samples were taken towards the end of summer (25 March to 6 April 1995) by using a General Oceanic rosette equipped with a set of 24 Niskin bottles. Sampling depths ranged betwen surface and 755 m. Measurements of enzymatic activity and bacterial production were performed at *in situ* temperature (8 ± 1°C) within 1 h after sampling.

Bacterial abundance and bacterial biomass. Immediately after sampling, 50 ml of seawater was preserved with 0.22 µm pore size filtered buffered formalin (2% final concentration). In order to prevent reduction of counts due to storage (Turley 1993, Gundersen et al. 1996), slides were prepared aboard the research vessel within 4 h after sampling. Cells were collected onto a 25 mm diameter black polycarbonate Nuclepore membrane (0.2 µm pore size) and stained with DAPI (4',6-diamidino-2-phenylindole) (Porter & Feig 1980). Slides were kept at −20°C until they were counted. Forty random fields per slide were counted with an Olympus BHA epifluorescence microscope coupled to an image analysis system (Van Wambeke

1988). Bacterial numbers were converted to carbon equivalents by using a conversion factor of 20 fg C cell^{-1} (Lee & Fuhrman 1987).

Bacterial production. Bacterial secondary production (BSP) was determined by the L-[4,5 ^{3}H]-leucine incorporation method (Kirchman et al. 1985), using a cold trichloroacetic acid (TCA) treatment followed by a cold ethanol wash step (Wicks & Robarts 1988). Triplicate water samples of 40 ml, including 1 TCA-killed blank, were incubated with 3 nM of L-[4,5 ^{3}H]-leucine (Amersham, 131 Ci mmol^{-1}) and 30 nM of unlabelled leucine (Sigma) for 2 h. Previous experiments indicated that this concentration (33 nM of total added leucine) was sufficient to obtain maximum uptake rates. Incubations were stopped by the addition of TCA to a final concentration of 5%. The samples were filtered onto 0.22 μm cellulose acetate filters, rinsed 4 times with 3 ml of ice-cold 5% TCA and twice with 2 ml of ice-cold 80% ethanol. The dried filters were then placed in scintillation vials and dissolved with 1 ml of ethyl acetate. Then, 5 ml of scintillation cocktail (PCS, Amersham) was added to each vial and radioactivity was determined on board using a Packard 1600 Tr liquid scintillation counter Quenching was corrected by external standards. L-[4,5 ^{3}H]-leucine incorporation was converted into bacterial net carbon production by an empirical conversion factor of 3.0 kg C mol^{-1} (Simon & Azam 1989, Bjørnsen & Kuparinen 1991).

Ectoproteolytic activity. The potential ectoproteolytic activity (PEA) was estimated by measuring the hydrolysis rate of L-leucine 7-amido-4-methyl coumarin (leu-MCA; Sigma), which competes well with easily degradable natural peptides (Chróst 1991b). Three 20 ml subsamples (2 replicates and 1 autoclaved control) were used per sample. The leu-MCA, dissolved in ethylene glycol monomethyl ether, was added to a 200 μM final concentration (experimentally verified saturated concentration). Upon hydrolysis, the leu-MCA releases the highly fluorescent product 7-amido-4-methyl coumarin (MCA) (Hoppe et al. 1988). The increase in fluorescence with time was monitored over 2 h using a Hoefer TKO 100 fluorometer (excitation: 365 nm; emission: 460 nm) The average difference between the 2 replicates was less than 10%. A standard curve was obtained with a range of MCA concentrations.

RESULTS

By considering the surface (0 to 50 m) layer of the water column, both the BSP and the PEA showed the highest values at the western station (Stn 1; BSP 228.2 ng C l^{-1} h^{-1}; PEA: 12.2 nmol l^{-1} h^{-1}), while the lowest values were typical of the central part of the Strait (Stn 6; BSP: 32.6 ng C l^{-1} h^{-1}; PEA: 4.6 nmol l^{-1} h^{-1}) (Table 1). In the Paso Ancho basin, intermediate values were recorded for BSP (80.1 and 88.7 ng C l^{-1} h^{-1}, Stns 9 and 18 respectively), whereas values for PEA were similar to Stn 1 (11.7 nmol l^{-1} h^{-1}, Stn 9).

At all of the stations except Stn 18, BSP and PEA showed similar vertical profiles, characterized by decreasing values of activity from the surface to the deeper layers (Fig 2). At the shallow Stn 18, the maximum value was measured in the deepest layers (50 and 80 m), probably because of a positive stimulation by the sediment on bacterial activities (Fig. 2). The BSP and the PEA vertical profiles were closely parallel and showed a high positive correlation (r = 0.88, p < 0.001, n = 51) (Table 2). This coupling between ectoproteolytic activity and bacterial production is expected to increase the efficiency of organic matter utilization by bacteria in aquatic ecosystems (Somville & Billen 1983, Chróst 1991a). The BSP values were also closely correlated to chlorophyll a (chl a) concentrations (r = 0.84, p < 0.001, n = 51). The phytoplanktonic biomass was calculated by applying a C to chl a ratio of 50 (Redalje 1983) to chl a data measured during the same cruise by Carrada et al. (1996). Chl a concentrations were also correlated with PEA, and inversely correlated with the concentrations of monomeric compounds, i.e. total free amino-acids (TFAA) (Table 2). On one hand, chl a is a good indicator of the phytoplanktonic biomass, and on the other hand, most of the organic compounds produced by phytoplankton have a polymeric structure, thus, the relations

Table 1 Maximum surface or subsurface values of different parameters. Data for Stn 9 are the mean of 3 samplings in different tidal conditions (data in parentheses are the extreme values). BSP: bacterial secondary production; PEA: potential ectoproteolytic activity; BA: bacterial abundance; GR: growth rate

Stn	BSP (ng C l^{-1} h^{-1})	PEA (nmol l^{-1} h^{-1})	BA (10^5 cells ml^{-1})	GR (d^{-1})	PEA/BSP[b]
1	228.2	12.2	14.3	0.19	3.8
2	54.0	10.3	7.1	0.09	13.7
4	57.4	11.8	5.8	0.12	14.8
6	32.6	4.6	10.5	0.04	10.2
9	80.1 (77 4–83.7)	11.7 (9.6–15.6)	9.7 (8.1–15.3)	0.13 (0.10–0.17)	10.5 (8.3–13.6)
18	88.7	8.2	13.0	0.08 (0.22[a])	6.6

[a]For the deepest sample (80 m)
[b]For the ratio calculation, PEA are expressed in the same units as BSP, ng C l^{-1} h^{-1}, assuming 1 molecule of leucine is released from each enzymatic cleavage
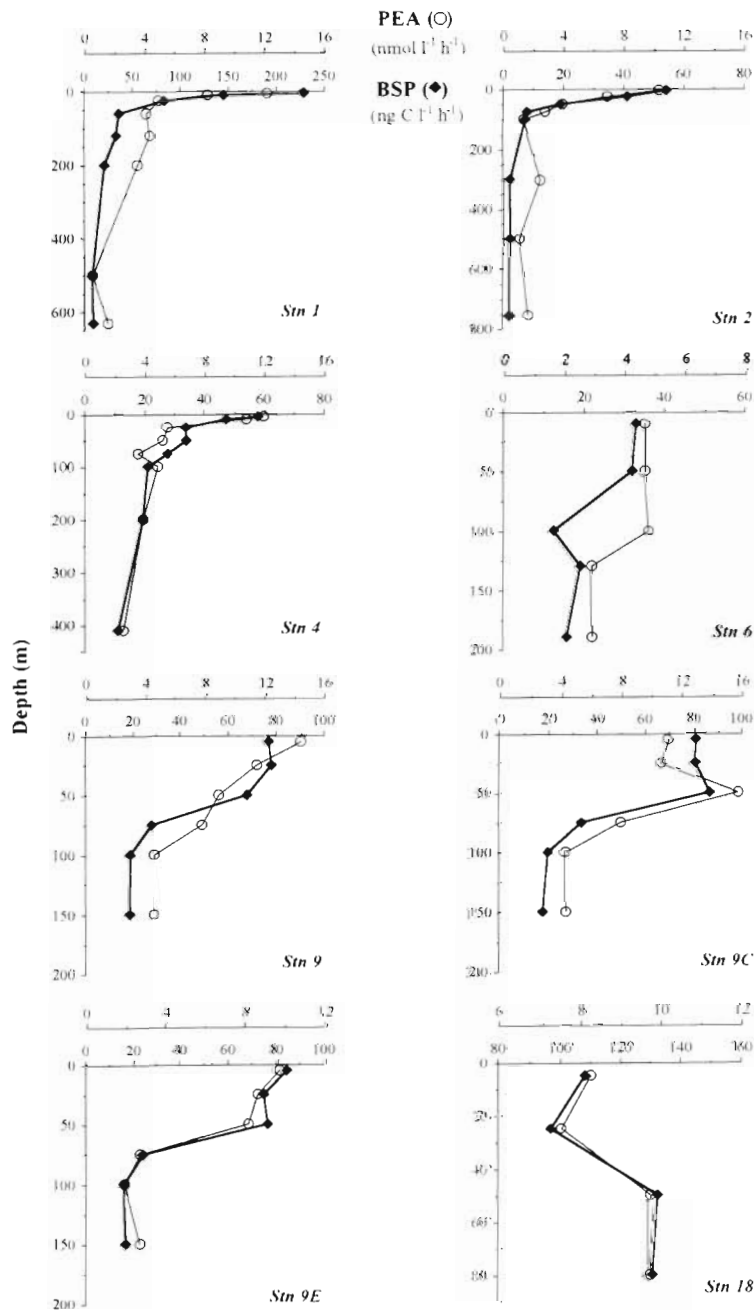
Fig. 2. Depth distributions of bacterial secondary production (BSP) and potential ectoproteolytic activity (PEA). Stns 9, 9C and 9E: conditions of low tide, high tide, and mid-tide respectively

10^5 cells ml^{-1}). As for the rates of bacterial activities, bacterial numbers decreased with increasing depth (Fig. 3) Because of the different patterns of vertical distributions of BSP, PEA and bacterial abundance at the different stations, integrated values were calculated for a 0 to 50 m depth layer (Fig. 4). The maximum values of integrated BSP were found in the Paso Ancho basin (3.89 and 4.84 mg C m^{-2} h^{-1} for Stns 9 and 18 respectively) and in the Pacific opening (5.22 mg C m^{-2} h^{-1}, Stn 1). Between these 2 extremities of the studied zone, lower BSP rates were observed in the Paso Largo area (Stns 2 and 4) and in the central part of the Strait, near Cape Froward (Stn 6). Bacterial biomass had similar spatial distributions, except at Stn 6, which showed a higher abundance of bacteria than in the other stations of the central area (Fig. 4). The distribution patterns of integrated PEA and BSP did not show a co-geographical distribution at all the stations. High PEA was concomitant with high BSP in the Paso Ancho basin (Stns 9 and 18), whereas at the Pacific border (Stn 1) low PEA and high BSP were simultaneously recorded (Fig. 4). For this period of the austral summer, the bacterial biomass at Stns 1 and 6, estimated using a conversion factor of 20 fg C cell^{-1} (Lee & Fuhrman 1987), exceeded the phytoplanktonic biomass (from Carrada et al. 1996) (Fig. 4).

Bacterial abundances, BSP and PEA were measured in high, low and mid-tide conditions at Stn 9 in the Paso Ancho basin (Fig 5), where tides of very high amplitude were recorded by Medeiros & Kjervfe (1988) and Michelato et al. (1991). Whatever the tide conditions, the salinity and temperature profiles (G. Budillon pers. comm.) as well as profiles of BSP (Fig. 5) were similar The profiles of bacterial abundance and PEA demonstrated variations with time, but they could not be related to the tide. The peripheric circulation of currents around the Paso Ancho basin (data from current meters deployed during the cruise; G. Budillon pers. comm.) may explain the weak influence of tidal currents on physical, chemical and bacteriological parameters at Stn 9. Further investigations with several tidal cycles covering a wider area of study need to be undertaken to better define the possible influence of the tide on the functioning of the ecosystem.

between chl a and bacterial enzymatic activity were easily understandable (Lancelot & Billen 1984, Fuhrman et al. 1985, Chróst et al. 1989).

The distributions of bacterial densities in the surface layers were similar to those observed for BSP and PEA at all stations (Fig. 3). The highest bacterial counts were measured at both extremities of the Strait (Stn 1 14.3 × 10^5 cells ml^{-1}, maximum value, and Stn 18: 13.0 ×

Table 2. Spearman's rank correlation between different parameters. Correlation coefficients (Spearman's rhos) shown, with n = 51 (excepted correlation with TFAA and TOC, n = 37) and $\cdots$p < 0.001, $\cdot\cdot$p < 0.01, $\cdot$p < 0.1 BSP: bacterial secondary production; PEA: potential ectoproteolytic activity; BA: bacterial abundance; TOC: total organic carbon; POC: particulate organic carbon; TFAA: total free amino-acids; Sal: salinity. TOC and TFAA values from R. Sempéré et al. (unpubl.). POC values from Povero et al. (1996)

	BSP	PEA	BA	TOC	POC	TFAA	Chl a
PEA	0.88$\cdots$						
BA	0.74$\cdots$	0.66$\cdots$					
TOC	0.32$\cdot$	0.54$\cdot\cdot$	0.46$\cdot\cdot$				
POC	0.91$\cdots$	0.86$\cdots$	0.70$\cdots$	0.36$\cdot$			
TFAA	-0.01	-0.14	0.14	0.15	-0.08		
Chl a	0.84$\cdots$	0.80$\cdots$	0.65$\cdots$	0.38$\cdot$	0.90$\cdots$	-0.40$\cdot$	
Sal	-0.85$\cdots$	-0.80$\cdots$	-0.80$\cdots$	-0.59$\cdot\cdot$	0.82$\cdots$	-0.07	-0.77$\cdots$

DISCUSSION

Proceeding eastwards from the Pacific entrance of the Strait of Magellan, in the 3 subsystems identified by land and sea forcing factors, the bacterial populations displayed specific characteristics: (1) the zone of the Pacific opening (Stn 1) with, in surface water, high bacterial abundance and production but with relatively low ectoproteolytic activity; (2) the Paso Largo/Cape Froward zone (Stns 2, 4 and 6) with low bacterial abundance and

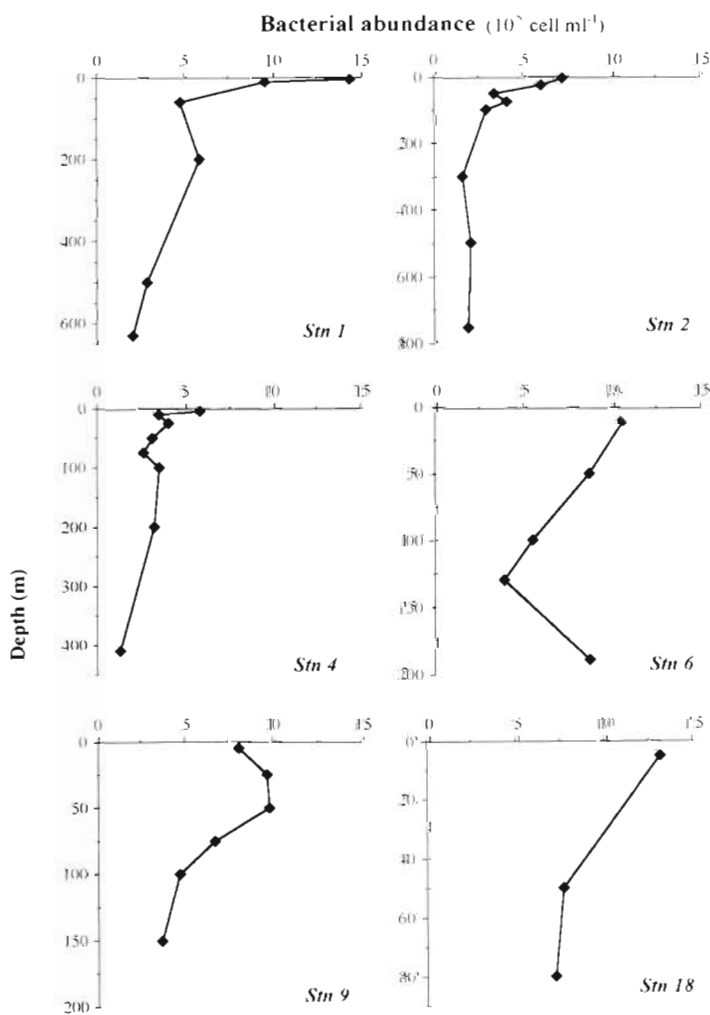
Fig. 3. Depth distributions of bacterial abundances. Values for Stn 9 are mean of 3 samplings in different tidal conditions
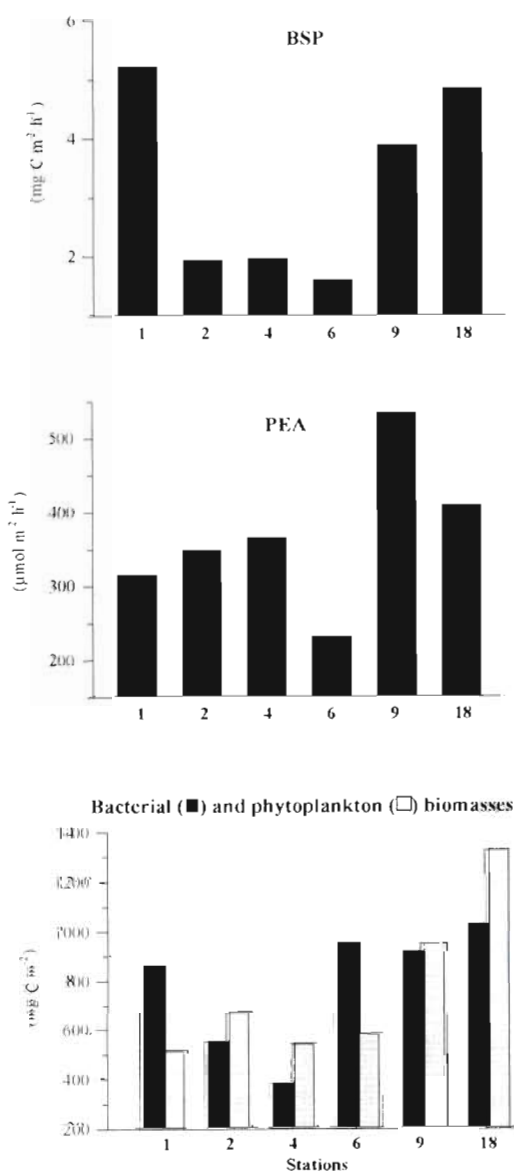

Fig. 4. Spatial distributions of integrated values of BSP, PEA, and bacterial biomass and phytoplankton biomass (values are integrated for 0 to 50 m layer)
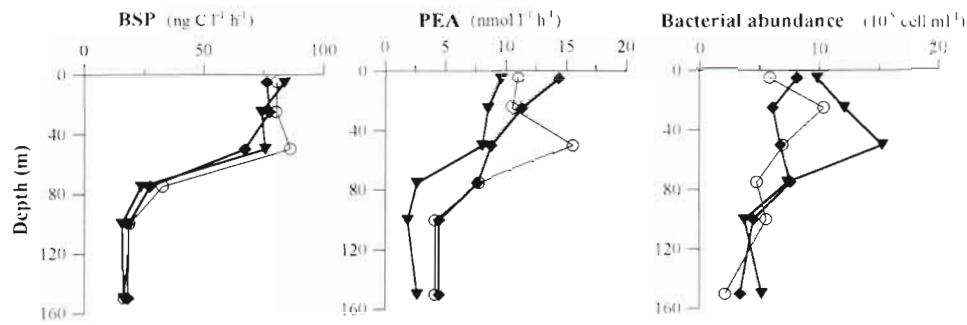
Fig. 5. Depth distributions of BSP, PEA and bacterial abundance at Stn 9 in low tide (◆), high tide (O) and mid-tide (▼) conditions

activities; (3) the Paso Ancho zone (Stns 9 and 18) with high bacterial abundance and activities.

At the Pacific opening, the high negative correlations between salinity and other parameters (Table 2) indicated a strong influence of freshwater inputs. At Stn 1, a drastic drop of bacterial and chemical parameter values was correlated with a sharp halocline from 27.3 in surface water to 33.2 at 150 m (G. Budillon pers. comm.) (Fig. 6a). According to Panella et al. (1991), the superficial freshwater originated from heavy rainfalls, characteristic of the western part of the Strait (maximum of 5090 mm yr^{-1}; Pickard 1971), and from the ice-edge of the Andean glaciers. Previous studies in this sector demonstrated that freshwater run-off could supply degradable pigments (Saggiomo et al. 1994). Probably due to these freshwater enrichment effects, the water column of Stn 1 was characterized by the largest organic fraction of total particulate matter (98%; Povero et al. 1996, data from the same cruise), by the highest concentration of total free amino-acids (TFAA) and by a clear decrease of total organic carbon (TOC) from 1.21 mg l^{-1} in surface water to 0.84 mg l^{-1} at 120 m depth (R. Sempere et al. unpubl.). Concomitantly, high BSP was coupled with relatively low PEA values. These chemical and biological characteristics could reflect the presence of an organic matter bulk which had already undergone the first steps (ectoenzyme hydrolysis) of degradation. The dominance of bacterial over phytoplanktonic biomass (Fig. 4) is usually characteristic of oligotrophic conditions (Simon et al. 1992), meanwhile in this Pacific opening area, such a ratio is due to the extra supply of organic matter by freshwater inputs favouring heterotrophic processes.

At the Pacific opening, the bacterial production was 3 times higher than in the central area (Paso Ancho), while the PEA values were similar both at the Pacific opening and in the Paso Ancho area. The high variability of the PEA to BSP ratio for the surface samples from the different stations may show the relative importance of each step involved in the bacterial process of degradation of the organic matter bulk, i.e. ectoenzymatic hydrolysis of polymers—uptake of monomers—bacterial production, along the Strait. At the Pacific opening,

a PEA to BSP ratio of 3.8 was 2 to 4 times lower than those measured at the other stations (Table 1), demonstrating a relatively low ectoenzymatic activity. At the same time, the highest growth rate (0.19 d^{-1}) for bacterial population was recorded in this area (Table 1). Most of the ectoenzymes produced by bacteria are inducible catabolic enzymes, whose synthesis is under the control of the repression/induction mechanism and therefore strongly correlated to the influx of polymeric com-
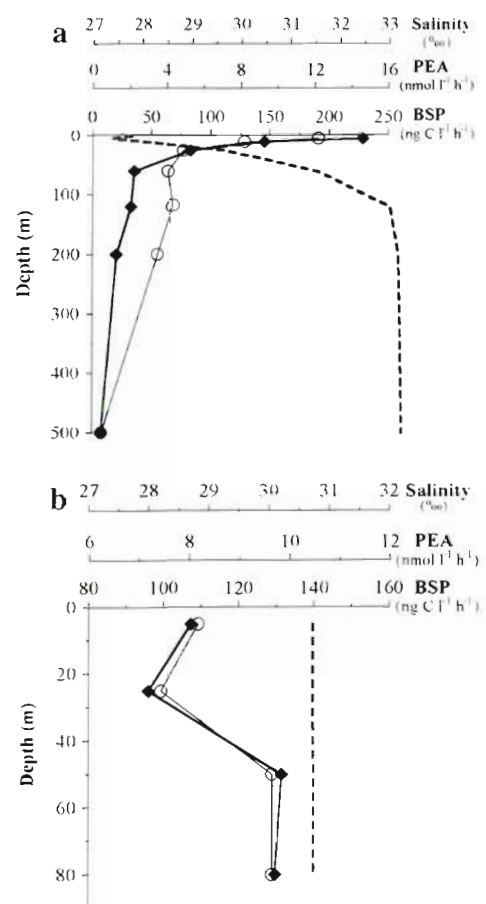

Fig. 6. Depth distributions of BSP (◆), PEA (O) and salinity (----) (G. Budillon pers. comm.) (a) at the Pacific opening (Stn 1), (b) at the Atlantic opening (Stn 18)

pounds, and/or to the availability of readily utilizable organic matter (Chróst 1990). Münster (1991) showed that high PEA is correlated with low dissolved free amino-acid concentrations. In our study, the highest concentration of TFAA was measured in the surface waters of Stn 1 located on the Pacific side of the Strait (192 nM; R. Sempéré et al. unpubl.). Consequently, due to this high concentration of readily utilizable nutrients, there was no need for an enhanced ectoenzyme synthesis. The low PEA combined with the high BSP measured in this Pacific area were in accordance with the environmental parameters describing organic matter which has already undergone the early stage of mineralization (i.e. the hydrolysis step), or which was originally rich in monomeric organic compounds available for bacterial growth.

Although BSP and PEA were positively correlated with bacterial abundance (Table 2), the PEA to BSP ratio was negatively correlated with bacterial abundance ($r = -0.72$, $p < 0.001$, $n = 22$) (Fig. 7). Several mechanisms could be involved to explain this negative correlation. (1) There is a lack of knowledge concerning the proportion of 'active' bacteria in natural communities (Grossman 1994, Zweifel & Hagström 1995, Bianchi & Giuliano 1996, Lovejoy et al. 1996); (2) it remains to be shown whether ectoenzymatic activity and BSP are mediated by the same organisms; (3) a low bacterial abundance may result either from a low substrate availability or a high predation pressure; and (4) if bacteria are commonly considered to be responsible for ectoenzymatic activity (Hoppe 1983, Vives-Rego et al. 1985), recent studies suggest a possible role of protozoa due to their grazing activity on bacteria (Karner et al. 1994, Karner & Rassoulzadegan 1995). In fact, a high proportion of free ectoenzymes could be the by-product of bacterial mortality due to protozoa grazing and thus explain the inverse relationship between the PEA to BSP ratio and bacterial abundance.

Another explanation for low bacterial abundance could be a limitation by resources. When easily utilizable monomers are lacking, ectoenzymatic hydrolytic processes could be favoured in order to increase the utilization of available substrates at the expense of growth processes. From a physiological point of view, energy used for bacterial metabolism would be monopolized for ectoenzyme synthesis rather than for cell production. Thus, to bypass the substrate limitation, bacteria would produce ectoenzymes at a higher rate, as suggested by Chróst & Rai (1993). After all, the correlation observed between bacterial abundance and PEA to BSP ratio could be specific of the peculiar conditions encountered in the Strait of Magellan (i.e. freshwater inputs). Thus, a concomitance of a high bacterial abundance and a low PEA relative to BSP
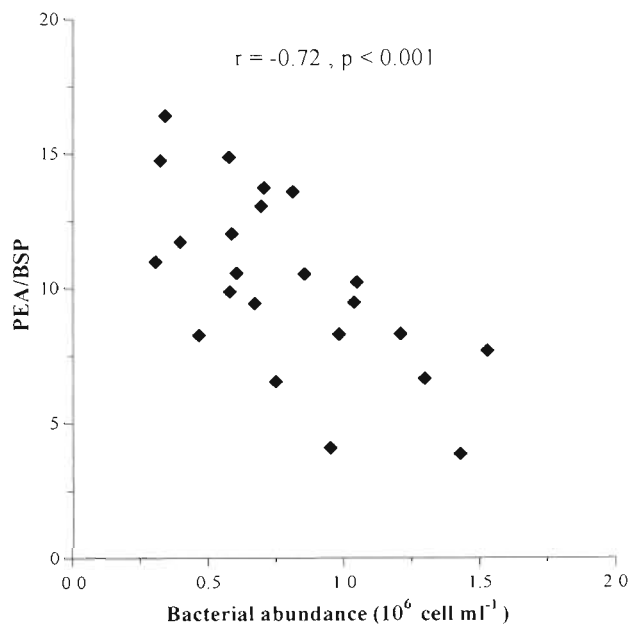

Fig. 7 Plot of potential ectoproteolytic activity to bacterial secondary production ratio (PEA/BSP) vs bacteria abundance in the euphotic zone

could be explained by the different mixture of organic matter sources. Consequently, the PEA to BSP ratio, as directly correlated with the bacterial abundance, appeared to be a reliable indicator of the trophic conditions in the different areas of the Strait.

The Paso Largo and Cape Froward zones (Stns 2, 4 and 6) presented similar integrated BSP, lower than those of neighbouring zones (Fig. 4). In spite of these low rates of bacterial production and ectoproteolytic activity, the central part of the Strait of Magellan (Stn 6) was characterized by a bacterial biomass 2 times greater than the phytoplanktonic biomass, demonstrating an oligotrophic trend in comparison with other studied stations (Cho & Azam 1990, Simon et al. 1992) (Fig. 4). Indeed, this section of the Strait has been shown to be oligotrophic, probably because of specific hydrological features (Saggiomo et al. 1994, Saggiomo pers. comm. for the present cruise). This area is submitted to strong vertical mixing connected with the tidal front of the eastern area inducing a homogeneous physical and chemical structure of the water column (G. Budillon pers. comm.). Moreover, the presence of the Carlos III Island sill, in the western boundary of this area, prevents the entrance of enriched waters from the Pacific opening (Medeiros & Kjerfve 1988, Mazzocchi et al. 1995, G. Budillon pers. comm.). The bacterial abundance and bacterial growth rate of this central area were also the lowest values in the Strait (Table 1, Fig. 3), except Stn 6 displaying high bacterial abundances at 190 m depth. Such increased

bacterial abundance did not correspond to any increase of bacterial activities. At Stn 6, a warmer and more salted water current was identified at the same depth (190 m) as incoming Pacific waters through the Magdalena channel (Artegiani & Paschini 1991, Saggiomo et al. 1994, G. Budillon pers. comm.).

The Paso Ancho basin (Stns 9 and 18) demonstrated eutrophic features, as already described by high chl *a* concentrations (2 mg m^{-3}), high primary production values (6 mg C m^{-3} h^{-1}) (Magazzu et al. 1991, Saggiomo et al. 1994) and the highest particulate organic carbon concentrations of the Strait, i.e. 150 μg l^{-1} at Stn 9 (Fabiano et al. 1991, Povero et al. 1996). Bacterial activities and biomass were also highest (Fig. 4). In contrast to the classical vertical profiles of bacterial activities in the Strait of Magellan, Stn 18, in the northern part of the Paso Ancho basin, showed the highest values of BSP and PEA in the deepest samples. Due to the shallow bottom (82 m), its location at the vicinity of a channel opening to the Atlantic Ocean and the resulting strong tidal currents (up to 4.5 m s^{-1}; Medeiros & Kjerfve 1988), Stn 18 showed a mixed water column confirmed by the homogenous vertical distributions of salinity (Fig. 6b). Sediment resuspension due to tidal currents could be an intermittent source of inorganic nutrients and organic matter for the microbial communities of the water column (Rowe et al. 1975), and could provoke strong ectoenzymatic bacterial activities (Chróst & Riemann 1994).

Table 3 shows that bacterial abundances and BSP values measured in the Strait of Magellan were higher than those from the Weddell Sea, collected during the same season of study (Cota et al. 1990), and from a subantarctic zone (SAZ), approximately at the same latitude (45° to 52° S), in the Indian sector of the Southern Ocean (Talbot 1995, Moriarty et al. 1997, Talbot & Bianchi 1997) or other regions of the Southern Ocean (Cota et al. 1990, Ducklow & Carlson 1992). With values of bacterial densities exceeding 10^6 cells ml^{-1}, the

waters of the Strait of Magellan appear closer to temperate or tropical offshore, or even coastal, than to Antarctic waters (Cho & Azam 1990, Cho et al. 1994, Caron et al. 1995).

High values of BSP (e.g. 279 nmol C l^{-1} h^{-1}) were recorded in the oligotrophic Southern Ocean, near the ice-edge (Gillespie et al. 1976, Hanson et al. 1983, Cota et al. 1990, Sullivan et al. 1990). Such values are of the same order as those we measured in the superficial waters of Stn 1 (228 nmol C l^{-1} h^{-1}). Several studies in the Southern Ocean have shown that the melting ice may seed the water column by releasing DOM and nanoplankton and thus, the ice-edge system constitutes an important area for enhanced bacterial activity (Ackley et al. 1979, Smith & Clement 1990, Talbot 1995). Similar favourable mechanisms could be considered for the Pacific opening of the Strait of Magellan (Stn 1), characterized by low salinity and high bacterial activity. In contrast with bacterial abundance and production values discussed above, all PEA values from coastal subantarctic areas were surprisingly similar to those measured in oligotrophic open ocean areas (Table 3). The values of PEA we measured in the Strait (4.5 to 15.6 nmol l^{-1} h^{-1}) were equivalent to those observed by Christian & Karl (1995) during several cruises in the Southern Ocean (mean of 10.8 nmol l^{-1} h^{-1}) and by Talbot (1995) in a subantarctic zone (5.9 to 16.1 nmol l^{-1} h^{-1}). The higher PEA activities (21 to 78 nmol l^{-1} h^{-1}) found in the same subantarctic zone by Talbot & Bianchi (1997) could be explained by a seasonal variation (March and May respectively).

Due to the lack of studies on bacterial activities concerning the coastal ecosystems of subantarctic zones, our nearshore data are compared to offshore data. We have to keep in mind that nearshore marine environments are expected to receive significant inputs of allochthonous organic matter. Nevertheless, by showing similar PEA rates, the waters of the Strait of Magellan seem to be weakly influenced by terrestrial poly-

Table 3. Estimates of bacterial abundance (BA), secondary production (BSP), growth rate (GR) and potential ectoproteolytic activity (PEA). Values are given as the ranges of observations for the euphotic zone or for depth <100 m. nd: no data. SAZ: subantarctic zone

Site and time	BA (10^5 cells ml^{-1})	BSP (ng C l^{-1} h^{-1})	GR (d^{-1})	PEA (nmol l^{-1} h^{-1})	Source
Indian Ocean Sector SAZ (45° to 52° S)					
March	4–6	10–21	0.02–0.05	6–16	Talbot (1995)
May	3–6	1–4.3	0.002–0.01	21–78	Moriarty et al. (1997), Talbot & Bianchi (1997)
Weddell Sea					
March	0.1–6	2–279	0.04–1.8	nd	Cota et al. (1990)
Strait of Magellan					
March	3–15	33–228	0.04–0.19	5–16	This study

meric organic matter inputs but strongly influenced by freshwater inputs rich in monomeric compounds enhancing the bacterial growth.

In conclusion, specific sets of bacterial parameters could be described for each of the 3 subsystems identified in the Strait of Magellan. The zone of the Pacific opening receiving freshwater inputs via rainfalls and melting of the ice-edge of glaciers showed high bacterial abundances in surface water, leading to a bacterial to phytoplanktonic biomass ratio higher than 1 The low ectoproteolytic activity associated with the bacteria of this area was probably a consequence of the nature of the external organic matter inputs. In the central part of the Strait, the Paso Largo/Cape Froward zone, bacterial parameters had the lowest values of this study, and the bacterial to phytoplanktonic biomass ratio was greater than 1, suggesting an oligotrophic trend in this area. The eastern side, corresponding to the Atlantic opening, was the Paso Ancho zone. In this shallow area, under the influence of strong tide currents, the highest values of bacterial parameters were measured. The ratio of bacterial to phytoplanktonic biomass was less than 1.

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