

The distribution of colonies of the bryozoan *Antarctothoa bougainvillei* on the red alga *Hymenena laciniata*

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Abstract The cheilostome bryozoan *Antarctothoa bougainvillei* (d'Orbigny) is the most frequent epibiont on the ribbon-like red alga *Hymenena laciniata* (Hooker f. & Harvey) Kylin in San Sebastián Bay (Tierra del Fuego, Argentina). Twenty-one thalli and 1,484 colonies were examined to analyse the relationship between both species. In most cases, number and area of colonies did not differ significantly at both sides of the thallus. Ancestrulae (i.e., founder zooids originating colonies by asexual budding) were mostly oriented facing the algal growing edge. Colonies were more frequent on central than on marginal zones of the thalli. The population of *A. bougainvillei* was mainly composed of very small colonies (<10 mm²). Larger colonies predominated and intraspecific competition was more intense near the basal portions of the thalli. Fecundity (number of ovicells) increased at a significantly higher rate in colonies with margins obstructed by conspecific neighbours than in free-growing colonies. Colonies were significantly larger on somatic than on reproductive algal tissues. As total and reproductive surfaces covered by colonies of *A. bougainvillei*

were on average very low (4.43% and 0.53%, respectively), this epibiont is not supposed to produce a negative effect on *H. laciniata*.

Keywords *Antarctothoa bougainvillei* · Bryozoa · *Hymenena laciniata* · Rhodophyta · Epibiosis · Argentina

Introduction

Algae are a suitable substratum for many epibionts, including bryozoans (Rogick & Croasdale, 1949; Ryland, 1962; Winston & Eiseman, 1980; Seed & O'Connor, 1981). An epibiotic association, however, creates a complex network of benefits and disadvantages between epibiont and basibiont (Wahl, 1989). Encrusting bryozoans increase frond loss (Dixon et al., 1981), decrease the photosynthetic rate and photon-flux density and affect the quality of the incident light reaching the thallus (Cancino et al., 1987; Muñoz et al., 1991). The plant may react by altering the relative concentration of photosynthetic pigments to compensate the reduction of incident light (Molina et al., 1991; Muñoz et al., 1991). In addition, CO₂ released from bryozoan cells may be used by the alga as a source of photosynthetic inorganic carbon (Muñoz et al., 1991; Mercado et al., 1998). Epibionts may as well benefit from substances produced by the basibiont, e.g., colonial survivorship and percentage of

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non-degenerated zooids are enhanced in bryozoan colonies which were allowed to absorb algal exudates (Manríquez & Cancino, 1996).

Algae possess different mechanical and chemical means to deter the settlement of fouling organisms (Dworjanyn et al., 1999, 2006; Nylund & Pavia, 2005). To maximize survival on these ephemeral substrata, solitary and colonial organisms show essentially different abilities to use space (Jackson, 1977). While both are able to select habitat during settlement, only colonial animals exhibit directional growth towards more favourable refuges on the substratum (Buss, 1979).

Bryozoan colonies are not randomly distributed on algae. In choice experiments, larvae show clear preferences related to the observed natural distribution of the adults (Ryland, 1959). Settlement mainly occurs on certain regions (Hayward & Harvey, 1974a) or on younger parts of the fronds (Stebbing, 1972), where life expectancy of the colonies is maximized (Cancino, 1986). Asexual budding of zooids may continue until the substratum is completely covered by a mosaic of colonies (Hayward & Ryland, 1975), whose fecundity is linearly related to colony area (Hayward, 1973). Crowding by conspecifics was experimentally shown to trigger the onset of sexual maturity (Harvell & Grosberg, 1988; Cancino et al., 1991; Harvell & Helling, 1993), but aggregation of colonies seems to have no effect on growth and mortality rates (Hayward & Harvey, 1974b). Studies analysing the orientation of bryozoan ancestrulae, i.e., founder zooids originating colonies by asexual budding, showed that they are mainly aligned parallel to the median axis of the frond, facing the growing tip (Ryland & Stebbing, 1971; Ryland, 1974a, b, 1977).

Most investigations on the distribution, demography and competitive interactions of epiphytic bryozoans, however, dealt with assemblages growing on brown algae (Stebbing, 1972, 1973; Hayward, 1973; Ryland, 1974a; Hayward & Ryland, 1975; Cancino, 1986; among others). Since different algal taxa show a vast array of chemical and mechanical defences to deter herbivory (Hay & Fenical, 1988; Hay, 1991) and fouling (Dworjanyn et al., 1999, 2006; Nylund & Pavia, 2005), it should be interesting to test whether these patterns occur also on the surface of red algae.

The abundance of *Antarctothoa bougainvillei* (d'Orbigny) (= *Celleporella bougainvillei*, see Wright

et al., 2007), a common encrusting cheilostome bryozoan in Magellanic and Antarctic coastal environments (López Gappa, 1985; Moyano, 1986; Hayward, 1995; Linse et al., 2006), gave us the opportunity to analyse the spatial pattern of its colonies on the ribbon-like thalli of the red alga *Hymenena laciniata* (Hooker f. & Harvey) Kylin. In the present study, we investigated: (1) how much of the algal surface and reproductive structures are covered by the bryozoan, (2) the relationship between intraspecific competition and fecundity in colonies of *A. bougainvillei*, (3) whether colonies are randomly scattered or show any preference for different areas of the algal thallus and (4) whether ancestrulae exhibit a clear orientation or are randomly placed with respect to the frond axis.

Materials and methods

Thalli of *Hymenena laciniata* are erect, mostly monostromatic, up to 25-cm tall, fixed to the substratum by hapteroid bases. Blades are initially flabellate and later strap-like, with branches 8–15 mm broad, smooth or crenulated margins and apices bordered by zones of meristematic cells. Most fronds have microscopic veins, which become coarse and prominent in the lower thallus (Ricker, 1987).

To analyse the distribution of *Antarctothoa bougainvillei* on *Hymenena laciniata*, 21 thalli with 1,484 colonies of this bryozoan from San Sebastián Bay (Tierra del Fuego, Argentina, 53°14'–15' S, 68°16'–17' W) were studied under a dissecting microscope. Algae were collected at 5–13 m depth using a rectangular dredge onboard the PSV *Laurel* on March 11, 2006. Thalli may have been separated by hundreds of metres from one another. To estimate bryozoan and algal area, contour of each colony and thallus was traced on paper, cut-out, weighed to the nearest mg and compared with the weight of a known surface. Area of reproductive and somatic tissues of each mature thallus was estimated similarly. Error was assessed by drawing and weighing 10 times the contour of one colony. A coefficient of variation of 0.7% was obtained.

The following data were recorded for each colony: (1) side of the thallus on which it was growing, (2) area and (3) number of ovicells.

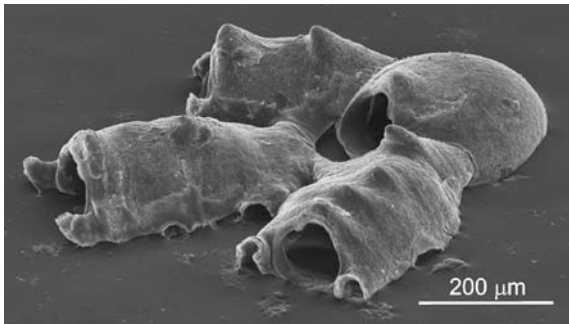


Fig. 1 Ancestrula and first zooids of *Antarctothoa bougainvillei*

In colonies undergoing intraspecific competition ($n = 223$), obstructed and free-growing margins were measured using a GIS software. All intraspecific encounters were recorded, irrespective of the length of the line of contact between colonies.

In colonies where the ancestrula (Fig. 1) was still present, we measured: (1) the distance from the ancestrula to the attachment disc of the thallus ($n = 874$), (2) the angle between the median longitudinal axis of the ancestrula and the frond and (3) the distance from the ancestrula to the right and left edges of the thallus ($n = 799$). Colonies adjacent to broken algal edges were not taken into account. A colony was defined as ‘marginal’ when the distance from the ancestrula to either edge was less than 1/4 of the thallus width. The remaining colonies were regarded as ‘central’.

The null hypothesis that ancestrulae were randomly oriented with relation to the frond axis was tested by means of the Rayleigh test (Zar, 1996).

Correlation between number of ovicells and (1) colony area or (2) percentage of intraspecific contact was calculated using the Spearman non-parametric test (Sokal & Rohlf, 1981).

In mature thalli ($n = 17$), we measured the distance from the zone of the thallus, where tetrasporangia, cystocarps or spermatangia begin to appear, to the attachment disc. Areas and distances from all *A. bougainvillei* colonies to the attachment disc were taken into account to estimate the proportion of algal reproductive tissues covered by this epibiont. In colonies where the ancestrula had disappeared, its most likely location was estimated by following the direction of zooidal budding backwards in the early astogenetic zone.

Number and area of colonies were compared between both sides of the thallus by the χ^2 test and

one-way ANOVA, respectively, taking into account only thalli with more than five colonies on each side ($n = 15$). Homogeneity of variances was verified by Cochran’s C test (Winer, 1971). The relationship between number of ovicells and colony area in obstructed and free-growing colonies was analysed using ANCOVA, but the homogeneity of adjusted means could not be tested because the slopes of the regression lines were not parallel (Sokal & Rohlf, 1981).

Results

Seventeen out of 21 thalli examined in this study were mature: 11 were female, 2 were male and 4 were tetrasporangial. Algal area varied between 1.02 and 672.77 cm² (Table 1).

The most common epibiont on *Hymenena laciniata* was the cheilostome *Antarctothoa bougainvillei*. Bivalves, ascidians, hydrozoans and the cyclostome bryozoan *Bicrisia biciliata* (Mac Gillivray) were extremely rare. Density of *A. bougainvillei* varied between 0.05 and 2.93 colonies cm⁻². The smallest and largest colonies measured 0.05 and 78.74 mm², respectively.

Percentage of the algal surface covered by *A. bougainvillei* (Table 1) was on average very low but extremely variable (mean: 4.43%, range: 0.02–35.76%). Percentage of algal reproductive tissues covered by this species was even lower (mean: 0.53%, range: 0–2.29%). Reproductive and somatic tissues of *H. laciniata* (ANOVA, $F = 0.58$, $P = 0.45$, Fig. 2A), and number of colonies of *A. bougainvillei* on each of these tissues (ANOVA, $F = 1.64$, $P = 0.21$, Fig. 2B) did not differ significantly. On the other hand, colonies were significantly larger on somatic than on reproductive algal tissues (logarithmic transformation, Cochran’s $C = 0.62$, $P = 0.32$; ANOVA, $F = 6.64$, $P = 0.01$, Fig. 2C).

Number of colonies was significantly higher on one side than on the other in only 1 out of 15 thalli (thallus No. 6, side A: 30, side B: 16, $\chi^2 = 4.26$, $P = 0.039$). Similarly, colony area was significantly larger on one side of *H. laciniata* than on the other in only 1 out of 15 thalli (thallus No. 7, Cochran’s $C = 0.57$, $P = 0.138$; mean: side A = 12.04 mm², side B = 8.04 mm²; ANOVA, $n = 217$, $F = 4.97$, $P = 0.027$).

Table 1 Percentage of algal surface and reproductive tissues of *Hymenena laciniata* covered by colonies of *Antarctothoa bougainvillei*

Thallus no.	Total area of thallus (cm ²)	Total number of colonies	Colony area (mm ²)	Colony area on algal reproductive tissues (mm ²)	% of thallus covered by colonies	% of reproductive tissues covered by colonies
1	672.77	121	696.4	95.9	1.04	0.23
2	488.96	386	1,606.3	310.5	3.29	0.88
3	132.29	155	1,573.8	264.0	11.90	2.29
4	273.12	42	204.2	29.5	0.75	0.11
5	162.56	56	401.4	0.0	2.47	0.00
6	329.16	46	283.4	6.1	0.86	0.06
7	514.49	217	2,216.3	27.7	4.31	0.12
8	90.09	16	23.8	10.8	0.26	0.13
9	142.00	54	516.0	3.0	3.63	0.34
10	194.81	75	321.3	50.5	1.65	0.35
11	48.35	10	49.1	–	1.02	–
12	19.06	1	0.3	0.0	0.02	0.00
13	174.64	106	985.2	56.8	5.64	0.68
14	32.22	7	21.2	21.2	0.66	0.80
15	258.56	59	333.9	4.6	1.29	0.07
16	84.41	23	89.7	66.0	1.06	0.84
17	179.15	70	341.5	245.8	1.91	1.47
18	108.40	17	24.8	13.5	0.23	0.56
19	53.61	9	48.9	–	0.91	–
20	10.36	11	148.1	–	14.30	–
21	1.02	3	36.6	–	35.76	–

Four thalli were immature

Central colonies were significantly more frequent than marginal ones (central: 494, marginal: 305, $\chi^2 = 44.71$, $P < 1 \times 10^{-4}$).

The null hypothesis that ancestrulae were randomly aligned with relation to the frond axis was rejected (Rayleigh test, $z = 365.2$, $P < 0.001$). Most ancestrulae (66.2%) faced the algal growing edge (315°–45°), showing an average angle of 0.4° (Fig. 3).

Correlation between colony area and distance from the ancestrula to the attachment disc was negative and highly significant (Spearman rank correlation, $n = 874$, $R_s = -0.287$, $P = 1 \times 10^{-6}$), since the largest colonies predominated near the basal portions of the thalli (Fig. 4).

Percentage of colonies undergoing intraspecific competition was 15.0%. Correlation between percentage of intraspecific contact and distance from the ancestrula to the attachment disc was also negative and highly significant (Spearman rank correlation,

$n = 874$, $R_s = -0.269$, $P < 1 \times 10^{-6}$, Fig. 5A), meaning that intraspecific competition was more intense in the basal portions of the thalli.

The size frequency distribution of *A. bougainvillei* on *H. laciniata* showed that 79% of the colonies were smaller than 10 mm² (Fig. 6). The smallest colony with ovicells measured 3.71 mm².

Correlation between colony area and number of ovicells was highly significant (Spearman rank correlation, $n = 1484$, $R_s = 0.420$, $P < 0.01$). Correlation between percentage of intraspecific contact and number of ovicells per unit area was positive and highly significant (Spearman rank correlation, $n = 1484$, $R_s = 0.552$, $P < 0.01$, Fig. 5B), meaning that fecundity increases with increasing intraspecific competition. The slope of the linear regression of ovicell number on colony area was significantly higher ($P < 0.0001$, Fig. 7) in obstructed ($y = -4.37 + 0.49x$) than in free-growing ($y = -0.33 + 0.12x$) colonies.

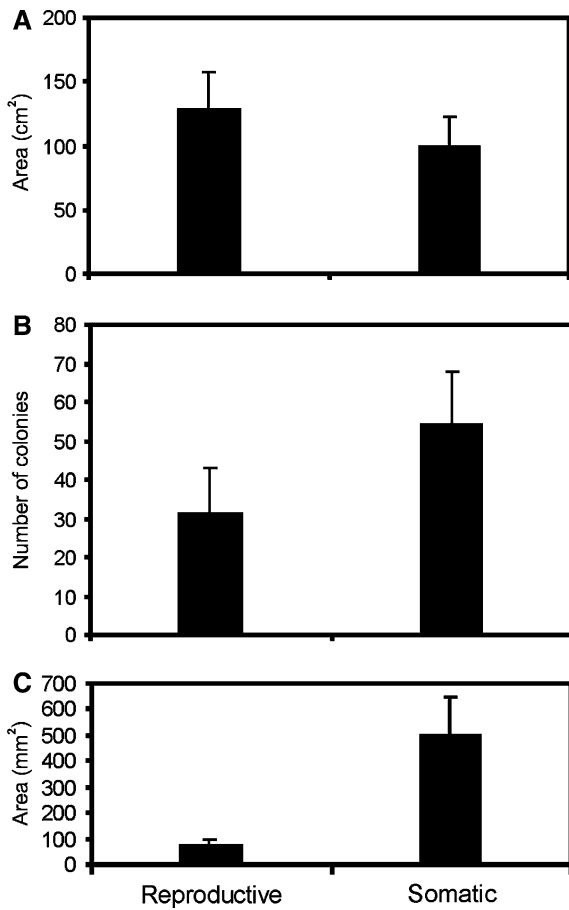


Fig. 2 (A) Reproductive and somatic tissues of *Hymenena laciniata* ($n = 17$ thalli), (B) number and (C) area of colonies of *Antarctothoa bougainvillei* growing on reproductive and somatic algal tissues (mean + SE)

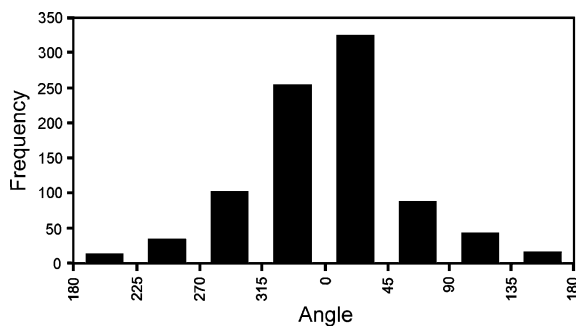


Fig. 3 Frequency distribution of the angles (in degrees) between the median longitudinal axis of the ancestrula and the frond

Discussion

In the shallow subtidal of San Sebastián Bay, algae attached to the bottom are probably swept to and fro

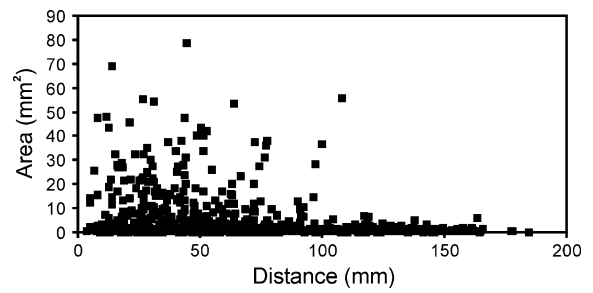


Fig. 4 Colony area of *Antarctothoa bougainvillei* plotted against distance from the ancestrula to the attachment disc of *Hymenena laciniata*

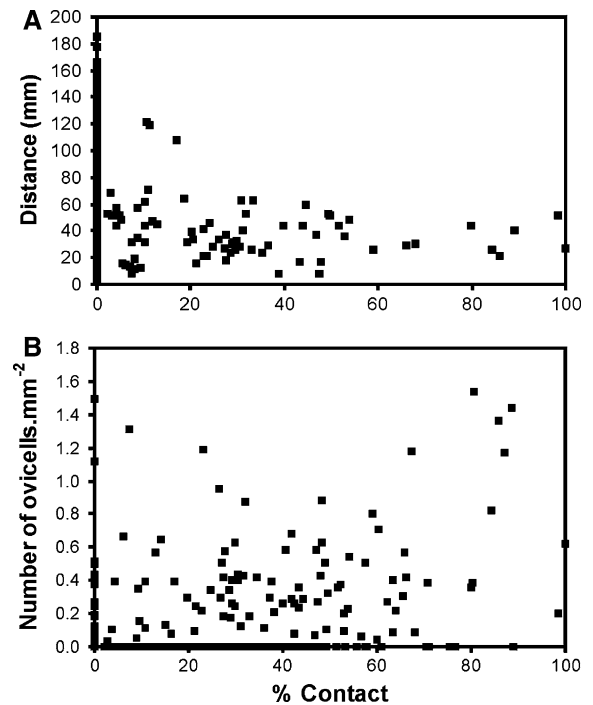


Fig. 5 Percentage of intraspecific contact plotted against (A) distance from the ancestrula to the attachment disc of *Hymenena laciniata*, (B) number of ovicells per unit area

by strong currents filling and draining the bay with each semidiurnal tidal cycle (Isla et al., 1991). Bryozoan colonies are usually much more abundant on lower than on upper surfaces of diverse substrata to avoid sediment deposition, which is clearly harmful for most species (e.g., Lagaaij & Gautier, 1965). Colonies of *Antarctothoa bougainvillei*, however, showed similar densities and sizes at both sides of most thalli of *Hymenena laciniata*, suggesting that any of the sides of this flexible red alga would be equally suitable for the bryozoan.

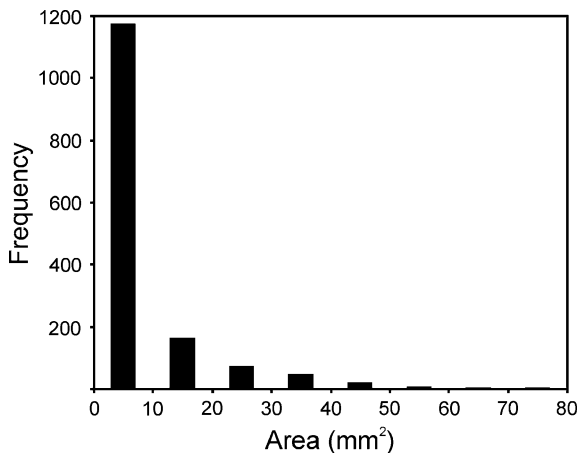


Fig. 6 Size frequency distribution of colonies of *Antarctothoa bougainvillei* growing on *Hymenena laciniata*

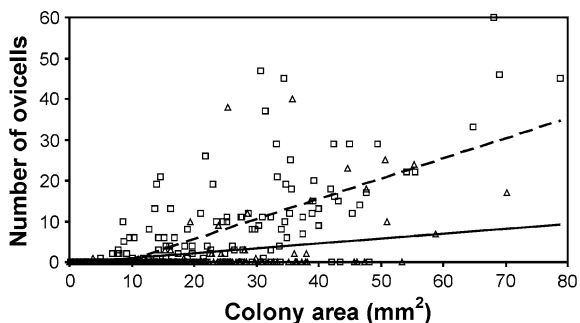


Fig. 7 Regression of number of ovicells on colony area in obstructed (squares, dashed line) and free-growing (triangles, solid line) colonies

Previous studies on the distribution of epiphytic bryozoans on algal surfaces showed clear spatial patterns. Colonies of *Alcyonidium hirsutum* (Fleming) settle preferentially along the grooves flanking the midrib of *Fucus serratus* L. but not on the midrib itself, and are more frequent around the midregion than on the basal and apical parts of the frond (Hayward & Harvey, 1974a). Unlike most of the brown algae whose epibiosis was analysed by previous authors, the morphology of *H. laciniata* is fairly simple. The main morphological features of this species are a system of microscopic veins, apical meristematic regions and reproductive organs (Mendoza, 1969; Ricker, 1987). In the present study, the higher number of colonies in central than in marginal areas could be interpreted as a larval choice to maximize future colony growth. As in other species (Stebbing, 1972; Hayward & Harvey, 1974a; Cancino, 1986), this pattern also seems to have

been produced by larval behaviour, since very small colonies or even ancestrulae were well preserved throughout the thallus, implying that any post-settlement mortality of marginal colonies would have been noticed.

As the meristems of *H. laciniata* are apical (Mendoza, 1969; Ricker, 1987), the occurrence of large colonies near the base of the thalli was expected, since this is the oldest part of the plant. Similarly, the anascan bryozoan *Jellyella* (= *Membranipora*) *tuberculata* (Bosc) is also found on the basal portions of the red alga *Gelidium rex* Santelices et Abbott (Cancino et al., 1987; Molina et al., 1991). The opposite pattern is observed in the brown alga *Laminaria*, where the oldest colonies and the highest biomass of epibionts are found near the distal end of the fronds, as in this species the meristematic regions are basal (Stebbing, 1972).

The surface of *H. laciniata* covered by colonies of *A. bougainvillei* in Tierra del Fuego is relatively low. In addition, the reproductive structures of this species are mainly located in the distal portions of the thallus (Ricker, 1987), where most bryozoan colonies are younger and smaller, whereas the larger and older zoaria grow mainly over somatic tissues near the basal region of the plant. The distribution of the colonies suggests that any negative effect of this epibiont on the photosynthetic and reproductive rates of *H. laciniata*, if present, should be minimal.

This study shows that most ancestrulae of *A. bougainvillei* are oriented towards the growing edge of *H. laciniata*. This pattern, probably a response to unidirectional water flow (Ryland, 1974b), has already been observed in *Electra pilosa* (L.) on *Fucus serratus* and also in *Jellyella tuberculata* on two species of *Sargassum* (Ryland & Stebbing, 1971; Ryland, 1974a; reviewed in Ryland, 1974b, 1977). The orientation of ancestrulae could be interpreted as an adaptation to spreading towards younger portions of the thallus, where more substratum is available and competition for space is still less intense than in older (i.e., basal) algal surfaces.

A. bougainvillei spans a large range in latitude in Antarctica and the Subantarctic region (Hayward, 1995), showing winter pauses in feeding and growth which lead to the formation of growth check lines (Barnes & Arnold, 2001; Linse et al., 2006). In this species, growth rate increases with latitude and is inversely correlated with lifespan (Linse et al., 2006).

Assuming that the Fuegian population of *A. bougainvillei* (53° S) grows at a similar rate ($38 \text{ mm}^2 \text{ y}^{-1}$; Linse et al., 2006) as in South Georgia (54° S), the age of 97.5% of the colonies examined in the present study can be estimated as less than 1 year. In just two colonies larger than 70 mm^2 we observed only one peripheral growth check line, with further development of relatively few zooids after resuming growth, suggesting that at least a small proportion of the colonies might be slightly older than 1 year. The growth rate of this bryozoan on Fuegian *H. laciniata* could be higher than that estimated by Linse et al. (2006) for South Georgia, since a colony of 78.7 mm^2 showed recent regrowth of relatively few zooids after its first check line.

Bryozoan lecithotrophic larvae brooded in ovicells have very short lifespans, usually settling in the vicinity of the maternal colony (e.g., Keough & Chernoff, 1987). The size frequency distribution observed in the present study, with a few large and many small colonies, suggests a massive recruitment of offspring generated by the earliest colonies, those that settled when the young thalli of *H. laciniata* were beginning to grow. The onset of reproduction occurs in colonies of 3.7 mm^2 , i.e., having an estimated age of just 1.2 months (Linse et al., 2006). This shows that *A. bougainvillei*, a species that loses most of its interspecific encounters against cheilostomes with spiny marginal zooids (López Gappa, 1989), assumes a strategy favouring early reproduction on ephemeral substrata, instead of allocating more resources to defend its colonies.

Algal surfaces are often the scenario where intense interspecific and interphyletic competition for space takes place (Stebbing, 1973). In the present material, however, virtually all encounters were intraspecific, due to the abundance of *A. bougainvillei* and the scarcity of other epibionts, and almost invariably resulted in growth arrest along the line of contact between colonies. This study shows that the rate of ovicell production of *A. bougainvillei* was significantly higher in colonies obstructed by conspecific neighbours than in free-growing colonies, and that the number of brood chambers per unit area increases with increasing intraspecific competition. Crowding by conspecifics also triggers the onset of sexual maturity in *Membranipora* spp. and *Celleporella hyalina* (L.) (Harvell & Grosberg, 1988; Cancino et al., 1991; Harvell & Helling, 1993). This process

could well be the result of diverting energy from growth to reproduction, but experimental work has shown that colonies of *C. hyalina* reared with conspecific neighbours produced viable larvae, while those reared in isolation never produced female zooids (Cancino et al., 1991).

Although the present study is based on material collected at a single location, results clearly indicate that the colonies of *A. bougainvillei* are equally frequent on either side of most thalli, but are more frequent on central than on marginal areas, and that ancestrulae are preferentially oriented towards the younger parts of the plant. Most of the population of *A. bougainvillei* is composed of young colonies ($<10 \text{ mm}^2$), while larger (i.e., older) colonies are mainly found on the basal portion of the thalli, where intraspecific competition is most intense and growth obstruction by conspecific neighbours increases ovicell production. The low proportion of somatic and reproductive algal tissues covered by this bryozoan suggests that its negative effect on the alga, if any, should be minimal.

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