Space utilisation patterns of bryozoans on the Patagonian scallop *Psychrochlamys patagonica*

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SUMMARY: We studied the bryozoan assemblage encrusting valves of the Patagonian scallop, *Psychrochlamys patagonica*, in 4 beds distributed along the continental shelf off Argentina to analyse (a) the distribution pattern of bryozoan colonies in different zones of the valves, (b) the influence of interspecific competition on assemblage composition, (c) whether encrusting species display different space utilisation strategies, and (d) whether bryozoan species richness and number of colonies vary in relation to host size. The assemblage was composed of 22 taxa and was dominated by *Arachnopusia monoceros* and *Osthimosia eatonensis*, which were at least one order of magnitude more abundant than any other species. Multivariate analyses based on coverage data of multiserial bryozoans separated the beds according to species richness rather than to geographic proximity and showed significant differences in assemblage structure between upper (left) and lower (right) valves and among beds. Competitive interactions occurred almost exclusively on lower valves, and more frequently in peripheral zones than in central zones of these valves. Correlations between valve area and number of bryozoan colonies, coverage and species richness were low but significant. Bryozoans were significantly more frequent, larger, and taxonomically diverse on lower valves than on upper valves. The uniserial colonies of *Neothoa* cf. *chiloensis*, the weakest bryozoan competitor, were as frequent in central zones as they were in peripheral zones, and usually spread out along channels on the scallop surface. This fugitive species was partially covered by multiserial colonies, but managed to persist even in peripheral areas of the lower valves.

Keywords: Bryozoa, Patagonian scallop, *Psychrochlamys patagonica*, interspecific competition, space utilisation patterns, Patagonian shelf, SW Atlantic.

RESUMEN: PATRONES DE UTILIZACIÓN DEL ESPACIO EN BRIOZOOS EPIBIONTES DE LA VIEIRA PATAGÓNICA *PSYCHROCHLAMYS PATAGONICA*. – Se estudiaron los briozoos que incrustan las valvas de *Psychrochlamys patagonica* en 4 bancos de la plataforma continental argentina para analizar su distribución sobre distintas zonas de las valvas, la influencia de la competencia interespecífica sobre la composición de la asociación, si las especies incrustantes exhiben distintas estrategias de utilización del espacio y si la riqueza específica y abundancia varían en relación al tamaño del huesped. Entre los 22 taxa presentes, *Arachnopusia monoceros* y *Osthimosia eatonensis* fueron al menos un orden de magnitud más abundantes que las demás especies. Análisis multivariantes basados en datos de cobertura de briozoos multiseriales separaron a los bancos por su riqueza específica más que por su proximidad geográfica y demostraron diferencias significativas en la estructura de las asociaciones entre valvas superiores (izquierdas) e inferiores (derechas) y entre bancos. Las interacciones competitivas ocurrieron casi exclusivamente sobre valvas inferiores y más frecuentemente en la periferia que en el centro. Las correlaciones entre el área de las valvas y el número de colonias, cobertura y riqueza específica de briozoos fueron bajas pero significativas. Los briozoos fueron más frecuentes, más grandes y más diversificados en las valvas inferiores que en las superiores. Las colonias uniseriales de *Neothoa* cf. *chiloensis*, el competidor más débil, fueron tan frecuentes en la zona central como en la periferia, extendiéndose a lo largo de los canales en la superficie de las valvas. Esta especie fugitiva resulta parcialmente cubierta por los briozoos multiseriales, pero logra persistir hasta en la periferia de las valvas inferiores.

Palabras clave: Bryozoa, vieira patagónica, *Psychrochlamys patagonica*, competencia interespecífica, patrones de utilización del espacio, plataforma patagónica, Atlántico Sudoccidental.

INTRODUCTION

Bivalve shells can be regarded as small habitat-islands (Ward and Thorpe, 1991) because they are discrete pieces of substratum isolated from the neighbouring environment and often represent the only hard surfaces available for prospecting larvae of sessile organisms. Analysing the distribution of sessile species on shells may provide useful insights for the paleoecological reconstruction of the life habit and orientation of the host (e.g. Villamil *et al.*, 1998).

Epifaunas dominated by bryozoans have existed since Paleozoic times (Taylor and Wilson, 2003) and despite the differences in taxonomic composition between fossil and recent biotas, the way in which species used and competed for substratum seems essentially the same as today (Taylor, 1984). Subtidal bryozoan assemblages that encrust hard substrata are often composed of a variety of species competing for space (López Gappa, 1989; Ward and Thorpe, 1989, 1991; Barnes and Clarke, 1995, 1998; Barnes and Rothery, 1996; Barnes *et al.*, 1996; Barnes and Dick, 2000; Barnes and Lehane, 2001) and food (Buss 1980a; Okamura *et al.*, 2001). Competitive interactions have been regarded either as highly deterministic, i.e. constituting clear hierarchies (Barnes and Rothery, 1996; Barnes and Arnold, 2001; Barnes and Lehane, 2001), or as intransitive networks characterised by a high proportion of reversals or stand-offs with none of the species able to monopolise the space (Buss and Jackson, 1979; Buss, 1980b; Russ, 1982).

Solitary and colonial organisms have different capacities of using space (Jackson, 1977). While both are able to select their habitat during settlement, only colonial animals exhibit directional growth towards more favourable refuges on the substratum (Buss, 1979). Sessile animals display several morphological strategies that enable them to pre-empt space and to cope with overgrowth competition (Jackson, 1979). Runners are more or less encrusting, linear or branching forms that lie parallel to the substratum, while sheets and mounds are two- or three-dimensional encrustations often completely attached to the substratum. Runners are entirely committed to a fugitive strategy, while sheets and mounds are committed to survival within and around their areas of settlement and to maintaining the integrity of their colony surfaces (Jackson, 1979).

The Patagonian scallop, *Psychrochlamys patagonica* (= *Zygochlamys patagonica*, see Jonkers,

2003), is distributed around the southern tip of South America from 42ºS in the Pacific to 35ºS in the Atlantic (Waloszek, 1991). Catches in the order of 50000 t yr^{-1} rank this species among the most important scallop fisheries in the world (Ciocco *et al.*, 2006). Scallop beds in the south-west Atlantic are mainly found along the 100-m depth isobath, where there are major frontal systems (Bogazzi *et al.*, 2005). The presence of a byssus in large individuals, and the considerable amount of epizoans (Waloszek and Waloszek, 1986; Waloszek, 1991; Sanfilippo, 1994; Schejter and Bremec, 2007) suggest that the mobility of this scallop is fairly low (Waloszek, 1991). *P. patagonica* lies on the substratum on its right valve (Rosso and Sanfilippo, 1991; Sanfilippo, 1994). The two valves are remarkably different: the left valve faces up in life position, it is convex and has many coloured ribs; the right (downward facing) valve is flatter and lighter in colour (Waloszek, 1991).

The role of *Psychrochlamys patagonica* as settlement substrate for different groups of benthic organisms has recently been analysed (López Gappa and Landoni, 2007; Schejter and Bremec, 2007). The frequency of occurrence of foraminifers, folliculinid ciliates, algae, sponges, hydrozoans, bryozoans, cirripedes, octocorals, bivalve molluscs, brachiopods, tunicates and serpulid, spirorbid and sabellarid polychaetes has already been quantified in several scallop beds along the continental shelf off Argentina (Schejter and Bremec, 2007). The encrusting sponge *Iophon proximum* is the most common and abundant epibiont on this pectinid (Schejter and Bremec, 2007). Other sessile groups are usually absent on sponge-covered scallops, which are significantly smaller than scallops without sponges (López Gappa and Landoni, 2007). Bryozoans, although frequently absent on scallops dominated by *I. proximum*, are one of the most common sessile groups, particularly in Patagonian beds (López Gappa and Landoni, 2007; Schejter and Bremec, 2007). Their abundance and interactions, however, have not yet been examined at lower taxonomic levels. Therefore, the aim of this study is to analyse (a) the distribution pattern of bryozoan colonies in different zones of the two valves of *Psychrochlamys patagonica*, (b) the influence of interspecific competition on assemblage composition, (c) whether encrusting species display different space utilisation strategies on the valves, and (d) whether bryozoan species richness and the number of colonies vary in relation to host size.

TABLE 1. – Basic data on the *Psychrochlamys patagonica* beds sampled by the F/V *Erin Bruce*, and number and size of the valves analysed in this study. Latitude and longitude in degrees, minutes and cables.

Bed	Latitude (S)	Longitude (W)	Depth (m)	Date	Number of valves analysed	Valve area $(cm^2, mean \pm SE)$
MDQ	38°50'52	54°33'85	105	28 June 1995	37	26.3 ± 1.05
San Blás	39°47'65	56°14'59	89	03 July 1995	53	25.9 ± 0.11
Valdés January	42°14'00	58°34'50	98	31 January 1995	100	27.0 ± 1.00
Valdés November	42°15'00	58°34'50	98	09 November 1995	100	30.5 ± 0.88
Tango B	42°32'81	59°15'71	96	18 April 1995	100	28.0 ± 0.61

MATERIALS AND METHODS

Samples of *Psychrochlamys patagonica* were collected along the continental shelf off Argentina by the scalloper F/V *Erin Bruce* (Table 1, Fig. 1). A complete description of the beds analysed in this study can be found in Lasta and Bremec (1998). Valdés bed was sampled twice, first in January 1995 and again in November 1995 (Table 1).

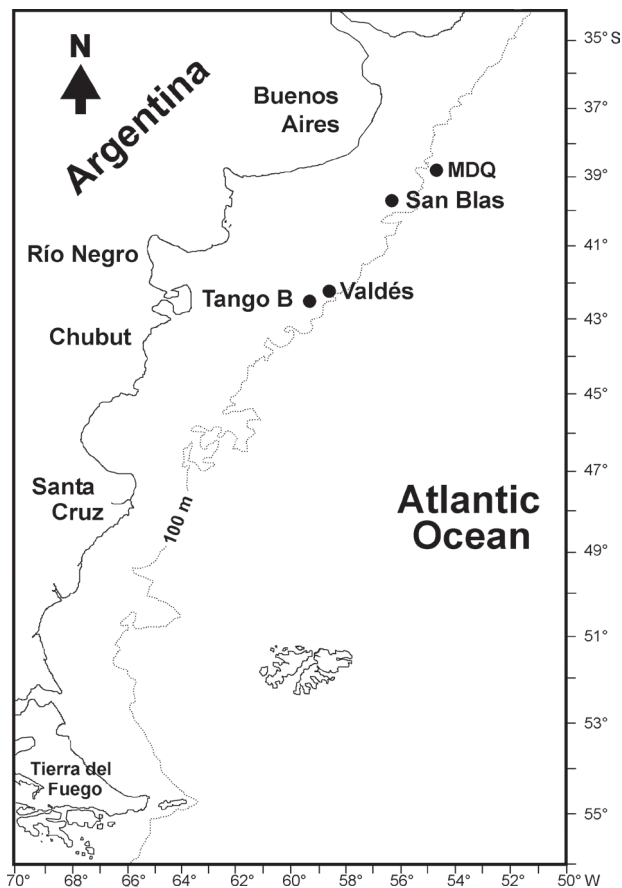The material was initially fixed in 10% formalin, and later transferred to 70% ethanol. Scallops

FIG. 1. – Distribution of *Psychrochlamys patagonica* beds sampled on the continental shelf off Argentina. The dotted line shows the 100 m isobath.

were alive at the time of collection, but since upper and lower valves were sometimes found separated from each other, they were all analysed individually. Broken valves whose length could not be measured were discarded. In beds where scallops were very abundant, 100 valves were randomly subsampled. Unrecognisable (i.e. eroded or highly fragmented) bryozoan colonies were not taken into account. Five bryozoan taxa were identified to genus or family level due to insufficient material or taxonomic difficulties.

Valve length (after Waloszek, 1984) was measured to the nearest 0.01 mm with a digital calliper. The position of each valve (i.e. whether they were left or right) was also recorded.

Valve area was estimated from length data after a regression analysis based on 48 valves (12 from each bed). The outline of each valve was traced on paper. Paper cuttings were weighed to the nearest 0.1 mg on an analytical balance, and then compared with the weight of a known area. The length-area relationship was calculated by fitting an exponential model (Area = a Length ^{b}), which resulted in the following equation:

$$Area = 1.6636 \, Length^{1.8145} \; (R^2 = 0.996, P<0.01)$$

The error was assessed by measuring the length of the same valve 10 times, and by drawing the contour of one valve 10 times on paper. Coefficients of variation for measuring length and area were 0.5% and 0.9% respectively. Areas calculated using this method may have been slightly underestimated due to the existence of channels and ribs on the valves.

A radius (R) that divided the valve into two zones of equal area was calculated in order to classify each colony as either growing in the central zone or in the peripheral zone. In the case of a circle, this radius is:

$$R \; central = (R \; peripheral^2 \, / \, 2)^{1/2}$$

This represents 35.4% of the valve length. Since scallops are not perfectly circular, a correction factor was calculated empirically in order to compensate the overestimation of the central zone. After analysing 10 valves, the excess of the central zone was found to be very small, and was compensated for by tracing a circle with a radius that represented 34.5% of the valve length.

Bryozoans with encrusting, multiserial colonies (sheets and mounds, see Jackson, 1979) were identified, their location recorded as central or peripheral, and their areas estimated by the method described above for *Psychrochlamys patagonica* valves, but in this case with the aid of a dissecting microscope fitted with a camera lucida. Colonies that spread across both the central and peripheral zones of a valve were assigned to the zone in which they were best represented. Species with runner-like (*Neothoa* cf. *chiloensis, Aetea ligulata*), or erect colonies (*Cellaria malvinensis, Menipea flagellifera, Notoplites elongatus* and *Caberea darwinii*) were just recorded as present or absent. Special attention was paid to avoid missing the tiny and translucent colonies of *Neothoa* cf. *chiloensis*.

Coverage data (cm²) were processed by multivariate analysis to compare bryozoan assemblage structure among beds. The basic data matrix (16 multiserial species x 5 samples, see Table 3) was square-root transformed to downweight the influence of dominant species. Cluster analysis using group-average linking was performed on a Bray-Curtis similarity matrix (Clarke and Warwick, 1994). The same analysis was repeated on a second matrix in which species coverage in each bed was partitioned between upper and lower valves. The null hypotheses of no differences in structure among beds and between upper and lower valves were tested by a two-way crossed ANOSIM (Clarke and Warwick, 1994), based on a data matrix of 16 species x 254 valves with bryozoans. The remaining 136 valves, without bryozoans, were not included in this analysis.

Interspecific encounters among different bryozoan taxa were recorded. Intraspecific competition was not analysed because a study on bryozoan overgrowth competition in the Magellan fauna showed that most encounters between colonies belonging to the same species resulted in redirection of growth towards free colony margins (López Gappa, 1989). The result of spatial competition was defined as: (a) overgrowth, when the elevation of the growing edge of a colony over another covered the aperture of zooids; or (b) tie

or cessation of growth, when a suture line was observed between two colonies and growth had been redirected towards their free margins. Based on previous studies (Barnes, 2002a and references therein), tied outcomes were interpreted as stable results and not as transitory phases. Since the number of encounters per valve was low, and no reversals were observed on the same valve, we counted the number of different types of encounters among species, not the actual number of encounters among colonies. The theoretical maximum of interspecific interactions (MI) among n species on each valve was calculated as:

$$MI = [n \ (n - 1)]/2$$

Statistical comparisons were performed by one-way ANOVAs after verifying the assumptions of normality (Kolmogorov-Smirnov's test; Sokal and Rohlf, 1981) and homogeneity of variances (Cochran's C test, Winer, 1971). In two instances, the Mann-Whitney non-parametric test was used instead of ANOVA when assumptions were not met after transformation (Sokal and Rohlf, 1981).

The relationships between valve size and bryozoan coverage, as well as the species richness and number of colonies were analysed with the Pearson's product-moment correlation coefficient.

Bryozoan frequencies between (1) left and right valves, (2) central and peripheral zones of the valve, and the number of wins and losses in interspecific encounters, were compared with the Yates-corrected chi-square test. Competitive interactions were only analysed statistically in 3 cases which involved the most frequent species (*Osthimosia eatonensis, Arachnopusia monoceros, Neothoa* cf. *chiloensis*). The low number of encounters recorded between pairs of rare species is also given in the interaction matrix (see Fig. 7), but was not used for statistical inference. Frequencies of *Neothoa* cf. *chiloensis* in the central and peripheral zones of the left and right valves were tested with the Fisher's exact test (Sokal and Rohlf, 1981).

RESULTS

The total number of colonies was significantly higher on lower valves than on upper valves [lower: 1029 (73.7%), upper: 368 (26.3%), chi-square, P<0.0001]. The numbers of bryozoan species and colonies per valve were significantly higher on
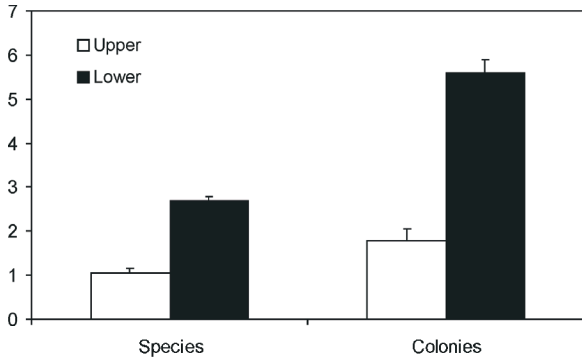
FIG. 2. – Number of bryozoan species and colonies per valve (mean + standard error) on upper and lower valves.

FIG. 3. – Colony area (mean + standard error) of multiserial encrusting bryozoans on central and peripheral zones of upper and lower valves.

lower valves compared to upper valves (Fig. 2, Mann-Whitney's U test, species: U = 9970, P<1 x 10^{-6}; colonies: U = 11212, P<1 x 10^{-6}).

The area of 1397 multiserial colonies was estimated. Mean colony area was significantly larger on lower valves compared to upper valves (ANOVA, lower: 0.37 cm², upper: 0.29 cm², df = 1, 1395, F = 39.6, P<1 x 10^{-6}).

The number of colonies was significantly higher in peripheral zones than in central zones of the valves [peripheral: 1113 (79.7%), central: 284 (20.3%), chi-square, P<0.0001]. If data are expressed as the percentage of available valve space occupied by multiserial colonies (summed up across all valves), it can be seen that bryozoan coverage was one order of magnitude higher in the peripheral zone of lower valves than elsewhere (upper-central: 1.72%, upper-peripheral: 2.13%, lower-central: 1.09%, lower-peripheral: 13.02%).

The area of multiserial colonies was also significantly larger in peripheral zones compared to central zones of both valves (ANOVA, peripheral: 0.35 cm², central: 0.27 cm², df = 1, 1395, F = 35.9, P<1 x 10^{-6}). However, when colony areas were compared separately on upper and lower valves it became evident that colonies were larger in peripheral zones than in central zones only on the lower valves, and not on the upper valves (ANOVA, upper valves: peripheral: 0.23 cm², central: 0.45 cm², df = 1, 366, F = 1.81, P = 0.18; lower valves: peripheral: 0.41 cm², central: 0.16 cm², df = 1, 1027, F = 31.5, P<1 x 10^{-6}; Fig. 3).

A maximum number of 8 bryozoan species per valve was observed. Bryozoan coverage, species richness and number of colonies were significantly correlated with valve area (Fig. 4). Correlations, however, were rather low, and were higher on lower valves than on upper valves (Table 2).
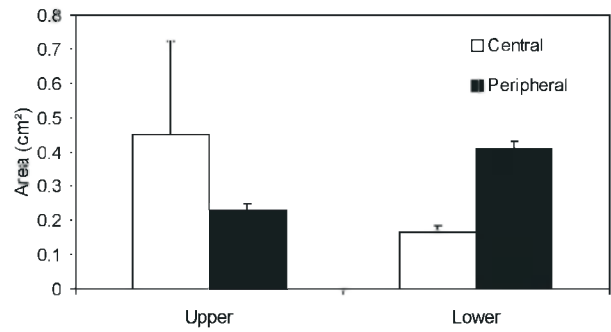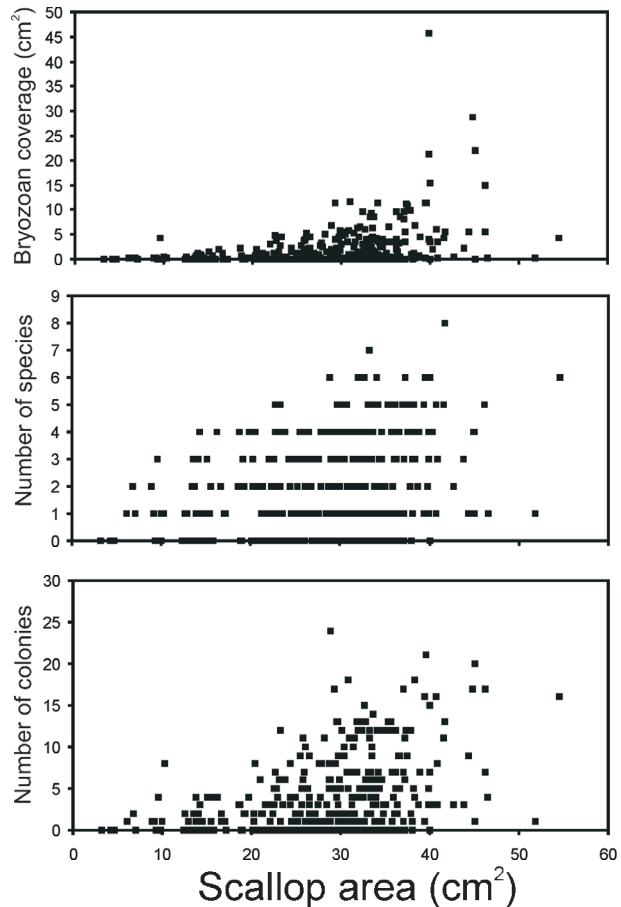

FIG. 4. – Correlations between scallop area and bryozoan coverage, species richness and number of colonies per valve (n = 390).

Twenty-two bryozoan taxa were identified, 18 of which were encrusting (16 multiserial, 2 runner-like) and 4 erect (Table 3). Four species were present in all beds: *Arachnopusia monoceros*, *Osthimosia eatonensis*, *Smittina leptodentata* and *Neothoa* cf. *chiloensis*. Valdés had the highest species richness, with 10 taxa present exclusively in this bed: *Aetea ligulata*, *Andreella uncifera*, *Caberea darwinii*, *Fenestrulina* sp., *Lacerna hosteensis*, *Menipea flagel-*

TABLE 2. – Relationship between valve area and bryozoan coverage, species richness and abundance. r: product-moment correlation coefficient.

	N	Coverage (cm²)		Number of species		Number of colonies	
		r	P	r	P	r	P
Lower valves	184	0.516	<0.0001	0.485	<0.0001	0.526	<0.0001
Upper valves	206	0.189	0.0065	0.181	0.0092	0.271	<0.0001
Total	390	0.379	<0.0001	0.367	<0.0001	0.423	<0.0001

TABLE 3. – Percent of colonised valves and coverage of 22 bryozoan taxa growing on *Psychrochlamys patagonica*. The area was not measured in runner-like or erect colonies. MDQ: MDQ, SB: San Blás, VJ: Valdés January, VN: Valdés November, TB: Tango B.

Species	% of colonised valves					Coverage (cm²)				
	MDQ	SB	VJ	VN	TB	MDQ	SB	VJ	VN	TB
Aetea ligulata	-	-	1	-	-					
Andreella uncifera	-	-	15	7	-	-	-	6.58	7.18	-
Arachnopusia monoceros	3	36	38	42	31	0.10	16.31	56.25	122.14	52.21
Buffonellodes glabra	-	4	11	32	1	-	0.77	5.89	8.27	0.73
Caberea darwinii	-	-	1	-	-					
Cellaria malvinensis	3	-	-	-	-					
Fenestrulina sp.	-	-	3	2	-	-	-	0.32	0.13	-
Lacerna hosteensis	-	-	1	-	-	-	-	0.41	-	-
Lichenoporidae	-	4	-	-	-	-	0.23	-	-	-
Menipea flagellifera	-	-	1	-	-					
Microporella sp.	-	-	-	1	-	-	-	-	0.01	-
Neothoa cf. *chiloensis*	3	17	41	50	46					
Notoplites elongatus	-	-	-	1	-					
Odontoporella adpressa	-	-	-	2	-	-	-	-	1.23	-
Osthimosia bicornis	-	2	6	32	-	-	0.42	2.12	6.94	-
Osthimosia eatonensis	11	49	56	71	62	0.21	15.81	41.29	43.80	27.48
Plagioecia dichotoma	-	13	1	14	-	-	1.93	0.51	1.92	-
Smittina jullieni	-	6	3	2	4	-	1.50	3.19	0.18	3.57
Smittina leptodentata	5	11	13	10	8	0.14	1.44	2.73	0.95	2.36
Smittina smittiana	-	-	5	3	-	-	-	33.20	12.57	-
Smittina sp.	-	-	-	-	2	-	-	-	-	0.25
Tubulipora sp.	-	-	-	7	1	-	-	-	0.20	0.03

lifera, Notoplites elongatus, Odontoporella adpressa, Microporella sp. and *Smittina smittiana*. Sample size for the Valdés bed was, however, greater than those of the remaining beds (Table 1). Other taxa also appeared in only one bed: *Cellaria malvinensis* in MDQ, a lichenoporid in San Blás, and *Smittina* sp. in Tango B.

The bryozoan assemblage was dominated by two species, *Osthimosia eatonensis* and *Arachnopusia monoceros*, which were at least one order of magnitude more abundant than any other taxa (Fig. 5). Colonies of the two species together made up 78% and 73% in number and area of the whole bryozoan assemblage in all beds respectively. *O. eatonensis* was the most abundant bryozoan, while *A. monoceros* was the main space occupier, since its colonies were larger (Fig. 5).

The case of *Smittina smittiana* was remarkable. With just 12 colonies found in all samples, it was the third most important species in coverage (Fig. 5), since its average colony area was at least 6 to 7
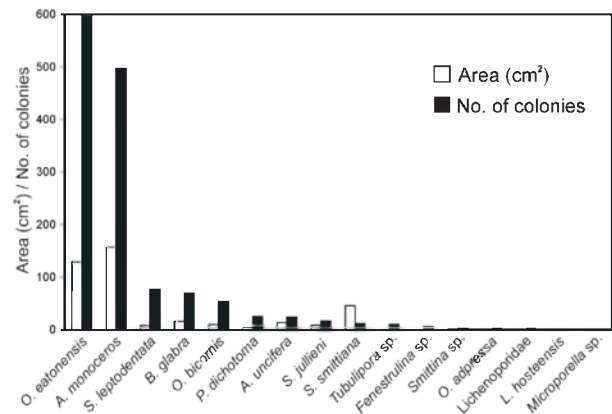

FIG. 5. – Coverage and abundance of each bryozoan species in all beds.

times larger than those of the remaining multiserial species. One valve of *Psychrochlamys patagonica* had more than half of its surface covered with just one colony of *S. smittiana*.

In the dendrogram based on square-root transformed coverage data of multiserial colonies (Fig.
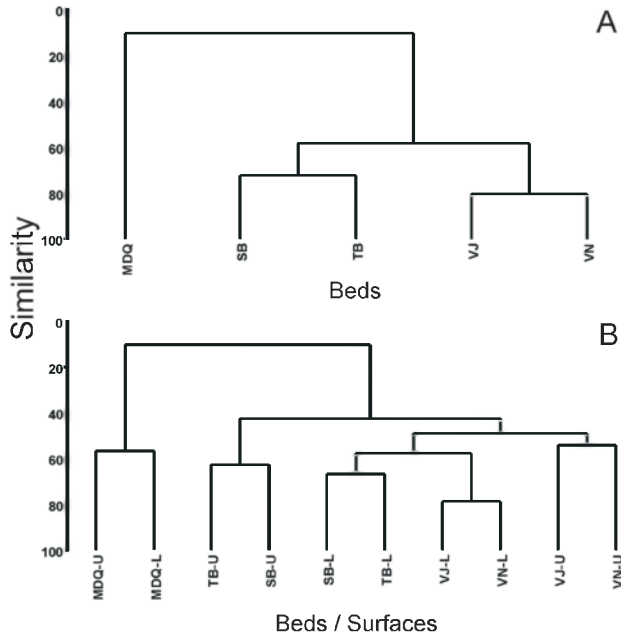
FIG. 6. – Cluster analysis of beds based on (A) square-root transformed coverage data of 16 multiserial species. (B) The same analysis, but with coverage data at each bed divided between the upper and lower valves. Abbreviations of beds as in Table 3. U: upper, L: lower.

6A), beds were separated by species richness (see Table 3) rather than by geographic proximity (see Fig. 1). The richest samples (11 to 13 species), obtained at different dates in Valdés bed, showed the highest affinity between each other. MDQ (3 species) showed the lowest affinity with all remaining beds. The cluster formed by San Blás and Tango B (7-8 species) was closer to Valdés than to MDQ. The position of the valve (i.e., upper or lower) seemed relatively less important than the bed in determining the structure of the bryozoan assemblage growing on *Psychrochlamys patagonica* (Fig. 6B). Both surfaces showed a high level of similarity at the poorest station (MDQ), but low-order clusters tended to join assemblages on valves of a similar position when differences in structure among beds were not so clear (i.e., Valdés, Tango B, San Blás). The null hypotheses of no difference in bryozoan assemblage structure between upper and lower valves and among beds were rejected by the two-way ANOSIM test (upper and lower surfaces: Global R = 0.443, P = 0.001, beds: Global R = 0.091, P = 0.001).

The interaction matrix (Fig. 7) shows the outcome of 123 interspecific encounters among 11 bryozoan species. More than 10 interspecific encounters occurred only among *Osthimosia eatonensis*, *Arachnopusia monoceros* and *Neothoa* cf. *chiloensis*. The runner-like, ramifying colonies of *Neothoa* cf. *chiloensis* lost all interactions against the multiserial *A. monoceros* and *O. eatonensis*, as well as most encounters against all other species. No significant winner resulted from competition between *A. monoceros* and *O. eatonensis*.

The actual number of observed interactions represented a very low proportion of the theoretical maximum number of possible encounters calculated as a function of bryozoan species richness per valve (123/899, 13.7%). Interspecific encounters were unevenly distributed on the valves, and occurred almost exclusively on lower valves, and more frequently in peripheral zones than in central zones (Table 4).

	Osthimosia eatonensis	Arachnopusia monoceros	Plagioecia dichotoma	Osthimosia bicornis	Smittina leptodentata	Buffonellodes glabra	Smittina smittiana	Smittina jullieni	Fenestrulina sp.	Andreella uncifera
Neothoa cf. chiloensis	↑17 / 0 0	↑31 / 0 0	1 / 0 0	1 / 0 0	6 / 1 0	4 / 0 0	1 / 0 0			3 / 0 0
Osthimosia eatonensis		NS 11 / 7 5		0 / 1 1	1 / 2 0	0 / 0 2				1 / 1 1
Arachnopusia monoceros			0 / 1 0	0 / 0 1	1 / 6 0	1 / 0 2	1 / 0 1	0 / 0 1		2 / 2 2
Plagioecia dichotoma								1 / 0 0		
Osthimosia bicornis								0 / 1 0	0 / 1 0	
Smittina leptodentata								1 / 0 0		

FIG. 7. – Matrix of competitive interactions among 11 encrusting bryozoan species. The figures in the top right corner and in the bottom left corner of each box are the numbers of wins and losses of the species shown above respectively. The figure in the bottom right corner is the number of ties recorded between the 2 interacting species. An arrow points out the significant winner in a chi-square test. NS: P>0.05. Only interactions involving more than 10 encounters were statistically tested.

TABLE 4. – Distribution of interspecific encounters on upper and lower valves, and on central and peripheral zones of the valves.

	Lower	Upper	Total
Peripheral	96 (78.0%)	1 (0.8%)	97 (78.9%)
Central	25 (20.3%)	1 (0.8%)	26 (21.1%)
Total	121 (98.4%)	2 (1.6%)	123 (100%)

The runner-like, ramifying colonies of *Neothoa* cf. *chiloensis* were frequently found spreading out along the channels that separated shell ribs. Their zooids etch the shell surface, leaving marks that remain clearly visible after zooids are lost due to abrasion (see Fig. 4g in Waloszek and Waloszek, 1986, as *Cliona* sp.?). Colonies of *N.* cf. *chiloensis* were also significantly more frequent on lower valves than upper valves [lower: n = 121 (82.3%), upper: 26 (17.7%), chi-square, P<0.001], but unlike multiserial species, they were evenly distributed in central and peripheral zones of the valves [central: n = 75 (51.0%), peripheral: n = 72 (49.0%), chi-square, P = 0.82]. Although the number of colonies of *N.* cf. *chiloensis* observed in peripheral zones of lower valves was slightly lower than expected (observed: 57, expected: 61.7), the null hypothesis of independence of distribution in central and peripheral zones of upper and lower valves could not be rejected (Fisher's exact test, P = 0.052).

DISCUSSION

It is well known that the interphyletic competition among the groups that compose the epibiota of bivalve molluscs is essentially hierarchical: tunicates overgrow sponges, which overgrow bryozoans, which overgrow tubicolous polychaetes (Kay and Keough, 1981). Competitive dominance of sponges over bryozoans has been well documented in several studies (Jackson and Winston, 1982; Nandakumar *et al.*, 1993; Barnes, 1995; Barnes and Clarke, 1995). The encrusting sponge *Iophon proximum*, the most common and abundant epibiont on *Psychrochlamys patagonica* in the south-west Atlantic (Schejter and Bremec, 2007), often monopolises the substratum, displacing all other groups of sessile invertebrates (López Gappa and Landoni, 2007). As a consequence of this process, bryozoan colonies are often confined to scallops where *I. proximum* is absent or still not fully developed (López Gappa and Landoni, 2007).

Interspecific competition for space among bryozoans on *Psychrochlamys patagonica* did not seem to influence species richness at the scale of individual valves. The actual number of encounters represented a very low proportion of the theoretical maximum number of possible interspecific contacts. This was obviously related to the relatively small percentage of valve space occupied by multiserial colonies. Patterns of bryozoan abundance and coverage were highly variable among species. Four species occurred in all samples, while most other taxa were rare and appeared in just one or two beds. Two dominant species, *Arachnopusia monoceros* and *Osthimosia eatonensis*, were responsible for around 75% of the abundance and coverage of the whole bryozoan assemblage. *A. monoceros*, the main space occupier, was one of the competitive dominants in an assemblage growing on artificial panels in Patagonia (López Gappa, 1989), and is widely distributed throughout the continental shelf off Argentina (Hayward and Thorpe, 1988; López Gappa, 2000). The colonies of *Smittina smittiana* were much larger than those of any other species and they seemed capable of monopolising extensive areas of the substratum, which suggests that their growth rate may be relatively high. There seems to be more species of epibiotic bryozoans along the entire geographic range of *P. patagonica* than the number recorded in the present study, since 64 cheilostomes were reportedly found on this scallop during the extensive collections made by the FFS *Walther Herwig* in the south-west Atlantic (Hayward and Ristedt, unpublished results quoted in Waloszek, 1991). Many bryozoan species may be restricted to shelf areas off Santa Cruz and Tierra del Fuego (see Fig. 1), where bryozoans reach maximum biodiversity in the southernmost sector of the south-west Atlantic (López Gappa, 2000).

Runner-like growth has been regarded as a strategy for avoiding enemies through the rapid location and exploitation of spatial refuges (Buss, 1979; Okamura *et al.*, 2001). In a study on overgrowth competition in an encrusting assemblage in Patagonia, the runner-like colonies of *Neothoa patagonica* (= *Celleporella patagonica*) lost all their competitive encounters with several multiserial species (López Gappa, 1989). A similar scenario occurs on the valves of the Patagonian scallop, where the uniserial colonies of *Neothoa* cf. *chiloensis* were partially covered by *Arachnopusia monoceros* and *Osthimosia eatonensis*, the two main space occupiers, as well as by all remaining multiserial species. *N.* cf. *chiloensis*, however, was

not completely eliminated even from the peripheral zones of lower valves, where bryozoan coverage and competitive interactions reached a maximum, as the species is best adapted to exploiting the central area of the lower valves due to its ability to spread out along channels. By growing within valve channels, this species may find a different hydrodynamic environment and also benefit from protection against abrasion. Since scallops lie on the substratum on the central part of the right valve, this zone seems to be an unsuitable habitat for mounds or sheet-like colonies, which allows *N.* cf. *chiloensis* to avoid competition by displaying the typical fugitive strategy of runner-like colonies (Jackson, 1979; Taylor, 1984). This competitive pattern has a long fossil history, as species with linear growth-forms were more susceptible to overgrowth than species with discoidal colonies in encrusting assemblages on Jurassic bivalves (Taylor, 1979). Similar marks to those left by *N.* cf. *chiloensis* have been described as a Pleistocene ichnogenus. The mechanism by which the bryozoan etches the calcareous substratum is unknown but is almost certainly chemical (Taylor *et al.*, 1999).

We found that correlations between valve size and bryozoan coverage, number of colonies and species richness were low but significant, which means that scallop size alone is a poor predictor of colony abundance, size and biodiversity of the bryozoan assemblage. A positive relationship between bryozoan coverage and scallop size has already been observed in *Psychrochlamys patagonica* from the Magellan Strait (Rosso and Sanfilippo, 1991). Epibiotic cover, including bryozoans, also increases with valve size in several species of Antarctic and New Zealand brachiopods (Barnes and Clarke, 1995; Barnes and Peck, 1996). Larger individuals of the giant marine isopod *Glyptonotus antarcticus* have significantly more epizoic bryozoan species and colonies than smaller ones (Key and Barnes, 1999). Similarly, epizoites are more abundant on larger shells than on smaller shells of the Brazilian cerith *Cerithium atratum* (Creed, 2000).

The present results show that bryozoan abundance, coverage and mean colony area were significantly higher on lower valves than on upper valves, and also in peripheral areas compared to central areas. Therefore, interspecific competition for space occurred mainly in peripheral areas of the lower valves. Preference for lower valves may be due to active larval behaviour during settlement, since larvae of sponges and other invertebrates settle mainly on the under-

surfaces of the artificial substrata they are offered, regardless of which microhabitat they are placed in (Maldonado and Young, 1996). The bryozoan assemblage of the subtidal pectinid *Chlamys opercularis* was also more abundant and diverse on the lower valves (Ward and Thorpe, 1991). Bryozoans were almost entirely confined to the undersurfaces of rocks in encrusting communities from the Antarctic sublittoral, and the proportion of colonies occurring on the upper surfaces decreased in the deepest samples, where silt deposition became a major influence (Barnes *et al.*, 1996). In samples of *Psychrochlamys patagonica* obtained at a depth of 80 m in the Magellan Strait, epibionts were common along the edges of the lower valves, but abundance of bryozoans was higher on the upper valves than on the lower valves (Rosso and Sanfilippo, 1991). Hydrodynamics and sediment deposition may be critical factors for explaining this difference. Scallops from the Magellan Strait were associated with coarse sediments (Rosso and Sanfilippo, 1991), which suggests that siltation was probably low or absent, and thus an abundant and diverse assemblage of bryozoans could develop on the upper valves.

Marine litter has doubled the rafting opportunities for biota, particularly at high latitudes, and has become the most common sea-going transport system. It is responsible for the widespread distribution of many marine animals (Barnes, 2002b). Fouling species such as the bryozoans living on *Psychrochlamys patagonica* may be likely candidates for invading remote areas of the Southern Ocean, transported on ship hulls and plastic debris; freezing temperatures are presently the main barrier preventing marine bioinvasions beyond the Antarctic circumpolar current. Global climate change, however, may lift this constraint, since polar regions such as the Antarctic Peninsula are one of the most rapidly warming areas of the world (Clarke *et al.*, 2007).

In conclusion, the results of this study show that bryozoans are mainly found on peripheral areas of the lower valves of *Psychrochlamys patagonica*. The assemblage is dominated by *Arachnopusia monoceros* and *Osthimosia eatonesis*, two multiserial species that win in overgrowth competition against the uniserial, ramified colonies of *Neothoa* cf. *chiloensis*. This bryozoan displays a fugitive strategy, and spreads out along channels on the scallop surface to find refuge from competition in the central area of the valve. Bryozoan species richness does not decrease with increasing host size, as

would be expected if a few competitive dominants progressively excluded weaker species, and even the weakest competitor still manages to persist in the assemblage.

ACKNOWLEDGEMENTS

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