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The ecology of an assemblage dominant: the encrusting bryozoan *Fenestrulina rugula*

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Abstract. The cheilostome bryozoan *Fenestrulina rugula* is a major component of the encrusting fauna of physically disturbed shallow water habitats in Antarctica. On rocks collected from Rothera Point, Adelaide Island, *F. rugula* was the dominant occupier of space (88% of all bryozoans, 76% of all fauna), though spirorbid polychaetes showed more colonisation events per unit area. Growth rate was relatively rapid in comparison with other polar bryozoans, but slower than temperate or tropical species. In fully reproductive colonies almost 80% of zooids carried ovicells. Colonies whose growth brought them into contact with other encrusting fauna (usually another colony of *F. rugula*) produced smaller zooids and initiated ovicell production earlier than unrestrained colonies. Analysis of overgrowth interactions showed that *F. rugula* was a relatively poor competitor compared with other encrusting bryozoans, and most within-species interactions were indeterminate. Population mortality was relatively high, averaging 89% per annum, although not as high as in some other species from ephemeral habitats. *F. rugula* is thus a typical early coloniser in being relatively fast-growing, quick to mature, short-lived and a relatively poor competitor. The population dynamics and ecology of this assemblage dominant appear to have been influenced primarily by the ephemeral nature of its habitat.

Additional key words: population dynamics, growth, competition, reproduction, mortality.

Organisms growing on hard substrata form assemblages whose structure and function are influenced strongly by biological interactions. Early colonisers will typically be gradually replaced by slower growing but more competitive forms, resulting eventually in a broadly equilibrium assemblage (Horn 1974).

The process of succession will be influenced by seasonal and interannual variability in biological factors such as larval abundance, settlement, and mortality, as well as interactions within the assemblage itself. In some habitats, however, assemblage composition and dynamics will also be influenced heavily by physical factors such as mesoscale and local oceanography (perhaps governing larval supply), or physical disturbance of settled larvae, early recruits, or developed assemblages. The structure and dynamics of such communities will thus vary with the nature, magnitude, and frequency of physical disturbance. In certain environments a degree of physical disturbance may maintain overall assemblage diversity at a relatively high level through the prevention of space monopolization by competitive dominants (Dayton 1971,

Barnes 1995b) or by transporting species to new localities (Dobbs & Vozarik 1983). Furthermore, the persistence of certain species may benefit from being coupled to disturbance (Barry 1989, Allen & Star 1982). Generally, however, assemblages affected heavily by physical disturbances, such as storm erosion (Yeo & Risk 1979), fresh-water runoff (Thomas & White 1969), anoxia (Jorgensen 1980), high water flow (De Kluijver 1993) or ice-scour (Barnes 1995a) are comparatively species-poor.

The encrusting fauna of Antarctic shallow subtidal habitats provide a typical example of an assemblage suffering frequent catastrophic physical disturbance and dominated by a small number of species. The combination of the formation of a winter icefoot which encases the intertidal and immediate subtidal in solid ice (Barnes 1995a), scour from floating ice, mortality from anchor ice formation directly onto organisms, and wave action results in a greatly impoverished fauna dominated by one or two fast growing, though poorly competitive species of bryozoans (Barnes 1995b, Barnes 1996). Here we present a preliminary study of aspects of the population dynamics of an important pioneer organism of the physically disturbed Antarctic subtidal, the bryozoan *Fenestrulina rugula*.

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Table 1. Colonising organisms on shallow subtidal rocks at Rothera Point, Antarctica.

Colonising taxa	Total number of col-	
	onists	Mean number of colonists per rock (SE)
Cheilostome bryozoans		
<i>Fenestulina rugula</i> HAYWARD & THORPE	869	124.1 (52.4)
<i>Aimulosia antarctica</i> (POWELL)	61	8.7 (2.5)
<i>Celleporella antarctica</i> MOYANO & GORDON	22	3.7 (0.6)
<i>Xylochostridens rangifer</i> HAWARD & THORPE	17	3.4 (1.3)
<i>Ellisina antarctica</i> HASTINGS	12	1.7 (0.4)
<i>Arachnopusoa inchoata</i> HAYWARD & THORPE	10	1.4 (0.7)
<i>Smittina</i> sp.	9	1.3 (0.3)
<i>Celleporella bougainvillei</i> (D'ORBIGNY)	4	0.6 (0.2)
<i>Hippadanella inerma</i> (CALVET)	3	0.4 (0.3)
<i>Escharoides tridens</i> (CALVET)	1	0.1 (0.1)
<i>Micropora brevissima</i> WATERS	1	0.1 (0.1)
Cyclostomatid bryozoans	15	2.1 (0.8)
Spirorbinid polychaetes	3,267	466.7 (172.8)

Methods

A representative sample of seven rocks (more or less rectangular cobbles) with surface areas ranging from 55–368 cm² were collected by SCUBA divers in the austral summer of 1993/94 from a subtidal site at Rothera Point (67°34'S, 68°07'W), Adelaide Island, Antarctic Peninsula. The samples examined were typical of the local substratum at the sampling depth of 20 m. Here the bottom is a mixture of cobbles and boulders, and the average slope is steep, typically between 40% and 80% (Coggan 1994). The rocks and associated epifauna were dried, wrapped in tissue paper, and transported to the UK for analysis.

The surface area of the rock substratum and of each individual epifaunal colonist was measured using an inelastic net marked with a 1 × 1 cm grid, following the method of Barnes and Clarke (1995) and Barnes *et al.* (1996). All colonising organisms were counted and identified to the highest possible taxonomic resolution with the aid of a binocular microscope. Particular attention was paid to the cheilostome bryozoans, which were the major colonising taxa, and a total of 1024 colonies were examined. One species, *Fenestulina rugula* HAYWARD & RYLAND 1990, dominated the bryozoan fauna and the following measurements were made on all colonies: the number of autozooids in a line from the ancestrula (the central and original zooid of the colony) to the furthest colony margin (in other words, the maximum colony radius measured in number of autozooids), the total number of autozooids in the colony, the total number of sexually active zooids (as determined by the presence of ovicells), the number of growth rings, the degree of crowding (the percentage of the colony periphery which was in direct

contact with other colonies), and whether the colony was of asexual origin (clonally budded from a fragment of an established colony) or had formed sexually by clonal budding from a metamorphosed larva on settlement (ancestrula).

Where colonies were in direct contact, the outcome of all inter- and intra-specific competitive interactions was recorded as either a win, loss, or tie. Interactions were scored only if both colonies were living at the time of collection (this is easily determined even in a dried specimen) and overgrowth was not the result of one colony settling directly on top of another. Overgrowth (a win for one competitor and a loss for the other) was determined from the obstruction of the loser's zooid apertures by the growing margin of the winner, following the protocol established by Stebbing (1973). Cessation of growth by both colonies along the contact zone was scored as a tied outcome.

Results

The average cover of the sample rocks by encrusting organisms was 28.9% (SE 3.4). Cheilostome bryozoans were the most important colonisers whether measured in terms of area covered or by the number of recruits. Cyclostome bryozoans, spirorbid polychaetes, and coralline algae were the only other colonising taxa present. Although eleven species of cheilostomatid bryozoans were present (Table 1) one species, *Fenestulina rugula*, dominated the assemblage in terms of the area of substratum occupied (87.5% of all bryozoans, 76.2% of the total fauna). Colonies of *F. rugula* also dominated the bryozoan fauna in terms of actual recruitment or colonisation events (85.9%) but formed only 26.6% of the total colonists, because the assem-

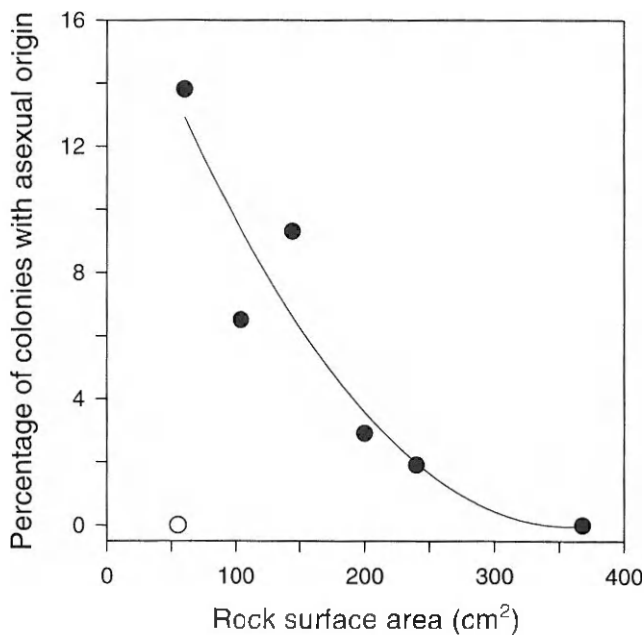


Fig. 1. Relationship between proportion of colonies formed asexually and substratum surface area (cm²), with fitted quadratic model. Unfilled point (at 55 cm²) may represent evidence of a breakdown of the relationship at smaller substratum surface areas, and has been excluded from the model fit.

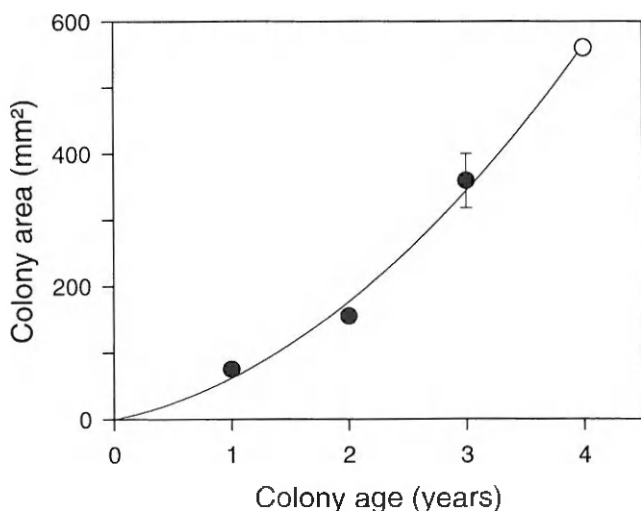


Fig. 2. Annual growth over four years. Colony size is expressed as area (mm²) and data are shown as mean \pm SE (bar). For colonies of age one and two years the SE bar is smaller than the plotted symbol. The open symbol (four-year-old colony) represents data for a single colony. The line is a quadratic fit.

blages were dominated numerically by spirorbid polychaetes.

Bryozoan colonies may form in two distinct ways: by settlement of a sexually produced larva to form an ancestrula, or by asexual fragmentation of an existing colony. Typically a sexually formed larva settles and metamorphoses into an ancestrula, the first zooid of a colony. The ancestrula then buds other zooids, clonally, in a variety of patterns radiating out from itself. Fragmentation may result from mechanical damage through predation or physical abrasion, and the various fragments may then each form new colonies. Sexual origins accounted for most of the colonies of *Fenestrulina rugula* examined in this study. However, the proportion of colonies with an asexual origin varied between 0 and 14%, and showed a complex relationship with substratum surface area (Fig. 1). For rock areas greater than 60 cm², the proportion of *F. rugula* colonies formed asexually decreased with rock size. The value of zero (all colonies formed sexually) for the rock of area 55 cm² suggests the possibility that the relationship between colony origin and substratum surface area breaks down below about this size, possibly because of the dynamics of rock turnover. Alternatively, these data may have been influenced by local hydrography. This relationship clearly needs further investigation as Fig. 1 is based on a very small sample of rocks.

Distinct concentric rings could be detected in most of the larger colonies of *Fenestrulina rugula*, and these rings had clearly been formed by periodic cessation and reinitiation of growth. Similar skeletal markings were shown to be annual growth checks in the erect Antarctic bryozoan *Cellarinella watersi* (Barnes 1995c). Furthermore, single growth rings were observed only in the larger bryozoan colonies of *Inversiula nutrix* and *Celleporella bougainvillei* on settlement panels deployed for a two year period (data from Barnes 1996), suggesting an annual formation of such growth checks in encrusting cheilostome bryozoa. Assuming an annual periodicity of growth rings in *F. rugula*, a size (area) at age plot was constructed (Fig. 2) illustrating the pattern of growth in zooids from origin to an age of four years (the oldest specimen present in the sample). The average growth rate of *F. rugula* at this site was 0.52 zooids per day, or in terms of area 0.22 mm² per day. Whilst most colonies grew at a broadly similar rate, there was a substantial difference between the fastest and slowest colonies, with 2-year old colonies varying in size from 25–470 mm².

Unobstructed colonies were circular in growth form, but the density of *F. rugula* on rocks caused many colonies to be crowded as a result of the growing margin coming into contact with other colonies. The in-

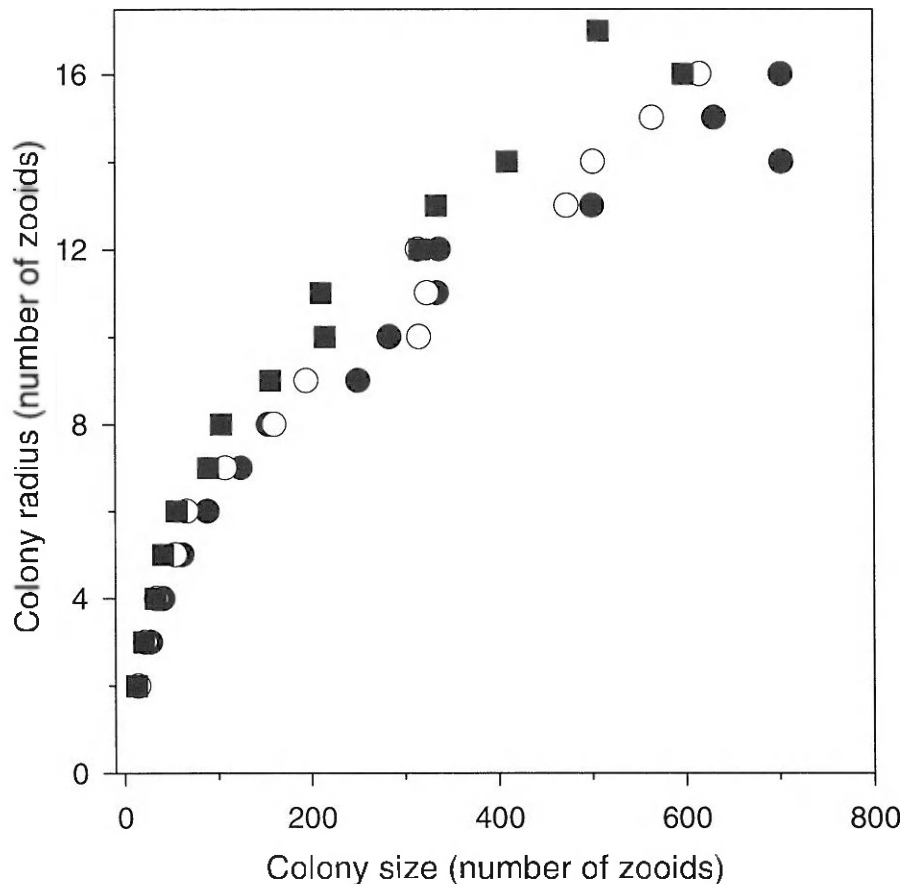


Fig. 3. Relationship between maximum colony radius (measured as the number of zooids) and the total number zooids for colonies having 0–25% (filled circles), 26–50% (open circles) and 51–90% (filled squares) of their colony periphery in contact with other colonies. Analysis of covariance (logarithmically transformed data) indicated statistically significant differences between colonies growing in different degrees of crowding ($P < 0.05$).

fluence of crowding on colony growth was studied by comparing the colony radius measured in zooids with the total number of zooids in the colony, and grouping colonies into those with 0–25%, 26–50% and 51–90% of their periphery obstructed (Fig. 3). Analysis of covariance showed that colonies whose growth brought them into contact with other colonies had significantly smaller zooids, and hence crowded colonies had a significantly smaller total area for a given number of zooids (ANCOVA, logarithmically transformed data, $F = 14.8$, $p < 0.01$). These smaller zooids were, obviously, those closest to the zone of contact.

Once bryozoan colonies reach a threshold size or age, some zooids become sexually active and start to form ovicells. In the populations of *Fenestrulina rugula* studied here, ovicells were first produced by colonies above about 150 zooids in size. This proportion increased to a maximum of about 75% total colony zooids with associated ovicells in colonies above about 900 zooids in size. In addition to the inhibitory influence on growth, crowding also had a pronounced and progressive effect on the onset and development of sexual activity. Thus with increased crowding there was a decrease in the size at which colonies first pro-

duced ovicells, and the size at which the maximum proportion of zooids with associated ovicells was reached (Fig. 4). The size at which a typical colony had 50% of its zooids sexually reproductive decreased by ~60% for a colony which was heavily crowded compared with one growing unobstructed. Colony crowding did not, however, have any apparent effect on the actual magnitude of the maximum proportion of sexually active zooids.

Many young colonies were found to be clustered around more developed colonies, suggesting that the older colonies are the parents of the smaller ones and that the period of time spent by at least some larvae in the water column is short. The proportion of larvae which settle nearby and the proportion (if any) which travel a significant distance is, of course, unknown. However, since these colonies are found largely on the undersides of rocks in a shallow water cobble/boulder field, it would seem likely that most colonies are formed by larvae settling close to their parents.

The result of crowding and competition for space among bryozoan colonies, as with sessile representatives of any group of organisms, inevitably results in interactions between adjacent colonies (Jackson 1979).

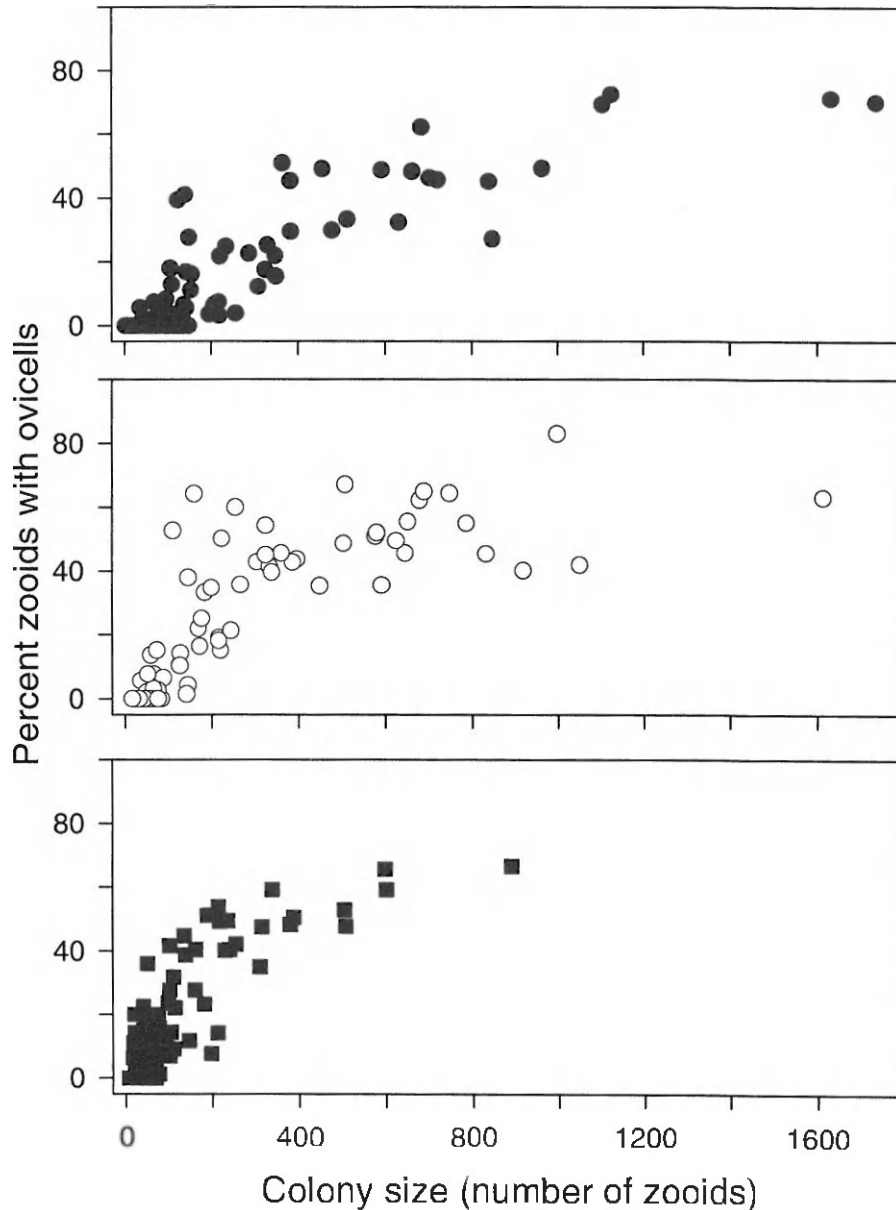


Fig. 4. Relationship between percentage of total colony zooids carrying ovicells and colony size. Individual plots are given for colonies having 0–25% (filled circle), 26–50% (open circles) and 51–90% (filled squares) of their colony periphery in contact with other colonies.

The results of such interactions may be either standoffs (tied outcome) or growth by one colony over another. As ten other species of cheilostome bryozoans were present in addition to the assemblage dominant, *Fenestrulina rugula*, there was potential for both interspecific and intraspecific interactions. Of the 456 total number of interactions observed, the great majority (402, 88.2%) involved *F. rugula*. Intraspecific interactions accounted for 343 of the total observed, of which all but two were indeterminate (that is, they resulted in a tie as opposed to a win or loss). Encoun-

ters between colonies of *F. rugula* almost invariably resulted in immediate cessation of growth in the direction of the neighbour, irrespective of colony size, encounter angle, or crowding. A degree of morphological plasticity also developed in zooids growing obliquely towards neighbouring colonies, such that in some the direction of growth was changed mid-zooid, and zooids also became a fraction of their normal width. Occasionally a zooid from one colony even fused with another from the neighbour colony. In contrast to the indeterminate nature of interactions be-

Table 2. Matrix showing outcome of interactions between encrusting cheilostome bryozoans on rocks at Rothera Point, Antarctica. Each box shows the outcome of interactions between the species at the top of the matrix, and the species to the left of the matrix. In each box the data shown are the number of ties (upper left), the number of wins by the species to the top of the matrix (upper right), the number of wins by the species to the left of the matrix (bottom left), and the total number of interactions (bottom right). This presentation follows that of Turner & Todd (1994).

	<i>A. inchoata</i>	<i>M. brevisissima</i>	<i>X. rangifer</i>	<i>E. antarctica</i>	<i>E. tridens</i>	<i>Smittina</i> sp.	<i>H. inerma</i>	<i>C. bougainvillei</i>	<i>F. rugula</i>	<i>C. antarctica</i>	<i>A. antarctica</i>
<i>Archnopusia inchoata</i> Hayward & Thorpe	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0
<i>Micropora brevisissima</i> Waters	0 0 0 0	0 0 2 2	0 0 1 1	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	18 18 3 3	0 0 0 0	0 0 0 0
<i>Xylochoatridens rangifer</i> Hayward & Thorpe	0 0 0 0	0 0 2 3	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	4 4 0 0	0 0 0 0	0 0 0 0
<i>Ellisina antarctica</i> Hastings	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	4 4 0 0	0 0 0 0	0 0 0 0
<i>Escharoides tridens</i> (Calvet)	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	1 1 3 3	0 0 0 0	0 0 0 0
<i>Smittina</i> sp.	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	9 9 11 11	0 0 0 0	0 0 0 0
<i>Hippadanella inerma</i> (Calvet)	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	2 2 4 4	0 0 0 0	0 0 0 0
<i>Celleporella bougainvillei</i> (d'Orbigny)	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	1 1 0 0	0 0 0 0	0 0 0 0
<i>Fenestulina rugula</i> Hayward & Ryland	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	338 2 0 1	1 1 3 3	0 0 0 0
<i>Celleporella antarctica</i> Moyano & Gordon	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	2 340 4 5	7 7 11 11	0 0 0 0
<i>Aimulosia antarctica</i> (Powell)	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0	0 0 0 0

tween colonies of *F. rugula*, almost all (97.3%) of the interactions involving two different species were determinate. Some species, such as the dominant overgrowth competitor *Archnopusia inchoata* (which won all encounters in which it was involved), had entirely determinate outcomes to all interactions (Table 2). Although the study species have been ranked according to win/loss scores (increasing in interaction strength from right to left in Table 2), because there are relatively few interactions not involving *F. rugula*, the only species whose position in the sequence can be viewed with confidence is *F. rugula* itself. *F. rugula*, despite being the major space occupier, was a relatively weak overgrowth competitor winning just 19.2% of encounters with other species.

The level of annual mortality in the overall population of *Fenestulina rugula* at Rothera was investigated by comparing the surviving number of recruits within each year group (Fig. 5). Whereas there were 724 first-year recruits, only one four-year-old colony was present. The slope of the regression line indicates that the average mortality in the study population of *F. rugula* was 89%, and the close fit of the statistical model suggests relatively little variation in mortality or recruitment over the four-year period. For some colonies, such as some of those formed asexually by col-

ony fragmentation, age was difficult to ascertain. The estimate of population mortality may thus be slightly higher than the real value.

Discussion

Much of community ecology has been concerned with the role of biological interactions in structuring the community (Hall *et al.* 1992). A small number of communities have, however, been studied where the structure is influenced primarily by physical disturbance (Dayton 1992). In the Southern Ocean, marine communities below the range of frequent direct impact by ice tend to be structured primarily by biological interactions (Dayton *et al.*, 1974). At shallower depths, however, assemblage structure is influenced primarily by physical disturbance, and most importantly by ice scour (Barnes *et al.*, 1996). Even within communities subject to frequent catastrophic disturbance by ice, however, it is relatively unusual for a community to be entirely dominated by just one species as is clearly the case in the sublittoral Antarctic community studied here. Thus, whilst Barnes *et al.* (1996) found a similar number of bryozoan colonies on rocks of similar size and depth at Signy Island, Antarctica (60°43'S, 45°36'W, 1400 km NE of Rothera Point), the number

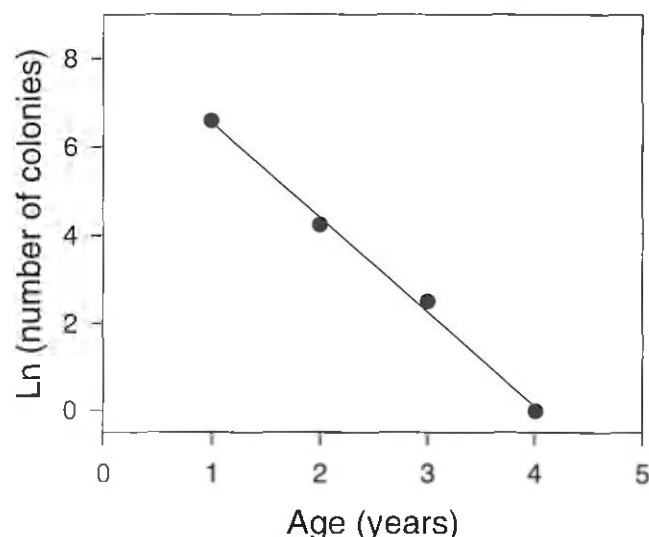


Fig. 5. Survival of colonies with time. The fitted least-squares regression shows the relationship between the number of colonies (transformed to natural logarithms) and colony age. The slope of the regression line indicates a mean annual mortality of 89%.

of bryozoan species on the larger rocks at Signy Island was nearly twice that of the present study (Barnes & Arnold in press). Furthermore, no one species comprised more than 13.6% of all colonies at Signy Island, whereas *Fenestrulina rugula* represented 85.9% of all colonies at Rothera Point. Whittaker (1965) and McNaughton & Wolf (1970) have suggested four measures of the importance of a given species within the community; these are cover, biomass, relative abundance, and productivity. While *Fenestrulina rugula* has the largest cover and almost certainly biomass, there were on average nearly four times as many spirorbid individuals than colonies of *F. rugula* (Table 1). These figures are problematical to compare, however, not only because there may be more than one spirorbid

Table 3. Growth in two polar (*Fenestrulina rugula*, *Celleporella antarctica*) and one temperate (*Celleporella hyalina*) species of cheilostomatid bryozoan. The data are the mean number of zooids in a colony as a function of age. Differences in growth rate between polar and temperate species combine the effects of inherent growth rate and differing lengths of growing season.

Age (years)	<i>Fenestrulina rugula</i>	<i>Celleporella antarctica</i>	<i>Celleporella hyalina</i>
1	178	102	>4,000
2	383	291	
3	931	509	
4	1,632	707	

species involved, but also because of the difficulty in comparing colonial (modular) and solitary (unitary) growth forms. Overall, however, the data suggest clearly that in this physically heavily-disturbed habitat, the assemblage is dominated by *Fenestrulina rugula*.

The proportion of *Fenestrulina rugula* colonies examined here with asexual (fragmentation) rather than sexual origins ranged from 0–14%. Jackson & Winston (1981) also found a relatively high incidence of colony formation through fragmentation in the fast growing encrusting tropical species *Drepanophora tuberculatum*. In contrast, a study of 26 (fossil) bryozoan species by Thomsen & Hakansson (1995) found no examples of asexual colony origins in the 10 encrusting species examined, although they found high proportions of asexual origins in erect species. Studies of Recent erect bryozoan species have also confirmed that substantial proportions of the population may be initiated by fragmentation, particularly in the Antarctic (Winston 1983, Barnes 1995c). One of the major conclusions of Thomsen & Hakansson (1995) was that growth habit or habitat determined the prevalence of asexual reproduction by fragmentation. In the present study, the level of disturbance (rock turnover) is clearly responsible for the partial damage of colonies causing new colony formation from remaining fragments. Whilst it is clear from the relationship shown in Fig. 1 that the proportion of asexually derived colonies generally decreases with rock surface area (presumably because of decreased frequency of turnover), it is possible that the inverse is true below a certain rock size (~50–60 cm²). This may be because whilst a small pebble may be frequently moved or overturned by physical disturbance, its own weight results in less damage to the encrusting biota. Given the small number of rocks examined in this study, more data are needed on the relationship between substratum rock size, disturbance frequency, and *Fenestrulina rugula* ecology.

The only other data on the growth rate of encrusting polar bryozoans are from two studies using artificial substrata (Barnes 1996, Stanwell-Smith & Barnes 1997). The present study provides data on the annual growth of *Fenestrulina rugula* over a four-year period. These data do, however, assume that the growth checks are annual. Table 3 compares the mean annual growth with age of *F. rugula* from Rothera Point with that of an ecologically similar species from Signy Island, *Celleporella antarctica* (Barnes unpubl. data), and a species from temperate waters (R.N. Hughes pers. com.). Clearly the growth rates of the two polar species are considerably slower than the temperate species *Celleporella hyalina*. The fastest growing colony of *F. rugula* (at 0.64 mm² per day) was also nearly

five times slower than the average of the fastest growing colonies of the tropical encrusting species examined by Winston & Jackson (1984). The fact that the colonies of *F. rugula* generally were larger than those of the other encrusting bryozoan species present in this study suggests *F. rugula* is, however, probably one of the faster-growing encrusting Antarctic bryozoans. The variation of growth rates between *F. rugula* colonies found here is typical of the high intra-specific variation which has been found not only in temperate bryozoans (Vail & Wass 1981, Winston & Jackson 1984, Bayer & Todd 1997), but also in those encrusting Antarctic bryozoans studied to date (Stanwell-Smith & Barnes 1997).

Cancino & Hughes (1987) found that water flow, food supply and probably sedimentation influenced the growth of *Celleporella hyalina*. Bayer et al. (1994) found that in addition to food concentration, there was also a strong genetic component to variation in colony growth rate and form of another temperate species, *Electra pilosa*. Despite the overall variation in within-year growth, there was still significant variation related to the immediate environs of the colony. The most obvious influence on growth (and reproduction) in the populations of *Fenestrulina rugula* studied here was that of crowding (mostly by other colonies of *F. rugula*). A similar result has been described for the anascan *Membranipora membranacea* (Harvell et al. 1990). In addition to the irregularity of shape imposed on crowded colonies (and zooids) of *F. rugula*, the rate of zooid production decreased and many of the zooids produced were smaller. This was because of the reduced active region of the growth margin and the decreased area available for zooids to fit between neighbours.

Crowding also had a pronounced influence on the onset and ratio of ovicell formation (sexual reproduction). A switch from growth to sexual reproduction on exhaustion of available substratum has been recorded in a variety of clonal taxa (reviewed by Hughes, 1989). A colony with over 50% of its growth margin bordering other colonies may reach the ratio of one ovicell to every other autozooid within a year's growth, half the time taken by a colony growing without obstructions. The proportion of autozooids of *Fenestrulina rugula* with associated ovicells peaked at about 80% (regardless of the degree of crowding), compared to between just 12–25% in the erect Antarctic bryozoans studied to date (Barnes & Clarke 1998). The capacity for relatively fast growth coupled with an early onset and high rate of ovicell production contrasts with the findings of Winston & Jackson (1984), who showed that fast-growing tropical species did so at the expense of delayed sexual maturity.

Benthic assemblages that encrust hard substrata are characterised by intense competition for space once growing individuals or colonies come into contact with their neighbours. The resulting interactions have been studied widely in a variety of benthic assemblages and taxa, and across most latitudes (Jackson 1979, Rubin 1982, Lopez Gappa 1989, Tanaka & Nandukumar 1994, Turner & Todd 1994). The interactions observed in this study show that *F. rugula* is a poor overgrowth competitor relative to other bryozoan species present in the assemblage. In the only other study of competitive interactions in a polar bryozoan assemblage (at Signy Island: Barnes & Rothery, 1996), *F. rugula* was also found to be a poor overgrowth competitor relative to other species present. This poses the question as to why *F. rugula* has not come to dominate similar substrata at Signy Island in the way that it does so further south at Rothera, despite being similarly abundant at the two sites. The answer is probably related to differences in the frequency of disturbance between the two sites.

Ward & Thorpe (1989) found that the related temperate species *Fenestrulina malusii* exhibited a similarly low relative competitive ability within an assemblage of bryozoans encrusting ephemeral habitats, and it is possible that the combination of poor competitive ability and relatively fast growth are a genus trait. *F. malusii* was also similar to *F. rugula* in that the high numbers of within-species interactions resulted in very few cases (<0.6%) of overgrowth, together with occasional instances of zooids from different colonies fusing together (homosyndrome) (Ward & Thorpe 1989).

The maximum lifespan in any of the colonies observed was four years. It is possible, however, that some of the colonies with fragmental asexual origins were older; because of their incomplete nature these colonies cannot be aged from growth rings. The annual population mortality of 89% in *Fenestrulina rugula* at Rothera, whilst appearing high, is lower than reported for some other populations of encrusting cheilostome bryozoans (Vail & Wass 1981, Cancino & Hughes 1987, Hughes 1990, Turner & Todd 1993). Individuals of many species are probably capable of living much longer (Winston & Jackson 1984, Rubin 1985), and the population mortality curve is dictated primarily by the frequency of physical disturbance. Each rock therefore appears to have a lower than annual frequency of catastrophic disturbance, with probably only substratum microtopography and chance deciding which colonies survive. The sample of rocks used in this study was too small to test for any effects of rock size on mortality in *F. rugula*. Future studies are planned to examine the turnover rate of rocks of different sizes,

and relate these to the population dynamics of the encrusting bryozoan fauna.

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References

- Allen TFH & Starr TB 1982. Hierachy: Perspectives for ecological complexity. University of Chicago press, Chicago.
- Barnes DKA 1995a. Sublittoral epifaunal communities at Signy Island, Antarctica: I. The ice foot zone. *Mar. Biol.* 121: 555–563.
- 1995b. Sublittoral epifaunal communities at Signy Island, Antarctica: II. Below the ice foot zone. *Mar. Biol.* 121: 565–572.
- 1995c. Seasonal and annual growth in erect species of Antarctic bryozoans. *J. Exp. Mar. Biol. Ecol.* 188: 181–198.
- 1996. Low levels of colonisation in Antarctica: the role of bryozoans in early community development. In *Bryozoans in space and time*. Gordon DP, Smith AM & J.A. Grant-Mackie, eds, pp. 19–28. Wellington, New Zealand.
- Barnes DKA & Arnold RJ (in press). Possible latitudinal clines in Antarctic intertidal and subtidal zone communities encrusting ephemeral hard substrata. *J. Biogeogr.*
- Barnes DKA & Clarke A 1995. Epibiotic communities on sublittoral macroinvertebrates at Signy Island, Antarctica. *J. Mar. Biol. Ass. U. K.* 65: 689–703.
- 1998. Seasonality of polypide recycling and sexual reproduction in some erect Antarctic bryozoans. *Mar. Biol.* 131: 647–658.
- Barnes DKA & Rothery P 1996. Competition in encrusting Antarctic bryozoan assemblages: outcomes, influences and implications. *J. exp. Mar. Biol. Ecol.* 196: 267–287.
- Barnes DKA, Rothery P, & Clarke A 1996. Colonisation and development in encrusting communities in the antarctic intertidal and sublittoral. *J. Exp. Mar. Biol. Ecol.* 196: 251–265.
- Barry JP 1989. Reproductive responses of a marine annelid to winter storms: an analog to fire adaptation in plants? *Mar. Ecol. Prog. Ser.* 54: 99–107.
- Bayer MM, Cormack RM, & Todd CD 1994. Influence of food concentration on polypide regression in the marine bryozoan *Electra pilosa* (L.) (Bryozoa: Cheilostomata). *J. Exp. Mar. Biol. Ecol.* 178: 35–50.
- Bayer MM & Todd CD 1997. Evidence for zooid senescence in the marine bryozoan *Electra pilosa*. *Invert. Biol.* 116: 331–340.
- Cancino JM, & Hughes RN 1987. The effect of water flow on growth and reproduction of *Celleporella antarctica* (L.) (Bryozoa: Cheilostomata). *J. Exp. Mar. Biol. Ecol.* 112: 109–130.
- Coggan R 1994. Rothera marine survey 1993–1994 — Biological report. Unpublished British Antarctic Survey report R/93/Nm, British Antarctic Survey, Cambridge
- Dayton PK 1971. Competition, disturbance, and community organisation: The provision and subsequent utilisation of space in a rocky intertidal community. *Ecol. Monogr.* 41: 351–389.
- 1992. Community landscape: Scale and stability in hard bottom marine communities. In: *Aquatic ecology, scale, pattern and process*. Giller PS, Hildrew AG & Raffaelli DG, eds., pp. 289–332. Blackwell Scientific, Oxford.
- Dayton, Robilliard GA, Paine RT, & Dayton LB 1974. Biological accommodation in the benthic community at McMurdo Sound, Antarctica. *Ecol. Monogr.* 44: 105–128.
- De Kluijver MJ 1993. Sublittoral hard-substratum communities off Orkney and St. Abbs (Scotland). *J. Mar. Biol. Ass. U.K.* 73: 733–754.
- Dobbs FC & Vozarik JM 1983. Immediate effects of a storm on coastal infauna. *Mar. Ecol. Prog. Ser.* 11: 273–279.
- Hall SJ, Raffaelli D, & Thrush SF 1992. Patchiness and disturbance in shallow water benthic assemblages. In: *Aquatic ecology, scale, pattern and process*. Giller PS, Hildrew AG & Raffaelli DG, eds., pp. 333–375. Blackwell Scientific, Oxford.
- Harvell CD, Caswell H, & Simpson P 1990. Density effects in a colonial monoculture: experimental studies with a marine bryozoan (*Membranipora membranacea*). *Oecologia* 82: 227–237.
- Horn HS 1974. The ecology of secondary succession. *Annual Review of Ecological Systems* 5: 25–37.
- Hughes RN 1989. *A functional biology of clonal animals*. London, Chapman and Hall. 331 pp.
- Hughes TP 1990. Recruitment limitation, mortality, and population regulation in open systems: a case study. *Ecology* 71: 12–20.
- Jackson JBC 1979. Overgrowth competition between encrusting cheilostome ectoprocts in a Jamaican cryptic reef environment. *J. Animal Ecol.* 48: 805–823.
- Jackson JBC & Winston JE 1981. Modular growth and longevity in bryozoans. In: *Recent and fossil Bryozoa*. Larwood GP & Nielsen C, eds., pp 121–126. Olsen and Olsen, Denmark.
- Jorgensen BB 1980. Seasonal oxygen depletion in the bottom waters of a Danish fjord and its effect on the benthic community. *Oikos* 34: 68–76.
- Lopez Gappa JJ 1989. Overgrowth in an assemblage of encrusting bryozoans settled on artificial substrata. *Mar. Ecol. Prog. Ser.* 51: 121–130.
- McNaughton SJ & Wolf LL 1970. Dominance and the niche in ecological systems. *Science* 167: 131–142.
- Rubin JA 1982. The degree of intransivity and its measurement in an assemblage of encrusting cheilostome Bryozoa. *J. Exp. Mar. Biol. Ecol.* 60: 119–128.
- 1985. Mortality and avoidance of competitive overgrowth in encrusting Bryozoa. *Mar. Ecol. Prog. Ser.* 23: 291–299.
- Stanwell-Smith DP & Barnes DKA 1997. Benthic community development in Antarctica: recruitment and growth on settlement panels at Signy Island. *J. exp. mar. Biol. Ecol.* 212: 61–79.
- Stebbing ARD 1973. Competition for space between the epi-

- phytes of *Fucus serratus* L. J. Mar. Biol. Ass. U. K. 53: 247–261.
- Tanaka M & Nandakumar K 1994. Measurement of the degree of intransitivity in a community of sessile organisms. J. Exp. Mar. Biol. Ecol. 182: 85–95.
- Thomas MLH & White GN 1969. Mass mortality of estuarine fauna at Bideford P.E.I., associated with abnormally low salinities. J. Fish. Res. Board Canada 26: 701–704.
- Thomsen E & Hakansson E 1995. Sexual versus asexual dispersal in clonal animals: examples from cheilostome bryozoans. Paleobiology 21: 496–508.
- Turner SJ & Todd CD 1993. The early development of epifaunal assemblages on artificial substrata at two intertidal sites on an exposed rocky shore in St. Andrews Bay, N.E. Scotland. J. Exp. Mar. Biol. Ecol. 166: 251–272.
- 1994. Competition for space in encrusting bryozoan assemblages: the influence of encounter angle, site and year on outcome variability. J. mar. biol. Ass. U. K. 74: 203–220.
- Vail LL & Wass RE 1981. Experimental studies on the settlement and growth of bryozoa in the natural environment. Aust. J. Mar. Freshwater Res. 32: 639–656.
- Ward MA & Thorpe JP 1989. Assessment of space utilisation in a subtidal temperate bryozoan community. Mar. Biol. 103: 215–224.
- Whittaker RH 1965. Dominance and diversity in land plant communities. Science 147: 250–260.
- Winston JE 1983. Patterns of growth, reproduction and mortality in bryozoans from the Ross Sea, Antarctica. Bull. mar. Sci. 33: 688–702.
- Winston JE & Jackson JBC 1984. Ecology of cryptic reef communities. IV. community development and life histories of encrusting cheilostome bryozoa. J. Exp. Mar. Biol. Ecol. 76: 1–21.
- Yeo RK & Risk MJ 1979. Intertidal catastrophies : effect of storms and hurricanes on intertidal benthos of the Minas Basin, Bay of Fundy. J. Fish. Res. Board Canada 36: 667–669.