

Do life patterns differ between two Scotia Arc localities? A preliminary investigation of three erect Antarctic bryozoan species

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Abstract: Erect bryozoans are extremely abundant and diverse in polar waters and individual species may span a wide range in latitude and bathymetry. A number of aspects of lifestyle, including polypide recycling, embryo production, distribution, growth form and epibiosis were compared in three species of erect bryozoans. These were collected from two locations; Signy Island (60°S) and Rothera Point, Adelaide Island (68°S) and a variety of depths. All three species were in similar stages of polypide cycling within and between the two sites. In the species *Isosecuriflustra rubefacta* and *Nematoflustra flagellata* the rate of brown body production (polypide generations) was slower at Signy Island than at Rothera Point. There was little difference between localities (within species) in the pattern of embryo production and no change in embryo size with depth. Embryos of *I. rubefacta*, however, were significantly larger at Rothera Point than at Signy Island. The proportion of the community occupied by each species changed with depth, but all three species occurred in shallower water at Rothera Point than at Signy Island. Fouling by epibionts decreased with increasing depth and from Signy Island to Rothera Point, both in terms of per cent cover and number of colonizing taxa. Possible trends with depth and latitude are compared with other studies involving bryozoans. The literature on Antarctic benthic taxa, in general, is also considered to determine whether trends within the Bryozoa are reflected in other groups.

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Introduction

The extension of detailed investigation of latitudinal trends in ecology into polar waters has only become possible in the last few decades. Some of the hypotheses and 'rules' have held under closer scrutiny, e.g. that of slower growth rates, greater longevity, reduced basal metabolic rates and lowered tempo of reproduction (Clarke 1991, Pearse *et al.* 1991). There have been notable, though rare, exceptions to some of these generalizations including annual bryozoans (Winston & Heimberg 1988) and fast growing sponges (Dayton 1989). Other generalizations, most famously Thorson's rule (Mileikovsky 1971) on the frequency of a suite of reproductive and larval characters, have proved true for only a few taxa (Pearse *et al.* 1991, Stanwell-Smith *et al.* 1999). The duration of phytoplankton abundance has, for certain fractions (nanoplanktonic ciliates and flagellates), been found to be greater than previously believed (Clarke & Leakey 1996). Polar suspension feeders have been found to be active (in terms of feeding and growth) for much or even all of the year (Barnes & Clarke 1994). Members of a number of phyla have been found in intertidal zones experiencing a daily level of temperature and salinity fluctuation an order of magnitude greater than typical annual levels in the subtidal zone (Barnes *et al.* 1996). This casts doubt on how stenothermal many Antarctic species are and whether they will thus be highly sensitive indicators of global warming (Copley 1998). Even

the levels of benthic diversity in Antarctica have been found to be locally as high as some tropical regions (Brey *et al.* 1994) suggesting that the trend of decreased diversity away from the tropics (Stehli *et al.* 1967, Clarke 1992) does not hold in the Southern Hemisphere.

Bryozoans are modular animals formed by serial budding of clonal units called zooids from an original sexually produced base or ancestrula. Cheilostomatid bryozoans may have a variety of types of zooids each specialized for a particular function; e.g. autozooids which suspension feed using a lophophorate arrangement of tentacles. The colony form may be encrusting or in a variety of erect morphologies. Both the range of morphologies, individual abundance and species richness of the order Cheilostomatida and the phylum Bryozoa are high in Antarctic waters (Hayward 1995). With the exception of another lophophorate phylum, the brachiopods (Foster 1974), a polar centre for diversity and abundance is unique. Polar bryozoans typically grow more slowly but may be comparable to similar forms in temperate or tropical regions (Winston 1983, Barnes 1995a, Brey *et al.* 1999). The lifetime of both the functional feeding unit, the polypide, and the zooid (which may have a number of generations of polypides) are exceptionally long in polar waters; up to nine months and five years respectively (Barnes & Clarke 1998a). Therefore colonies of polar bryozoans, as with many other

unitary Antarctic taxa (e.g. brachiopods, Peck & Brey 1996), have extended life spans (Barnes 1995a). This has made the taxon a valuable one for the analysis of seasonal and interannual variations characteristic of the polar environment (Clarke 1988, Arntz *et al.* 1994).

Latitudinal changes in the growth and mortality of encrusting bryozoans have been found along the Scotia Arc from South Georgia to Adelaide Island (Barnes & Arnold 1999). Mortality was found to increase with latitude, mediated through the catastrophic disturbance of shallow water rocks probably by increased rates of ice scour. An associated finding was increased sublethal mortality reducing a colony to several fragments of asexual origin, a phenomenon also documented from the fossil record (see McKinney & Jackson 1991, Thomsen & Håkansson 1995). In very shallow water the elevated frequency of disturbance also results in encrusting assemblages at 68°S being dominated by just one very fast growing (though competitively inferior in overgrowth competition) species (Barnes & Clarke 1998b). Surprisingly, though, there is some evidence for increased growth rates with increased latitude, the converse to the normal pattern of growth rate from the tropics to the poles (Barnes & Arnold 1999).

This study compares polypide recycling, embryo production, distribution, growth form and epibiosis of three species of erect bryozoans from two locations; Signy Island (60°S) and Adelaide Island (68°S). The seasonal life patterns of two of these three species, *Isosecuriflustra rubefacta* Moyano and *Nematoflustra flagellata* (Waters), have been studied in depth and provide an important reference point for this work (Barnes & Clarke 1998a). The purpose of the comparison is to investigate what type and magnitude of differences occur between three of the most ubiquitous erect species of bryozoans in shallow Antarctic assemblages (Winston & Heimberg 1988, Barnes 1995b).

Study sites and species

The two study sites used in this investigation were adjacent to the British Antarctic Survey research stations on Signy Island (60.5°S, South Orkney Islands) and Rothera Point, Adelaide Island (68°S, Antarctic Peninsula). The seasonal cycle of nutrients, chlorophyll and various environmental parameters have been described in detail at Signy Island by Clarke *et al.* (1988) and Clarke & Leakey (1996). Both sites are characterized by rocky boulder scree with occasional rock faces and an alternation of open water and fast ice periods. Although anchor ice is undescribed from either site (see Dayton *et al.* 1970) both sites experience frequent ice scour during open water periods, Rothera Point more so than Signy Island (Barnes & Arnold 1999). Erect cheilostomatid bryozoans were collected from Signy Island at 40 m, 100 m and 150 m using SCUBA and a towed Aggasiz trawl in December 1992. Specimens were also collected from Rothera Point using SCUBA in December 1994 and December 1997.

Abundance of each species was estimated in terms of relative numbers of individuals per trawl/dive. Differences of all examined parameters in relation to the year of collection are assumed to be minor as this was found to be the case for two of the study species (*Isosecuriflustra rubefacta* and *Nematoflustra flagellata*) between 1990 and 1993 (Barnes, unpublished data). All material was preserved in 4% buffered formalin and analysed under binocular microscope in Ireland.

Erect cheilostomatid bryozoans were chosen for study for a number of reasons:

- 1) They were extremely abundant at both sites and across a range of depths.
- 2) Their translucent nature facilitates study of polypide recycling and embryo development.
- 3) Recent advances in taxonomy (Hayward 1995) have made identification relatively easy.
- 4) Three abundant species were common to the two sites and across depths.

Of the three species selected for investigation, the ecology of two (*Isosecuriflustra rubefacta* [formerly known as *Alloeflustra tenuis* see Moyano 1996] and *Nematoflustra flagellata*) has been the subject of a number of ecological studies. These have included polypide recycling and sexual reproduction (Barnes & Clarke 1998a), epibiotic colonization (Barnes 1994), vertical distribution (Barnes 1995b) and growth (Barnes 1995a). These were aspects considered in the present study (albeit briefly in the case of growth). The third species, *Kymella polaris* (Waters), is one of the most abundant and ubiquitous Antarctic bryozoans and has been described from many locations (e.g. Winston & Heimberg 1988, Winston & Hayward 1994, Barnes 1995b).

All specimens were examined for patterns of polypide activity/recycling as per the methods of Dyrinda & Ryland (1982). Polypides in zooids from the growth margin (growing tip) to 60 zooids back (towards the colony base) were assigned to one of three classes 'differentiating', 'active' or 'degenerated' (brown bodies). The patterns of polypides in each class were plotted in relation to the growth margin. The number of brown bodies (previous polypide generations) was also plotted relative to the growth margin. The regression lines resulting from the linear component of such plots were compared, between sites for equality of slope, using the Generalized Linear Model (GLM). The presence of developing embryos was recorded in each specimen in terms of the number of embryo 'bands', the proportion of zooids with embryos and the diameter of embryos. Differences between sites, in these embryo parameters, were analysed using Mann Whitney non-parametric tests. The gross colony morphology was recorded for each species at each depth and site. The approximate age of specimens (for *Isosecuriflustra rubefacta* and *Nematoflustra flagellata*) was recorded using the data from the previous study of Barnes (1995a). This involved the assumption that the rate of growth was not significantly different between

depths or sites. Unlike the former two species the growth of *Kymella polaris* showed discontinuities, which were assumed, as with previously measured species (Winston 1983, Barnes 1995a), to be typically annual.

Epibiota was recorded in the form of percent cover of the front surface (that which active polypides emerge from, not applicable in the bilaminar species *Kymella polaris*) and back surface of each colony. The number of epibiont species on the front and back surfaces, along with the total number of epibiont phyla were also recorded. These were compared between depths and sites (again) using the Mann Whitney non-parametric statistic. Differences in abundance and vertical distribution are discussed using data from both the present study and the existing literature.

Results

Polypide recycling

The patterns of polypide activity are similar between all three species (Fig. 1). Most of the zooids at the GM (growth margin) are differentiating. From the GM to about 25 zooids back towards the base, the majority of zooids contain active polypides, after which point the majority are in the state of degeneration or brown body. The subtle differences between the three species are most evident at 20–40 zooids back from the GM: the extent of active zooids was greater in *Isosecuriflustra rubefacta* than either of the other species. There was little apparent difference in the polypide activity in either *I. rubefacta* and *Nematoflustra flagellata* between Signy Island and Rothera Point. One possible difference was that, in both species, the zone of completely degenerated polypides occurred closer to the GM at Rothera Point than at Signy Island.

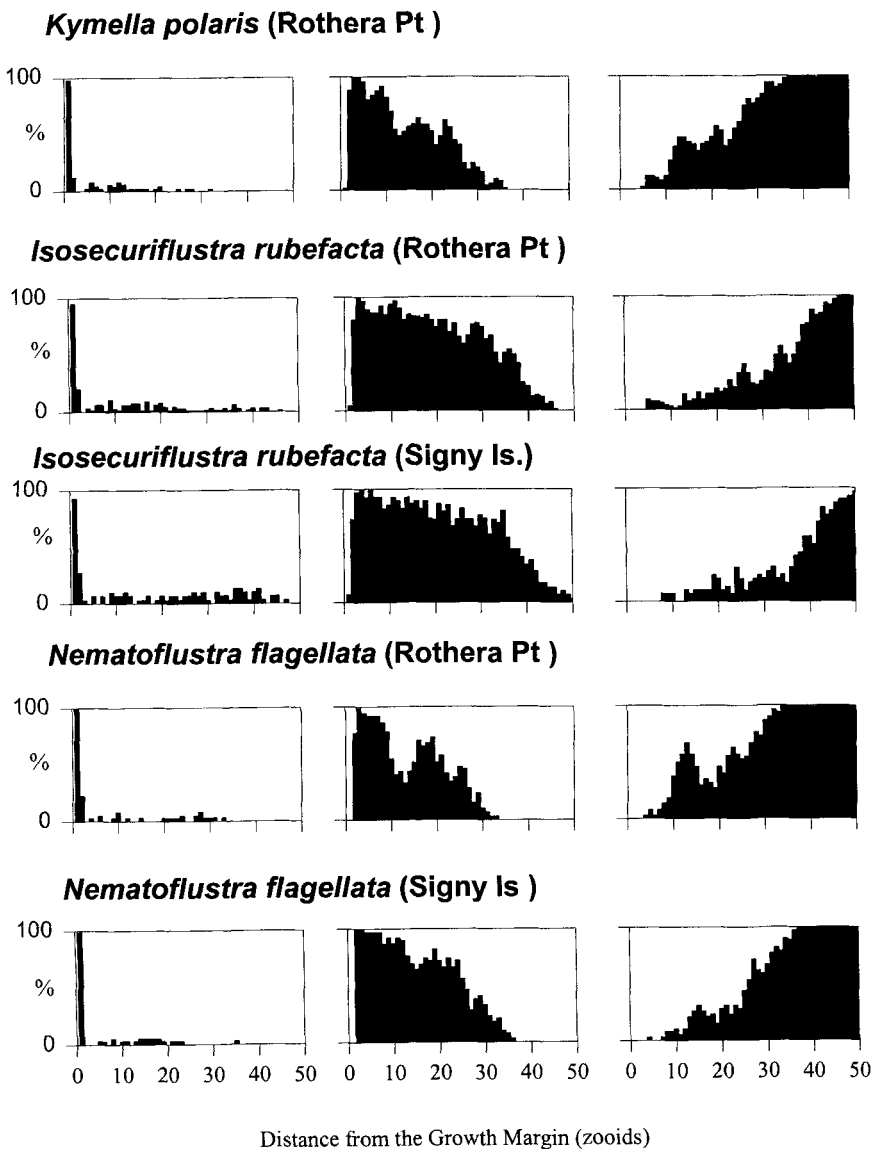


Fig. 1. Proportion (%) of polypides differentiating/redifferentiating (left) active (centre) and degenerating/in brown body (right) with distance from the growth margin in zooids.

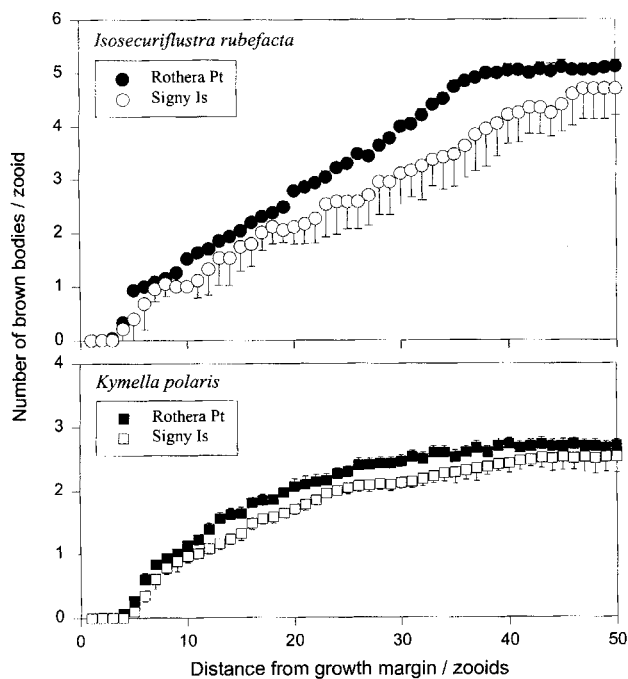


Fig. 2. Number of brown bodies per zooid with distance from the growth margin in zooids. Data are shown for *Isolecuriflustra tenuis* and *Kymella polaris* for Rothera Point (●) and Signy Island (○). Data are presented as mean with standard error bars.

The region of polypide inactivity may be examined using a different method; that of plotting the number of brown bodies per zooid with distance from the GM (Fig. 2). In both *Isolecuriflustra rubefacta* and *Nematoflustra flagellata* the rate of brown body production (polypide generations) was slower at Signy Island than Rothera Point (*I. rubefacta* illustrated only). GLM comparison of the region from 0–40 zooids from the GM (the part of the graphs to which a regression line can be fitted) showed a significant difference between the slopes ($F = 99.2, P < 0.001$). The rate of brown body production in *Kymella polaris* was similar to that of *I. rubefacta* and *N. flagellata* up to about 15 zooids from the GM. After this point the number of brown bodies with distance from the GM reach plateaux. If brown body formation is synonymous with polypide generations (Barnes & Clarke 1998a) only half the number of polypide generations occurred in *K. polaris*. Although brown body production was slower at Signy Island than Rothera Point in *K. polaris*, these differences were insignificant ($F = 1.4, P = 0.2$).

Sexual reproduction (embryo production)

The proportion of zooids with embryos and the number of 'bands' of embryos increased in all three species above a certain threshold size (illustrated for *Isolecuriflustra rubefacta*, Fig. 3). The largest colonies had 6–7 bands and 20–25% zooids with embryos. Figure 3 shows proportion of zooids with embryos in relation to colony length is similar in

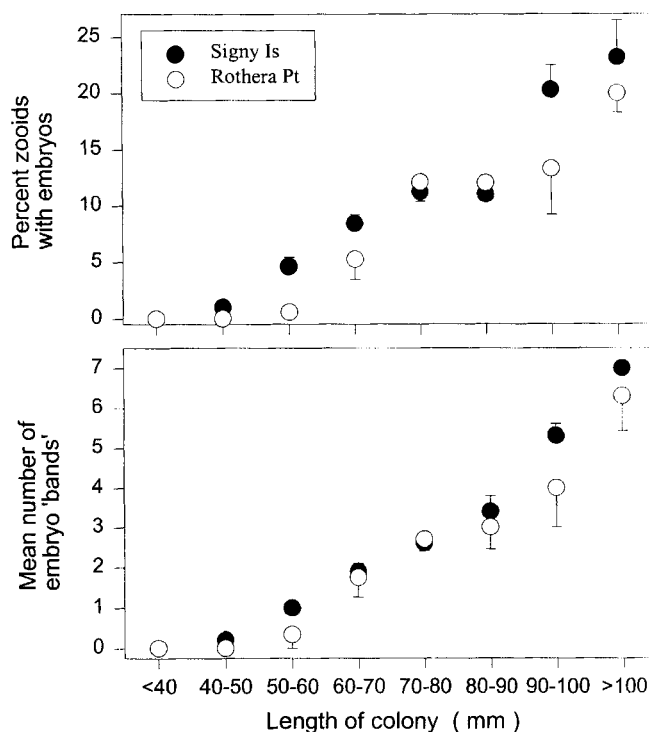


Fig. 3. a. Proportion (%) of zooids bearing ovicells with colony length in mm. b. Number of ovicell 'bands' with colony length in mm. The species are *Isolecuriflustra tenuis* for Signy Island (●) and Rothera Point (○). Data are presented as mean with standard error bars.

I. rubefacta at Signy Island and Rothera Point. In the specimens sampled, however, both *I. rubefacta* and *N. flagellata* had more bands of embryos at Rothera Point and a higher proportion of embryos per colony (as there were few small colonies) (Table I). There were more embryo bands and greater proportions of embryos in both *I. rubefacta* and *N. flagellata* with increased depth, but not significantly so (Mann Whitney *U* test, all $P > 0.05$). There was no change in embryo size with depth (in *N. flagellata*), but embryos of *I. rubefacta* were significantly larger at Rothera Point than at Signy Island (Mann Whitney *U* test, $P < 0.05$).

Abundance and vertical distribution

The proportion of *Isolecuriflustra rubefacta* and *Nematoflustra flagellata* (relative to other erect bryozoans) decreased with depth from 40–150 m, whilst the proportion of *Kymella polaris* increased. The proportion of *I. rubefacta* and *N. flagellata* in shallow water (20 m) at Rothera Point was lower than in shallow water at Signy Island, but higher than in deeper water at Signy Island. In contrast, *K. polaris* was nearly an order of magnitude more important at Rothera Point than at Signy Island in terms of the population proportion. *I. rubefacta* was not found occurring any shallower than 20 m and not abundantly occurring shallower than 38 m at Signy Island. *Nematoflustra flagellata* and *K. polaris* were not

Table I. Age, reproductive status and proportion of bryozoan species with depth and latitude for the three study species (data are presented as median and range (min-max) age in years, total number of bands of ovicells (embryos) per colony, total % of zooids with ovicells per colony, embryo width and proportion (%) of erect bryozoans at each site). Change in epibiont assemblage associated with the three study species with depth and latitude (data are presented as median and range (min-max); parameters are percent frontal and abfrontal surface covered by epibionts, number of epibiont species on front and back surfaces, the total number of phyla occurring as epibionts and the sample size).

Species Location	<i>Isoecuriflustra rubefacta</i>				<i>Nematoflustra flagellata</i>				<i>Kymella polaris</i>			
	60.5°S (Signy Island)			68°S	60.5°S (Signy Island)			68°S	60.5°S (Signy Island)			68°S
Depth	40 m	100 m	150 m	20 m	40 m	100 m	150 m	20 m	40 m	100 m	150 m	20 m
Sample age	13 (1–25)	15+ (1–6)	15+ (1–7)	10 (4–17)	12 (1–25)	15+ (0–4)	15+ (1–5)	8 (1–14)	9 (1–15)	10+ (1–3)	13+ (1–4)	7 (4–12)
Ovicell band	2 (0–5)	3 (1–6)	3 (1–7)	3 (0–8)	2 (0–4)	2 (0–4)	3 (1–5)	1 (0–6)	1 (0–3)	2 (1–3)	2 (1–4)	1 (0–3)
% Ovicells	8.3 (0–27)	11.7 (2–20)	13.3 (2–22)	10 (0–21.7)	8.3 (0–20)	10 (0–25)	11.7 (3–25)	8.5 (0–18)	2 (0–10)	2.5 (0–12)	2.5 (1–12)	2.5 (0–14)
Embryo Ø (mm)	294 (283–310)	nd (288–325)	nd (249–272)	300 (250–269)	259 (253–268)	258	259	nd	nd (263–288)	nd	nd	275
% Erect bryos	42.1	7.2	3.6	24.1	32.8	14.2	10.8	13.8	0.7	3.9	4.3	39.7
Epibiota												
% Frontal	3.2 (0–54)	1.0 (0–6)	0.5 (0–2)	0.2 (0–2)	1.1 (0–10)	0.2 (0–2)	0 (0–1)	0 (0–1.5)	4.0 (0–40)	1.0 (0–10)	0.5 (0–6.5)	0.6 (0–11)
% Abfrontal	75 (0–99)	14 (0–40)	10 (2–25)	1.0 (0–2.7)	67 (0–99)	5.0 (0–32)	3.0 (1–20)	2.0 (0–10)	–	–	–	–
Species front	3 (0–6)	1 (0–3)	1 (0–1)	1 (0–3)	2 (0–4)	0 (0–2)	0 (0–1)	0 (0–1)	2 (0–6)	1 (0–3)	1 (0–3)	1 (0–5)
Species back	3 (0–7)	2 (0–5)	2 (0–4)	1 (0–5)	2 (0–9)	1 (0–6)	1 (0–4)	2 (0–5)	–	–	–	–
Total phyla	10	5	4	8	10	5	5	7	9	5	4	10
Sample size	123	18	9	14	123	33	16	10	13	20	21	23

found shallower than 38 m. At Rothera Point, however, all three species are common at 20 m depth.

Growth and colony morphology

The youngest colonies were generally found in shallow water at Signy Island but the median age of colonies was lowest at Rothera Point, where the maximum age was also lowest (Table I). The growth morphology was similar in all three species at Signy Island and Rothera Point, but the branches of *Isoecuriflustra rubefacta* and *Nematoflustra flagellata* became thinner and more elongate with depth. *N. flagellata*, curled in shallow water, had straight branches at the deeper sites of 100 and 150 m. The morphology of *Kymella polaris* was unchanged with depth.

Epibiota

The degree of colonization of active (frontal in the case of *Isoecuriflustra rubefacta* and *Nematoflustra flagellata*) surfaces significantly decreased with depth at Signy Island (regressions, ANOVA, all $P < 0.03$) (Table I). The degree of colonization was also significantly lower on the frontal surfaces of all three species at Rothera Point than at Signy Island (Mann Whitney U test, all $P < 0.01$). Similar patterns of decreased epibiont colonization with depth occurred on the abfrontal surfaces (of *I. rubefacta* and *N. flagellata*) (regressions, ANOVA, all $P < 0.04$). As with the frontal surfaces, the degree

of colonization was significantly lower on the abfrontal surfaces of *I. rubefacta* and *N. flagellata* at Rothera Point than at Signy Island (Mann Whitney U test, all $P < 0.03$). At each depth and site the frontal surfaces (with avicularia or vibracula present) were significantly less colonized than the back surfaces (of *I. rubefacta* and *N. flagellata*) (Mann Whitney U test, all $P < 0.02$). The number of epibiont species on the surfaces of all three bryozoans also decreased with depth (regressions, ANOVA, all $P < 0.05$). The total number of epibiont phyla associated with each bryozoan species are also shown in Table I, these also seem to decrease with depth.

Discussion

Does latitude influence life patterns within Antarctic bryozoan species?

Ecologically, the high Antarctic marine environment around the continental coast differs substantially from that of the Antarctic Peninsula which in turn differs from the outlying island groups (e.g. South Orkney Islands in the present study). Apart from the obvious change in light climate, there are changes in the variability in sea temperature (Clarke 1988), duration of fast-ice (thus influencing phytoplankton 'bloom' timing and duration) and the frequency of ice impacts (Arntz *et al.* 1994). There has been much discussion of wide scale latitudinal influences on life processes, such as basal metabolism, growth, reproduction and feeding. Ikeda (1974),

Ivleva (1980) and Luxmoore (1984) have, respectively, found decreased oxygen consumption relationships with temperature in zooplankton, crustaceans and isopods. Extrapolation of this data, however, shows there to be virtually no difference in oxygen consumption within the range of sea temperatures likely to be encountered within polar regions.

Two of the study species, *Isosecuriflustra rubefacta* and *Nematoflustra flagellata*, have been found to show distinct seasonality of activity with reduced growth, cessation of feeding and degeneration of polypides into brown bodies during the winter period (Barnes & Clarke 1994, 1998a). A similar level of seasonality has been found in northern temperate/boreal cheilostomatid bryozoan species (Eggleston 1972, Dyrinda & Ryland 1982) compared to an aseasonal pattern in those from low latitudes (Jackson & Wertheimer 1985). Whilst there are clear differences between *I. rubefacta* and the other two species (greater proportion of polypides active in the former) there is little apparent variation (within a species) between the localities. The subtle increase in proportion (Fig. 1) and proximity to the growth margin (Fig. 2) of brown bodies (degenerated polypides) suggests the process of polypide recycling takes place faster at the more southerly Rothera Point. These rates of polypide generation and degeneration are very slow and the lifetime of polypides (9–10 months) and zooids (5 yr) may be an order of magnitude longer than non-polar species (see Gordon 1977).

The seasonal pattern of embryo production in erect cheilostomatid bryozoans has been described for three Antarctic species by Barnes & Clarke (1998a). A band of ovicells is formed at the growth margin in mid-summer, brooded for 10 months and released as larvae early next summer. In the present study, the number of bands or proportion of embryos did not differ between localities when size of colony was taken into account (Fig. 3, Table I). The overall population capacity for sexual proliferation (embryo production) was considerably higher in the Signy Island population due to the younger age structure of the population than at Rothera Point. This is probably due to a greater level of ice scour at Rothera Point causing a higher probability of catastrophic disturbance for any given area (Barnes 1999). Mortality and sublethal disturbance has been found to increase in encrusting bryozoans southwards along the Scotia Arc from South Georgia to Rothera Point (Barnes & Arnold 1999). In association with this the mean age of encrusting bryozoans has been found to decrease along a similar gradient, but the patterns of embryo production are complicated by relationships with crowding and competition with neighbours (Barnes & Clarke 1998b). The significance of the larger size of embryos in *Isosecuriflustra rubefacta* is difficult to interpret. It could result from either a larger embryo/larva *per se* or due to larval release at Rothera Point being earlier than at Signy Island, so embryos were at a later stage of development.

Erect flustrid (fan shaped) species occur in much shallower water at Rothera Point than at more northerly locations along the Scotia Arc, such as Signy Island and the Falkland Islands

(Table I and author's unpublished data). There are also more erect species, such as *Kymella polaris*, which more commonly occur in shallow water at Rothera Point than at Signy Island. Winston (1983) and Winston & Heimberg (1988) have recorded many erect species around the margin of the continent and this may be the centre of their diversity (Hayward 1995). More northerly and isolated localities may have fewer shallow water species through just being further from a centre of diversity or from biogeographic effects (MacArthur & Wilson 1967). Why these growth forms should occur in shallower water at Rothera Point is unclear.

Bryozoans are a major fouling agent at most marine localities to have been studied world wide, including the surfaces of erect flexible cheilostomatids (Stebbing 1971, Barnes 1994). Although similar levels of fouling may occur in temperate and polar flustrids (personal observation), the fouling on both the frontal and abfrontal surfaces of *Isosecuriflustra rubefacta* and *Nematoflustra flagellata* was significantly lower at Rothera Point than at Signy Island. This may also be a result (indirectly) from increased shallow water scouring intensity. The number of encrusting bryozoan species in shallow water may increase southwards along the Scotia Arc, but the community at Rothera Point may be dominated by just one fast growing species (Barnes & Clarke 1998b). This species rarely occurs as an epibiont, so the local supply of potential epibiont larvae may be very low.

Does depth influence life patterns within Antarctic bryozoan species?

Depth has been found to have three important influences on encrusting bryozoans; one is reduction of light penetration reducing competition with algae. The second is an increase of numbers of species (of fauna) and therefore intensity and complexity of competition for space and predation (Barnes 1995b). The other major influence of depth is mediated through reduction of disturbance (mainly ice scour) levels resulting in longer assemblage persistence and therefore greater monopolization by overgrowth dominants (Barnes 1995a, 1999). The increase in species number is also true of erect bryozoans and explains the reduction in the proportion of bryozoans that each of the study species occupies with increasing depth (Table I). The change in disturbance is probably responsible for a greater variety of morphologies with depth compared to just encrusting forms in the immediate subtidal zone (Barnes 1995a). The colony longevity of each of these species appears to be greater than is possible in shallow water where ice scour is frequent. The lowered disturbance at depth, therefore, results in colonies surviving to greater age and higher reproductive output (Table I).

Colonies of both *Isosecuriflustra rubefacta* and *Nematoflustra flagellata* were found to have reduced width to height ratios at depth compared to shallow water forms. Being suspension feeders and dependent on water-borne particles, differences in growth morphology may be an adaptation to

protrude further into the water column to obtain better access to food. The structure of *Kymella polaris*, the third study species, remained unchanged with depth, but is of similar structure to deep water flustrids anyway. The number of and space occupied by, epibionts decreased by an order of magnitude with depth, probably due to reduced larval supply sources as a result of less available hard substratum for colonies (Barnes & Peck 1996). The reduced architectural strength of longer/thinner colonies may not be viable in shallow water as the high loading of epibionts may weigh them down, which even happens to stronger shallow morphological forms (personal observation). This may explain why *K. polaris* is rare in shallow water but increases in abundance with depth at Signy Island, but was abundant in shallow water at Rothera Point where epibiont loading was very low. So depth may have an important influence on bryozoan life patterns in Antarctic waters, but these are mediated through change in other factors. There are parallels between depth and latitude in that many factors, e.g. epibiont loading, number of bryozoan species and proportion of erect forms change similarly along both gradients. In contrast, other factors change inversely with increased depth and latitude, e.g. ice scour frequency, bryozoan age structure and community complexity (Barnes & Arnold 1999).

Are trends in erect bryozoans reflective of those for other taxa?

In some respects (e.g. light climate and probably primary productivity and ice influences) the high Antarctic is more seasonal than the environment of the maritime Antarctic. In others, however, such as sea temperature (and probably salinity and macronutrient) variation (Clarke 1988) it is more aseasonal. Initial observations suggest that the more intense seasonality of phytoplankton productivity reduces the period of feeding of both bryozoans and other fauna compared to the maritime fauna at Signy Island (Simon Brockington, personal communication). That some processes, e.g. recycling of functional units and possibly embryo production and clonal growth (Barnes & Arnold 1999), occur at a faster rate at a higher latitude location is unusual. These may be linked to a shorter period of food availability and thus the time available for essential processes to occur. The timing of initiation of sexual reproduction in bryozoans appears to be similar to many other taxa (Pearse *et al.* 1991, Stanwell-Smith & Clarke 1998), as is the slower tempo of the process. Despite the advantage of mobility (for faster recolonization) in many taxa, younger age structures of populations should also be the case in areas of higher ice scour as the process is indiscriminate (Barnes 1999).

A number of taxa have been found to occur at shallower depths at Rothera Point than at Signy Island, including various asteroid and crinoid echinoderms, nudibranch molluscs and sponges (Simon Brockington, personal communication). Other taxa have also been found to be considerably less fouled at

depth, e.g. brachiopods (Barnes & Peck 1996), but this is the only study, to date, of fouling at high polar latitudes known to the author. So this preliminary study, in combination with other work on Bryozoa, suggests both latitude and depth have a substantial influence on many different aspects of the biology and ecology of the study species. Comparison with the literature and current studies shows some of these trends are also common to other taxa, but the abundance, depth and latitudinal range of bryozoans make the group ideal for future studies of such trends.

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