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Influence of seasonal variation in temperature, salinity and food availability on module size and colony growth of the estuarine bryozoan *Conopeum seurati*

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Abstract Zooid size and colony growth of the estuarine bryozoan *Conopeum seurati* (Canu) (order: Cheilostomata; suborder: Malacostegina) were examined over 15 mo at Avonmouth Dock, Avon, England. Data were analysed in conjunction with synchronous measurements of temperature, salinity and food availability. Zooid length, width and area were strongly temperature-dependent, while both food availability and colony growth rate had no significant effect on zooid length, width or area. Salinity and the interaction of temperature and salinity significantly influenced zooid length and area, suggesting that changes in zooid size may result from oxygen limitation in warm waters. The validity of a number of other mechanisms proposed to account for temperature-related changes in zooid size is discussed. The results support the use of zooid size as an indicator of both long-term trends and seasonal variations in temperature in Recent and fossil assemblages as long as data sets are large and the effects of other factors on zooid size are considered. Colony growth rate was found to be significantly influenced by both the amount of food available to the colonies and the combined effect of temperature and food availability, suggesting that growth rate increases as food increases, but that the former may be limited at low temperatures when metabolic rates are low.

Introduction

The morphology or phenotype of an organism is a product of its genetic makeup or genotype, and the effect of the environment in which it has developed and lived. Temperature–size adaptation is one well-documented response to environmental changes based on the common and long-standing observation that larger body size is achieved in cooler environments. Atkinson (1994) reviewed 109 studies that had investigated temperature-mediated size responses, and found that 84% reported body size to be larger at lower temperatures. Atkinson's review incorporated examples from nine phyla and included research on both ectothermic and endothermic animals. Of the studies, 11% reported an opposite trend, but the results of half of these were invalid as the organisms had been reared at inappropriately extreme temperatures.

Cheilostome bryozoans are major space-occupiers on a variety of marine substrata, where they grow as colonies composed of asexually-budded modules termed zooids (see Fig. 2). A variety of studies have indicated that the zooids in cheilostome bryozoans conform to the temperature–size rule. Laboratory-based studies have shown that *Membranipora membranacea*, *Conopeum reticulum*, and *Celleporella hyalina* produce smaller zooids at higher temperatures under controlled conditions (Menon 1972; Hunter and Hughes 1994). These findings are mirrored by natural patterns of variation in zooid size. The genera *Haplopoma* and *Hippothoa*, and the species *Haplopoma sciaphilum* display variation in zooid size along latitudinal, and therefore temperature, gradients (Ryland 1963; Morris 1976; Silén and Harmelin 1976). Zooid size has also been found to vary for a number of species in Recent and fossil assemblages in accordance with known temperature regimes (Okamura and Bishop 1988; O'Dea and Okamura 1999). These latter studies provide evidence that changes in zooid size within a species over geological time may be used to infer relative changes in palaeotemperature. Finally, a

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decrease in zooid size during warmer summer months in the bryozoan *Electra pilosa* suggests that the temperature–size effect also occurs on a seasonal basis (Okamura 1987). Okamura speculated that this seasonal variation in size arose from variation in temperature not food availability; however, since neither temperature nor food availability were monitored, their relative effects could not be assessed.

Despite the ubiquity of the temperature–size effect, the mechanism(s) behind the effect remain unknown (see Atkinson and Sibly 1997), although a number of hypotheses have been proposed since the pattern was first noted. Following observations that cell size in animals tends to increase with decreasing temperature (Masry and Robertson 1979; Romero and Baguna 1991; Partridge et al. 1994), Van Voorhies (1996) suggested that changes in cell size may be the underlying mechanism behind the temperature–size rule, since bigger cells will produce bigger bodies as long as cell number remains constant. For ectotherms, Sebens (1982) proposed that the temperature–size effect might be the result of changes in metabolic rate at varying temperatures. Increased metabolism at increased temperature will reduce growth if energy intake is constant. More recently, Atkinson (1994) suggested that the availability of oxygen may affect body size. As temperature increases, metabolic rate increases and oxygen requirements correspondingly increase, but unless the diffusion rate or supply of oxygen increases in line with temperature, body size may be reduced. This may be particularly critical for aquatic organisms, since the maximum amount of oxygen that can be dissolved in a volume of water is ≈ 20 times less than in an equal volume of air and the solubility of oxygen decreases rapidly with increasing temperature.

With regard to bryozoans, several other mechanistic explanations for the temperature–size effect may pertain. Dzik (1975) believed that zooid size in bryozoans is a direct function of the amount of food that has been made available to “parent” zooids. Sebens (1979) proposed that changes in module size in colonial suspension-feeders may reflect changes in food availability since, under increased food levels, it could be advantageous for a single module (polyp or zooid) to become two smaller units because of the resultant increase in surface area for prey intake. Hunter and Hughes (1994) thus suggested that bryozoans use temperature as an extrinsic cue to predict productivity and thereby attain the optimum zooid size for the amount of food available. Under this scenario, zooid size would appear to be the result of temperature, even under laboratory conditions. Another possibility is that zooid size may increase as a response to the increased viscosity of seawater at lower temperatures (Denny 1990). This higher viscosity may require the production of stronger feeding currents, which could be achieved by an increase in lophophore (the feeding crown) size and, hence, zooid size. Finally, changes in zooid size could be determined by variations in the amount of energy allocated by the colony to the formation of new zooids as a result of changes in the

status of the colonies. For example, as colony growth-rate increases in warmer waters (Jebram 1977), zooid size may be correspondingly reduced or, as a result of gamete production during the warmer months, changes in the energy demands of the colony may similarly result in the production of smaller zooids.

Because colonies of cheilostome bryozoans are composed of iterated zooids that reach a determinate final size, application of the temperature–size rule to the Bryozoa at the zooidal level provides a unique opportunity to infer temperature regimes experienced by colonies. Cheilostome bryozoans may therefore represent a potentially powerful tool for investigating temperature trends on both long-term (Okamura and Bishop 1988; Hunter and Hughes 1994) and seasonal scales (O’Dea and Okamura 1999) in Recent and fossil environments.

The aim of this study was to document temporal variation in zooid size and colony growth in the estuarine bryozoan *Conopeum seurati*, and to determine the extent to which such variation might be related to changes in environmental variables (temperature, salinity and food availability) and the status of the colony (growth-rate and reproduction). These analyses provide the first explicit and detailed documentation of the nature of growth in bryozoans in a natural setting. In addition, our research provides an important foundation for studies that use zooid size to infer temperature regimes in Recent and fossil assemblages (Okamura and Bishop 1988; O’Dea and Okamura 1999). Finally, our results provide support for various hypotheses that have been proposed to explain the temperature–size rule.

Materials and methods

The Old Dock at Avonmouth Port lies on the northern side of the River Avon at its entrance to the Severn Estuary, Avon, England (Fig. 1). Brackish water enters the dock through a series of locks. The tidal range in the Old Dock is ≈ 3 to 4 m.

The encrusting bryozoan *Conopeum seurati* (Canu) (order: Cheilostomatida; suborder: Malacostegina) is one of the few euryhaline bryozoan species, and is found at the Old Dock. Zooids of *C. seurati* have a simple morphology (Fig. 2). They are lightly calcified, and have a translucent frontal membrane and easily distinguished lateral walls. Colonies generally develop by producing runner-like spokes, 4 to 7 zooids wide, which bud distally in a straight line away from the ancestrula (the founding zooid of the colony). Gaps between these spokes are subsequently filled in with zooids as the colony grows. On even substrata, colonies form regular lacy sheets, while on uneven surfaces colonies become irregular, and zooid size and shape can vary substantially (Ryland and Hayward 1977). Breeding in *C. seurati* in Britain takes place between June and October (Ryland and Hayward 1977).

Two Perspex racks, each holding 22 glass slides (7.5 cm²), were suspended in the Old Dock on the 18 June 1997 to a depth of ≈ 1 m at lowest tide. Larvae of *Conopeum seurati* then settled on the glass slides. Each slide had a smooth and a finely-abraded surface, providing the settling larvae with a choice of substratum texture.

Once a juvenile colony of *Conopeum seurati* began to develop on a slide, all other epibionts were removed from that slide throughout the lifetime of the colony. This ensured that a single colony was maintained per slide without hindrance or competition for space. Colonies that reached the edge of the slide were removed, apart from a small patch of living zooids which were then free to grow across the

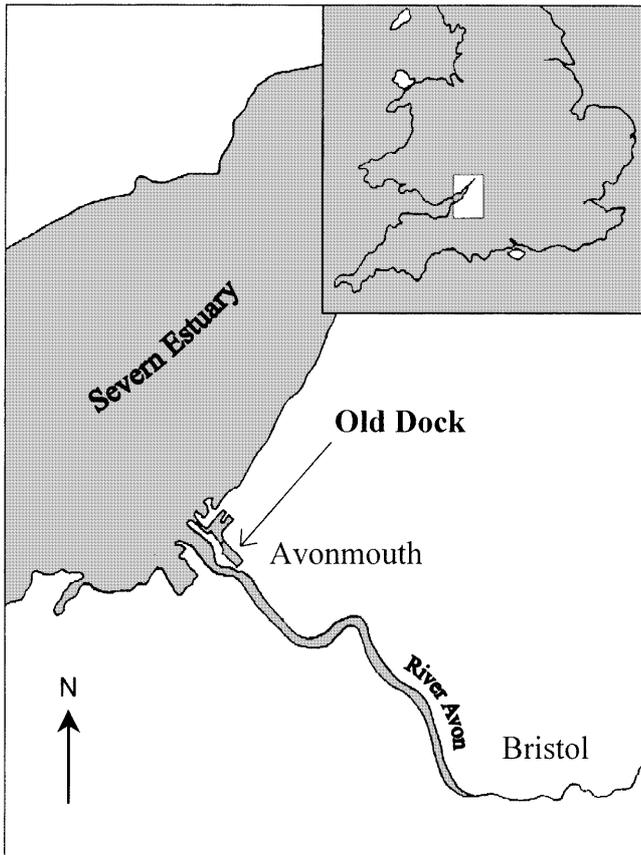
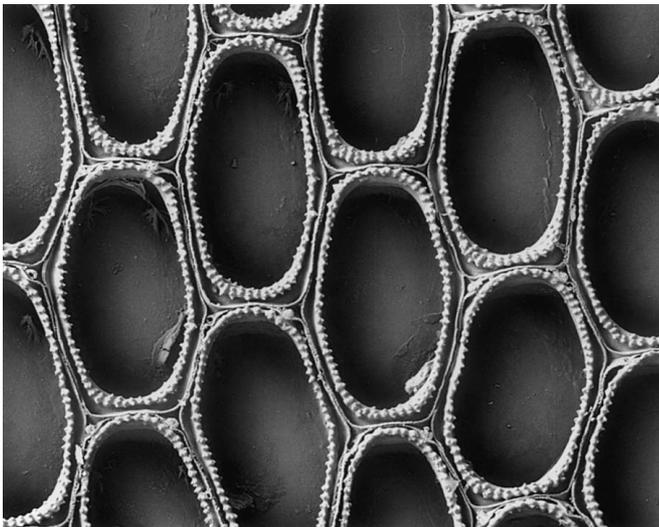


Fig. 1 Location of Old Dock at Avonmouth (51.47N; 2.71W)

cleared portion of the slide. This allowed data to be collected over a longer period of time for an individual colony, but was only carried out on very mature colonies in order to remove the effects of confounding astogenetic differences in colonies of differing maturity. If a colony stopped growing, it was removed from the slide altogether, the slide was then available for further larval settlement.

Fig. 2 *Conopeum seurati*. Scanning electron micrographs of different regions of same colony taken at same magnification ($\approx \times 80$) (Left graph zooids that budded at 22 °C; right graph zooids that budded at 14 °C)

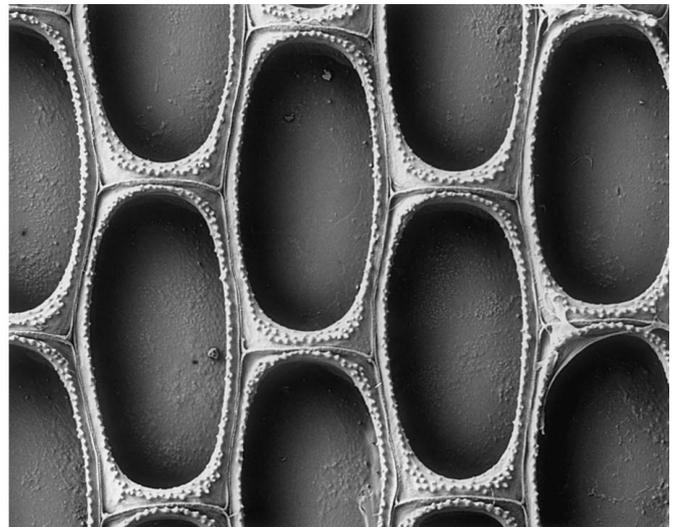


Data collection

Between 18 June 1997 and 1 October 1998, a total of 19 sampling visits were made. During periods of rapid growth these were approximately biweekly, but were less frequent during winter. Upon each visit, slides with colonies were removed from the racks, submerged in a tray with water from the dock, and observed on-site with a dissection-microscope. Within each colony, five zooids at the growing edge were haphazardly selected for morphometric study. Zooids were measured only if their lateral walls were complete enough to enable measurement and if they lay within the "spokes" of the colony. For each zooid selected, maximum length and width were measured, from which an index of frontal area was derived by multiplying maximum length by maximum width. Zooid dimensions were only obtained from those colonies for which it was considered that the growing edge was outside the zone of astogenetic change (where a regular sequence of changes in zooid morphology occurs during early colony development: Boardman et al. 1970). At each sampling, the radius of each colony was also determined, measured as the maximum distance from the ancestral zooid to the growing edge. The growth rate of each colony was then calculated as the increase in colony extent along the maximum radius since the previous sampling. Colony radius was deemed the most appropriate method of measuring growth rate in *Conopeum seurati* because we wanted to measure actual accretion rates of new zooids at colony margins rather than changes in growth form or colony area. Unlike colony area, using increase in radius as an index of growth rate allows comparisons of growth between colonies of different sizes.

During each sampling visit, water temperature and surface-water salinity were measured at the depth of the slide racks, the latter by means of a hand-held refractometer. In addition, three replicate 1-litre samples of water from around the racks were collected for chlorophyll *a* analysis. Chlorophyll *a* content was measured following the techniques of Parsons et al. (1992). Chlorophyll *a* concentration was considered the most effective method of obtaining an index of the amount of food available to the colonies, as a variety of evidence indicates that phytoplankton provides the most important food source for bryozoans (Winston 1977). However, bryozoans are known to selectively feed from the plankton, since some particles will be too large or too spiny to ingest (Winston 1977), and bryozoans also ingest non photo-autotrophic plankton (e.g. gametes: Best and Thorpe 1994). Thus, the use of chlorophyll concentration as an estimate of the amount of food available may not be wholly accurate. To improve our understanding of food availability, each water sample was examined microscopically to identify the dominant plankton.

The presence of eggs was observed in colonies during the summer period. However, as the study was designed to repeatedly measure growth over time, colonies could not be sacrificed to



document reproductive timing and effort. For statistical purposes, the reproductive state of colonies was presumed to occur between June and October (from Ryland and Hayward 1977).

Analysis of data

Data were analysed to determine how zooid length, width and frontal area varied within individual genotypes (colonies) as a function of seasonal fluctuations in temperature, salinity, food availability, the reproductive status of the colonies, and colony growth rate. An analysis was also conducted to determine the effects of temperature, salinity, food availability and genotype on the rate of colony growth.

Only data from colonies which survived at least six consecutive sampling sessions were used in statistical analyses, and it was assumed that all colonies were genetically dissimilar. This is a reasonable assumption, since all colonies were derived from long-lived, sexually-produced larvae. Data were analysed using a General Linear Model (GLM) with Minitab (Version 10). Factors in the analysis were; temperature, mean chlorophyll *a* concentration, surface water salinity, mean growth rate of colonies, reproductive state of colonies and genotype. Because a number of factors were found to be closely correlated, colinearity problems arose when a model with full interactions was implemented. We analysed the maximum number of interactions GLM would allow, and believe that all interactions of importance were incorporated.

Results

Environmental variables

During the study period, the waters in the Old Dock at Avonmouth underwent marked seasonal fluctuations in temperature (range 10 to 21.5 °C: Fig. 3) and salinity (range 18.5 to 27.5‰: Fig. 3). Mean chlorophyll *a* concentration fluctuated on a sub-seasonal basis (range 0.65 to 43.3 mg m⁻³: Fig. 3). Peaks in chlorophyll *a* were observed to be coincident with blooms of the flagellate *Cryptomonas* sp.

Zooid size in *Conopeum seurati*

Trends in the overall mean zooid length, zooid width and zooid area can be seen in the pooled data (data from all colonies: Fig. 4). Generally, the largest zooids were produced during the coolest periods and the smallest during the warmer summer months (Fig. 2), suggesting a clear correlation between zooid size and temperature. However, as the trends in these pooled data could potentially reflect genotypic changes through the study as old colonies die and new colonies are founded, it was necessary to correct for any genetic component of size using GLM.

GLM confirmed that zooid length, width and area were significantly dependent upon temperature (Tables 1, 2, 3). Food availability had no significant effect on zooid morphometrics (Table 1, 2, 3). Salinity significantly influenced zooid length (Table 1) and zooid area (Table 3) but not zooid width (Table 2). Colony identity (genotype) had a strong influence on zooid length (Table 1) and zooid area (Table 3), but not on

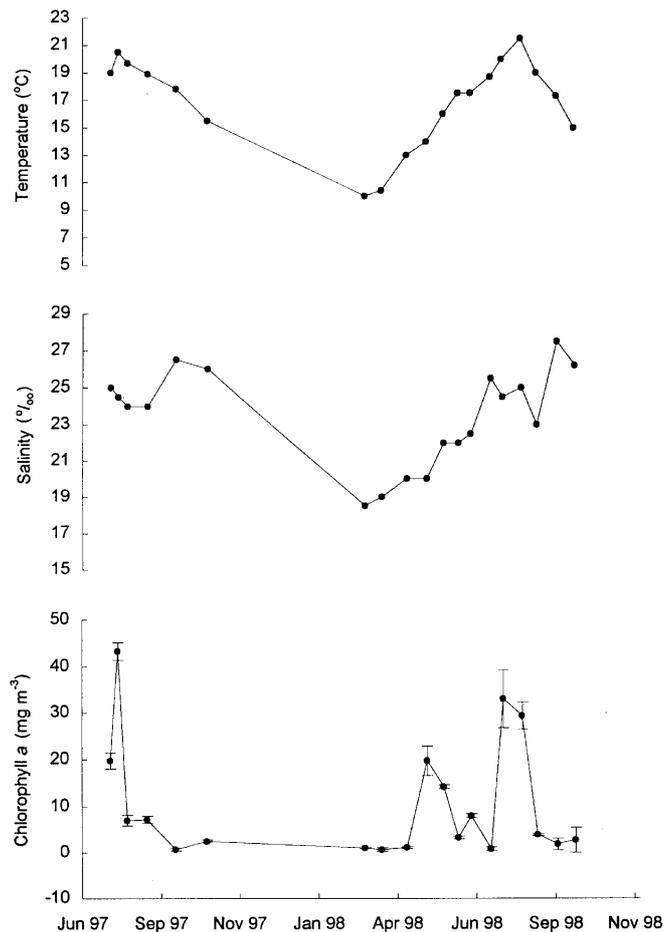


Fig. 3 Environmental variables over study period at the Old Dock. (Error bars ± 1 SD)

zooid width (Table 2). Neither the mean rate of growth nor the reproductive state of the colonies had a significant effect upon any measure of zooid size (Tables 1, 2, 3). Only one interaction term, the combined influence of temperature and salinity on zooid length and zooid area, proved to be significant (Tables 1 and 3).

Temperature consistently accounted for most variation in zooid length (31.83%), width (31.75%) and area (40.51%) (Table 4). Salinity, and the interaction between temperature and salinity, had the next strongest effects, accounting for roughly similar proportions of the variance (Table 4). The proportion of variance in the three measures of zooid size that is attributable to temperature suggests that zooid area is more sensitive to temperature than zooid length, while zooid length is more sensitive to temperature than zooid width.

Colony growth rate

The mean growth rate of the bryozoan colonies varied over the study period, reaching a maximum mean rate of nearly 1 mm d⁻¹ (Fig. 4). Comparison with the temperature and chlorophyll *a* profiles suggests that mean

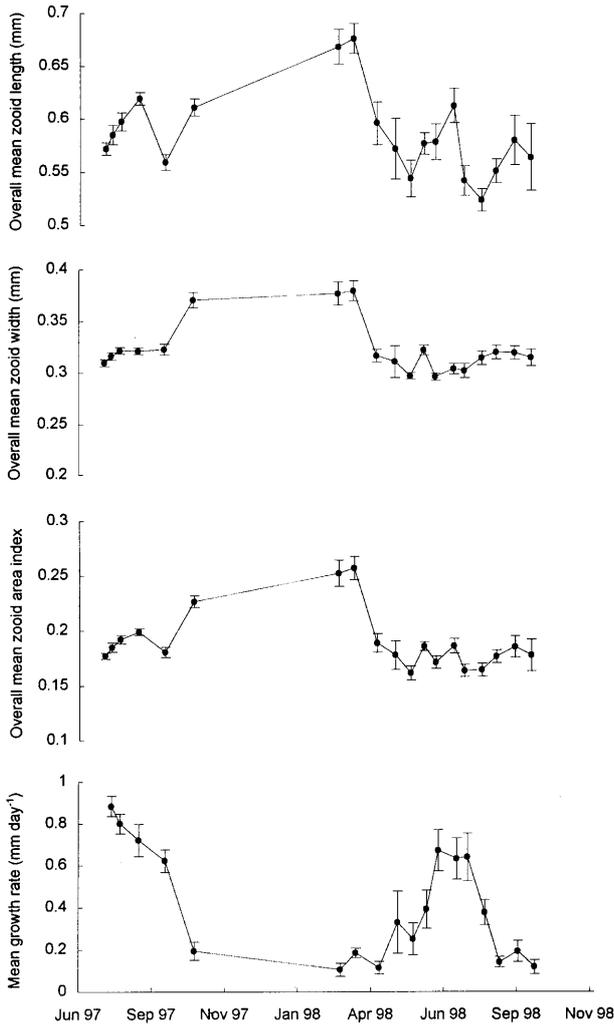


Fig. 4 *Conopeum seurati*. Morphometric responses over study period at Old Dock (Error bars standard errors)

Table 1 *Conopeum seurati*. General linear model (GLM) of zooid length for bryozoans grown at Avonmouth Docks as a function of temperature (*T*), mean chlorophyll *a* concentration (*Chl*), salinity (*S*), mean colony growth rate (*G.rate*), colony reproductive state (*Rep*) and individual colony (*Col*). *T*, *Chl*, *S* and *G.rate* were covariates. Sources of variation: *T* (*n* = 19); *Chl* (*n* = 19); *S* (*n* = 13); *G.rate* (*n* = 18); *Rep* (*n* = 2); *Col* (*n* = 22) (*Adj SS* adjusted sum of squares; *Adj MS* adjusted mean square; * significant at *p* < 0.05; ** significant at *p* < 0.01; *** significant at *p* < 0.001)

Source	GLM of zooid length				
	(<i>df</i>)	Adj SS	Adj MS	<i>F</i>	<i>p</i>
<i>T</i>	(1)	38.930	38.930	9.44	**
<i>Chl</i>	(1)	1.139	1.139	0.28	NS
<i>S</i>	(1)	21.435	21.435	5.20	*
<i>G.rate</i>	(1)	5.259	5.259	1.28	NS
<i>Rep</i>	(1)	0.086	0.086	0.02	NS
<i>Col</i>	(17)	311.388	18.317	4.44	***
<i>T</i> × <i>Chl</i>	(1)	3.487	3.487	0.85	NS
<i>T</i> × <i>S</i>	(1)	22.106	22.106	5.36	*
<i>T</i> × <i>G.rate</i>	(1)	7.420	7.420	1.80	NS
Error	(84)	346.413	4.124		

Table 2 *Conopeum seurati*. GLM of zooid width for bryozoans grown at Avonmouth Docks (Further details as in Table 1)

Source	GLM of zooid width				
	(<i>df</i>)	Adj SS	Adj MS	<i>F</i>	<i>p</i>
<i>T</i>	(1)	7.762	7.762	6.90	*
<i>Chl</i>	(1)	0.966	0.966	0.86	NS
<i>S</i>	(1)	3.806	3.806	3.38	NS
<i>G.rate</i>	(1)	0.293	0.293	0.26	NS
<i>Rep</i>	(1)	3.344	3.344	2.97	NS
<i>Col</i>	(17)	23.828	1.402	1.25	NS
<i>T</i> × <i>Chl</i>	(1)	1.128	1.128	1.00	NS
<i>T</i> × <i>S</i>	(1)	3.991	3.991	3.55	NS
<i>T</i> × <i>G.rate</i>	(1)	0.630	0.630	0.56	NS
Error	(84)	94.509	1.125		

Table 3 *Conopeum seurati*. GLM of zooid frontal area (length × width) for bryozoans grown at Avonmouth Docks (Further details as in Table 1)

Source	GLM of zooid area (length × width)				
	(<i>df</i>)	Adj SS	Adj MS	<i>F</i>	<i>p</i>
<i>T</i>	(1)	36222	36222	15.90	***
<i>Chl</i>	(1)	267	267	0.12	NS
<i>S</i>	(1)	18897	18897	8.29	**
<i>G.rate</i>	(1)	240	240	0.11	NS
<i>Rep</i>	(1)	2823	2823	1.24	NS
<i>Col</i>	(17)	148351	8727	3.83	***
<i>T</i> × <i>Chl</i>	(1)	46	46	0.02	NS
<i>T</i> × <i>S</i>	(1)	19704	19704	8.65	**
<i>T</i> × <i>G.rate</i>	(1)	216	216	0.09	NS
Error	(84)	191378	2278		

Table 4 *Conopeum seurati*. Proportion of mean sum-of-squares accounted for by each source of variation for zooid length, zooid width, and zooid area (length × width). Data are percentages of the adjusted mean squares (Further details as in Table 1)

Source	% variance		
	Zooid length	Zooid width	Zooid area
<i>T</i>	31.83	31.75	40.51
<i>Chl</i>	0.93	3.95	0.30
<i>S</i>	17.53	15.57	21.13
<i>G.rate</i>	4.30	1.20	0.27
<i>Col</i>	0.07	13.68	3.16
<i>Rep</i>	14.98	5.74	9.76
<i>T</i> × <i>Chl</i>	2.85	4.61	0.05
<i>T</i> × <i>S</i>	18.08	16.33	22.04
<i>T</i> × <i>G.rate</i>	6.07	2.58	0.24
Error	3.37	4.60	2.55

colony growth rate is strongly correlated with temperature. However, when analysed within genotypes using GLM, growth rate was significantly influenced by mean chlorophyll *a* concentration, while the effect of temperature alone was not significant (Table 5).

GLM revealed a significant positive relationship between the reproductive status of the colonies and the rate of colony growth (Table 5). The interaction of

Table 5 *Conopeum seurati*. GLM of colony growth-rate for bryozoans grown at Avonmouth Docks (Further details as in Table 1)

Source	GLM of growth-rate				
	(df)	Adj SS	Adj MS	F	p
T	(1)	0.025	0.025	0.88	NS
Chl	(1)	0.332	0.332	11.47	**
S	(1)	0.002	0.002	0.04	NS
Rep	(1)	0.970	0.970	33.56	***
Col	(17)	0.109	0.006	0.22	NS
T × Chl	(1)	0.242	0.242	8.37	**
T × S	(1)	0.007	0.007	0.26	NS
Error	(87)	2.487	0.029		

temperature and chlorophyll *a* concentration also had a significant positive effect on growth rate (Table 5).

During the investigation it became clear that *Conopeum seurati* larvae preferred to settle on the finely abraded side of the slides. A small number of colonies did settle and grow on the smooth surfaces, but this had no apparent detrimental effect on growth.

Discussion and conclusions

Changes in zooid size

This study demonstrates that, in a natural setting, zooids of the bryozoan *Conopeum seurati* vary significantly in length, width and area as a function of the temperature at which they develop. We regard these temperature–morphometric changes to reflect true changes in zooid size. However, as we were not able to measure zooid depth, we cannot claim unequivocally to have documented size-variation. Nonetheless, zooids did not noticeably become thicker or thinner with decreasing or increasing zooid lengths and widths, respectively. Indeed, colony thickness appeared to directly parallel variation in zooid lengths and widths. We are therefore confident that changes in zooid lengths and widths are reasonable correlates of zooid size, and thus we refer to changes in zooid size in the subsequent discussion.

The monitored levels of chlorophyll *a* revealed that zooid morphometrics do not respond to the amount of food available. In general, our results support evidence of the zooid size/temperature relationship noted in previous studies, but characterise further and more precisely the relationship between various environmental variables and zooid size. The use of zooid size as an indicator of temperature regimes (Okamura and Bishop 1988; Hunter and Hughes 1994; O’Dea and Okamura 1999) is thus upheld. However, because zooid size has a substantial genotypic component (see present Table 4, and also Hunter and Hughes 1994), it is crucial that studies using zooid size to infer temperature be based on clearly defined species and substantiated by large data sets. Provided these precautions are taken, the consistent

temperature–size relationship described in previous studies for bryozoans, and the explicit documentation we provide here, lead us to conclude that bryozoans present a unique opportunity of gaining insight into seasonal and longer-term temperature regimes in Recent and fossil assemblages.

Zooid width appears to be less sensitive than zooid length or zooid area to temperature, a conclusion also reached by Okamura and Bishop (1988). Since zooid width is instrumental in zooidal tessellation, it is likely that width is strongly controlled by the position of the zooid in the colony and the shape of its neighbouring zooids. We therefore recommend that zooid length or zooid area should be used to interpret temperature responses. However, as zooid area, which is a function of both length and width, in all cases accounted for a greater proportion of variance than zooid length alone, it is clear that the general response to temperature is to increase size in both dimensions, albeit less so in width.

Colony growth rate

Colony growth rate was greatest during periods of high chlorophyll *a* concentrations. The significant influence of food availability on the rate of colony growth has similarly been found in other studies of bryozoans (Winston 1976; Jebram 1977). We believe that our measure of food availability based on chlorophyll *a* concentration provided a reasonable estimate of the actual food available to *Conopeum seurati*. First, we observed that the flagellate *Cryptomonas* sp. was sufficiently abundant at times to cause bloom conditions, during which the water visibly turned brown. These periods correlated with the times of highest chlorophyll *a* concentrations. Flagellates are widely regarded to be important food items for bryozoans (Winston 1977), and *Cryptomonas* sp. lies within the range of plankton available to *Conopeum seurati* (*Cryptomonas* sp. size $\approx 25 \mu\text{m}$; *Conopeum seurati* mouth size $\approx 32 \mu\text{m}$). Second, Jebram (1968) and Menon (1972) found that *C. seurati* grew well under laboratory conditions when provided with *Cryptomonas* sp. as food source. Thus, reservations we had about using chlorophyll *a* as an index of food availability appear to be unfounded.

Colony growth as a function of food availability was influenced significantly by temperature (see interaction of temperature and food availability: Table 5). Growth rate increased as food availability increased, but growth is apparently compromised at lower temperatures, presumably because metabolic rate is low (see Fig. 3).

Our data also revealed a significant relationship between the reproductive state of the colonies and colony growth rate (Table 5), with gamete production occurring during times of increased growth rate. The explanation for this relationship is not known, but we believe it reflects the timing of energetically-expensive gamete production to coincide with periods of high productivity, and in this case, warm temperatures (Fig. 4).

Mechanisms responsible for changes in zooid size

Considering our results in the light of hypotheses explaining temperature-mediated changes in zooid size, we can readily discount hypotheses that zooid size changes as a direct response to the amount of food available (Dzik 1975; Sebens 1979), since in our study zooid size did not vary as a function of chlorophyll concentrations. However, Hunter and Hughes (1994) suggested that changes in zooid size may be adaptive responses to variations in food availability that are mediated by temperature, since bryozoans use temperatures as an extrinsic cue to predict the amount of food. We suggest that there are two fundamental weaknesses in this hypotheses: (1) productivity does not necessarily parallel temperature in a natural environment; (2) an autozooid will not only feed just after it has been budded, when it has supposedly attained optimum size, but will continue feeding long after the environment has changed and food availability has altered. Since zooids in cheilostome bryozoans do not change size after being budded, it appears that zooid size would have limited ability to parallel food availability, particularly in environments where productivity is rapidly changing. For similar reasons, we believe that the size changes observed in the zooids of *Conopeum seurati* are also unlikely to reflect an adaptive response to changes in seawater viscosity.

Zooid size was not influenced by the rate at which colonies grew. Consequently, variation in zooid size cannot be due to differential energy allocation to newly budding zooids arising from variations in growth rate. It could be argued that the production of a larger number of smaller zooids in the summer might be necessary to support reproduction in older, larger zooids; however, we regard this as an unlikely explanation since: (1) the inferred period of reproduction had no effect on variations in zooid size; (2) apart from newly-budded zooids at the growing edge of colonies and those budded at very early stages of colony growth, reproduction appeared to occur in all zooids, regardless of size or position.

It has been suggested that increasing oxygen demands at higher temperatures may play an important role in temperature-mediated changes in body size (Atkinson 1994). Our data provide some support for this scenario, since a decrease in zooid area occurred at higher temperatures. The significant effect of salinity and also the interaction of temperature and salinity on zooid area further suggest that oxygen limitation may influence zooid size, since both temperature and salinity affect the oxygen solubility of water. At Avonmouth, the combined effects of an increase in temperature and salinity would have reduced the maximum oxygen solubility of the water from 6.88 ml l⁻¹ in March to only 5.30 ml l⁻¹ in August 1998 (from Parsons et al. 1992). Thus, not only would oxygen demand have increased as temperatures increased, but oxygen availability would correspondingly have been reduced, thereby enhancing the effects of increased temperature and salinity.

More detailed study of the Bryozoa and other taxa is required to elucidate the mechanism(s) of the temperature-size effect. It is, however, apparent that the effect is not taxon-specific (see Atkinson 1994), as it applies to ectothermic and endothermic animals in terrestrial and aquatic environments as well as to solitary and colonial forms. This strongly suggests that the response reflects an unavoidable, fundamental biological phenomenon that has no adaptive basis. Thus, if size decreases are the result of reduced oxygen levels, they are more likely to represent a direct restriction on growth as oxygen becomes limited, than an adaptive response that allows organisms to maintain optimal surface-to-volume ratios. The size stability of mature zooids and their functional longevity combined with environmental fluctuations render the task of finding an adaptive explanation for zooid size-variation difficult.

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