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Bryozoan assemblages on hard substrata: species abundance distribution and competition for space

Romina Centurión · Juan López Gappa

Abstract Bryozoans are colonial invertebrates that often dominate epibenthic assemblages on the lower surfaces of hard substrata. Competition among neighbouring organisms is usually a critical process regulating biodiversity, and hard substrata have proved to be a suitable model habitat to analyse spatial interactions. We explored the relationships among abundance, species richness, diversity, competitive ability, coverage, available surface, depth and substratum size in an assemblage of bryozoans encrusting pebbles and cobbles in a bank off the eastern mouth of the Strait of Magellan. We also tested whether overgrowth competition can be regarded as hierarchical, and whether the species abundance distribution shows a mode of rare species and a decreasing frequency of increasingly abundant species. Abundance, species richness, diversity and overgrowth competition were highest on the largest substrata. Smaller pebbles tended to be encrusted by the commonest bryozoans, while the rarest species were mainly found on relatively larger clasts. A high proportion of the lower surfaces of most substrata was available for growth. Diversity values of relatively shallow stations were lower than expected under Caswell's neutral model. Interspecific competition was hierarchical, but the abundance of colonies was not related to the competitive ability of each species. The species abundance distribution was bimodal, with a main mode of rare species and a second one partly composed of relatively abundant bryozoans with poor competitive abilities. This study shows that even in an encrusting assemblage where competition is hierarchical, the weakest competitors persist and the dominant species are far from being capable of monopolizing space.

Keywords Overgrowth competition · Encrusting bryozoans · Species abundance distributions · Commonness and rarity of species · Hard substrata · Strait of Magellan

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Introduction

For decades, ecological studies have focused on the distribution of individuals among species and have tried to elucidate the underlying causes of the commonness and rarity of species (e.g. Preston, 1948; Magurran & Henderson, 2003; Gray et al., 2005). Different theories were developed to seek explanations for the observed patterns of species abundance distributions (SADs) in space and time, most of them emphasizing the central role of niche differences in promoting species coexistence (Chesson, 2000). Understanding the causes of SADs may tell ecologists

a great deal about how communities are structured (McGill, 2003), because one of the advantages of SADs is the ability to compare unrelated communities (McGill et al., 2007).

Applying a completely different approach, neutral models have achieved a surprising success in predicting relative species abundances, while assuming that all individuals in a community are ecologically equivalent (Chave, 2004). Neutral models attempt to eliminate all forces which might play a part in explaining an observed pattern of species abundance, such as interspecific biotic interactions or differential responses to biological or physical disturbance. Given the total number of species and individuals, the neutral model is then used to generate a predicted pattern against which to compare the observed pattern. Caswell's neutral model (Caswell, 1976) describes the stochastic development of a set of non-interacting populations which colonize a community, persist temporarily, and eventually become extinct. Biodiversity studies have concluded that the V statistic derived from Caswell's neutral model is a sensitive tool for analysing the effects of disturbance on species abundance patterns (Platt & Lambshead, 1985; Lambshead & Platt, 1988).

Competition among neighbouring organisms is regarded as a critical process regulating biodiversity in spatially structured habitats (Tilman, 1994). Discrete hard surfaces such as boulders have proved to be a suitable model habitat to analyse spatial competition as well as the influence of physical disturbance on the structure of epibenthic assemblages (Sousa, 1979a, b; McGuinness, 1987a, b). At high latitudes, interspecific overgrowth interactions among encrusting organisms are usually clearly hierarchical (Barnes & Kuklinski, 2003). A surface on which to grow is often regarded as a critical limiting resource in encrusting assemblages (Paine, 1984; Turner & Todd, 1994). The substratum, however, is often not monopolised by one or a few dominant species. Disturbances create a pattern of spatio-temporal heterogeneity by renewing a limiting resource that may be occupied by species that are not dominant competitors, but are often the first to take advantage of the new patches of free substratum (Levin & Paine, 1974). The result of this process is that maximum levels of benthic biodiversity are usually to be found under intermediate disturbance rates (Connell, 1978; Sousa, 1979a, 1984). In boulder fields, disturbance rates are related both to near-bottom hydrodynamic conditions and to substratum size, because smaller substrata are usually overturned more frequently than larger ones (Sousa, 1979a; McGuinness, 1987a).

Persistence of species with relatively lower competitive abilities may be achieved, among other factors, by preferential allocation of resources to reproduction (Jackson, 1979a; López Gappa, 1989), by the exploitation of spatial refuges (Buss, 1979; Okamura et al., 2001), or because in colonial organisms mortality caused by overgrowth may be partial (Buss, 1979; Barnes & Arnold, 2001). On the contrary, allocating relatively more resources to defence and maintenance of the integrity of colony surfaces may be a convenient strategy on hard surfaces where the available space is scarce and overgrowth competition is intense (Jackson, 1979a). Hence, the abundance of different encrusting species may be inversely related to their competitive ability.

Bryozoans are colonial and sessile filter-feeding invertebrates which often dominate epibenthic assemblages on natural (Barnes & Clarke, 1998) and artificial (López Gappa, 1989) hard substrata. They offer several advantages as model organisms for the study of spatial competition, as they can be easily identified under a dissecting microscope without disturbing their spatial relationships on the substratum, and may show relatively high levels of species richness at local scales (e.g. Maughan & Barnes, 2000). In addition, their calcareous skeletons persist after death, allowing the study of competitive interactions in interspecific encounters (Taylor & Wilson, 2003).

The aims of this study are to analyse (1) whether the SAD of an encrusting assemblage shows a mode of rare species and a monotonically decreasing frequency of increasingly abundant species, (2) whether overgrowth competition can be regarded as hierarchically dominant, and (3) to explore the relationships among abundance, species richness, diversity, competitive ability, colony size, available surface, depth and substratum size.

Materials and methods

Study area

Banco Sarmiento is an underwater extension of Cabo Vírgenes and is located between the Argentine
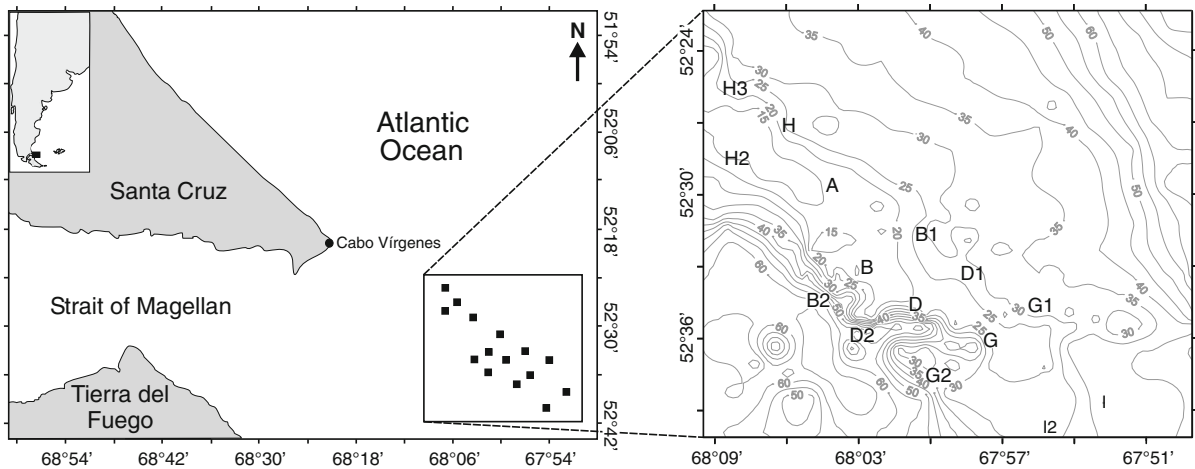
Fig. 1 Location of study area and stations. Isobaths in metre

provinces of Santa Cruz and Tierra del Fuego (Fig. 1). The study area is characterised by strong currents originated from semidiurnal tidal waves coming from the Atlantic Ocean that determine a macrotidal regime with an amplitude of up to 9 m during spring tides (Medeiros & Kjerfve, 1988). Currents between 80 and 100 cm s^{-1} flowing in an east–west direction have been recorded at 40 m depth in the eastern mouth of the Strait of Magellan, but these velocities may be greatly reduced near the bottom due to friction (Michelato et al., 1991).

Sampling

Sampling took place onboard the PSV *Golondrina de Mar* on 27–28 October, 2006, along an area of 13.0 × 33.4 km. The position of each station was recorded with a GPS (Table 1). Two or three quantitative samples were taken at each station with a 20.3 × 18.0 cm (3.654 dm^2) Van Veen grab. In addition, qualitative samples were also obtained at all stations with a 20 × 60 cm rectangular dredge with a mesh size of 3.5 cm. Depths were recorded with an echosounder and were later corrected according to the tidal height at the moment of sampling. Grab samples were immediately washed with seawater on a 1-mm sieve and then fixed in 10% formaldehyde. The material was later transferred to 70% ethanol in the laboratory to prevent acidification and loss of calcareous structures. Fifteen out of 21 stations yielded hard substrata encrusted with bryozoan colonies (Table 1). Their depths ranged from 16 to 65 m.

A distance of 30.5 km separated the two most distant stations where clasts with bryozoans were found.

Hard substrata

Clast weight was measured to the nearest 0.01 g on an analytical balance. The null hypothesis of no differences in the mean weight of clasts encrusted by each bryozoan species was tested with one-way ANOVA (Sokal & Rohlf, 1981). Only species represented by more than 10 colonies were included in this analysis.

Size of clasts analysed in this study (hereafter called pebbles) mostly fall within the range of 4 to 64 mm, although we also found a smaller proportion of larger substrata (cobbles, 64–256 mm). Epifaunal organisms were mostly represented by encrusting colonies or tube-dwelling polychaetes whose volume was negligible in comparison with that of the substratum.

Substratum area was estimated on a random subsample of 10 pebbles per station, except for stations with fewer pebbles, where all were included (total $n = 127$). Each pebble was wrapped in aluminium foil, the foil was cut and its outline was traced on a sheet of paper divided into 0.25-cm^2 squares. The number of squares completely enclosed (CE) or partially enclosed (PE) by the outline were counted. Then, the area (A) was estimated as $A = \mathrm{CE} + \mathrm{PE}/2$. Pebble surfaces were almost invariably smooth and regular. Therefore, pebble areas can be obtained from weights with a high level of

Table 1 Basic data of the 15 stations with pebbles encrusted by bryozoans in Banco Sarmiento

Station	Latitude (S)	Longitude (W)	Depth (m)	No. of pebbles with bryozoans	No. of species	No. of colonies	Coverage (%, mean ± SE)
H3	52°25.696′	68°08.330′	22	26	13	144	44.2 ± 15.9
H	52°27.239′	68°06.029′	26	6	5	8	13.3 ± 6.6
H2	52°28.598′	68°08.259′	16	76	26	736	36.7 ± 9.6
A	52°29.741′	68°04.208′	16	37	19	192	14.0 ± 5.1
B1	52°31.794′	68°00.304′	30	38	17	302	24.3 ± 7.0
B	52°33.155′	68°02.753′	16	17	13	54	4.5 ± 2.4
B2	52°34.540′	68°04.858′	65	45	12	180	13.3 ± 4.0
D2	52°35.995′	68°03.056′	64	54	13	137	14.5 ± 7.4
D	52°34.692′	68°00.773′	22	33	13	108	6.5 ± 2.6
D1	52°33.397′	67°58.411′	27	34	20	326	33.0 ± 9.8
G1	52°34.720′	67°55.600′	37	4	7	32	22.9 ± 14.6
G	52°36.181′	67°57.616′	23	102	16	867	19.8 ± 6.4
G2	52°37.662′	67°59.880′	29	14	17	140	17.0 ± 4.9
I2	52°40.131′	67°55.140′	29	4	7	13	12.6 ± 6.2
I	52°38.714′	67°52.777′	40	3	7	30	5.2 ± 2.5

Coverage is expressed as percentage of half the total area of each pebble occupied by bryozoan colonies

accuracy using the following linear equation: Area $(cm^2) = 8.129 + 0.568$ weight (g); $n = 127$, $R^2 = 0.92$, $P = 2.1 \times 10^{-70}$.

Biodiversity and species abundance distributions

Bryozoan colonies were identified to the lowest taxonomic level possible and counted under a dissecting microscope. A few colonies encrusting secondary substrata such as sabellarid tubes or barnacles (i.e. higher order epibiosis, Wahl & Mark, 1999) were not taken into account.

Species abundance data were plotted as number of species against number of individuals per species in log_2 classes called bins, following the Method 3 recommended by Gray et al. (2006).

Caswell's neutral model

The Shannon–Wiener's diversity index and Caswell's V statistic were calculated with the DIVERSE routine of the PRIMER package (Clarke & Warwick, 2001). The deviation statistic V (Caswell, 1976) is determined by comparing the observed diversity (H') with that predicted by Caswell's neutral model [$E(H')$]:

$$V = \frac{[H' - E(H')]}{SD(H')}$$

where $SD(H')$ is the standard deviation of diversity. A value of 0 for the V statistic indicates neutrality, positive values indicate greater diversity than predicted (due to excessive evenness) and negative values lower diversity (due to excessive dominance) (Platt & Lambshead, 1985).

Competition for space

All cases of competitive interactions between bryozoan colonies were recorded. Overgrowth was defined as the elevation of the growing edge of a colony over another so as to cover the aperture of zooids (Stebbing, 1973a). Apparent cessation of growth at the line of contact between colonies was regarded as stand-off. Tied outcomes were regarded as stable results and not simply as transitory phases in competition (see Barnes, 2002, 2006; Barnes & Kuklinski, 2003). Data were summarised in an interaction matrix where intraspecific competition appears in the main diagonal. Although all interactions were recorded, only cases of at least 5 wins/

losses were statistically tested using the Fisher's exact test (Sokal & Rohlf, 1981). Erect bryozoans [*Tricellaria aculeata* (d'Orbigny), *Cellaria malvinensis* (Busk), *Caberea darwinii* Busk] and three rare encrusting species [*Fenestrulina* sp., *Microporella personata* (Busk), *Romancheina labiosa* (Busk)] which did not interact with neighbouring colonies were not included in the matrix.

A ranking of competitive overgrowth abilities of all the encrusting species represented by more than 10 colonies ($n = 17$) was calculated using the wins/losses ratio (Jackson, 1979b).

The degree of hierarchy of the bryozoan assemblage was measured using the win index and the stand-off index (Tanaka & Nandakumar, 1994). The win index (WI) is expressed as:

$$WI = \sqrt{\frac{\sum_{i=1}^{n} \sum_{j=1}^{n} p_{ij}[W]^2}{\frac{n(n-1)}{2}}}$$

where $p_{ij}[W]$ is the probability that species i wins over species j, and n is the number of species.

The stand-off index (SI) is expressed as:

$$SI = \sqrt{\frac{\sum_{i=1}^{n} \sum_{j=i+1}^{n} p_{ij}[S]^2}{\frac{n(n-1)}{2}}}$$

where $p_{ij}[S]$ is the probability of a stand-off occurring between species i and j.

Both indices were calculated on a reduced matrix where all species interacted with each other. This smaller matrix included the nine commonest species and comprised 557 interactions, i.e. 77.6% of the total number of interspecific encounters.

In cases in which WI is larger than SI, Tanaka & Nandakumar (1994) proposed a procedure to characterise the type of competitive system under study. Briefly, a boundary value (BV) is calculated as an average of two WI values: one resulting from the rearrangement of the original matrix so as to get maximum possible hierarchy, leaving the stand-off probability intact, and the other rearranging the matrix so as to get maximum possible network, also leaving the stand-off probability intact. If the WI of the original data is larger than the BV, the system is regarded as hierarchically dominant.

Coverage

Colony areas were estimated by tracing the outline of each colony on paper under a dissecting microscope with the aid of camera lucida. Overgrown areas (i.e. portions covered by the winner of each interaction) were not measured. Paper cuttings were weighed to the nearest mg on an analytical balance and then compared with the weight of a known area. In this case, only colonies found in the random subsample of pebbles whose area was measured (see above) were taken into account ($n = 949$). The error of this technique was assessed by drawing the contour of the same colony and weighing the paper cuttings 10 times, which produced a coefficient of variation of 0.7%. As bryozoan colonies were found invariably on the lower or lateral sides, we expressed the space occupied by the sum of all colonies as a percentage of half the total surface of each pebble.

Correlation between variables

As 3–4 samples were taken at each station while the vessel was trying to maintain its position, geographic coordinates and depths may have been recorded with a certain degree of error. Therefore, the Spearman rank order correlation coefficient was preferred to the Pearson product–moment correlation, because it uses not the actual values of the variables but their ranks (Sokal & Rohlf, 1981).

Only interactions involving at least five interspecific encounters ($n = 36$) were taken into account when analysing the correlation between the percentage of tied outcomes and rank differences between competitors.

Results

Hard substrata

A total of 493 pebbles with bryozoans was analysed (mean $\pm$ SD: 16.84 ± 33.49 g, range: 0.08–350.90 g). The frequency distribution of weights was highly asymmetrical, with 93.1% of the pebbles weighing less than 50 g (Fig. 2).

Weight of pebbles with bryozoans was not significantly correlated to depth. On the contrary, significant
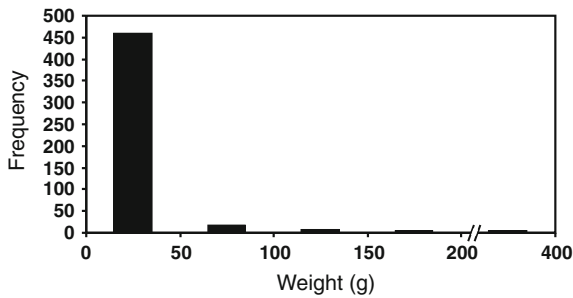
Fig. 2 Frequency distribution of weights of pebbles with bryozoans from 15 stations in Banco Sarmiento

Fig. 3 Weight of pebbles (mean + SE) encrusted by different bryozoans. Only species with more than 10 colonies were included

positive correlations were found between pebble weight and bryozoan species richness, diversity, abundance and intensity of overgrowth competition (Table 2). This means that on average more species, more colonies and more competitive encounters occurred on larger than on smaller substrata.

Significant differences existed among the weight of pebbles encrusted by different bryozoan species (one-way ANOVA, df = 17, $F = 8.23$, $P < 0.01$, Fig. 3). *Electra monostachys*, found on the smallest substrata (Fig. 3), was the only species with uniserial, runner-like colonies in the assemblage. Bryozoan abundance was negatively correlated to the weight of pebbles occupied by each species (Table 2), meaning that relatively smaller substrata tended to be encrusted by some of the commonest bryozoans (e.g. *E. monostachys*, *Chaperiopsis galeata*, *Umbonula alvareziana*) and that the rarest species were mainly found on relatively larger substrata (Fig. 3).
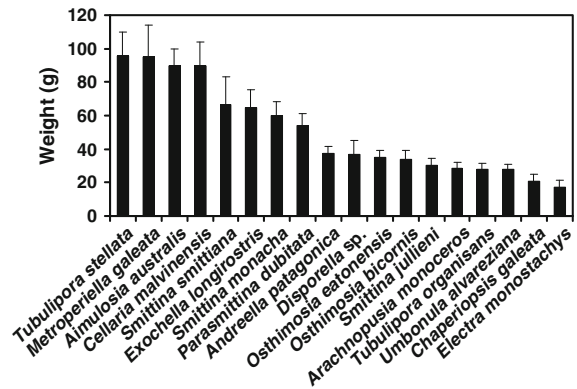
Biodiversity and species abundance distributions

Bryozoans were by far the dominant organisms of the encrusting assemblage, both in number and coverage. Spirorbid, serpulid and sabellarid polychaetes, as well as barnacles, sponges and compound ascidians, were relatively rare. We identified 3,269 bryozoan colonies belonging to 30 species (Fig. 4), 26 of which were encrusting and three erect. *Beania costata* (Busk) was unique in being prostrated, i.e. lying horizontally on the substratum but attached to it by rhizoids. The most abundant species were two ascophoran cheilostomes, *Umbonula alvareziana* and *Arachnopusia monoceros* (Busk).

The graph plotting the number of species against the abundance of colonies per species (Fig. 5) shows a mode of relatively rare bryozoans (bin 2, species

Table 2 Summary of Spearman rank order correlations (R_s) between pairs of variables analysed

Correlation	n	R_s	P
Mean pebble weight (g) vs. depth (m)	15	0.11	0.69
Species richness vs. pebble weight (g)	493	0.73	**$<1 \times 10^{-2}$**
Shannon–Wiener's diversity vs. pebble weight (g)	493	0.71	**$<1 \times 10^{-2}$**
Abundance (no. of colonies) vs. pebble weight (g)	493	0.75	**$<1 \times 10^{-2}$**
No. of encounters vs. pebble weight (g)	493	0.56	**$<1 \times 10^{-2}$**
Caswell's V vs. depth (m)	15	0.66	**$<1 \times 10^{-2}$**
Competitive ability (W/L ratio) vs. abundance (no. of colonies)	17	−0.35	0.17
Abundance (no. of colonies) vs. pebble weight per species (g)	17	−0.84	**$<1 \times 10^{-4}$**
Substratum area covered by bryozoan colonies (%) vs. depth (m)	15	−0.09	0.75
Colony area (cm^2) vs. abundance (no. of colonies)	17	−0.17	0.50
Colony area (cm^2) vs. competitive ability (W/L ratio)	17	0.21	0.40

Significant results are in bold

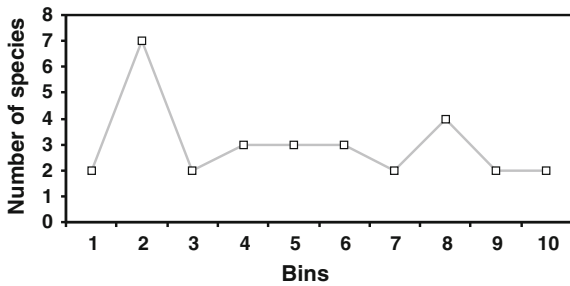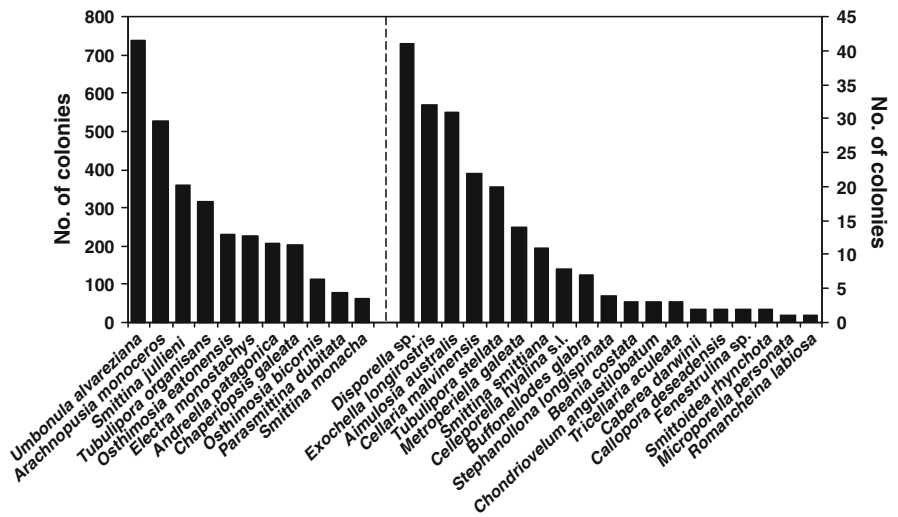**Fig. 4** Abundance of each bryozoan species

Fig. 5 Species abundance distribution of bryozoans

with 2–3 colonies each). The unexpectedly high number of species in bin 8 (i.e. those represented by 128–255 colonies) was due in part to the abundance of two anascan cheilostomes with poor competitive abilities (Table 3): *Electra monostachys* (Busk) and *Chaperiopsis galeata* (Busk).

Caswell's neutral model

Although none of the values of Caswell's V statistic obtained at the 15 stations sampled in this study (Table 4) departed from neutrality (i.e. $2 > V > -2$, see Clarke & Warwick, 2001), they were significantly correlated with depth (Table 2). In relatively shallow stations (Table 1), diversity was lower than expected under the neutral model (Table 4). Inspection of the matrix of species by samples showed that negative V values in stations A, D, H2 and I2 were due to excessive dominance of *Umbonula alvareziana* and *Arachnopusia monoceros*. On the contrary, in stations with high positive V values (i.e. B1, B2), several

Table 3 Rank of competitive ability of all encrusting bryozoans with more than 10 colonies

Species	W/L ratio
Smittina smittiana (Busk)	13.000
Osthimosia eatonensis (Busk)	4.636
Osthimosia bicornis (Busk)	3.286
Parasmittina dubitata Hayward	2.357
Disporella sp.	2.333
Arachnopusia monoceros (Busk)	2.164
Metroperiella galeata (Busk)	2.000
Smittina monacha (Jullien)	1.400
Tubulipora stellata Busk	1.000
Smittina jullieni Moyano	0.932
Andreella patagonica López Gappa	0.844
Aimulosia australis Jullien	0.750
Exochella longirostris Jullien	0.667
Chaperiopsis galeata (Busk)	0.500
Tubulipora organisans d'Orbigny	0.420
Umbonula alvareziana (d'Orbigny)	0.302
Electra monostachys (Busk)	0.083

W/L ratios can be calculated from data in Fig. 6

species were represented by relatively high numbers of colonies, including poor competitors like *Chaperiopsis galeata* and *Electra monostachys*.

Competition for space

Most of the observed interactions were interspecific (718/740, 97%) (Fig. 6). There were just 22

Table 4 Statistics calculated by Caswell's neutral model

Station	H'	$E[H']$	$SD[H']$	V
A	2.145	2.235	0.199	−0.452
B	2.158	2.116	0.155	0.268
B1	2.416	2.005	0.236	1.741
B2	2.146	1.732	0.246	1.683
D	1.801	1.936	0.207	−0.650
D1	2.517	2.171	0.222	1.560
D2	2.185	1.880	0.222	1.371
G	2.201	1.745	0.284	1.604
G1	1.750	1.528	0.180	1.231
G2	2.205	2.183	0.193	0.116
H	1.494	1.485	0.058	0.158
H2	2.128	2.295	0.227	−0.737
H3	2.084	1.868	0.225	0.957
I	1.725	1.543	0.174	1.041
I2	1.733	1.765	0.080	−0.398

H' observed diversity, $E(H')$ expected diversity according to the neutral model, $SD(H')$ standard deviation of diversity, V deviation statistic

intraspecific encounters (3%), involving only seven species. The most common outcome of intraspecific competition was a stand-off in the line of contact between colonies (73%), whereas overgrowth occurred in just six cases (27%). The number of different paired combinations taken from a set of 27 encrusting/prostrated bryozoan species is 351. As most species were rare, we observed just 103 (29.3%) different combinations of interspecific encounters, which can be seen as a majority of empty squares in the interaction matrix (Fig. 6). Interspecific overgrowth occurred in 509 instances (70.9%), while stand-offs were observed in the remaining 209 cases (29.1%). The percentage of tied outcomes was negatively correlated with the difference of competitive ability between pairs of interacting species (Fig. 7, Spearman rank correlation, $R_s = -0.41$, $P = 0.012$, $n = 36$), i.e. ties were relatively more frequent between species of similar competitive ability than between those showing great differences in their W/L ratios (see Table 3).

We did not find a significant correlation between competitive ability and abundance (Table 2). *Smittina smittiana* (Busk), a relatively rare species, had the highest W/L ratio, while *Umbonula alvareziana*, the most abundant bryozoan in the assemblage, occupied

one of the lowest ranks in the competitive hierarchy (cf. Fig. 4; Table 3).

The observed values of the win index (WI = 0.696), stand-off index (SI = 0.276), and the boundary value (BV = 0.657) calculated as a mean of WI assuming maximum (0.784) and minimum (0.529) hierarchy indicate that this system should be regarded as hierarchically dominant.

Coverage

Bryozoan coverage was highly variable across stations, ranging on average from 4.5 to 44.2% of half the pebble surfaces (Table 1). Most pebbles had plenty of space available for colony growth on their lower surfaces, except for just three pebbles with 111–137% coverage where the whole lower and lateral sides were occupied by colonies. Percentage of substratum area covered by bryozoans was not related to depth (Table 2). Twenty-one bryozoan species occurred on the subsample used to estimate species-specific colony areas. Among these, the smittinids *Smittina smittiana* and *Parasmittina dubitata* Hayward had the largest colonies (Fig. 8). Colony area was neither related to abundance nor to competitive ability (Table 2).

Discussion

This study shows that in an assemblage of encrusting bryozoans with enough available substratum for further growth, the best competitors were not the most abundant species, in spite of the fact that interspecific competition was hierarchical. In addition to the usual mode of rare species, the SAD of this epilithic association showed a second mode composed in part of relatively common bryozoans with poor competitive ability.

The surface occupied by bryozoan colonies was highly variable but usually fairly low, with plenty of space available for growth. As expected, most colonies were confined to lower (Barnes et al., 1996) or lateral surfaces, whereas the upper sides of the pebbles were usually devoid of sessile macrofauna. The orientation and position of substrata have large effects on epibiotic assemblages (Glasby & Connell, 2001). The combined influence of light and sedimentation rate produces a pattern in which the

Fig. 6 Matrix of competitive interactions among 1 prostrated and 23 encrusting species. The figures in the *top left corner* and in the *bottom right corner* of each *box* are the numbers of wins and losses of the species shown above, respectively. The figure in the *bottom left corner* is the number of stand-offs recorded between the two interacting species. *Arrows* point to significant winners in interspecific competition. NS: $P > 0.05$ in a Fisher's exact test. Only interspecific interactions involving five or more wins/losses were statistically tested. Intraspecific competition appears in the main diagonal. Species ordered by abundance. Ua, *Umbonula alvareziana*; Am, *Arachnopusia monoceros*; Sj, *Smittina jullieni*; To, *Tubulipora organisans*; Oe, *Osthimosia eatonensis*; Em, *Electra monostachys*; Ap, *Andreella patagonica*; Cg, *Chaperiopsis galeata*; Ob, *Osthimosia bicornis*; Pd, *Parasmittina dubitata*; Sm, *Smittina monacha*; Ds, *Disporella* sp.; El *Exochella longirostris*; Aa, *Aimulosia australis*; Ts, *Tubulipora stellata*; Mg, *Metroperiella galeata*; Ss, *Smittina smittiana*; Ch, *Celleporella hyalina* s.l.; Bg, *Buffonellodes glabra* Hayward; Sl, *Stephanollona longispinata* (Busk); Ca, *Chondriovelum angustilobatum* (Moyano); Bc, *Beania costata*; Cd, *Callopora deseadensis* López Gappa; Sr, *Smittoidea rhynchota* Hayward & Thorpe
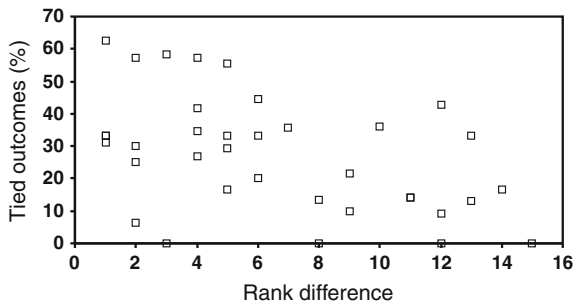
Fig. 7 Relationship between percentage of tied outcomes and rank differences between competitors

upper surfaces are dominated by algae while the lower sides are occupied by filter-feeding invertebrates (Irving & Connell, 2002). It has been shown that the area covered by the epilithic assemblage is usually greater on lower than on upper surfaces (Stark, 2008), regardless of conditions of sedimentation and light, suggesting geotaxic behaviour of some larvae (Maughan, 2001).
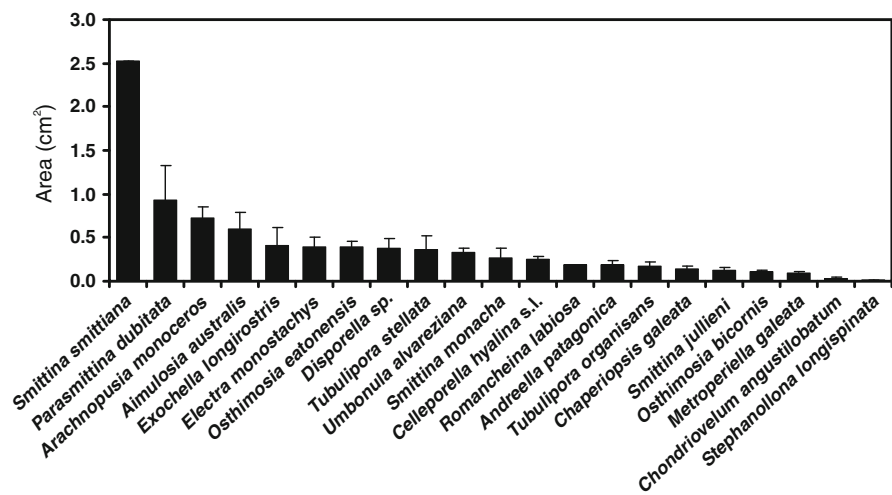
We found a significant correlation between Caswell's *V* statistic and depth, indicating a trend for lower or higher diversity than expected under the neutral model in shallower or deeper stations, respectively. On the other hand, no signs of frequent overturning were found on the pebbles. Bryozoan colonies showed a clear distribution pattern, occurring on the lower and lateral surfaces, which suggests a certain stability of the pebbles on the bottom surface. In addition, pebbles of different sizes may undergo different disturbance regimes at the same

depth, so the relationship between disturbance and depth is complex and should be analysed with caution.

As in most SADs, the encrusting bryozoans of Banco Sarmiento display a mode composed of species represented by 2–3 colonies in the whole assemblage. Rareness is also a dominant feature of marine soft sediment and tropical tree assemblages, where most species are represented by one or a few individuals while a few species are extremely common (Gray et al., 2005). A long-term data set obtained from an estuarine fish community (Magurran & Henderson, 2003) found that it could be separated in two components: core species, which were abundant and persistent, and occasional species, which occurred infrequently. An interesting result of this study was the occurrence of a second mode in the eighth bin of the distribution. This category contained four species, including two anascan cheilostomes with very poor competitive ability: *Electra monostachys* and *Chaperiopsis galeata*. The presence of a second mode composed of relatively abundant species agrees with the results obtained during a comprehensive coral reef survey performed at a single site, where the SAD of a sample of more than 40,000 coral colonies had at least three modes (Dornelas & Connolly, 2008).

In an analysis of the structuring influence of the substratum on assemblages of Arctic bryozoans, Kuklinski et al. (2006) found that the smallest substrata were dominated by *Electra arctica* Borg, a stoloniferous and pioneer species which releases

Fig. 8 Colony area (mean + SE) of 21 encrusting bryozoans. *Smittina smittiana*, *Romancheina labiosa* and *Stephanollona longispinata* are represented by one colony each

planktotrophic larvae in high numbers. Its congener, *Electra monostachys*, is one of the few cheilostome bryozoans in the epilithic assemblage of Banco Sarmiento that lacks ovicells, showing that the reproductive strategy of this species also involves the release of great numbers of larvae capable of feeding in the water column. When a species is found mainly on hard substrata of relatively smaller size, observational studies like the present one cannot discern whether this pattern was caused by active larval choices or by differential mortality after settlement. *Electra monostachys* is the weakest competitor of this assemblage and was found on the smallest pebbles. Both facts suggest that on larger (and more stable) substrata the abundance of this common species may have been reduced by overgrowth competition.

Umbonula alvareziana was the most common species on pebbles of Banco Sarmiento and also on artificial substrata immersed in Ría Deseado, Santa Cruz Province (López Gappa, 1989). This species seems to be the most abundant bryozoan on shallow hard substrata of southern Patagonia. Its rank in the competitive hierarchy is much lower in this study than in the assemblage which developed on experimental panels in Ría Deseado. Several poor competitors currently classified in the genera *Antarctothoa*, *Austrothoa* and *Neothoa* were absent in Banco Sarmiento but were abundant in Ría Deseado, where they were easily overgrown by the spiny colonies of *U. alvareziana*.

The cheilostome *Smittina smittiana* occupied the top rank among the competitors on pebbles of the Strait of Magellan in spite of lacking marginal spines. Spines in peripheral zooids of many encrusting cheilostome bryozoans appear to play a role in preventing overgrowth by other sessile organisms (e.g. Stebbing, 1973b). Colonies of *S. smittiana* were by far the largest both in this study and in a bryozoan assemblage encrusting shells of the Patagonian scallop (López Gappa & Landoni, 2009), which suggests that the great overgrowth ability of this species might be related to a high growth rate. In the remaining species of Banco Sarmiento, however, colony area was not correlated to competitive ability. It may be interesting to compare the number, length and cross-sectional area of the tentacles of *S. smittiana* with those of other bryozoans of this assemblage, as it has been shown that the size of

tentacular crowns may be associated with a higher growth rate due to a greater intake of nutrient energy per unit time (McKinney, 1993).

The intermediate disturbance hypothesis (Connell, 1978; Sousa, 1979a) predicts that species richness and diversity should be highest on medium-sized substrata. Space monopolisation by dominant competitors, however, did not occur on the largest substrata, which supported the richest and most diverse assemblages of encrusting bryozoans and had the highest rates of interspecific competition. The analysis of the bryozoan interaction matrix of Banco Sarmiento following the procedure proposed by Tanaka & Nandakumar (1994) showed that overgrowth competition was hierarchical, like in most other encrusting biotas at high latitudes or polar regions (e.g. Barnes & Arnold, 2001; Barnes & Lehane, 2001; Barnes & Kuklinski, 2003). As has been shown previously (Barnes & Rothery, 1996), the proportion of tied outcomes was higher between competitors with similar *W/L* ratios than between species occupying distant ranks in the competitive hierarchy. When both competitors display similar overgrowth abilities, the outcome may be influenced by colony size (Buss, 1980; López Gappa, 1989) or encounter angle (Turner & Todd, 1994), among other factors.

The weakest competitors managed to persist in the context of a competitive hierarchy. Some of them were among the most abundant members of the encrusting assemblage, a fact that can be explained because in this case space did not seem to be a limiting resource, as in most substrata a relatively high proportion of the lower surface was still available. Therefore, this study shows that even in an assemblage where competition is hierarchical, dominant species are far from being capable of monopolizing space.

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