

IN: *Bryozoa: Past and Present. Proceedings of the 7th International Conference on Bryozoa.* JRP Ross, Editor. Western Washington University Press, Bellingham, Washington, pp. 197-203.

SEASONAL CHANGES IN ZOOID SIZE AND FEEDING ACTIVITY
IN EPIFAUNAL COLONIES OF ELECTRA PILOSA

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ABSTRACT

Data collected during a larger study of the feeding of Electra pilosa colonies growing epifaunally on Fucus serratus revealed seasonal patterns in zooid size and feeding activity. Mean zooid sizes were found to decrease through the summer months, while feeding activity generally increased during the same period. These results are related to predictions based on hypotheses regarding body size vs. temperature and on food availability. Spatially and/or temporally induced changes in zooid size are rarely considered, despite broad implications for evolutionary and taxonomic studies.

INTRODUCTION

Variation in the architecture of clonal organisms has been suggested to relate to their competitive abilities and life history strategies. Jackson (1979) and Lovett-Doust (1981) proposed that the overall sizes and shapes of benthic marine invertebrates and plants were related to strategies of substratum procurement and maintenance. Variation in clones and colonies can occur at the module level as well. Functional variation of modules has allowed for a marked division of labor in a number of organisms (e.g. scyphomedusae, hydromedusae, bryozoans, anemones, ascidians, insect colonies). Recently, variation in the size of modules that form clones and colonies has been considered. Over evolutionary time scales, the risk of mortality and the degree of clonal integration have been suggested to explain observed differences in module size in bryozoans, anemones, ascidians, and corals (Coates & Jackson 1985). Over ecological time scales, changes in prey size and/or abundance have been considered to invoke module size changes in suspension-feeding organisms (Sebens 1979).

The size of bryozoan zooids is an important taxonomic character and is often used as a morphological character to indicate evolutionary change, yet spatial and/or temporal measures of zooid size changes are rarely considered (but see Taylor & Furness 1978). Ryland (1963) provided incidental data of a latitudinal gradient in zooid size for the genus Haplopoma. Silén and Harmelin (1976) found a similar latitudinal gradient in size for the species H. sciaphilum. Morris (1980) noted that fossil Hippothoa colonies had larger zooids in northern regions. In this paper I present observations of seasonal changes in zooid size and feeding activity that occurred in epifaunal colonies of Electra pilosa.

MATERIALS AND METHODS

The epifaunal assemblage of the furoid alga, Fucus serratus, has been the focus of numerous ecological investigations in Great Britain (for review see Seed & O'Connor 1981). In the Menai Straits, North Wales, Electra pilosa is one of the three most common bryozoans occurring on F. serratus blades (Wood & Seed 1980). E. pilosa is present on F. serratus year-round and is often overgrown by other epifauna (Wood & Seed 1980). In general, growth rates of bryozoans are low in winter (Nair 1962; Ryland 1970; Stebbing 1971; Seed et al. 1981), presumably due to colder temperatures (Menon 1972). Recruitment of E. pilosa to blades of F. serratus occurs throughout the year with a possible peak in early summer (Seed & O'Connor 1981; Okamura, pers. obs.).

In the early spring through summer of 1985 I collected relatively small colonies of Electra pilosa ($< 2 \text{ cm}^2$, most $< 1 \text{ cm}^2$) in the mid- to low intertidal of the Menai Straits, North Wales. Colonies were brought to the laboratory where I mapped them by drawing their outline onto a sheet of acetate. I then performed a series of feeding experiments designed to assess the effects of neighboring epifaunal bryozoans on feeding success. Colonies were placed in a recirculating flow tank containing a suspension of latex particles (13 microns in diameter) and were allowed to feed for 27 min. At the end of experiments colonies were placed, frontal surfaces upward, in dilute sodium hypochlorite. This treatment dissolves organic contents of colonies but leaves intact the exoskeleton, membranous material, and latex particles. Latex particles remained entrapped within the zooids that had ingested them because of the surrounding undissolved portions of the zooid and because of their relatively high density in dilute sodium hypochlorite. The number of particles captured per zooid were then quantified using a dissecting microscope. Very infrequently particles were lost from zooids during the release of air bubbles that ripped the frontal membrane as materials dissolved. However, the effect of particle loss was deemed minimal because it was rare and not biased across experimental treatments. In addition to the number of particles captured per feeding zooid, the total number of zooids per colony was determined. Newly-forming zooids at the edges of colonies were excluded in these counts.

Digitizing the mapped colonies provided measures of colony areas. To estimate the mean size of zooids in each colony I divided the colony area values by the total number of zooids in each colony. In the analysis of mean zooid sizes I excluded colonies that were being overgrown by other bryozoans as this phenomenon may possibly affect zooid size (Gordon 1972).

The mean percentage of the zooids per colony that ingested latex particles and the mean number of particles captured per feeding zooid per colony were used as measures of feeding activity. This technique may overestimate feeding activity as the method did not identify zooids that attempted to feed but were unsuccessful. Feeding activity was determined for isolated Electra pilosa colonies as well as colonies in association with and being overgrown by other epifaunal bryozoans. As these categories were relatively equally represented, the overall effect on feeding activity was deemed to be minimal, therefore the data were pooled.

RESULTS

Changes in Feeding Activity

A general but nonsignificant increase in feeding activity as measured by the mean % zooids feeding per colony can be seen from early March to early July (Fig. 1A). However, in late July feeding activity rose dramatically and significantly (ANOVA of arcsine transformed % feeding zooids vs. time: $F_{6,202} = 45.875$, $p < 0.001$; followed by Scheffe's method of a posteriori unplanned contrasts amongst means). Feeding activity, as measured by the mean number of particles captured per zooid in colonies, was significantly greater in late May as well as in late July (Fig. 1B) ($F_{6,202} = 35.033$, $p < 0.001$; ANOVA followed by Scheffe's method).

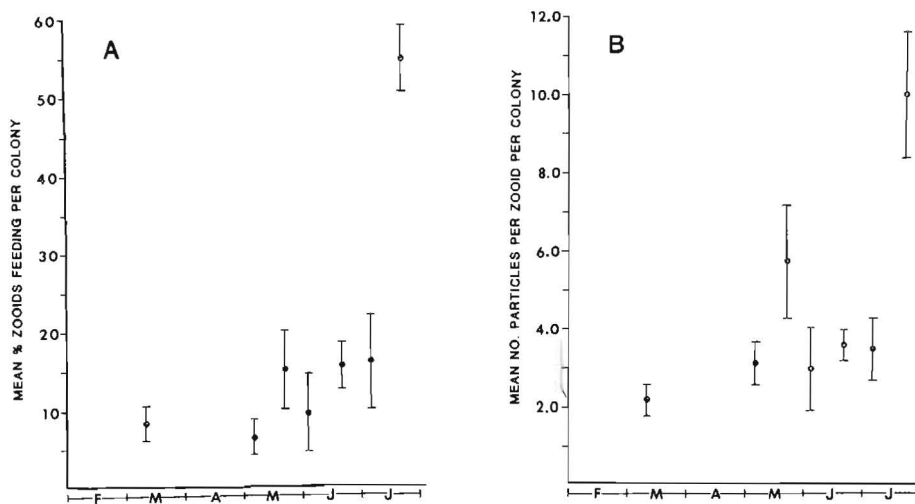


Fig. 1. The mean % zooids feeding per colony (A) and the mean number of particles captured per zooid in colonies (B) from early March to late July 1985 ($n = 8-63$ colonies). Bars represent 2 standard errors about the mean.

Zooidal Size Changes

Mean zooid sizes in the June and July samples were significantly smaller than in the May samples (Fig. 2) ($F_{6,222} = 4.83$, $p < 0.001$; ANOVA followed by Scheffe's method). Zooids sampled in March, however, were not significantly different in size from those in May nor from those in the summer months.

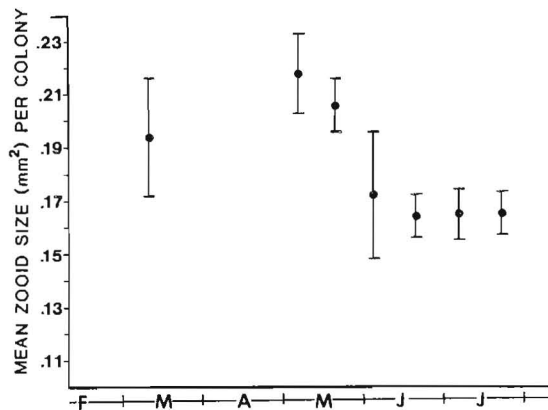
DISCUSSION

Seasonal Patterns in Feeding Activity

The two most likely environmental influences that may explain seasonal trends in feeding activity and zooid size are temperature and food availability. Temperatures in the Menai Straits during the months of observations have been measured to range from about 5°C in March up to 17°C in July (Buchan et al. 1967; O. Calvario-Martinez, pers. comm.). In winter, temperatures can reach as low as 0°C. (During periods of aerial exposure at low tides, bryozoans will experience a much greater range in temperature.) Peak levels of chlorophyll were measured in April while peak levels of phytoplankton primary productivity occurred in May (O. Calvario-Martinez, pers. comm.). In general, the Menai Straits experience spring and fall blooms of phytoplankton (Jones & Spencer 1970; Al-Hasan et al. 1975).

Feeding activity showed a slight increase through the period of the study with anomalously high levels (as measured by both estimates of activity) during the last sampling period. (Tidal period did not appear to be related to feeding activity.) The following considerations may serve, at least partially, to explain the feeding patterns: 1) certain species of phytoplankton may promote particularly high feeding rates; 2) higher temperatures incur greater energetic costs and hence may invoke greater feeding rates; 3) possible shock to colonies acclimated to the cold ambient temperatures of the Menai Straits early in the season (the suspension in the flow tank was at ambient laboratory temperature). Explanations 2 and 3, however, seem unlikely to explain the very dramatic difference in feeding activity between mid- and late July.

Fig. 2. The mean zooid size per colony from early March to late July of 1985 (n = 5-47 colonies). Bars represent 2 standard errors about the mean.



While the reasons for variation in feeding are unknown, the potential for such variation should be noted and accounted for in studies of bryozoan feeding. In an earlier study (Okamura 1985) I noted a similar seasonal change in the feeding activity of colonies of Conopeum reticulum from San Francisco Bay, California. In that study activity levels were higher earlier in the summer than later on. (Different experimental treatments were run concurrently during the study, thus there was no problem in interpreting the results.)

Seasonal Patterns in Zooid Size

Sebens (1979) suggested that changes in the body sizes of colonial suspension feeders may reflect changing food availability. He argued that if the prey sizes become smaller or if food availability is high, it is advantageous for a single polyp (or zooid) of any size to become two smaller polyps due to the concomitant increase in surface area for prey intake. The argument is based on the inverse scaling of surface area to volume.

The data collected in this study appear to counter Sebens's suggestion: larger zooids occurred at the time of peak primary productivity. However, it is possible that some lag occurs before size is expressed as a response to environmental influences. In addition, the measure of mean zooid size reflected the mean size of all zooids in the colony, not just those that were recently formed (see materials and methods section). Finally, since growth rates vary with temperature (see below), any lag between size expression and environmental influence will also vary temporally, making interpretation of a relationship in the data complex.

While food availability may explain the size changes observed in this study, I believe a stronger case can be made for temperature-induction of zooid size changes. Variation of body size with temperature and latitude appears to be a fundamental trait of both endotherms and ectotherms (e.g. Ray 1960; Kinne 1970; Mayr 1970; Vermeij 1978; Nevo et al. 1986) although the mechanisms of temperature-mediated changes in body size remain speculative. Postulated mechanisms include: 1) for endotherms, less heat will be lost through radiation at larger body sizes due to the inverse scaling of surface area to volume (commonly known as Bergmann's Rule) (Mayr 1963: 319); 2) for ectotherms, increased rates of metabolism at high temperature reduce growth if energy intake is constant (Sebens 1982); 3) the observed attainment of larger cell sizes at lower temperatures may produce organisms of larger body size (Vermeij 1978); and 4) differentiation and sexual maturation may be more strongly temperature-dependent than somatic growth, thus delayed ontogeny may result in growth to large size (Ray 1960; Vermeij 1978).

Experimental culture of bryozoans further support a temperature-induction of zooid size changes (Menon 1972). Both *Electra pilosa* and *Conopeum reticulatum* were found to produce smaller zooids at higher temperatures, although there was no significant size change in zooids of *Membranipora membranacea* (Menon 1972). However, as equal amounts of food were provided, zooid size changes may have reflected an energetic response: at higher temperatures the greater metabolic costs may have reduced zooid growth.

Implications of Zooid Size Changes

Variation in zooid size may occur both spatially, over latitudinal (Ryland 1963; Silén and Harmelin 1976; Morris 1980) and possibly depth gradients (Popofsky, 1908, cited in Kinne, 1970, reported increased sizes with depth for radiolarians) and temporally, over seasonal (this paper) and annual cycles. Such variation is notable for several reasons. Care should be taken when body size is considered as a taxonomic character since there appears to be the potential for considerable temporal and spatial variation in zooid size. In addition, changes in various dimensions of body size are often used as morphological characters to measure evolutionary rates. The relative importance of evolutionary processes (e.g. phyletic gradualism vs. punctuated equilibrium)

(Gould & Eldredge 1977) that influence rates of morphological change through geological time is a much-debated topic in evolutionary biology. To resolve this issue investigators have been studying biostratigraphic sequences for rates and patterns of morphological change (e.g. Dingus and Sadler 1982; Bell et al. 1985; Cheetham 1986). This study suggests that caution should be used when employing body size changes for the above arguments (see also Stanley 1985). Documented changes in body size may not reflect true evolutionary change but rather may simply represent displacement of assemblages in space or time.

ACKNOWLEDGEMENTS

I wish to acknowledge the help and encouragement provided by Dr. R. Seed during my studies in North Wales. J. Pell aided in field collections and laboratory experiments. Dr. A.H. Cheetham encouraged me to report these findings, and conversations with Dr. S. Lidgard clarified my thoughts. To all I am grateful. This is contribution no. 176 of the Smithsonian Marine Station at Link Port.

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