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RESEARCH ARTICLE

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Zooid size parallels contemporaneous oxygen isotopes in a large colony of *Pentapora foliacea* (Bryozoa)

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Abstract The relationship between seasonal changes in temperature and the size of zooids within cheilostome bryozoans is explored by comparing zooid size and contemporaneous carbonate mineralogy within a single colony of a perennial species that grew in a highly seasonal environment. Previously published oxygen isotope profile data from two fronds of a large colony of *Pentapora foliacea* from the Irish Sea record the cyclical patterns related to seasonal changes in temperature experienced by the colony over 3 years of growth. Zooid size data gathered from the same points at which the oxygen isotope data were taken reveal that zooid size and contemporaneous $\delta^{18}O$ values covary. These and previously published data show that zooid size profiling can be confidently used to easily estimate rates of growth and longevity of bryozoan colonies, and further illustrate the negative relationship between zooid size and ambient temperature. Some inconsistencies in timing between zooid size and $\delta^{18}O$ data may provide insights into the mechanisms behind temperature mediated body size changes in poikilothermic animals.

Introduction

Colonies of cheilostome bryozoans are composed of asexually budded modules termed zooids. Despite being genetically identical, zooids within a colony are often considerably variable in morphology, particularly with respect to the position or function the zooid serves within the colony (McKinney and Jackson 1989). External biotic and abiotic factors can also cause considerable morphological change. For example, encrusting forms often show changes in shape and size of zooids when the substrate they inhabit is irregular or growth is constrained by competitive interactions with other biota (see Jackson 1983).

In addition, several studies have shown that the size of zooids in cheilostome bryozoans varies with respect to the ambient temperature in which the zooid developed, both in the wild and under controlled laboratory conditions (Ryland 1963; Menon 1972; Morris 1976; Silén and Harmelin 1976; Okamura 1987; Okamura and Bishop 1988; Hunter and Hughes 1994; O'Dea and Okamura 1999, 2000a, 2000b, 2000c; O'Dea and Jackson 2002, 2003; O'Dea 2003). Results thus far show a clear inverse relationship between temperature and zooid length, zooid width and zooid frontal area. These results mirror a response termed the temperature-size rule that occurs in a wide number of animal taxa (Atkinson 1994, 1995, 1996; Atkinson and Sibly 1997; Angilletta and Dunham 2003). However, despite its ubiquity across taxa the mechanistic causes behind the temperature size-rule remain unknown (see Angilletta and Dunham 2003).

Interest in the processes and expression of the temperature-size rule within cheilostome bryozoans was fuelled by the proposed potential use of the response to investigate environmental conditions in ancient environments by evaluating zooid sizes in fossil bryozoans (Okamura and Bishop 1988; O'Dea and Okamura 2000a, 2000b). For example, if other factors are controlled, the amount of variation in zooid sizes within individual bryozoan colonies has been shown to be related to the amount of seasonal variation in temperature a colony experiences (O'Dea and Okamura 2000a, 2000b; O'Dea 2003; O'Dea and Jackson 2002). Thus, intracolony variation in zooid size from fossil colonies can be used to estimate the absolute range of seasonal variation in temperature in an ancient environment (O'Dea and Okamura 2000a, 2000b).

In addition, perennial colonies of bryozoans growing in a seasonal environment lay down a cyclical

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pattern of increasing and decreasing zooid size as the colony grows (O'Dea and Okamura 2000c; O'Dea and Jackson 2002) which can be used to investigate rates of growth in both fossil (O'Dea and Jackson 2003) and Recent (O'Dea and Okamura 2000c; O'Dea and Jackson 2002) colonies much in the same way as oxygen-isotope profiling (e.g. Jones 1988). In this respect, O'Dea and Okamura (2000c) showed that the perennial bryozoan *Flustra foliacea* produces cyclical changes in zooid size through the growth of a colony that are in synchrony with seasonal variations in temperature.

Despite the potential uses of zooid size variation to make environmental predictions, the mechanism(s) that account for temperature-mediated zooid size changes remain unknown. This is also true for the temperature-size rule in general (Stelzer 2002; Angilletta and Dunham 2003). Adaptive explanations that are taxon-specific appear to be inapplicable given that a wide range of taxa exhibit decreased body size at higher temperatures (O'Dea and Okamura 1999; Berrigan and Charnov 1994). In the Bryozoa, some data suggest that limits on oxygen levels, such as temperature and therefore oxygen demand increases, may help explain why zooids are smaller in warmer waters (O'Dea and Okamura 1999; S. Morley, personal communication). Additionally, recent work may be revealing that levels of food availability, previously shown by several workers to have little or no effect upon zooid size (Menon 1972; Hunter and Hughes 1994; O'Dea and Okamura 1999, 2000c; O'Dea and Jackson 2002; O'Dea 2003), may be accounting for some of the variation previously observed (Needham et al. 2003). Clearly, more investigations are required to further clarify the presence of the temperature size response in bryozoans and also to try and use new techniques to better understand the mechanisms responsible. With these aims, this study investigates the process of zooid size in a perennial bryozoan by comparing zooid size data to oxygen-isotope profiling data from the same colony.

Isotope profiling is a technique applicable to many shell-secreting animals (Jones 1988). The amount of ^{18}O relative to ^{16}O in skeletal carbonate, taken at regularly sampled spaces along a transect of growth, can reveal the seasonal patterns of temperature and/or salinity experienced by the animal during its growth, since the relative amount of ^{18}O to ^{16}O in carbonate is a function of temperature, as well as the oxygen-isotopic composition of the water during calcification. Isotope profiling allows inferences to be made on the levels of seasonal variation in temperature at the time of growth, as well as estimates of age if the animal lived in a seasonal environment. A number of studies have successfully used isotope profiling approaches to explore the potential of finding otherwise difficult to get data on rate of growth in bryozoans (Pätzold et al 1987; Brey et al. 1998; Bader 2000), but few studies have utilised the approach to its full potential to assess life histories, demographies and population structures of bryozoans.

For the purpose of this study, isotope-profile data from a cheilostome colony provides a means of both testing and investigating the zooid size response to temperature. By comparing data on zooid size to contemporaneous isotopic data on skeletal carbonate composition it should be possible to retrospectively observe how zooids respond to environmental variations in temperature.

The first bryozoan to have been profiled for oxygen isotopes was a colony of *Pentapora foliacea* from the Bristol Channel, UK (Pätzold et al. 1987). Two profiles were made along separate fronds that came from the same colony (Pätzold et al. 1987; see Fig. 2). Results revealed clear seasonal cycles in carbonate composition that enabled the authors to estimate a colony growth rate of around 2 cm per year and demonstrating the usefulness of the approach in studying life histories in the Bryozoa. In this study, the same colony used by Pätzold et al. (1987) is used to compare zooid sizes to the isotopic composition of contemporaneous bryozoan skeleton.

Materials and methods

Pätzold et al. (1987) made two separate isotope profiles along two fronds taken from a single colony of the bryozoan *Pentapora foliacea*. For this study, the same fronds were borrowed from the Institut für Paläontologie, Universität Bonn. The fronds originally came from a large colony approximately 20 cm in diameter and 10 cm high (Pätzold et al. 1987; Fig. 1). The colony was collected at a depth of around 20 m from a locality off

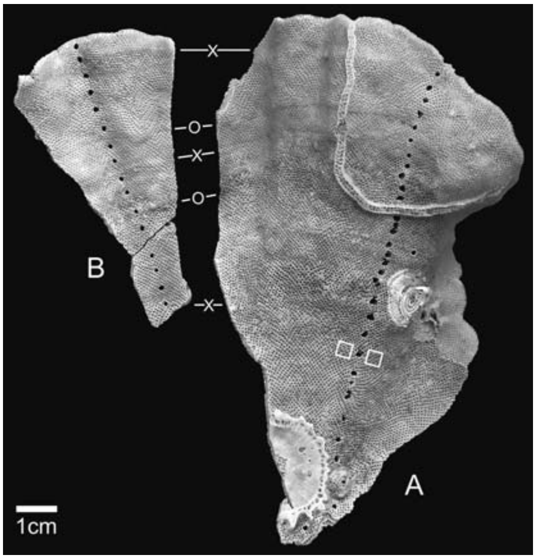

Fig. 1 *Pentapora foliacea*. Bilaminar fronds *A* and *B* showing locations of original samples taken for stable oxygen isotopic analysis by Pätzold et al. (1987). *White squares* demonstrate the method of determining mean zooid density. Growth bands are delineated by *white lines* between fronds. Growth bands discussed by Pätzold et al. (1987) are marked with a *circle* while growth bands visible on colony surface but not discussed by Pätzold et al. (1987) are marked with a *cross*

Martins Haven, Pembrokeshire, UK, in the Irish Sea on 6 October 1978. The two fronds analysed for isotopic composition had been removed from opposite sides of the colony. The largest frond is approximately 93 mm long while the smaller is approximately 53 mm long (Fig. 1).

Samples for isotopic analysis had been taken at roughly 3-mm intervals (Fig. 1). Twenty-eight samples had been taken from the larger frond and 16 from the smaller frond, each weighing approximately 0.5 mg. Values of δ^{18}O were measured using V.G. Micromass 602 D mass spectrometer that reportedly had a precision of 0.1 ‰ (Pätzold et al. 1987).

In order to compare zooid morphology with contemporaneous oxygen-isotope values, zooid density was used as an index of zooid size. Zooid density, or the number of zooids within an area, increases as mean zooid size decreases and has already been shown to be a valuable technique for making profiles of zooid size in bryozoans (O’Dea and Okamura 2000c). Zooid density was measured as the number of whole zooids contained within a square area of 4.84 mm^2 formed by an eyepiece grid graticule on a stereo microscope. Zooids that were not entirely contained within the square were counted only if they spanned the top or right border of the square.

Adjacent to each hole in the colony (produced from the isotopic analysis) zooid density was measured (Fig. 1). Because *P. foliacea* produces bilaminar sheets, it was possible to take two measurements on each side of the fronds at each sample, making a total of four measurements of zooid density from which a mean and 95% confidence interval could be derived.

If the area adjacent to the hole was obscured by epibionts, or the zooids were unusual in shape due to growth patterns, the square was moved sideways, lateral to the direction of growth, and always contemporaneous with the isotope location, until a suitable place for measurement could be found.

The only time the isotope and zooid density samples were not contemporaneous was the 16th sample of the largest frond, 37.2 mm proximal to the growing tip. Here, the isotope sample crosses a growth check line (Pätzold et al. 1987) that has obscured and deformed the shape and size of the zooids making the data unsuitable for zooid size analysis (O’Dea and Okamura 2000b). For this sample, zooid density data was measured at the first available location distal to the growth check line.

For each isotope sampling point, the four measurements of zooid density were used to calculate mean zooid density in zooids per 4.84 mm^2, which was than converted to zooid density/mm^2. For each frond, mean zooid density data were then plotted in the same form as the original isotopic data presented by Pätzold et al. (1987) for direct comparison.

Correlating mean zooid density and δ^{18}O values tested the strength of a relationship between the isotope and zooid size. Because the two profiles come from the same colony, there were no intercolonial genetic effects upon zooid size and thus data from both profiles were combined in the analysis. Pearson’s correlation was tested using *t*-test.

Results

Variations in mean zooid density (Table 1) mirror the seasonal cyclical patterns recorded by skeletal isotopic composition in both fronds of *Pentapora foliacea* by Pätzold et al. (1987) (Fig. 2). Generally, during times of increased δ^{18}O values, representing cooler water, zooid density is lower. Thus, because zooid density is inversely related to mean zooid size, larger zooids were produced during times of cold water and smaller zooids during times of warmer water.

Correlating mean zooid density and δ^{18}O values for each point along both transects reveals a highly significant negative relationship ($r = -0.60$; $t = -4.80$; $df = 42$; $P < 0.001$; Fig. 3). Thus, zooid size in *Pentapora foliacea* parallels patterns of seasonal temperature changes, providing further support for the presence of the temperature-size rule in the cheilostomes.

Discussion

The synchronicity between zooid size and the oxygen isotope composition observed in *Pentapora foliacea* is clear enough to allow zooid size profiling to be used to make estimates of rate of growth in perennial bryozoans (Fig. 2). Zooid size data are not as precise as oxygen isotope data; the noise in the zooid size data is likely to be controlled by various biotic and abiotic factors (see O’Dea and Okamura 1999).

In both profiles, the highest δ^{18}O values, representing the times of coldest water, occur slightly proximal to the lowest point in the troughs of zooid density data (Fig. 2). This lack of synchronicity may be due to the noise discussed above, or may be due to a factor of how a bryozoan colony grows and zooids are calcified. Marginal colony growth in bryozoans occurs through the budding of new zooids. As a zooid buds it is not immediately calcified. Complete calcification always occurs after budding and, depending upon the species, this process can take some time to finish. Moreover, in some species, calcification of a zooid often continues as the colony increases in age (McKinney and Jackson 1989). Thus, the deposition of skeletal carbonate of a zooid takes place after the zooid bud has formed and the zooid size and shape been determined. As a result, at any given point along a colony profile, isotopic data will represent carbonate deposition at a time *after* budding, while morphology data will represent the time exactly *at* budding. The degree to which the two are not contemporaneous depends upon the growth strategy and rate of calcification of the bryozoan in question. Isotope profile studies should be aware of this potential lag, particularly in fast growing species.

Table 1 Replicate zooid density along profiles on both sides of two fronds of a colony of *Pentapora foliacea* from the Irish Sea. Zooid density measured as the number of whole zooids (z) within an area of 4.84 mm^2 and converted to z/mm^2. 95% confidence intervals (Ci) given for z/mm^2 data

Frond and sample number	Distance from growing tip (mm)	Zooid density replicates (z/4.84 mm^2)				Mean zooid density		
		Side 1		Side 2				
		1	2	1	2	(z/4.84 mm^2)	(z/mm^{-2})	95% Ci
A1	2.3	16	16	14	17	15.75	3.25	0.25
A2	5.2	17	18	15	19	17.25	3.56	0.35
A3	7.6	13	12	11	13	12.25	2.53	0.19
A4	10.1	15	12	14	15	14.00	2.89	0.29
A5	12.3	12	14	12	15	13.25	2.74	0.30
A6	14.5	11	14	14	16	13.75	2.84	0.42
A7	17.6	14	12	14	13	13.25	2.74	0.19
A8	19.5	13	18	17	17	16.25	3.36	0.45
A9	21.9	16	18	15	18	16.75	3.46	0.30
A10	23.7	18	17	17	13	16.25	3.36	0.45
A11	25.6	14	12	13	13	13.00	2.69	0.17
A12	29.0	13	12	12	13	12.50	2.58	0.12
A13	31.4	12	16	12	14	13.50	2.79	0.39
A14	33.7	13	12	14	14	13.25	2.74	0.19
A15	35.5	14	12	16	11	13.25	2.74	0.45
A16	37.2	11	12	16	13	13.00	2.69	0.44
A17	39.0	13	13	15	13	13.50	2.79	0.20
A18	41.0	17	15	13	17	15.50	3.20	0.39
A19	44.6	14	15	14	15	14.50	3.00	0.12
A20	47.3	14	15	14	16	14.75	3.05	0.19
A21	50.5	15	16	15	15	15.25	3.15	0.10
A22	54.4	11	14	14	13	13.00	2.69	0.29
A23	57.8	14	13	13	13	13.25	2.74	0.10
A24	60.0	14	13	13	15	13.75	2.84	0.19
A25	62.0	12	13	14	13	13.00	2.69	0.17
A26	66.3	14	13	14	13	13.50	2.79	0.12
A27	70.6	13	15	14	18	15.00	3.10	0.44
A28	74.0	13	15	17	15	15.00	3.10	0.33
B1	0.3	16	15	16	13	15.00	3.10	0.29
B2	3.1	16	14	15	14	14.75	3.05	0.19
B3	6.7	18	15	18	15	16.50	3.41	0.35
B4	9.3	18	17	14	14	15.75	3.25	0.42
B5	12.9	15	17	14	10	14.00	2.89	0.60
B6	16.5	13	14	13	14	13.50	2.79	0.12
B7	20.4	14	12	15	15	14.00	2.89	0.29
B8	22.9	16	13	15	16	15.00	3.10	0.29
B9	26.4	17	17	17	13	16.00	3.31	0.40
B10	29.1	16	17	16	16	16.25	3.36	0.10
B11	33.1	16	17	12	11	14.00	2.89	0.60
B12	35.9	8	11	13	11	10.75	2.22	0.42
B13	41.8	11	12	13	14	12.50	2.58	0.26
B14	44.6	14	16	15	15	15.00	3.10	0.17
B15	47.7	14	14	17	16	15.25	3.15	0.30
B16	50.6	17	15	14	15	15.25	3.15	0.25

Needham et al. (2003) presented results suggesting that food availability may have a significant effect upon zooid size in the encrusting cheilostome *Electra pilosa*. This is despite previous studies showing there to be little effect (Hunter and Hughes 1994; O'Dea and Okamura 1999, 2000c). At the locality where the *Pentapora foliacea* colony was collected, levels of primary production would have fluctuated with respect to temperature, levels of nutrients available and intensity of grazing by zooplankton. Because of these interwoven effects, the amount of food that would have been available to the colony of *P. foliacea* (mostly soft-bodied small phytoplankton) would very likely have followed a double peaked annual pattern of spring and autumn blooms, as occurs at other Irish Sea locations (e.g. Blight et al. 1995; Gowen and Bloomefield 1996), with relatively low levels available during the high summer months when grazing rates are high and nutrients depleted. Using contemporaneous morphometric and temperature estimates from the isotope data, it is possible to see that zooid size does not follow this double peaked pattern. The influence of temperature upon zooid size is apparently much more important than food availability. The data therefore corroborate previous results that the level of food made

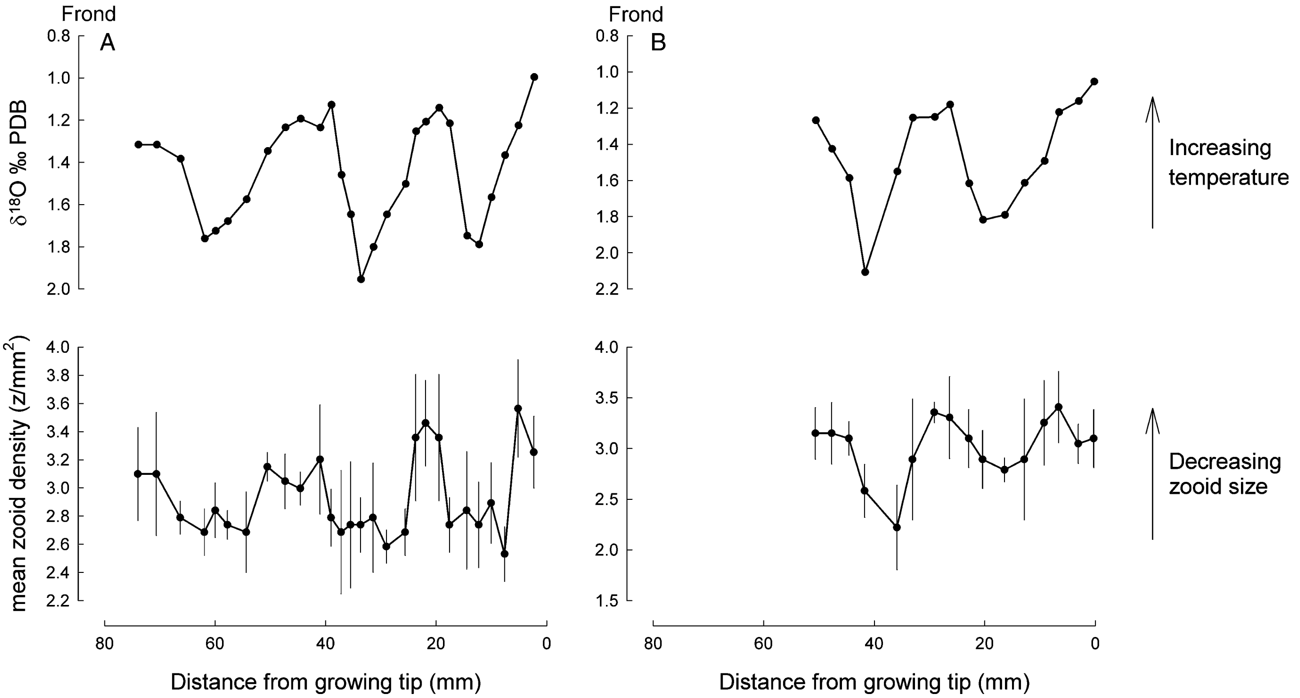

Fig. 2 Profiles of stable oxygen isotopes and zooid size from two fronds of *Pentapora foliacea*. *Top row*: δ^{18}O values from Pätzold et al. (1987)(note inverted scale). *Bottom row*: mean zooid densities (z/mm^2). *Vertical bars* represent 95% confidence intervals. $n = 4$ for each sample point

available to cheilostomes has minimal effect upon zooid size (Hunter and Hughes 1994; O'Dea and Okamura 1999, 2000b, 2000c).

Levels of food availability may nonetheless influence zooid size, and its effects in combination with temperature may be observable in the results of this study. Fig. 3 illustrates a combined model of growth whereby temperature has an inverse effect on size while food availability has a positive effect on size (as found by Needham et al. 2003). During the winter, temperature is low and therefore zooids are large. In the spring, as temperatures rise, zooid size should decrease but the first phytoplankton bloom dramatically increases food levels keeping zooid sizes large. Only when food is depleted *and* temperatures are high during the summer months (illustrated by the grey band in Fig. 3) do zooids become small. As temperatures decrease into the autumn, zooid size increases more rapidly than if temperature was the only factor as the autumn phytoplankton bloom starts.

The resulting pattern of growth from this model is one of greater and more rapid variation in zooid size, leading to large zooids during the winter and small zooids during the summer and few zooids of intermediate size (Fig. 4). This pattern appears to occur in the profile from the large frond, but is not apparent in the profile from the small frond (Fig. 2).

Because Pätzold et al. (1987) did not find values of δ^{18}O that corresponded with the minimum temperatures that occur in the area the colony was collected, the authors concluded that growth ceased during wintertime. Growth cessation is a common phenomenon in many bryozoan species that grow in a seasonal environment and is likely to be the result of decreased food availability rather than reduced temperatures (Stebbing 1971; Barnes 1995; Brey et al. 1998; Smith and Key 2004). In *Pentapora foliacea*, Pätzold et al. (1987) demonstrated the presence of two growth bands that corresponded with δ^{18}O maxima and therefore colder waters. However, the authors failed to mention that similar, and on occasion even clearer, lines can be observed across the fronds that do not correspond to any regularity

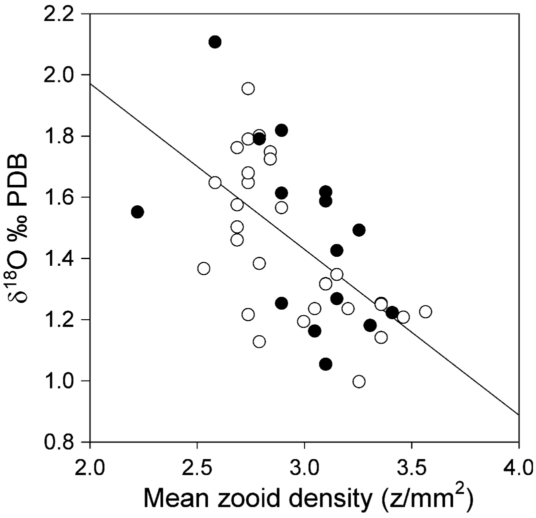

Fig. 3 Correlation of δ^{18}O values and contemporaneous mean zooid density (z/mm^2) measures from two fronds of *Pentapora foliacea* ($r = -0.60$). *Open circles* from frond A, *closed circles* from the smaller frond B. δ^{18}O values from Pätzold et al. (1987). *Line* of best fit is plotted

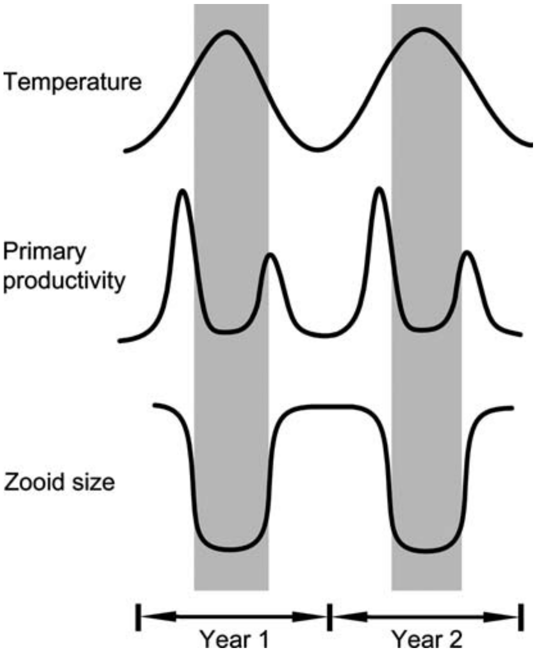

Fig. 4 Schematic model of growth in cheilostome bryozoans over a 2-year period illustrating the potential cumulative effects of temperature and levels of primary productivity upon zooid size. See text for further details

either in the growth of the colony or the isotopic values (see Fig. 1). Because of this, I would not recommend that growth bands be used to measure rates of growth or colony longevities in bryozoans without first clarifying the periodicity of the production of such lines within individual species.

The data presented here provide further support that zooid size in cheilostomes varies with respect to temperature. The data demonstrate that zooid size profiling is able to estimate growth rates and colony longevities, and highlights the value of the technique for making life history inferences from both fossil and Recent bryozoan colonies.

Further work is needed to elucidate the response of zooid size to abiotic and biotic variables. In particular, meticulous studies are required to measure the absolute importance of levels of food upon size. Nonetheless, in each study so far, the effects of food availability appear to be substantially less than those of temperature, and the results gathered here reinforce such a conclusion. The importance of food upon size may be so small that it would be impractical or impossible to measure from colonies grown in natural situations where myriad and multiple factors, including temperature, are much more influential.

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