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D. K. A. Barnes · A. Clarke

Seasonality of polypide recycling and sexual reproduction in some erect Antarctic bryozoans

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Abstract The seasonality of polypide cycling has been investigated for three species of erect bryozoans from Antarctica: *Isoseculiflustra rubefacta* (Kluge, 1914), *Nematoflustra flagellata* (Waters, 1904) and *Himantozoum antarcticum* (Calvet, 1905). Approximately ten colonies of each species were collected monthly by SCUBA divers over a 14 mo period during 1992/1993, and the status of each individual zooid was classified as differentiating/regenerating, active (feeding autozooids), degenerate (brown body) or sexually reproductive (ovicells present, or zooid containing a larva). Polypide cycling in all three species was distinctly seasonal. New zooids formed at the growth margin and typically contained actively feeding polypides for ≃9 mo before these polypides degenerated into brown bodies in the austral winter (June). Very few polypides were active in the period from June to August, when water-column food levels were at their lowest; after this period new polypides differentiated. Individual zooids typically underwent a total of five (*I. rubefacta* and *N. flagellata*), or at least four (*H. antarcticum*) complete polypide cycles before becoming senescent. Polypide lifetimes generally became shorter as the age of the zooid increased. Sexual reproduction was also distinctly seasonal in these species, with bands of ovicells or sexually reproductive zooids being formed each year in late summer once a given colony had grown to a threshold size (or age). Larvae were then brooded for ≃10 mo before being released in January/February (*N. flagellata*) or February/March (*H. antarcticum*). The seasonal patterns of polypide cycling are related clearly to the variations in food availability, and these species appear to have the longest zooid lifetime (≃5 yr) and the slowest polypide cycling (once per year with polypide lifetimes up to 10 mo) reported for any bryozoan so far.

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D.K.A. Barnes
Department of Zoology and Animal Ecology,
University College, Cork, Lee Maltings,
Cork, Ireland

A. Clarke (✉)
British Antarctic Survey, High Cross, Madingley Road,
Cambridge CB3 0ET, England

Introduction

Clonal animals offer valuable opportunities for ecologists to study the factors affecting sexual and asexual reproduction in the same individual. They are also ecologically important, with taxa such as ascidians, sponges and bryozoans being major components of hard-substratum fouling assemblages. Typically, a bryozoan colony will start with the settlement of a sexually produced larva, followed by metamorphosis to produce the ancestrula. This is then followed by asexual growth, in which new modules (zooids) are added to the colony which thereby grows in size. Some bryozoans also, however, form new colonies by fragmentation of an existing colony, a process which is asexual, for it propagates the maternal genome (McKinney and Jackson 1989, pp 167–189; Thomsen and Håkansson 1995). Whether a new colony forms sexually by the settlement of a larva or by fragmentation, subsequent growth is always modular by addition of zooids.

Cheilostomatids, the most successful living order of bryozoans, are also characterised by extensive polymorphism in zooids. Many zooids are specialised for feeding (autozooids), others for sexual reproduction, colony protection (avicularia), or even movement (Ryland 1970). Bryozoans thus form valuable model systems for investigating the influence of biotic and abiotic factors on sexual reproduction and modular growth. Of particular relevance in high latitudes are the seasonal variations in many important environmental factors, variations which tend to induce a corresponding seasonality in the biology of polar organisms (Clarke 1988).

The shallow shelf-waters around the Antarctic continent and the outlying island groups are characterised by low seawater temperatures with only slight seasonal

variation, together with marked seasonal variations in light climate, primary production, and physical disturbance by both ice and water movement (Clarke et al. 1988; Clarke and Leakey 1996). However, these waters have been known since the time of the "Challenger" and the "Discovery" expeditions to support a rich and diverse benthos, in which various suspension-feeding taxa can be locally dominant (reviewed recently by Arntz et al. 1994). Bryozoans are almost ubiquitous in the southern ocean; they have been found to be extremely abundant on both hard and soft substrata, including other organisms (Barnes 1995b; Barnes and Clarke 1995b), and from the shallow sublittoral to deep-sea environments (Bullivant 1961; Barnes 1995a). A few species have even been shown to inhabit intertidal pools where daily salinity and temperature variations may greatly exceed normal annual variability of the local marine environment (Barnes et al. 1996).

The pattern of annual variation in phytoplankton production in the southern ocean might suggest that the reproductive activity of the benthos would generally be constrained to summer. Recent studies of a variety of suspension-feeding taxa, including many bryozoans, have, however, suggested that for organisms feeding on smaller cells such as nanoflagellates, the period of winter food-scarcity can be very short (Barnes and Clarke 1994, 1995a). Indeed, one species of Antarctic bryozoan, *Arachnopusia inchoata*, has been shown to feed continuously throughout the year.

The seasonality of reproductive activity has been described only rarely in its entirety for any bryozoan species. In general, species from more seasonal environments, such as boreal and temperate shallow waters, exhibit distinct seasonality (Ryland 1970; Eggleston 1972), whilst tropical, deep-water or more cosmopolitan species have aseasonal, effectively continuous reproductive cycles (Gautier 1962; Jackson and Wertheimer 1985). Reproductive seasonality has also been linked to lifestyle, with short-lived annual or biennial species tending to be more seasonal than perennial species (Eggleston 1972). Certain epiphytic species also synchronise their reproductive timing to aspects of the host organism's ecology (Eggleston 1972; Cancino 1986).

In this study, we have investigated the seasonality of polypide cycling in the erect cheilostomatids *Isoseculiflustra rubefacta*, *Nematoflustra flagellata* and *Himantozoum antarcticum* at Signy Island, Antarctica. Seasonal patterns of polypide cycling are compared with data on feeding activity and growth rate, and preliminary observations on sexual reproduction are included to produce an overall picture of life-history in relation to the key biotic and physical features of the environment.

Materials and methods

Specimens of three erect cheilostomatid bryozoan species were sampled from Outer Island, a location close to the British Antarctic Survey research station on Signy Island, Antarctica (60°43′S; 45°36′W). The study site was at a depth of ≃40 m; the substratum was gently sloping and consisted primarily of pebbles and small boulders overlain by silty sand; the site is described in more detail in Barnes and Clarke (1994). The species studied were *Isoseculiflustra rubefacta* (Kluge, 1914), *Nematoflustra flagellata* (Waters, 1904) and *Himantozoum antarcticum* (Calvet, 1905). *I. rubefacta* is one of two species (the other being *I. tenuis*) now recognised as forming what was previously known as *Alloeoflustra tenuis* (see Moyano 1996).

Samples of each species (usually ten colonies of each) were collected monthly by SCUBA divers over a 14 mo period during 1992/1993. Although considerations of underwater safety meant that each set of monthly samples came from a small area, during the course of the study samples were collected randomly from large beds of each species. Immediately on return to the laboratory, two strips, each ≃15 to 20 zooids wide, were cut along the entire length of each individual colony sampled. One strip was fixed and preserved in 4% buffered formal-saline, and the other was fixed in 10% gluteraldehyde in sodium cacodylate buffer and then preserved in sodium cacodylate. The samples were held at 4 °C and transported to the UK for subsequent examination.

Seasonal patterns of polypide recycling were documented by microscope examination of the monthly samples. Every zooid in each sample strip from every colony was examined, and the developmental stage of individual polypides was assigned to one of the three classes used by Dyrynda and Ryland (1982), namely: "differentiating", "active" (fully developed zooids), or "degenerated" (brown bodies). The position of each polypide relative to the growing margin (which represents the youngest part at the top of the colony), and the overall length of the colony were also recorded.

Whilst examining the samples for polypide status, some preliminary observations of sexual reproductive activity were also recorded. These were the overall length of the colony, and the number and location of all reproductively active zooids.

Results

Polypide cycling

In bryozoans, whereas larvae produced by sexual reproduction are the primary means of dispersal and new colony formation, once the larva has settled and metamorphosed to form the ancestrula, increase in colony size takes place solely by asexual modular growth. New zooids are formed by budding, hence growth is modular, and the polypide within a non-reproductive zooid differentiates to become fully developed for feeding. The lifetime of an individual polypide is transient, and after a while the polypide degenerates leaving a small residue of insoluble material (the brown body). A new polypide then regenerates within the same zooid from undegenerated body-wall tissue (Ryland 1970). In many of the species studied to date, several cycles of polypide differentiation, activity and degeneration may take place in a given zooid within a single summer season (Reed 1991).

In the flexible erect species examined in this study, new polypides formed at the growth margin (GM); they then differentiated and became fully developed, as indicated by actively feeding, at two or three zooids distance from the GM. In all three species, a few degenerated polypides could be detected quite close to the GM, indicating that polypide recycling had started very soon after initial differentiation. Data from colonies sampled during the austral summer indicated that polypide

recycling effectively ceased (that is, the proportion of active and/or regenerating polypides was zero and all zooids had degenerated), at 35 zooids behind the GM in *Nematoflustra flagellata* and *Himantozoum antarcticum*, and 50 zooids behind the GM in *Isoseculiflustra rubefacta* (Fig. 1).

The data presented in Fig. 1 are means calculated from ≃10 colonies per species per month (median 11 colonies, range 8 to 13), and there was relatively little variation between individual colonies. There was also a high degree of synchrony in patterns of polypide recycling between individual fronds of the same colony, although detailed examination of individual fronds from a single colony of *Nematoflustra flagellata* revealed subtle differences in the detailed patterns of polypide recycling obscured in the mean data (Fig. 2). Thus in Frond B, there were sharp peaks in the incidence of degenerated polypides matched by peaks in differentiation and dips in the proportion of fully active polypides (Fig. 2). In Frond B, there were distinct peaks in the proportion of fully active polypides at 14 and 21 zooids behind the GM, suggesting that a typical individual zooid underwent a cycle of polypide regeneration in the time it took the GM to extend by seven zooids. Since in *N. flagellata* the overall zone of actively feeding zooids extended to ≃35 zooids behind the GM, this would suggest that the maximum number of polypide generations per zooid in this species is ≃5.

An independent estimate of the number of polypide generations per zooid was made for all three species by counting the number of individual brown bodies per zooid and plotting this as a function of distance from the growing margin. Since each cycle of regeneration results in one brown body, the number of brown bodies per zooid should increase with distance from the GM and reach a plateau once polypide recycling has ceased. The data shown in Fig. 3 confirms this pattern in *Nematoflustra flagellata*, which averaged ≃5 polypide generations per zooid before recycling ceased at ≃35 zooids from the GM. *Isoseculiflustra rubefacta* also had ≃5 polypide generations in total, whereas *Himantozoum antarcticum* had ≃4. In *I. rubefacta*, a clear plateau of just under five brown bodies was reached at ≃45 zooids from the GM, whereas in *H. antarcticum* there was no sign of a plateau by 50 zooids from the GM (Fig. 3).

Seasonality of polypide activity

All three species illustrated a marked seasonal pattern in polypide activity and recycling (Fig. 1). On average, approximately half the total zooids in the zone from the GM to 50 zooids behind the GM had active polypides during the austral summer, with almost all zooids close to the GM being active and the proportion decreasing with distance from the GM. As the austral summer progressed, this zone of highest activity gradually contracted towards the GM, although the proportion of polypides active within this zone changed little until June. This means that younger zooids closer to the GM had were, on average, active for longer throughout the year than older zooids further from the GM (Fig. 4). Few zooids were active for the 3 mo period from June to August (the height of the austral winter), when virtually all the autozooids of the colony contained only brown bodies. Differentiating zooids were present at the GM throughout the year, although differentiation was particularly intense during July and August. In September, the proportion of active zooids increased manyfold and the zone of active feeding expanded once again towards the base of the colony.

Although the broad seasonal pattern of zooid differentiation, activity and degeneration were similar in the three species studied, clear differences were detected between them. The zone of feeding activity was much broader throughout the entire year in *Isoseculiflustra rubefacta* than in either of the other two species (Fig. 1a), whereas *Nematoflustra flagellata* was distinguished by the intense winter contraction of the activity zone to a single zooid band, where the peak of activity remained >70% (Fig. 1b). The length of the winter period of inactivity was greatest in *Himantozoum antarcticum*, which had no polypides active during July, and <10% active in August (Fig. 1c).

Sexual reproduction

In *Isoseculiflustra rubefacta*, *Nematoflustra flagellata* and *Himantozoum antarcticum*, once a colony reached a threshold size (which was typically 40 to 50 mm for the two flustrids and somewhat less for *H. antarcticum*) a proportion of zooids became sexually active and formed ovicells or brooded larvae. No ovicells or other signs of sexual reproductive activity were ever detected in specimens below the threshold size (or age) characteristic of the species at this particular sampling location. Ovicells were usually formed in bands, several zooids wide, across each colony. The zooids of *I. rubefacta* and *H. antarcticum* formed ovicells at the anterior part of the zooid, thereby altering its external appearance (Fig. 5). In contrast, the zooids of *N. flagellata* brooding larvae were otherwise similar in external appearance to normal autozooids. Ovicells were only produced on some branches of *H. antarcticum*, and usually at points where the colony branches were widest, immediately prior to bifurcation. Ovicells were formed during zooid differentiation at the growth margin in *I. rubefacta* and *H. antarcticum*, and hence whether a particular zooid had the potential to become reproductively active was determined on creation. In contrast, the timing of sexual determination in *N. flagellata* was not obvious and brooded larvae did not become apparent until the reproductive zooids were some distance from the growing margin. Reproductive zooids in *N. flagellata* and *H. antarcticum* did not have functional polypides, whereas those in *I. rubefacta* retained fully functional polypides, and hence the ability to feed (Fig. 5).

Fig. 1a

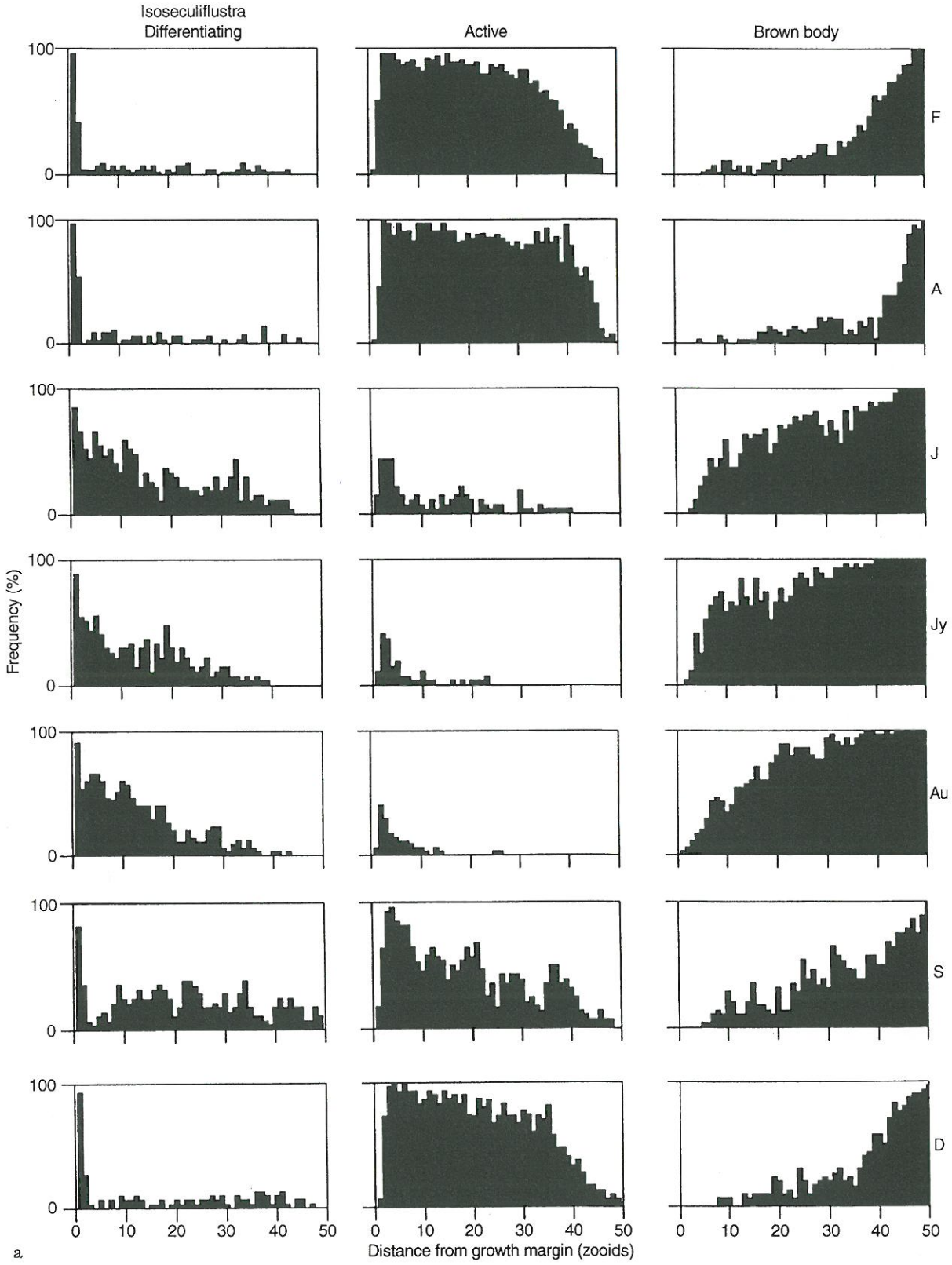

Fig. 1 *Isoseculiflustra rubefacta* (**a**), *Nematoflustra flagellata* (**b**), and *Himantozoum antarcticum* (**c**). Seasonal variation in proportion of polypides classified as either differentiating/redifferentiating, active, or degenerating in brown body as a function of distance from growth margin (measured as number of zooids) (*F* February; *A* April; *J* June; *Jy* July; *Au* August; *S* September; *D* December) Data were collected for all months; the five months not shown exhibited patterns intermediate between those on either side

Fig. 1b

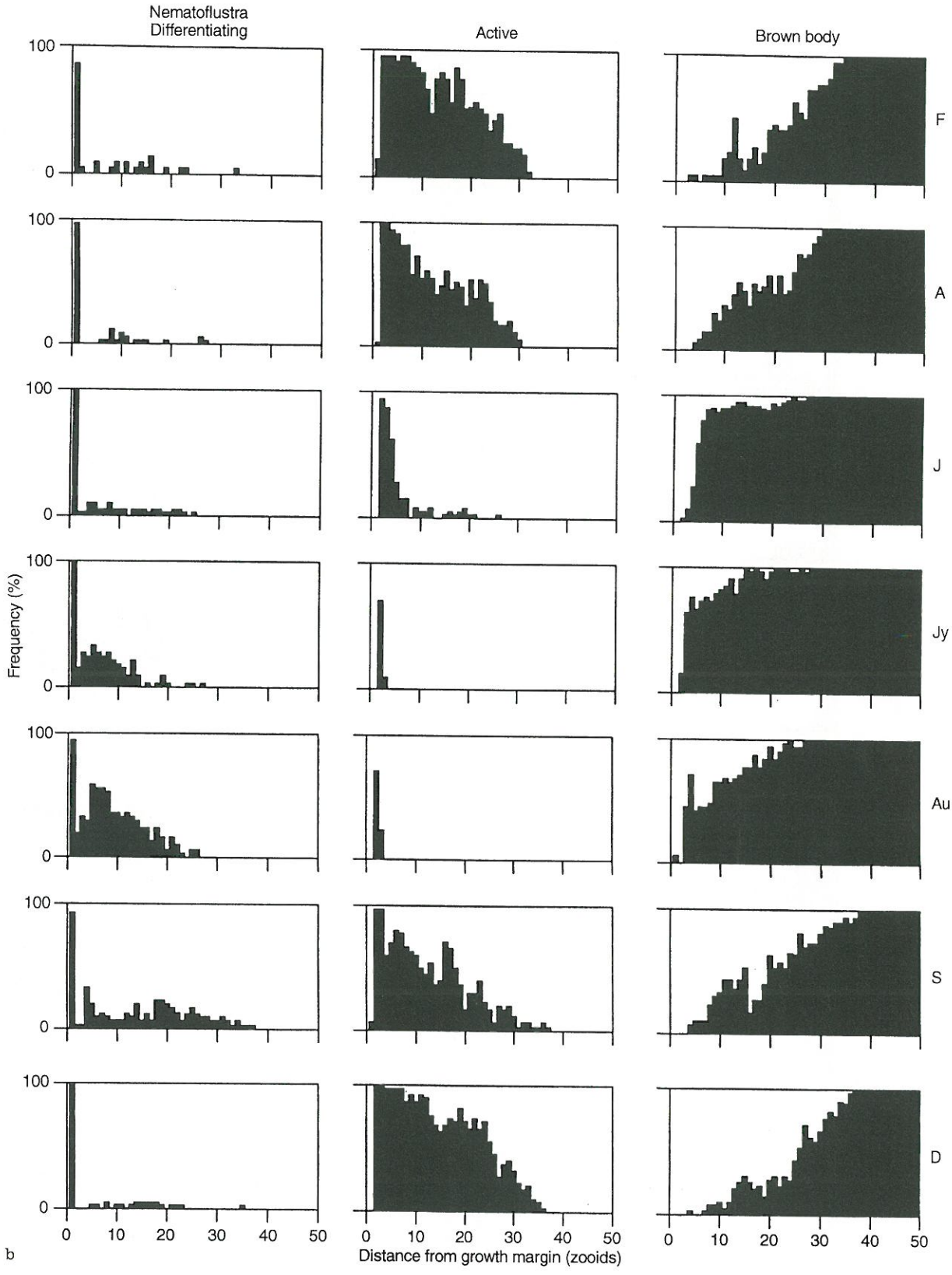

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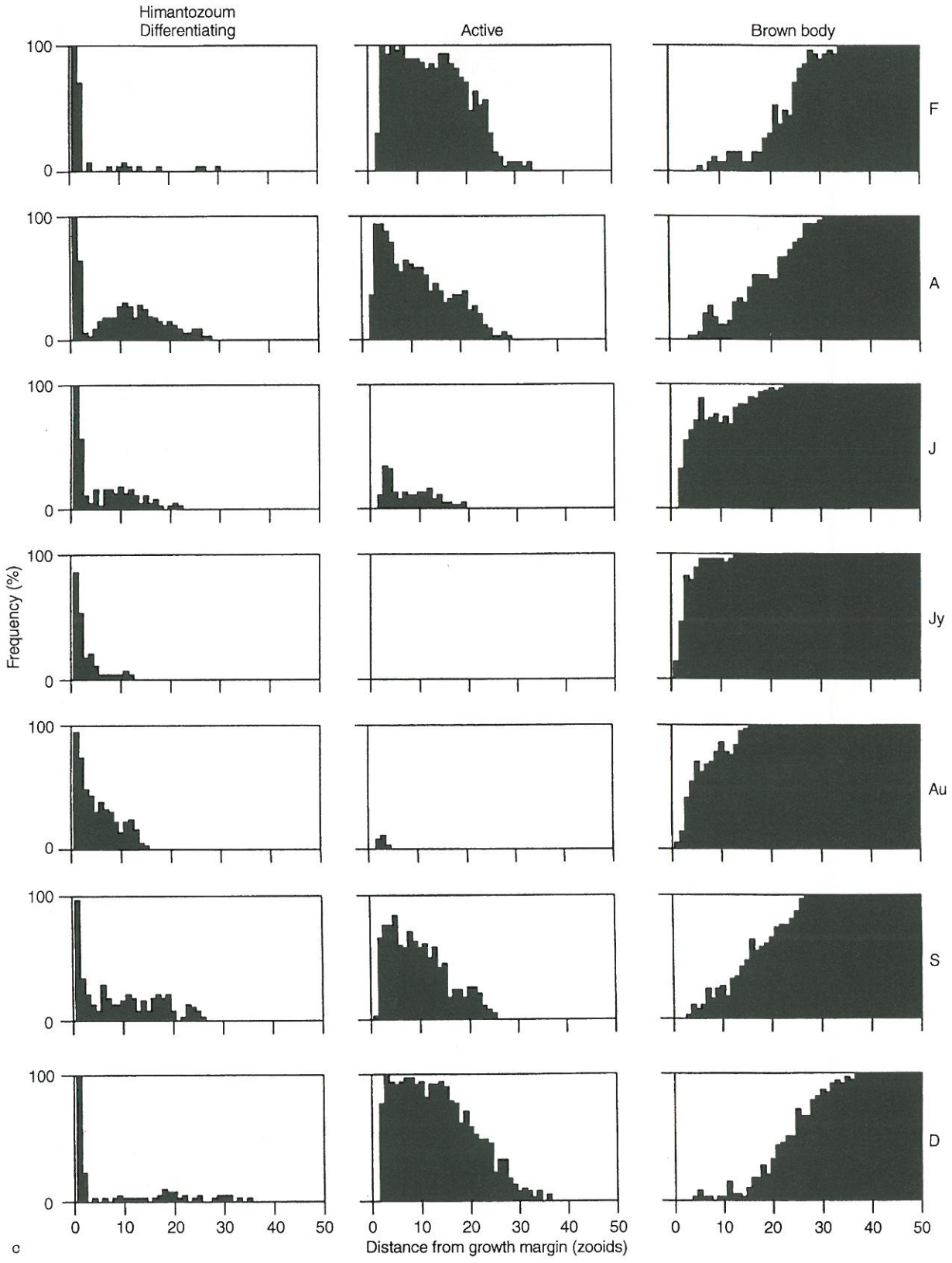
Fig. 1c (continued)



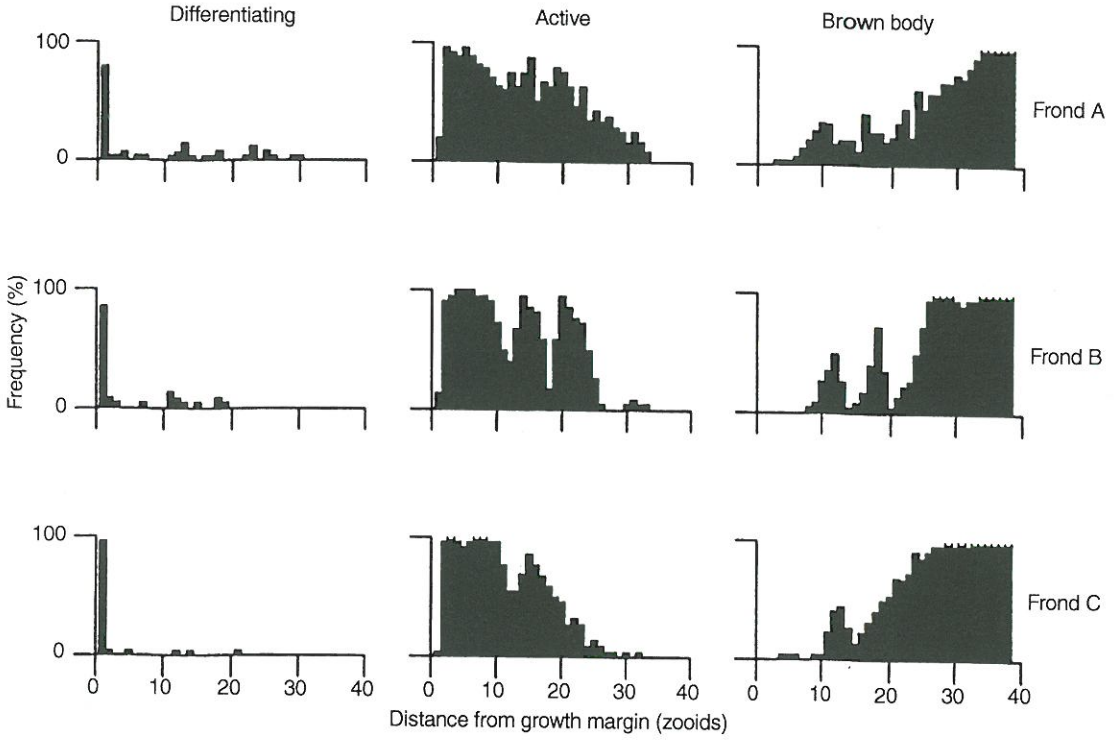


Fig. 2 *Nematoflustra flagellata*. Proportion of polypides differentiating/redifferentiating, active, or degenerating/in brown body from three different fronds as a function of distance from growth margin, measured as number of zooids

Small colonies of *Isoseculiflustra rubefacta* and *Nematoflustra flagellata* were not sexually active, and growth was directed exclusively at zooid proliferation in addition to factors such as colony strengthening and attachment. Ovicells were only detectable in these two species once the colony exceeded a size of 40 to 50 mm (Fig. 6; we cannot, of course, distinguish from our data whether the functional threshold is one of colony size or colony age). Above this threshold, both the percentage of sexually reproductive zooids and the number of ovicell bands per colony increased with colony size, although the patterns in the two species differed. In *I. rubefacta* the mean number of ovicell bands increased from 1 in colonies of 50 to 60 mm, to 7 in the largest colonies (> 100 mm). At the same time, the percentage of total zooids bearing ovicells increased to

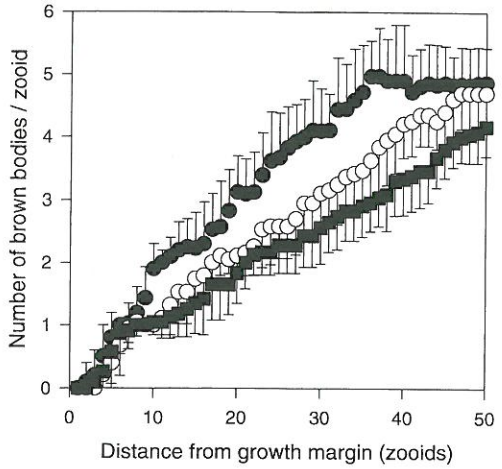


Fig. 3 *Isoseculiflustra rubefacta* (○), *Nematoflustra flagellata* (●), and *Himantozoum antarcticum* (■). Number of brown bodies per zooid as a function of distance from growth margin, measured as number of zooids. Data are means ±1 SE (*bars*)

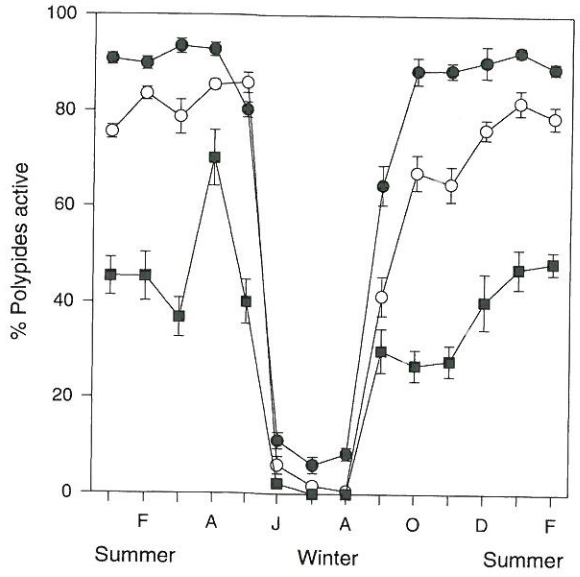


Fig. 4 *Isoseculiflustra rubefacta*. Seasonal variation in proportion of autozooids actively feeding in three zones at increasing distance from growing margin, GM: 0 to 10 zooids from GM (○), 20 to 30 zooids from GM (●), and 40 to 50 zooids from GM (■). (*Nematoflustra flagellata* and *Himantozoum antarcticum* showed qualitatively similar seasonality, although neither of these species have feeding autozooids in the zone 40 to 50 zooids from the GM)

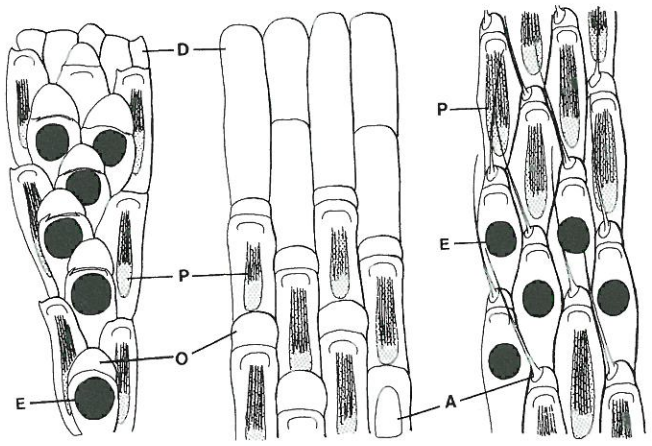


Fig. 5 *Isoseculiflustra rubefacta* (*centre*), *Nematoflustra flagellata* (*right*) and *Himantozoum antarcticum* (*left*). Sexually reproductive zooids [*D* differentiating zooids (at growth margin); *P* polypide; *O* ovicell (*I. rubefacta* and *H. antarcticum*); *E* brooded embryo (*N. flagellata*); *A* avicularia (these are also present in *H. antarcticum*, but are small)]

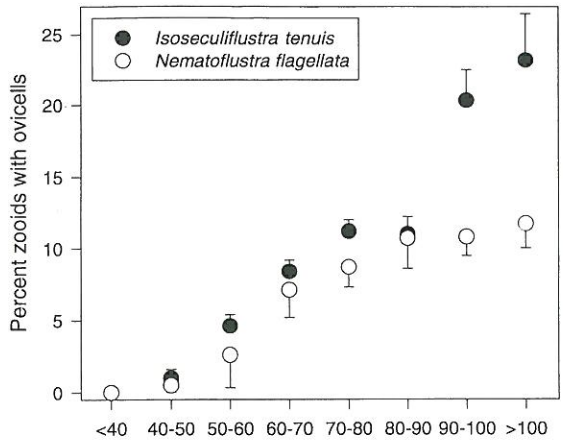


Fig. 6 *Isoseculiflustra rubefacta* and *Nematoflustra flagellata*. Proportion of zooids bearing ovicells as a function of colony length (mm). Data are means ± 1 SE (*bars*)

almost 25%; in contrast, over the same range of colony sizes, *N. flagellata* developed a maximum of 3 bands of sexually reproductive zooids and only 12% total zooids with brooded larvae. For a colony of given size, *I. rubefacta* thus had approximately twice the number of bands of sexually reproductive zooids as did *N. flagellata*. These bands were on average 2.7 zooids wide and separated by 8.1 zooids in *I. rubefacta*, whereas in *N. flagellata* the bands averaged 2.3 zooids in width and were 6.7 zooids apart. The greater overall investment in reproductive zooids by *I. rubefacta* was thus primarily the result of more, rather than larger, bands of ovicells.

Estimating the proportion of zooids bearing ovicells was difficult in *Himantozoum antarcticum* because of its very different colony-growth form. Whereas the two flustrids were fan-shaped, *H. antarcticum* grew as a series of multiple, thin, bifurcating branches. There was only rarely more than one band of ovicells between the colony base and a given branch terminus in *H. antarcticum*, and overall the largest colonies were estimated to have approximately 25% zooids with ovicells. This suggests a similar investment in the proportion of reproductive zooids as for *Isoseculiflustra rubefacta*, although the growth form was very different. No male gametes were observed in any of the specimens.

In *Isoseculiflustra rubefacta*, the ovicells did not change in size after creation. Ovicell bands were formed at the growth margin in the austral summer, between January and April each year, although not in all specimens. As the colony grew in size, the most recently formed ovicell band then became progressively distant from the growth margin. The change in maturity of embryos within the ovicells was indicated by a change in colour from pale white to orange, and an increase in opacity. No obvious point of larval release was noted during the year in this species, although the timing of the initial formation of zooids with ovicells at the growth margin would suggest that development of the brooded embryo was both synchronous and seasonal.

In contrast, the development of embryos could be followed easily in the monthly samples of both *Nematoflustra flagellata* and *Himantozoum antarcticum*. In *N. flagellata* embryos first became apparent in March when they were ≃75 μm in diameter, and filled the width of the zooid. All larvae from all colonies examined were released between January and February. The pattern of reproductive development in *H. antarcticum* was similar to that of *N. flagellata*, although offset by 1 mo, such that release of larvae was between February and March.

Discussion

Over the past three decades, there has been a substantial increase in research into benthic marine communities at polar latitudes, most of which has taken place in shallow waters around Antarctica. Although a significant fraction of this work has considered aspects of reproduction in a variety of taxa, such work has been confined almost entirely to solitary (unitary or non-colonial) animals (see Pearse et al. 1991). This is perhaps surprising considering the overwhelming importance of modular taxa such as ascidians, bryozoans, sponges and certain cnidarians (hydroids and octocorals) in many areas of the Antarctic benthic environment (Winston and Heimberg 1988; Dayton 1990; Gerdes et al. 1992; Arntz et al. 1994). The present study thus provides the first year-round study of the life-history of any colonial marine invertebrate from Antarctica.

Bryozoan life-histories in Antarctica

The three species of erect bryozoans examined in this study (*Isoseculiflustra rubefacta*, *Nematoflustra flagellata*

and *Himantozoum antarticum*) all exhibit a marked seasonality in modular growth, polypide recycling and sexual reproduction. In all three species there is a complete cessation of polypide activity in the middle of winter (typically June to August). During this period almost no polypides can be classified as active, and most have degenerated to the brown-body stage (Figs. 1 and 4). In late winter, zooids at the growth margin start to differentiate actively, and by spring there is a zone of polypides behind the growth margin which is formed predominantly of actively feeding polypides. Feeding then continues throughout the summer and well into the following winter before the polypides degenerate once more, and the zooid accumulates a further brown body. This end-of-season cessation of feeding activity occurs earlier in the older polypides further from the growing margin. The average number of brown bodies per zooid thus increases from the growing margin towards the base, to the point where zooids are sufficiently old that they cease further differentiation. At this point they are effectively senescent/dead and presumably have a purely structural role.

The onset of sexual reproduction could be determined easily in all three species: ovicell bands were created at the growing margin during the second half of the austral summer (January to April) in *Isoseculiflustra rubefacta*, and embryos first became visible in *Nematoflustra flagellata* and *Himantozoum antarcticum* in March. In the latter two species, larval release took place in the following February or March, whereas the timing of larval release could not be determined in *I. rubefacta*. The coupling of polypide recycling and sexual reproduction in the two flustrid species is indicated by the increase in the mean number of brown bodies per autozooid polypide by an average of one in each bands of feeding autozooids between successive band of ovicells moving from the growing margin towards the base of the colony.

The most parsimonious interpretation of these data is that all three species of Antarctic bryozoans examined in this study have a distinctly seasonal pattern to their biology. Each year in late winter, a cycle of polypide differentiation is initiated. Typically, a given feeding autozooid undergoes a single polypide cycle, lasting up to 10 mo in younger zooids, but much less (perhaps 5 mo) in older zooids, in each year. The lifetime of a typical autozooid is thus 5 yr in both *Isoseculiflustra rubefacta* and *Nematoflustra flagellata*, but probably >5 yr in *Himantozoum antarcticum* (where the number of brown bodies per polypide had not reached a plateau up to 50 zooids from the growing margin). All three species also show a strongly seasonal pattern of sexual reproduction, with a new band of sexually reproductive zooids being produced each year and larval development taking $\simeq 1$ yr. The growth pattern for the two flustrid species is shown diagrammatically in Fig. 7. Data from this study suggest that some polypide recycling occurs throughout the year, but the vast majority of polypides are created in August and are active from September until April or May. They then degenerate for the non-feeding period,

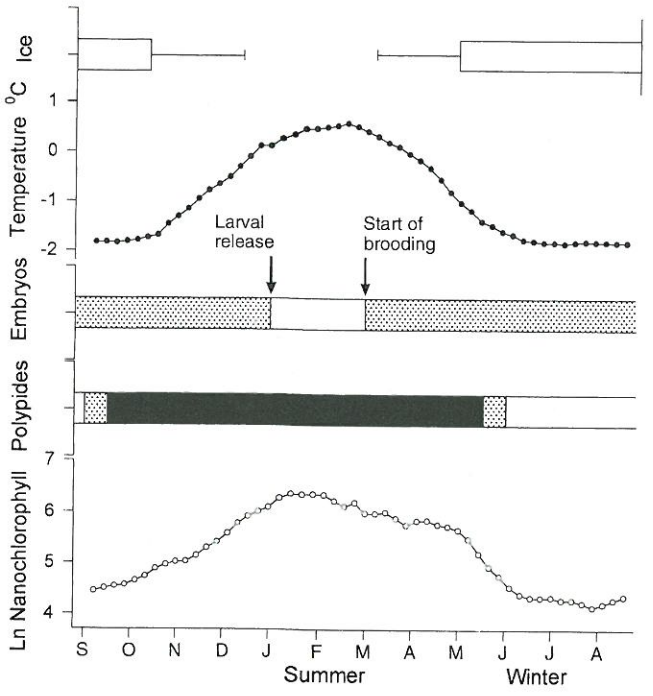


Fig. 7 *Isoseculiflustra rubefacta* and *Nematoflustra flagellata*. Diagramatic representation of life-cycle of flustrid bryozoans at Signy in relation to selected environment variables. Data for winter fast-ice ("Ice") show mean period of sea-ice presence (*bar*) with ranges; temperature data are weekly means for a single station at 10 m depth; chlorophyll data are weekly mean concentrations (mg m^{-3}) for 20-2 μm fraction (both temperature and chlorophyll data are weekly means pooled over period 1989 to 1994: Clarke and Leakey 1996). Period of embryo brooding is also shown (*stippled*), together with mean timing of larval release; and period of polypide feeding (*black*), winter non-feeding period (*open*) and period of change (*stippled*)

which is typically June to August, before regenerating for the next season. During the non-feeding period, however, polypides at the growth margin continue to differentiate (see Fig. 1). This may explain why these species do not show a growth band (in contrast, for example, to *Flustra foliacea*: Stebbing 1971), but it does suggest that although not feeding, bryozoan colonies are translocating reserves from more mature zooids to fuel the continuing differentiation during the non-feeding period.

This interpretation is of course dependent on the assumption that no brown bodies are ejected by newly regenerated polypides (although the pattern in Fig. 3 suggests this does not occur). Assuming that each colony produces a new band of sexually reproductive zooids every year in late summer allows the average rate of distal zooidal budding to be estimated. In *Isoseculiflustra rubefacta*, the band of zooids bearing ovicells averaged 2.7 zooids in width, and the band of feeding autozooids 8.1 zooids; this makes a total of 10.8 zooids budded per year in *I. rubefacta*. The same calculation for *Nematoflustra flagellata*, based on feeding autozooids (average 6.7 zooids per band) and zooids containing visible brooded larvae (average 2.3 zooids per band) yields a total of 9 frontally budded zooids per year. These values

do not, of course, represent total zooid production per year, for this depends on overall colony size (and specifically the width of the growing margin). Neither do they reflect the overall production of colony organic matter per year (which is greater in *N. flagellata* than in *I. rubefacta* by a factor of ≃3: Barnes 1995c). Nevertheless, the rate of production of new zooids by distal budding is clearly much slower than the few data available for temperate-water species: in *Membranipora membranacea* growing in the laboratory a new transverse partition at the growing margin may separate a new zooecium every 4 to 6 h, with full development of the polypide taking ≃2 d (Lutaud 1961). In *Bowerbankia gracilis*, polypide formation in the ancestrula takes 4 d at 12.5 °C (Reed and Cloney 1982).

With so few data available in the literature for comparison, it is currently not possible to control for the influence of ecology or phylogeny to ensure that we are comparing like with like. Nevertheless, the formation of new zooids is clearly very slow in the polar species examined here, at roughly one zooid budded distally per month in the polar species compared with one every one or two days in the temperate species studied to date. A greatly reduced overall rate of colony zooid-production was also reported for the polar *Cellarinella watersi* compared with the temperate *Flustra foliacea* (Barnes 1995c), although these two species differ greatly in the investment in skeletal structures. Coupled with this is a very slow rate of polypide cycling in the polar species. In *Isoseculiflustra rubefacta* and *Nematoflustra flagellata*, young (first generation) polypides lasted ≃9 to 10 mo compared with polypide lifetimes of 1 to 10 wk in temperate species (Gordon 1977).

It is well recognised that a severe mismatch between the frequency of sampling and the time-course of the process under study can lead to error. Thus, monthly samples are likely to miss processes occurring on a timescale of hours or days. It is possible, therefore, that the monthly samples taken in this study may have failed to detect polypide cycling occurring at rates reported previously for temperate bryozoans. A number of lines of evidence, some of them quite independent, suggest that this is not the case and that polypide cycling is genuinely slow in the polar bryozoans studied here. The first is the pattern of accumulation of brown bodies with distance from the GM (Fig. 3) which, on the assumption that no brown bodies are ejected, indicates a maximum of ≃5 cycles of polypide regeneration per zooid lifetime. The second is the detailed distribution of differentiating polypides in individual fronds (Fig. 2), which indicates that an individual polypide has an average lifetime equivalent to the time it takes to add seven zooid modules to the GM. The third is the average increment of one brown body per zooid to each zone of autozooids separated by a band of reproductive zooids when moving from the GM to the base of the colony; coupled with the clear time-stamp provided by the annual release of larvae this is very strong evidence for the average lifetime of a polypide being one year. Finally the average rate of addition of new zooids to the GM required by this interpretation matches that established from the measurements of overall colony-growth rate made from marked colonies growing in situ (Barnes 1995c).

Although the two flustrid species exhibited a more or less seasonally determined pattern of polypide recycling, with one polypide generation per year on average, the lifetime of an individual polypide tended to decrease with zooid age. Despite each zooid being genetically identical with those around it, there was also a marked variation in the pattern of polypide lifetimes in adjacent zooids. Analysis of fixed samples, however, does not allow any judgement as to how much of this variability is the result of stochastic variations in ecological conditions for each zooid (perhaps reflecting influence of neighbours on an individual polypide's ability to capture food), and how much reflects internal differences between the zooids. Overall, the polypide cycling observed in the three polar species studied here was much less synchronous than that described for *Chartella papyracea* (Dyrynda and Ryland 1982).

Seasonality of biology of Antarctic bryozoans

The species examined in this study exhibit a strong seasonality in their biology, with a pattern of one generation of polypide degeneration and regeneration per year. This is integrated with sexual reproduction in that each ovicell appears to be active for one year, releasing a single larva after ≃12 mo incubation. Studies of some erect temperate bryozoans have also demonstrated a pattern of one generation of polypides completing one gametogenic cycle (Dyrynda 1981; Dyrynda and King 1982; Dyrynda and Ryland 1982). Ryland (1963, 1970) has also demonstrated seasonality in the sexual reproduction of fjord-dwelling bryozoans at a similar latitude to the present study in the northern hemisphere (although at a site where the environment is boreal rather than truly polar). This seasonality was found to be cued mainly by variations in temperature and day length (Ryland 1970; Eggleston 1972), although other processes may also be involved. The pattern of zooid life-history in the polar species examined in this study is thus similar to some temperate species, with a temporal coupling of zooid proliferation (modular growth), polypide cycling and sexual reproduction, but over a much longer time-span.

The life-history of the two polar flustrid species studied is also shown diagrammatically in Fig. 7. Also shown are the seasonal variations in key environmental variables which may influence the biology of polar suspension-feeders such as bryozoans. Although the annual variation in sea temperature in the maritime Antarctic is very small, usually < 2.5 C°, there is nevertheless a distinct seasonal pattern (Clarke et al. 1988; Clarke and Leakey 1996). It has been suggested (Pearse 1965; Picken 1980), that despite being small, this variation could cue sexual reproduction in Antarctic waters. Recent studies at Signy Island (60°S) have, however, found that short-

term (tidal, daily or on a time-scale of days) variation of seawater temperature in summer may be as much as 20% of the annual range, suggesting that sea temperature is unlikely to be a proximate control mechanism (Clarke unpublished data). Furthermore, a comparison of the timing of spawning in the Antarctic limpet *Nacella concinna* with seawater temperature at Signy Island over 10 yr revealed no correlation whatsoever (Stanwell-Smith and Clarke 1997). Although underwater light intensity is influenced greatly by the presence or absence of ice cover, and particularly the amount of snow lying on the surface ice (Gilbert 1991; Brouwer 1996), the seasonal change in photoperiod would seem to be the likely major environmental cue at these latitudes. Most important of all, however, is the seasonal variation in the standing crop of chlorophyll in the size range taken by bryozoans. Although the precise size-range of particles taken by polar species is not known, it is likely to fall within the nanoplankton range (20 to 2 μm), and a previous study has shown a tight correlation between the amount of annual growth in *Cellarinella watersi* at Signy Island and the duration of the nanoplankton chlorophyll bloom (Barnes 1995c).

The coupling of the seasonal pattern of feeding, polypide cycling and sexual reproduction to those of food availability in the environment suggest that the results from this study will be generally true of erect bryozoans in the general locale. Whilst individual colonies living in close proximity might be genetically closely related through being founded either by fragmentation or limited dispersal of larvae, it does not seem intuitively probable that genetic factors will cause major differences in the response of separate colonies to factors such as broad patterns in food availability.

Why do polar bryozoans grow so slowly?

The reason for the slow rate of production of new zooids and the unusually long polypide life-spans in the polar bryozoans examined in this study is not clear. Although the data for *Cellarinella watersi* indicate that the length of time in the year when sufficient food is available to allow feeding is critical to the number of new zooids produced annually at the growing margin, these data do not explain why growth in polar bryozoans is usually so slow when it does take place. In many polar marine invertebrates there is a suite of associated life-history characteristics which includes a slow growth rate, an extended life-span and a reduced basal metabolic rate (Clarke 1991). It is not yet clear as to the extent to which a reduced maintenance cost is necessarily related to a slow growth rate, but the present study shows that bryozoans fit the general picture emerging for polar benthos (Brey and Clarke 1993). It is possible that one consequence of molecular adaptation to low temperature is a reduced capacity for maximum energy throughput, thereby limiting maximal growth rates (Clarke 1991; Clarke and North 1991; Johnston and Battram 1993; Johnston et al. 1995; Clarke 1998). It is also possible that somewhere in the biochemical machinery required for growth is a rate-limiting step which evolution cannot circumvent. The place to look is perhaps the faster-growing early-colonising species which have to complete their life-cycle before either being overgrown by superior competitors or destroyed by ice (Barnes 1995a, b).

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