



ELSEVIER

Palaeogeography, Palaeoclimatology, Palaeoecology 185 (2002) 77–94

**PALAEO**

www.elsevier.com/locate/palaeo

# Bryozoan growth mirrors contrasting seasonal regimes across the Isthmus of Panama

Aaron O'Dea<sup>a,\*</sup>, Jeremy B.C. Jackson<sup>b,c</sup>

<sup>a</sup> 14 Ninetree Hill, Kingsdown, Bristol BS1 3SQ, UK

<sup>b</sup> Scripps Institute of Oceanography, La Jolla, CA 92093-00244, USA

<sup>c</sup> Center for Tropical Paleocology and Archeology, Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Panama

Received 20 September 2001; accepted 27 March 2002

## Abstract

Two highly environmentally contrasting localities on either side of the Isthmus of Panama were chosen to investigate the response of zooid size to differing seasonal regimes within colonies of cupuladriid bryozoans. The Bocas del Toro region in the southern Caribbean experiences a very low mean annual range of temperature (MART) while, as a result of seasonal upwelling, the Gulf of Panama in the eastern Pacific experiences a high MART. Profiles of zooid size, from ancestrula to colony margins, were made on colonies from both localities. Results reveal that in colonies from the Gulf of Panama zooid size varies cyclically, while in colonies from the Bocas del Toro region no strong trends are observed, hence paralleling the respective seasonal temperature regimes. These data support previous evidence that zooid size varies inversely with temperature. We propose that given good taxonomic understanding, profiling zooid size in this way could provide important information on aspects of life histories in both fossil and Recent cupuladriids. We were also able to show that the amount of variation in zooid size within cupuladriid colonies correlates well with the MART which the colony experiences. This approach may be used to provide data on absolute MARTs over geological time by analysing zooid sizes in fossil cupuladriids. The abundance of cupuladriids in the Neogene of Central America suggests that this technique could provide important corroborative data on regional environmental changes associated with the closure of the Central American Isthmus. © 2002 Published by Elsevier Science B.V.

*Keywords:* Cupuladriidae; growth; zooid; seasonality; tropical America

## 1. Introduction

Cheilostome bryozoans are colonial, mostly marine animals which grow through the asexual budding of modules termed zooids with calcare-

ous skeletons (McKinney and Jackson, 1989). A large number of studies have demonstrated that the ultimate size of zooids in cheilostomes is controlled to a significant extent by the ambient temperature in which the zooid was budded, such that in warmer waters smaller zooids are produced compared to those in cooler waters (Ryland, 1963; Menon, 1972; Morris, 1976; Silén and Harmélin, 1976; Okamura, 1987; Okamura and Bishop, 1988; Hunter and Hughes, 1994;

\* Corresponding author.

E-mail addresses: aaronodea@yahoo.com (A. O'Dea), jbjackson@ucsd.edu (J.B.C. Jackson).

O'Dea and Okamura, 1999, 2000a,b,c, S. Morley and R. Hughes, unpublished data).

The inverse relationship between environmental temperature and body size is a phenomenon commonly observed in a large number of ectothermic and endothermic animals encompassing over eight phyla (see Atkinson, 1994). Indeed, although the mechanism(s) behind the response are not currently fully understood, its biotic ubiquity led Atkinson and Sibly (1997) to describe the response as the temperature–size rule.

In the Bryozoa, the scaling of zooid size to temperature has been documented to occur at different hierarchical levels. Thus, the relationship has been observed between colonies of the same species across climatic boundaries (Ryland, 1963; Morris, 1976, Silén and Harmélin, 1976; O'Dea and Okamura, 2000b,c); within species over geological (Okamura and Bishop, 1988; O'Dea, 1999) and seasonal time scales (Okamura, 1987); within colonies over seasonal time scales (Hageman, 1995; O'Dea and Okamura, 1999, 2000a,b,c); and within colonies under differing laboratory conditions (Menon, 1972; Hunter and Hughes, 1994, S. Morley and R. Hughes, personal communication).

Of these studies, perhaps the most important are those to have documented the response under cultured conditions where many potential size-influencing variables were either measured or controlled. As a result, these studies were able to discriminate the relative effects of numerous environmental and biotic influences upon zooid size including temperature (Hunter and Hughes, 1994; O'Dea and Okamura, 1999; Morley and Hughes, personal communication). In each of these studies, temperature was consistently found to account for the largest response in zooid size, while other factors, such as food availability, oxygen levels, growth rates, and energetic allocation to reproduction, appeared to have little significant influence on size. These studies also reveal that across colonies of perceived species, zooid size is highly influenced by genotype. This has important implications for the use of zooid morphology in determining biological species using morphometric techniques (Jackson and Cheetham, 1990; Hageman et al., 1999).

### 1.1. *Environmental inferences from zooid size*

The observation that zooid size varies with environmental temperature led workers to propose the potential use of zooid size as a thermometer to investigate environmental change over time. Firstly, Okamura and Bishop (1988) suggested that trends in zooid size within species over geologic time could be used to indicate relative changes in palaeotemperature. Even though similar techniques have previously been widely applied to different taxa (e.g. Malmgren and Kennet, 1978; Strauch, 1968), this approach, however, has inherent problems, including the inability to distinguish confidently the relative effects of environmental change and any phyletic trends in zooid size over time (O'Dea, 1999). This is of particular importance considering that genetic differences within species have shown to have a significant effect upon zooid size (Hunter and Hughes, 1994; O'Dea and Okamura, 1999).

In an attempt to remove the confounding element of these genetic effects and to produce a more sophisticated approach to using zooid size as a palaeoenvironmental tool, O'Dea and Okamura (2000a,b) investigated the theory that the amount of variation in zooid size within bryozoan colonies is related to the amount of seasonal variation in temperature experienced by the colony. Because the approach measured the variation of zooid size within colonies, and carefully avoided size differences associated with changing genetic expression (e.g. polymorphism), it was possible to create a model that assumed no genetic component of zooid size. Formulation of the model involved the measurement of over 3000 zooids from over 150 carefully selected colonies of 30 species from a wide variety of seasonally differing environments (tropical to polar and deep to subtidal waters). The approach was able to show that the intracolony coefficient of variation (CV) in zooid size was significantly related to the mean annual range of temperature (MART) which the colony had experienced through its growth. Regression analysis of these data produced the following linear equation:

$$\text{MART} = 3 + 0.745(b)$$

where MART = the mean annual range of temperature experienced by the colony ( $^{\circ}\text{C}$ ), and  $b$  = the mean intracolony CV of zooid frontal area (O'Dea and Okamura, 2000b).

This equation was then successfully used to predict values of the MART of two ancient seas by applying zooid size data from fossil colonies (O'Dea and Okamura, 2000a,b). This novel approach to utilising within-colony variation is of particular value to palaeoclimatologists as it provides an absolute estimate of the range of seasonal variation in temperature at the time of deposition and is able to circumvent a number of potential problems associated with other techniques for assessing marine palaeoseasonality (O'Dea and Okamura, 2000b).

A further study of variation in morphology within bryozoan colonies analysed changes in zooid size through profiles along the fronds of the perennial Recent bryozoan *Flustra foliacea* (O'Dea and Okamura, 2000c). Results showed that as colonies grew, zooid size varied in a cyclical pattern which was in synchrony with seasonal changes in temperature. The authors proposed that such zooid size profiles provide a unique opportunity to assess aspects of environmental change and the life histories of both fossil and Recent bryozoan species. For example, annual growth rates of a colony could easily be quantified by measuring the mean wavelength of cycles within a profile, thereby leading to inferences about environmental productivity, growth rates, and longevity within and among bryozoan colonies (O'Dea and Okamura, 2000c). This approach has many similarities with the oxygen isotope profiling technique which can be used to advance the understanding of the biology of Recent shell secreting organisms and has provided a powerful approach for making palaeobiological and palaeoenvironmental inferences based upon profiles from fossil organisms (Jones, 1998), including bryozoans (Pätzold et al., 1987; Brey et al., 1998; Bader, 2000).

Thus, these two approaches of analysing variation in zooid size within bryozoan colonies present a number of opportunities to investigate aspects of environmental change and life histories in perennial bryozoans. In the present study this



Fig. 1. Localities on either side of the Isthmus of Panama used in this study: Bocas del Toro in the south-west Caribbean and the Gulf of Panama in the eastern Pacific. Circles represent position of sampled sites.

potential is examined in colonies of free-living tropical American cupuladriid bryozoans. The study uses Recent colonies of *Cupuladria* and *Discoporella* from two environmentally contrasting coastal waters around Panama, specifically from the Bocas del Toro region in the south-western Caribbean, and the Gulf of Panama in the eastern Pacific (Fig. 1). Firstly, the potential of the zooid size profiling approach to make environmental and life history predictions is investigated. Secondly, the potential of the MART approach to make accurate estimates of seasonality is tested.

### 1.2. Mechanisms explaining zooid size changes

It is important to introduce and review the proposed mechanisms behind the response of zooid size to temperature to provide the reader with a more complete understanding of the current state of knowledge into zooid size variation within the Bryozoa. Hunter and Hughes (1994) and O'Dea and Okamura (1999) provide more detailed reviews. The mechanisms that have been proposed either attribute size changes to an adaptive response (e.g. temperature-related changes in levels of food supply (Sebens, 1979; Hunter and Hughes, 1994) or sea water viscosity (O'Dea and Okamura, 1999)), or have been explained as an unavoidable biological phenomenon (e.g. temperature-derived changes in metabolic rate (Sebens, 1982), a response to changes in oxygen demand (O'Dea and Okamura, 1999; Morley and Hughes, personal communication) or as a simple increase in the size of cells at lower temperatures (van

Voorhies, 1996)). In terms of zooid size changes that occur within colonies and are not associated with astogenetic or other known fixed stages of colony growth, O'Dea and Okamura (1999) argued that it is difficult to reconcile the idea that zooids are responding adaptively to a particular environmental cue at a particular time. It was maintained that size adaptation to a distinct environmental level will become invalid as soon as that environment has altered since zooids in cheilostomes remain a fixed size once budded and zooecial chambers are often re-used through the growth of the colony. For this reason, plus the fact that temperature-related zooid size changes have been observed to occur within genotypes across environmental gradients and that the temperature–size rule occurs across a wide variety of taxa (Atkinson, 1994; Atkinson and Sibly, 1997), we feel confident that the numerous studies documenting temperature-related zooid size changes are recognising a tangible ecophenotypic process.

We do not claim that temperature is the only factor that can affect zooid size within colonies; indeed, a number of other biotic and abiotic factors have been shown to influence zooid size including: water flow (Okamura and Partridge, 1999), substrate irregularities (O'Dea and Okamura, 2000b), and biotic competition for space (Polluzzi and Coppa, 1991). However, through the careful collection of data, these confounding factors can be minimised (Hageman et al., 1999; O'Dea and Okamura, 2000b).

Zooid size has strong adaptive implications, particularly since it correlates well with the size and therefore the type of food which the bryozoan can ingest (McKinney and Jackson, 1989). Across bryozoan species, zooid size also has consequences upon ecological dominance, growth rates and maximum colony sizes (McKinney and Jackson, 1989) and ranges of zooid size within a bryozoan assemblage may be constrained by the historical level of environmental stability (Jackson and Herrera-Cubilla, 2000). Thus, ecological and environmental size adaptation and constraint should be expected to occur across and within species. The patterns expressed through these processes cannot however be invoked to explain intracolony ecophenotypic changes in zooid size

unless of course clearly defined somatic changes have occurred during the growth of the colony.

Thus, there is strong evidence suggesting that the temperature-related zooid changes that have been observed in the Bryozoa are temperature-mediated.

## 2. The Cupuladriidae

The family Cupuladriidae are a group of free-living cheilostome bryozoans that are commonly found in tropical and subtropical marine habitats around the world (Cook and Chimonides, 1983). Unlike the majority of cheilostomes however, the cupuladriids are not fixed to the substratum but are motile, being able to rest free from the surface and unbury themselves through the use of polymorphic zooids (Marcus and Marcus, 1962; Cook, 1963; Greeley, 1967). This free-living life mode allows them to inhabit regions where sediment instability would normally preclude the settlement of other bryozoan species.

Two cupuladriid genera, *Cupuladria* and *Discoporella*, are abundant both today and as fossils in tropical and subtropical regions particularly around Central America and the Caribbean (Cheetham and Jackson, 2000). The family is believed to have originated in the Palaeocene and underwent a major diversification during the Neogene (Cook and Chimonides, 1983).

As in other cheilostomes, cupuladriid colony growth occurs through the asexual budding of zooids which, once budded and calcified, remain fixed in size throughout the life of the colony. Colonies can originate in one of three distinct ways: (1) from sexually produced, short-lived larvae which form an ancestrular triad (the founding zooids of the colony); (2) by colonial budding from a parent colony; or (3) by regeneration of fragments of older broken colonies (Håkansson and Thomsen, 2001). In all forms, growth of the colony is maintained through the radial budding of zooids away from the most proximal region of the colony, resulting in more or less circular, cap-shaped colonies (Fig. 3).

As with most bryozoans the life histories of cupuladriids are not well known. Winston (1988)

investigated the population-size structure of *Discoporella* and *Cupuladria* from Florida. However, there are no data on growth rates and timing of reproduction or recruitment for any cupuladriid species.

### 3. Contrasting environments across the Central American Isthmus (CAI)

Formation of the CAI during the Neogene (Coates and Obando, 1996) has resulted in the Pacific and Caribbean waters around Panama experiencing very different seasonal environmental regimes (Jackson and D'Croz, 1997). Prior to the formation of the CAI, waters flowed freely at abyssal depths across the region and there is a wide variety of evidence to suggest that environmental conditions were relatively homogeneous between the eastern Pacific and the Caribbean (e.g. Keigwin, 1982; Collins, 1996; Teranes et al., 1996).

Today, the two coasts of Panama experience dramatically different environmental regimes. Generally, the Caribbean experiences overall high temperatures with little seasonal change, high salinities and low primary productivity (Keigwin, 1982), while on the opposite side the Gulf of Panama in the eastern Pacific is characterised by marked seasonal changes in temperature, lower salinities and strong shifts in primary productivity (D'Croz et al., 1991). These differences are caused by strong seasonal upwelling in the Gulf of Panama which occurs as a result of trade winds blowing across the isthmus from late December to late March bringing cold, nutrient-rich deep water into coastal waters. Furthermore, the eastern Pacific is also affected by El Niño events which can suppress the yearly cycle of seasonal upwelling, resulting in high interannual variability in the seasonal thermal and primary productivity regimes.

The two sites in this study were chosen for their contrasting seasonal regimes in temperature and primary productivity, and because of the availability of cupuladriid collections. Temperature, chlorophyll and salinity data demonstrate the contrasting seasonal environments of the two sites

(Fig. 2). The MART in the Bocas del Toro region in the Caribbean is roughly 3.8°C and is relatively stable interannually (STRI Marine Environmental Science Program unpublished data). The MART for the Gulf of Panama in the Pacific is 8.2°C but this value can vary by up to as much as 6°C between years. The phytoplankton regime in the Gulf of Panama corresponds with the input of nutrient-rich waters during the period of upwelling, while chlorophyll measures from the Bocas del Toro region reveal an exactly opposite trend in seasonal phytoplankton abundance (Fig. 2). This may be a response to a decrease in terrestrial run-off into coastal waters during the period February to April as a result of the dry season which affects the whole of Panama during this time. This association between phytoplankton abundance and terrestrial run-off has been documented further east along the Caribbean coast in the San Blas (Kuna Yala) region of Panama (D'Croz et al., 1999). Salinity in the Gulf of Panama is consistently lower than in Bocas del Toro but neither locality appears to show strong seasonal trends in salinity (Fig. 2).

#### 4.5. Environmental data details

the sources of environmental data used in this study.

These contrasting environments on either side of the isthmus today, plus the relatively recent separation of the two faunas and therefore the possible occurrence of very closely related taxa (Lessios, 1990; Knowlton, 1993), present a unique opportunity to examine the phenotypic responses in marine biota to differing seasonal clines (e.g. Birkeland, 1987; Lessios, 1990; Anderson, 2001; Jackson and Herrera-Cubilla, 2000). We present here the first trans-isthmian study to utilise bryozoans as a tool to investigate within-genotype morphological responses to seasonally different environments.

## 4. Materials and methods

### 4.1. Species and colony selection

Material for this study came from dredge and trawl collections made by the Panama Paleontology Project (PPP) between the years 1996 and

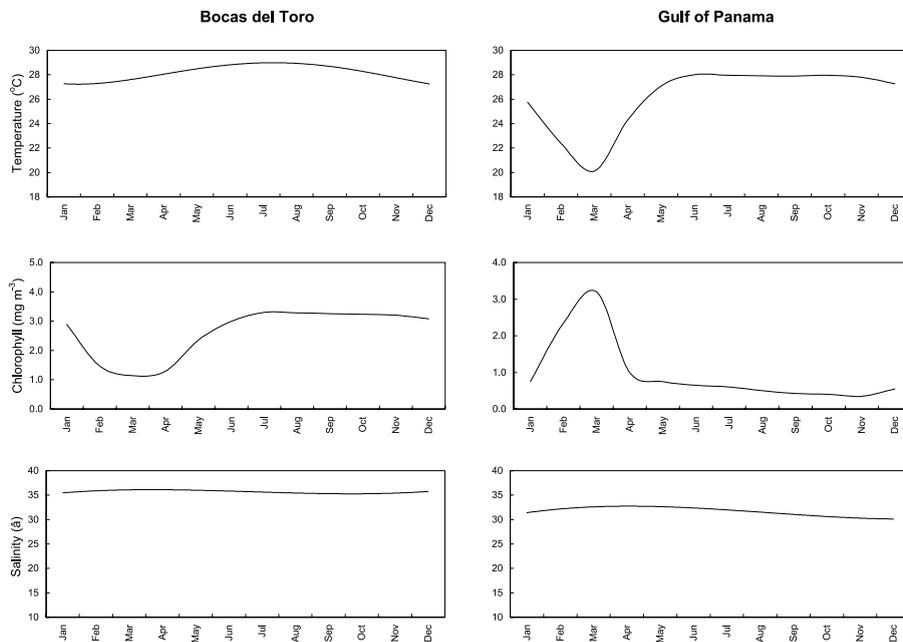


Fig. 2. Contrasting seasonal environmental regimes across the Isthmus of Panama: typical annual trends in temperature, chlorophyll, and salinity for the Bocas del Toro region and the Gulf of Panama. Data averaged from various sources (see text for details).

2000 (Fig. 1) and is housed at the Smithsonian Institution, Washington, DC, USA (USNM Catalogue Nos. 511817–511841).

The selection of cupuladriid species was based on the availability of sorted material in the PPP collections. Only species which produce large colonies were chosen. Colonies within species were chosen only if they were preserved well enough to allow adequate morphological identification to the level of species.

The systematic status of the members of the family Cupuladriidae is currently under revision. Identifications for this study are based upon preliminary species groupings (A. Herrera-Cubilla and M. Dick, unpublished data). In this study, we use codes to identify separate species taken from systematic work in progress (Herrera-Cubilla, submitted).

A total of 20 colonies were analysed. Ten colonies were selected from two localities in the Bocas del Toro region in the Caribbean (Fig. 1), each of which was identified as *Cupuladria* aff. *biporosa* Cbi4. Ten colonies were selected from four localities in the Gulf of Panama, in the east-

ern Pacific (Fig. 1), comprising five colonies of *Cupuladria* aff. *biporosa* Cbi5, four colonies of *Discoporella* aff. *umbellata* Dsp6 and one colony of *Discoporella* aff. *umbellata* Dsp5.

#### 4.2. Method of zooid size profile analysis

Fig. 3 demonstrates the process of collecting data on zooid size in a colony of *Cupuladria* aff. *biporosa* Cbi4.1. Within each colony, four proximal–distal transects were created, beginning at the main ancestral zooid from the ancestrular triad (or most proximal region of growth if the colony was a regenerated fragment) and moving outwards towards the colony margin. Profiles followed sequential generations of disto-laterally budded zooids (Fig. 3). Along the profile, maximum zooid length and zooid width were measured for each zooid generation. Length and width data for each zooid were combined to provide an index of zooid frontal area (length  $\times$  width) and zooid shape (length  $\div$  width).

Through each profile, zooids were chosen for measurement only if they were normal, complete

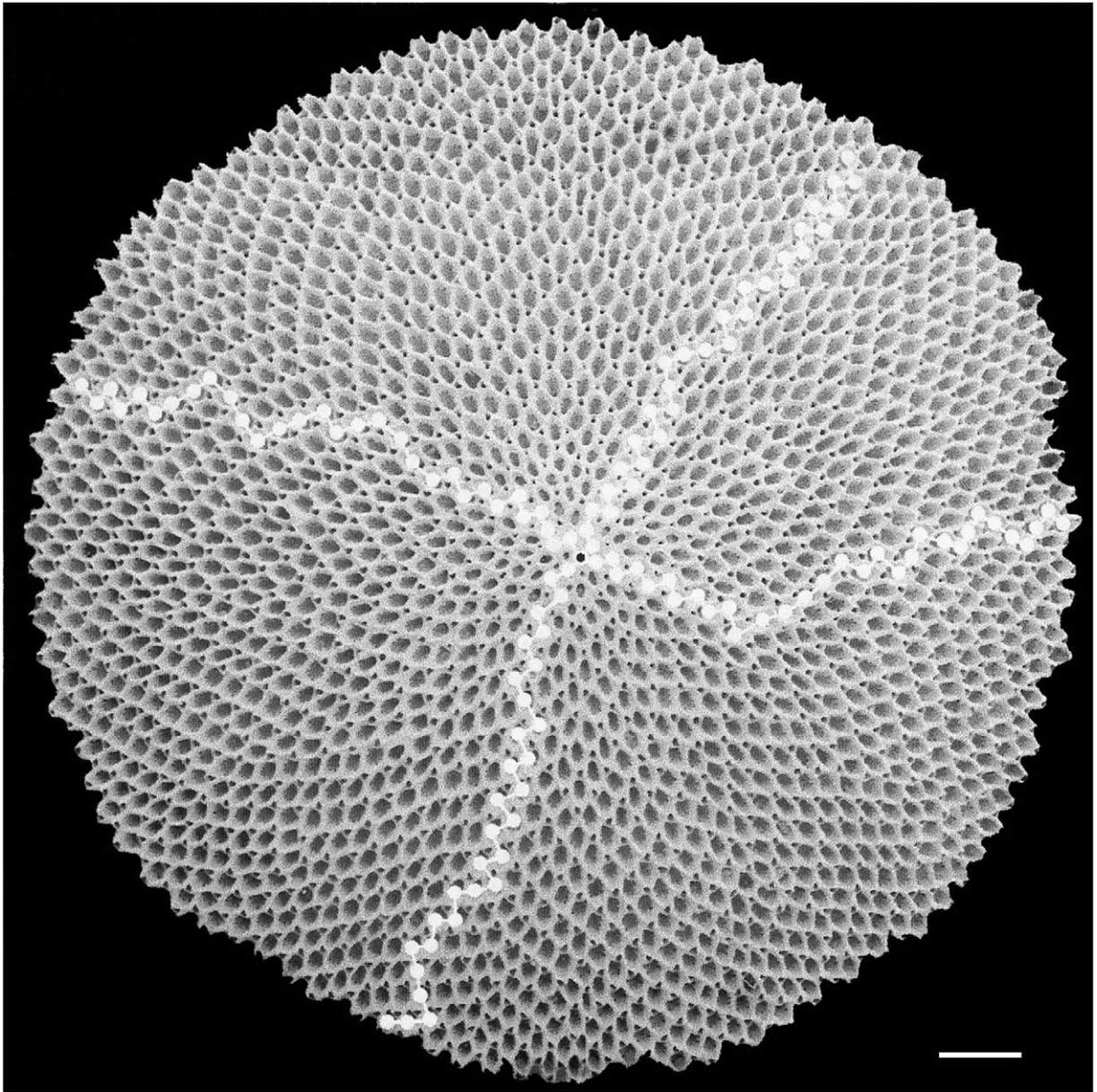


Fig. 3. Scanning electron microgram (SEM) of a sexually derived colony of *Cupuladria* aff. *biporosa* Cbi4.1 (colony BdT 5) illustrating the method of zoid area profiling. White lines represent the paths of the four profiles away from the ancestrula to the colony margin, and dots indicate the zooids chosen for measurement. Scale bar = 1 mm.

autozooids. Zooids were not measured if they represented a bifurcation in the normal budding series (which serves to increase the numbers of zooids as the colony extends radially), or if they lay distal to such a bifurcation as zooids in these

regions are more susceptible to changes in size and shape in order to conform to tessellation as the colony grows. If a zooid or a region was chosen not to be included in the profile, the path of the profile was altered to try to ensure zooid size

data were not affected by such problems. In regenerated colonies, care was taken not to allow profiles to cross regions of the colony where budding direction had changed considerably as a result of lateral budding of zooids in the region of the previous fracture since these zooids were also often unusual in size and shape (see O'Dea and Okamura, 2000b for more information on the selection of species and colonies for zooid size analysis).

For each zooid generation, area data from each of the four transects were combined and averaged and profiles compiled for each individual colony to show how mean zooid area varies throughout the growth of a single colony and to assess growth in the two seasonally different environments.

#### 4.3. Method of growth rate analysis

In those colonies where cyclical fluctuations in zooid size were observed in the profiles, growth rates and minimum colony ages were estimated. This was achieved by counting the number of cycles within a colony to gain minimum colony age in years and by subjectively calculating the mean wavelength of the cycles to gain growth rate data. Measures of growth rate are therefore presented as the mean amount of peripheral incremental growth from distal to proximal regions of the colony per year. This approach is based upon the assumption that cyclical trends in zooid size within colonies are annual. Growth rate data were analysed using analysis of variance (AN-OVA).

#### 4.4. Method of MART analysis

The zooid size data collected for the zooid area profiling approach were also analysed by the technique presented by O'Dea and Okamura (2000b) which can estimate absolute values of MART by measuring the amount of variation in zooid areas within colonies (see 1.1. Environmental inferences from zooid size).

It was important not to include those zooids within the zone of astogenetic change, where zooids become progressively larger (Boardman et al., 1969). The position of the zone of astogenetic

change within colonies was established using a slightly modified approach originally described by Taylor and Furness (1978) who applied it to determine the nature of astogeny in the Jurassic cyclostome *Stomatopora*. Here, the approach involved fitting a series of linear regressions to the zooid area profile plots, beginning with the inclusion of the first three zooidal generations from the ancestrula and sequentially adding older generations until a point is reached when a non-significant regression is obtained. The point at which the regression is no longer significant plus one further zooid generation is the point at which the zone of astogenetic change was considered to end and the zone of astogenetic repetition begins. This approach provides a standardised and conservative method of determining the position in the zooidal series where the zone of astogenetic change ends and the zone of astogenetic repetition begins, thereby minimising any problems associated with subjectively determining the position of this zone. Regenerated colonies, where the ancestral region is absent, were not suitable for the regression approach. To ascertain whether the zone of astogenetic change still remained within the first few zooidal generations in regenerated colonies, colony morphologies were examined in detail and a conservative decision made as to the location of the boundary between the zones of change and repetition.

Within each colony, those data from the zone of astogenetic change were removed leaving only zooid area data from the zone of astogenetic repetition to calculate the intracolony CV in zooid area. The position of the zone of astogenetic change is indicated by filled circles in the zooid area profiles (Figs. 4 and 5).

For each colony, the CV of zooid frontal area was applied directly to the equation presented by O'Dea and Okamura (2000b) (see 1.1. Environmental inferences from zooid size) to estimate the MART which the colony experienced. By comparing the predicted MART from colonies with actual environmental data, an assessment on the effectiveness of this approach to make palaeoenvironmental inferences can be made. Zooid size and MART data were analysed using AN-OVA.

#### 4.5. Environmental data

Data on the seasonal temperature, chlorophyll and salinity regimes in the Bocas del Toro and Gulf of Panama regions were derived and averaged from a variety of sources.

For the Bocas del Toro region, temperature data were derived from the STRI Marine Environmental Science Program (data collected at 10 m depth from five sites in the Bocas del Toro region) and Sadler et al. (1987) (data collected from 1 m depth). Chlorophyll data were derived from Feldman et al. (1989) (originating from the NASA's Coastal Zone Color Scanner), and Conkright et al. (1998). Salinity data were derived from the STRI Marine Environmental Science Program (unpublished data) and Boyer et al. (1998).

For the Gulf of Panama, temperature data were derived from D'Croz et al. (1991), Glynn and Maté (1997), Sadler et al. (1987), Kwiecinski and Chial (1983), Podestá and Glynn (1997) and D'Croz and Robertson (1997). Chlorophyll data were derived from D'Croz et al. (1991), D'Croz and Robertson (1997), Feldman et al. (1989), and Conkright et al. (1998). Salinity data were derived from D'Croz et al. (1991) and Boyer et al. (1998).

The seasonal environmental data compiled from these varied sources therefore represents typical trends within a region over a year. The data do not claim to represent exactly the environmental regimes experienced by the cupuladriid colonies used in this study.

## 5. Results

### 5.1. Zooid area profiles

Twenty profiles of zooid area (length × width) through colonies of *Cupuladria* and *Discoporella* from the Bocas Del Toro region and the Gulf of Panama are presented respectively in Figs. 4 and 5.

Omitting the zone of astogenetic change, substantial differences can be seen between colonies from the two localities. In all colonies from Bocas del Toro little or no trends in zooid area are apparent (Fig. 4), while a sinusoidal pattern of in-

creasing and decreasing zooid area is apparent in almost all of the colonies from the Gulf of Panama (Fig. 5). The only exception, colony GoP 7 (Fig. 5), exhibits an unusual pattern which begins as if normal but after the second cycle zooid area remains low throughout the rest of the colony's growth. As described in 6.1. Zooid area profiles, there is no way of correlating this unusual pattern to actual environmental data. However, the pattern expressed in colony GoP 7 is similar to what would be expected if the colony had developed during a period of continued increased temperatures and the suppression of seasonal upwelling (i.e. a strong El Niño event).

Cyclical trends in zooid area in material from the Gulf of Panama and the lack of similar trends in material from Bocas Del Toro appear to parallel known temperature data (Fig. 2).

### 5.2. Growth rate analysis

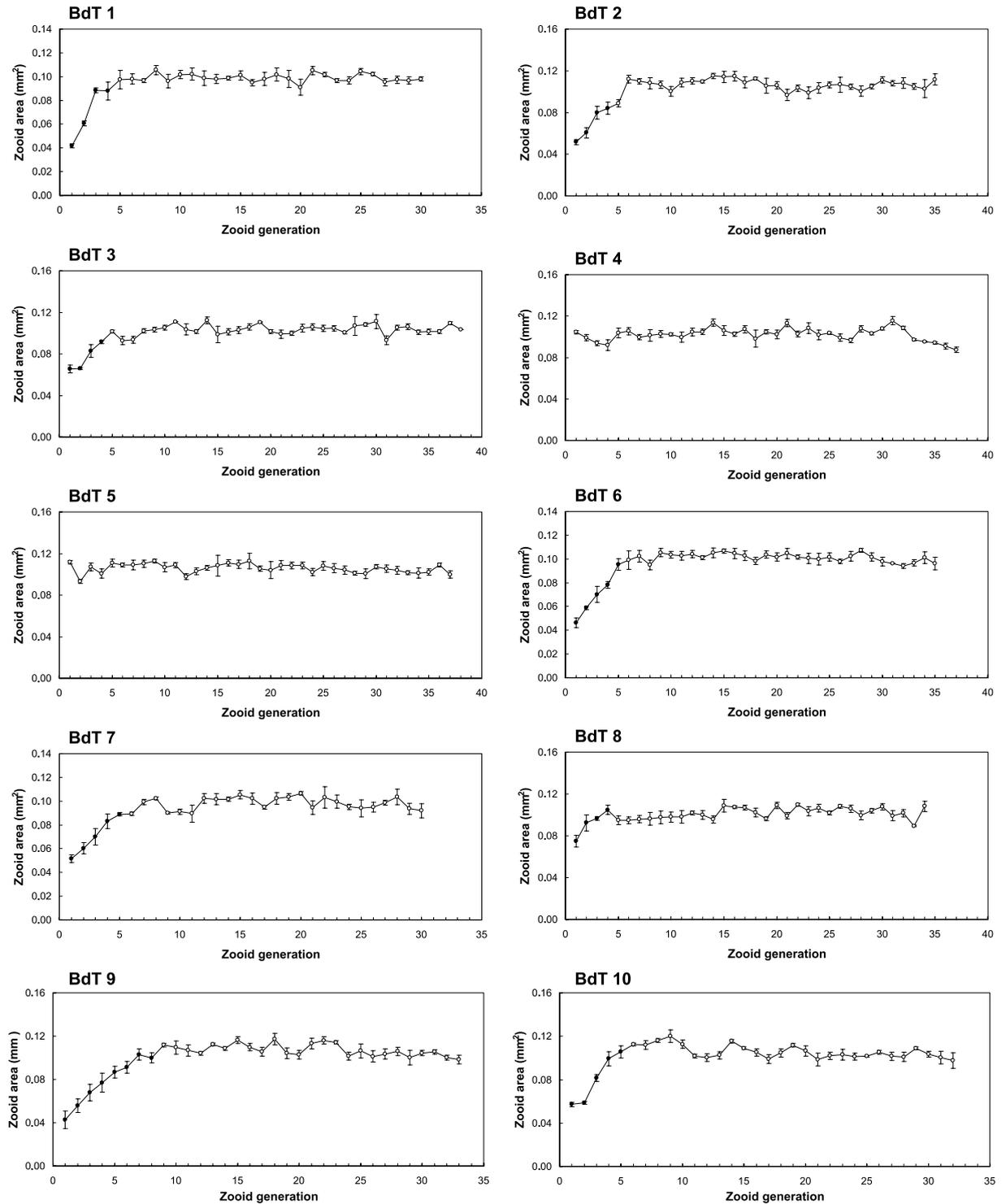
Excluding the anomalous GoP 7 colony, the profiles of all colonies from the Gulf of Panama were examined to estimate the rate of growth and colony age (Table 1). These results rest upon the assumption that the cyclical changes in zooid size observed occur in response to seasonal changes in temperature (see 6.1. Zooid area profiles). Colonies of *Cupuladria* grew at a slightly, although not significantly ( $F=0.479$ ,  $P=0.51$ ), slower rate than colonies of *Discoporella*. As a result of this slower growth and the production of generally larger colonies, *Cupuladria* reached on average an older minimum age than *Discoporella* (Table 1). There is no evidence for variation in growth rate between years.

### 5.3. MART analysis

Intracolony CV of zooid area for each of the colonies analysed is listed in Table 2, together with the respective predicted MARTs and the actual MARTs for each locality. This was found to be significantly greater in colonies from the Gulf of Panama (mean = 15.27) than in colonies from the Bocas del Toro (mean = 8.17) (Table 1) ( $F=47.64$ ,  $P<0.001$ ).

For Bocas del Toro, these data allow MART to

## Bocas del Toro



be estimated as 3.1°C. The MART estimated individually by the 10 specimens ranged from 2.4 to 4.2°C, and the standard deviation of the mean was 0.5°C. The actual MART for the Bocas del Toro region is 3.8°C and has a 95% confidence interval of 0.7°C (data from: STRI Marine Environmental Science Program (unpublished data from five localities), Sadler et al., 1987).

For the Gulf of Panama, a MART of 8.4°C is estimated. The MART estimated individually by the 10 specimens ranged from 6.0 to 13.4°C and the standard deviation of the mean was 2.4°C. The actual MART for the Gulf of Panama derived from various sources averages 8.2°C and ranges from 4.8 to 11.0°C depending upon the year of collection and therefore has a 95% confidence interval of 6.1°C (data from: Kwiecinski and Chial, 1983; Sadler et al., 1987; D'Croz et al., 1991; D'Croz and Robertson, 1997; Glynn and Maté, 1997; Podestá and Glynn, 1997).

The MARTs estimated here through the analysis of zooid sizes therefore are in close agreement and lie within the 95% confidence intervals of the actual MARTs for both localities.

## 6. Discussion

### 6.1. Zooid area profiles

Results of profiling through colonies of *Cupuladria* and *Discoporella* reveal that trends in zooid area through colony growth correspond with the respective seasonal temperature regimes which the colonies experienced. Thus, in the Gulf of Panama where strong seasonal changes in temperature occur (Fig. 2), zooid area tends to vary cyclically (Fig. 5), while at Bocas del Toro, which typically experiences very low seasonal changes in temperature (Fig. 2), colonies reveal no clear trends in zooid area (Fig. 4).

There is compelling evidence to assume that these distinct morphometric trends are the direct

result of the different temperature regimes between the two localities, and not, for example, the result of the differences in primary productivity that occur between the sites (Fig. 2). Much previous work has shown a direct link between ambient temperature and zooid size in cheilostome bryozoans and not with food availability or other environmental factors (Okamura, 1987; Hunter and Hughes, 1994; O'Dea and Okamura, 1999; Morley and Hughes, personal communication). The data we present here also provide further support for this assumption: not only do trends in zooid size within colonies from either side of the isthmus correspond to the respective seasonal trends in temperature of each locality, but they wholly contradict the typical trend observed in primary productivity (chlorophyll). In both localities, levels of chlorophyll are strongly seasonal (Fig. 2) and thus the contrasting zooid size data from either side of the isthmus do not correspond to levels of food availability. Similarly, because both localities exhibit little annual trend in salinity (Fig. 2) this gives further evidence that zooid size does not vary with decreasing salinity. Thus, the data presented here provide yet further evidence that temperature is a strong correlate of zooid size.

It could perhaps be argued that the differences might be the result of differing genetic expression between the populations from the two localities. However, since cyclical trends in zooid area occur in colonies from two genera (*Cupuladria* and *Discoporella*) this hypothesis seems to be highly unlikely, unless the expression is of an adaptive nature (although see 1.2. Mechanisms explaining zooid size changes for why this is improbable). Furthermore, the mirroring of growth trends on either side of the isthmus occurs in populations that are apparently closely related (i.e. the taxonomic group *Cupuladria biporosa*).

There is no effective method of statistically correlating these trends in zooid size to actual temperature data for a number of reasons. First, it is

---

Fig. 4. Mean zooid area (length×width) profiles through colonies of *Cupuladria* aff. *biporosa* Cbi4.1 (BdT 1–10) from Bocas del Toro. Filled circles represent the zone of astogenetic change; open circles represent the zone of astogenetic repetition (see text). Error bars represent standard error.

## Gulf of Panama

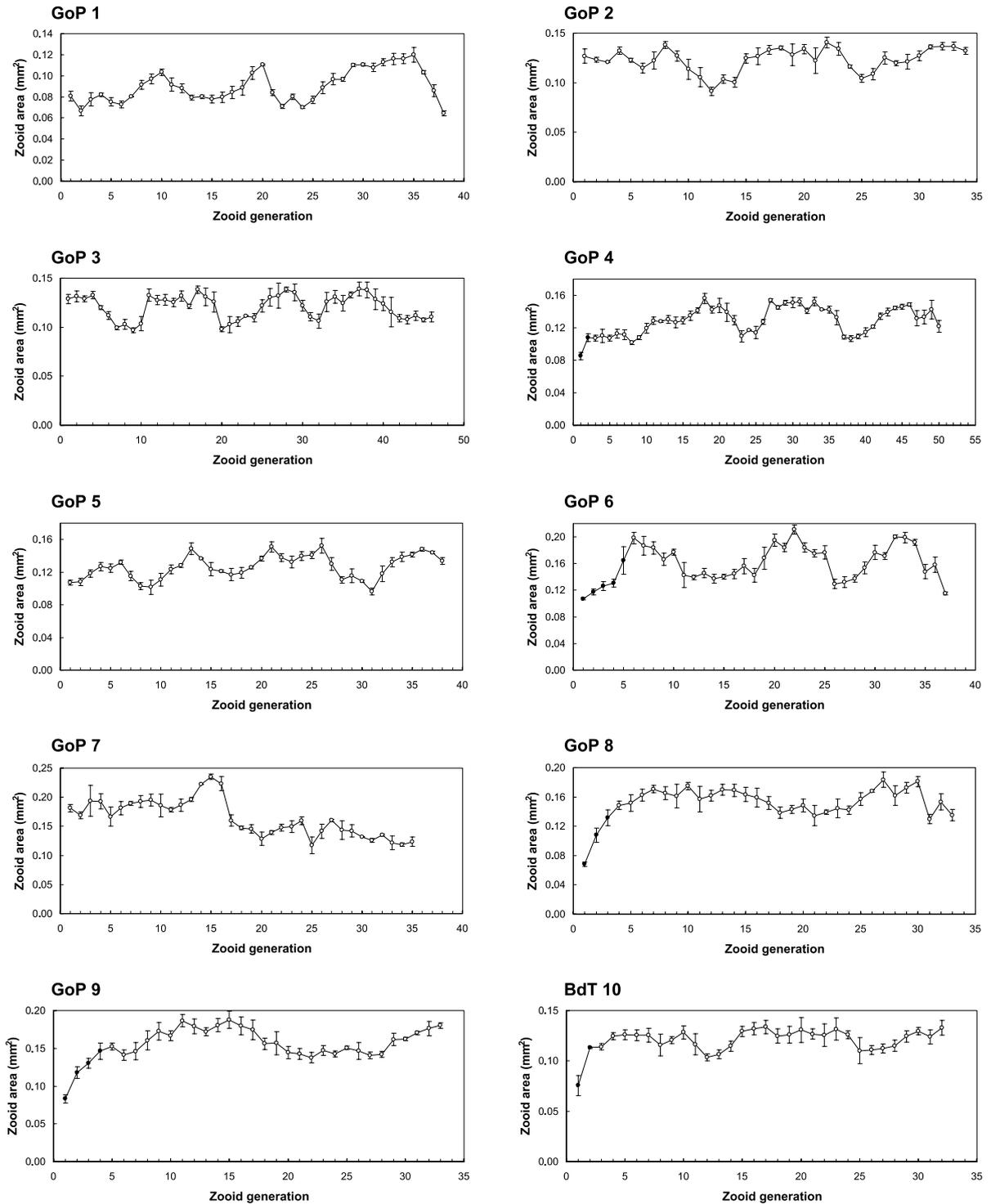


Table 1

Colony growth data for *Cupuladria* and *Discoporella* colonies from the Gulf of Panama estimated from the analysis of zooid area profiles

Colony number	Species (code)	Maximum colony radius (mm)	Minimum age at collection (yr)	Mean growth rate (mm yr <sup>-1</sup> )
GoP 1	<i>Cupuladria</i> aff. <i>biporosa</i> (Cbi5)	10.8	3	3.3
GoP 2	<i>Cupuladria</i> aff. <i>biporosa</i> (Cbi5)	10.2	3	3.6
GoP 3	<i>Cupuladria</i> aff. <i>biporosa</i> (Cbi5)	12.0	4	3.0
GoP 4	<i>Cupuladria</i> aff. <i>biporosa</i> (Cbi5)	15.0	3	4.2
GoP 5	<i>Cupuladria</i> aff. <i>biporosa</i> (Cbi5)	10.8	4	3.0
	Mean	11.8	3.4	3.4
	(S.D.)	(1.93)	(0.55)	(0.5)
GoP 6	<i>Discoporella</i> aff. <i>umbellata</i> (Dsp6)	7.5	3	2.5
GoP 8	<i>Discoporella</i> aff. <i>umbellata</i> (Dsp6)	8.3	2	4.6
GoP 9	<i>Discoporella</i> aff. <i>umbellata</i> (Dsp6)	9.0	2	5.5
GoP 10	<i>Discoporella</i> aff. <i>umbellata</i> (Dsp5)	7.5	3	2.9
	Mean	8.1	2.5	3.9
	(S.D.)	(0.72)	(0.58)	(1.4)

not possible to be confident that all the colonies used were alive when collected; this is of particular importance if we were to try to correlate trends in zooid size to intradecadal events such as El Niño in the Gulf of Panama (see 5.1. Zooid area profiles). Second, the overall rate of growth of cupuladriid colonies has not been effectively estimated elsewhere (see 6.2. Growth rate analysis), thereby precluding the correlation of interannual trends in size and known temperature regimes. Third, the rate of incremental accretion of zooids at colony margins will almost certainly vary seasonally and it will therefore be virtually impossible to estimate accurately the timing of budding for a particular region in a colony.

Overcoming these and the problems resulting from a dearth of growth rate information (6.2. Growth rate analysis) requires empirical, real-time data on the life histories of cupuladriid bryozoans. In particular, the reproduction, recruitment and demography of cupuladriids remain little understood yet is of great importance for furthering the potential applications of approaches such as that presented here and in

understanding the ecology and evolution of the cupuladriid group in general.

## 6.2. Growth rate analysis

By assuming that the trends in zooid size observed in colonies from the Gulf of Panama are synchronous with seasonal variations in temperature, we have been able to derive estimates of growth rate and colony longevity. These growth data suggest that *Cupuladria* grows at roughly the same rate, but produces slightly larger colonies and as a result reaches, on average, an older age than *Discoporella*. It was not possible to derive growth data from the Bocas del Toro colonies simply because of the lack of seasonal variations in temperature in that region. No current estimates on the rate of growth for cupuladriid species currently exist with which to compare these results, although circumstantial evidence from size–frequency diagrams of *Cupuladria* and *Discoporella* colonies from Florida suggests a similarly slow rate of growth of approximately 1–5 mm per year (Winston, 1988, figs. 7 and 8). Compared

Fig. 5. Mean zooid area (length×width) profiles through colonies of *Cupuladria* aff. *biporosa* Cbi5 (GoP 1–5), *Discoporella* aff. *umbellata* Dsp6 (GoP 6–9) and *Discoporella* aff. *umbellata* Dsp5 (GoP 10) from the Gulf of Panama. Filled circles represent the zone of astogenetic change, open circles represent the zone of astogenetic repetition (see text). Error bars represent standard error.

Table 2

Species utilised in this study from Bocas del Toro (top) and the Gulf of Panama (bottom)

Bocas del Toro – Caribbean					
Colony number	USNM Cat.	No. Species (code)	Colony status	CV zooid area	Estimated MART (°C)
BdT 1	511817	<i>Cupuladria</i> aff. <i>biporosa</i> (Cbi4.1)	sex.	8.25	3.2
BdT 2	511818	<i>Cupuladria</i> aff. <i>biporosa</i> (Cbi4.1)	sex.	8.28	3.2
BdT 3	511819	<i>Cupuladria</i> aff. <i>biporosa</i> (Cbi4.1)	regen.	7.46	2.6
BdT 4	511820	<i>Cupuladria</i> aff. <i>biporosa</i> (Cbi4.1)	regen.	7.91	2.9
BdT 5	511821	<i>Cupuladria</i> aff. <i>biporosa</i> (Cbi4.1)	regen.	7.92	2.9
BdT 6	511822	<i>Cupuladria</i> aff. <i>biporosa</i> (Cbi4.1)	sex.	7.27	2.4
BdT 7	511825	<i>Cupuladria</i> aff. <i>biporosa</i> (Cbi4.1)	sex.	9.62	4.2
BdT 8	511826	<i>Cupuladria</i> aff. <i>biporosa</i> (Cbi4.1)	regen.	8.29	3.2
BdT 9	511827	<i>Cupuladria</i> aff. <i>biporosa</i> (Cbi4.1)	sex.	8.42	3.3
BdT 10	511828	<i>Cupuladria</i> aff. <i>biporosa</i> (Cbi4.1)	sex.	8.23	3.1
			Mean	8.17	3.1
			Range	2.35	1.8
			S.D.	0.64	0.5
			Actual MART for locality:		3.8
Gulf of Panama – Pacific					
GoP 1	511829	<i>Cupuladria</i> aff. <i>biporosa</i> (Cbi5)	sex.	18.64	10.9
GoP 2	511830	<i>Cupuladria</i> aff. <i>biporosa</i> (Cbi5)	regen.	12.84	6.6
GoP 3	511833	<i>Cupuladria</i> aff. <i>biporosa</i> (Cbi5)	regen.	13.82	7.3
GoP 4	511834	<i>Cupuladria</i> aff. <i>biporosa</i> (Cbi5)	regen.	14.09	7.5
GoP 5	511835	<i>Cupuladria</i> aff. <i>biporosa</i> (Cbi5)	regen.	13.80	7.3
GoP 6	511837	<i>Discoporella</i> aff. <i>umbellata</i> (Dsp6)	regen.	17.85	10.3
GoP 7	511838	<i>Discoporella</i> aff. <i>umbellata</i> (Dsp6)	regen.	22.06	13.4
GoP 8	511839	<i>Discoporella</i> aff. <i>umbellata</i> (Dsp6)	sex.	13.97	7.4
GoP 9	511840	<i>Discoporella</i> aff. <i>umbellata</i> (Dsp6)	regen.	13.50	7.1
GoP 10	511841	<i>Discoporella</i> aff. <i>umbellata</i> (Dsp5)	regen.	12.14	6.0
			Mean	15.27	8.4
			Range	9.92	7.4
			S.D.	3.12	2.4
			Actual MART for locality:		8.2

Intracolony CV of zooid area for each colony (not including data from the zone of astogenetic change) together with respective derived estimates of MART, and for comparison, the actual MART of each locality (see text for details). Species codes from A. Herrera-Cubilla and M. Dick (unpublished data). Colony status as either sexually produced (sex.) or a regenerated fragment (regen.).

with the limited amount of data on the rates of growth in other cheilostomes, these growth rates are on the slow side (McKinney and Jackson, 1989). This is not surprising considering the sizeable energy allocation presumably required to sustain the motile habit, cuticle moulting (Winston and Håkansson, 1989) and high level of colony defence which characterise the cupuladriids.

### 6.3. MART analysis

By comparing the MARTs estimated in this study and the actual MARTs for the respective

localities, the robustness of the MART approach when applied to the cupuladriids can be tested. Indeed, the means of the estimated MARTs are comparably very similar to the actual MARTs (Table 2) and lie well within the 95% confidence limits for the approach (see O'Dea and Okamura, 2000c; Fig. 2) and the 95% confidence intervals calculated from the actual MARTs experienced. The range of MARTs estimated individually by the colonies also corresponds well with the temperature regimes of the two seas. The range of MARTs is low in colonies from Bocas del Toro, where interannual variability of MART is corre-

spondingly low and the range of MARTs is high in colonies from the Gulf of Panama, where actual MARTs can vary widely between years (see 3. Contrasting environments across the Central American Isthmus (CAI)). These results support the application of the MART approach to estimate absolute values of seasonality in ancient environments using colonies of cupuladriid bryozoans so long as all the requirements outlined by O'Dea and Okamura (2000b) are fulfilled.

The development of the MART approach was originally based upon erect and encrusting species only (O'Dea and Okamura, 2000b). The results of this study show that it is equally applicable to the free-living cupuladriids. Indeed, this group may circumvent a number of problems which hinder the approach when applied to encrusting and erect species. In particular, the problems associated with frontal budding and irregularities in the substratum are both avoided in the Cupuladriidae. Also, a free-living habit will reduce the effects of resource competition (e.g. space) on zooid size. The clearly defined pattern of normal zooids and vibracula within the cupuladriids (see Fig. 2) means that it is easy to distinguish between the two, thus leading to fewer problems associated with the discrimination of polymorphic zooids that occurs in some groups. The cupuladriids do not produce ovicells which often affect the size of zooids in colonies (O'Dea and Okamura, 2000b) and in general both *Cupuladria* and *Discoporella* produce low numbers of embryos (Winston, 1988).

The free-living life mode of cupuladriids can therefore be argued to be potentially the most appropriate for application of zooid size MART analysis. Although the lunulitids exhibit a similar life mode and can produce very large colonies, their highly integrated colonies and zooidal sexual dimorphism (Chimonides and Cook, 1981) may preclude them from being used for zooid size analysis.

#### 6.4. Zooid size and environment across the isthmus

The data presented here demonstrate trends in zooid size in cupuladriid bryozoans that mirror contrasting seasonal environmental regimes across

the isthmus of Panama and consequently provide further evidence that zooid size in cheilostome bryozoans varies inversely with environmental temperature.

Data from a previous study on transisthmian zooid sizes (Jackson and Herrera-Cubilla, 2000) reported on average larger zooid sizes in the warmer Caribbean compared with the seasonally cooler Gulf of Panama, thereby suggesting that zooid sizes in tropical American cheilostomes were not consistent to the model of increasing zooid sizes in cooler waters. However, it is important to note this study considered only variation between species across the region and could therefore not claim to describe a purely phenotypic response of zooid size. As discussed here and elsewhere (O'Dea and Okamura, 1999; Hageman et al., 1999), the ecophenotypic response of zooid size to temperature can only confidently be claimed to have been partitioned if genotype is controlled. This is of particular importance considering that genotype within species accounts for significant differences in zooid size (Hunter and Hughes, 1994; O'Dea and Okamura, 1999).

#### 6.5. Potential of zooid size analysis in the cupuladriids

The zooid size profile and MART approaches described here may provide potentially useful environmental and life history information in both fossil and Recent cupuladriid bryozoans.

Although zooid sizes through colonies mirror natural seasonal variations in temperature, the potential of the zooid size profile approach to infer palaeoenvironments from fossil colonies may be modest. To derive useful information on the level of seasonality it would be necessary to measure the amplitude of the cycles. However, the amount of noise within the data limits the quality of any derived information. In addition, the information gained would only provide relative and not absolute data on seasonality. Conversely, we have shown that the MART approach, when applied to the cupuladriids, provides accurate estimates of the amount of seasonal variation in temperature that the colonies experienced during their growth and we propose that this approach is most

effective when making palaeoenvironmental inferences.

Perhaps the most important use of zooid size analysis as described here would be as a technique for assessing regional and temporal changes in the seasonal environment around Central America associated with the closure of the CAI (see Teranes et al., 1996 on the potential of this kind of approach). For this purpose, as shown here, the MART approach produces accurate absolute values of seasonality and may provide complementary evidence to other approaches of palaeoenvironmental investigation including isotope profiling. The MART approach may be particularly useful considering that well preserved cupuladriid assemblages are common as fossils throughout the Neogene in tropical America, colonies are small and easily collected, and that, unlike isotope profiling, collection of data is cheap and efficient, thereby making it relatively easy to gather large amounts of replicate data.

On the other hand, we conclude that the zooid size profiling approach may provide only limited palaeoenvironmental information but can be used to derive highly desirable longevity and growth rate information from both fossil and Recent cupuladriid populations. Such an approach could be used to enhance and support a broader study into the life histories of cupuladriids. However, it is essential that the taxonomic status of the Cupuladriidae be well understood before the latter can be attempted with confidence.

### Acknowledgements

We are very grateful to members of the STRI, in particular: Amalia Herrera-Cubilla for her continued help with identification, logistical support and advice; Helena Fortunata for her help with the collection of material, her encouragement and support; and Luis D'Croz for allowing us to use unpublished climatic data from the Bocas del Toro region and for making valuable comments to the manuscript. Matt Dick acted as super-stooge. Alan Cheetham and JoAnn Sanner gave valuable taxonomic assistance. Bob Porter and Ruth Dewel helped produce the SEMs. We would

like to thank Paul Taylor, Steve Hageman, Alison Washbrook and Beth Okamura who all kindly made useful comments on the manuscript. A.O'D. would like to give special thanks to Steve Hageman for his support and advice during the writing of this paper and for obtaining funds for a visit Appalachian State University. This work was supported by a fellowship from the STRI to A.O'D.

### References

- Anderson, L.C., 2001. Temporal and geographic size trends in Neogene Corbulidae (Bivalvia) of tropical America: using environmental sensitivity to decipher causes of morphologic trends. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 166, 101–120.
- Atkinson, D., 1994. Temperature and organism size – A biological law for ectotherms? *Adv. Ecol. Res.* 25, 1–58.
- Atkinson, D., Sibly, R.M., 1997. Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends Ecol. Evol.* 12, 235–239.
- Bader, B., 2000. Life cycle, growth rate and carbonate production of *Cellaria sinuosa*. In: Herrera-Cubilla, A., Jackson, J.B.C. (Eds.), Proc. 11th International Bryozoology Association Conference. Smithsonian Tropical Research Institute, Balboa.
- Birkeland, C., 1987. Nutrient availability as a major determinant of differences among coastal hard-substratum communities in different regions of the tropics. In: Birkeland, C. (Ed.), Comparison between Atlantic and Pacific Tropical Marine Coastal Ecosystems: Community Structure, Ecological Processes and Productivity. UNESCO Reports in Marine Science 46, Paris, pp. 45–97.
- Boardman, R.S., Cheetham, A.H., Cook, P.L., 1969. Intra-colony variation and the genus concept in Bryozoa. In: Proc. North American Paleontological Convention, pp. 294–320.
- Boyer, T.P., Levitus, S., Antonov, J.I., Conkright, M.E., O'Brien, T., Stephens, C., 1998. World Ocean Atlas 1998, Vol. 4: Salinity of the Atlantic Ocean. NOAA Atlas NESDIS 30. US Gov. Printing Office, Washington, DC.
- Brey, T., Gutt, J., Mackensen, A., Starmens, A., 1998. Growth and productivity of the high Antarctic bryozoan *Melicerita obliqua*. *Mar. Biol.* 132, 327–333.
- Cheetham, A.H., Jackson, J.B.C., 2000. Neogene history of cheilostome Bryozoa in Tropical America. In: Herrera-Cubilla, A., Jackson, J.B.C. (Eds.), Proc. 11th International Bryozoology Association Conference. Smithsonian Tropical Research Institute, Balboa.
- Chimonides, P.J., Cook, P.L., 1981. Observations on living colonies of *Selenaria* (Bryozoa, Cheilostomata). II. *Cah. Biol. Mar.* 22, 207–219.
- Coates, A.G., Obando, J.A., 1996. The geological evolution of the Central American Isthmus. In: Jackson, J.B.C., Budd,

- A.F., Coates, A.G. (Eds.), *Evolution and Environment in Tropical America*. Chicago University, Chicago, IL, pp. 21–56.
- Collins, L.S., 1996. Environmental changes in Caribbean shallow waters relative to the closing of the tropical American seaway. In: Jackson, J.B.C., Budd, A.F., Coates, A.G. (Eds.), *Evolution and Environment in Tropical America*. Chicago University, Chicago, IL, pp. 130–167.
- Conkright, M.E., O'Brien, T.D., Levitus, S., Boyer, T.P., Stephens, C., Antonov, J.I., 1998. *World Ocean Atlas Vol. 10: Nutrient and Chlorophyll of the Atlantic Ocean*. NOAA Atlas NESDIS 36. US Gov. Printing Office, Washington, DC.
- Cook, P.L., 1963. Observations on live lunulitiform zoaria of *Polysphaera*. *Cah. Biol. Mar.* 4, 407–413.
- Cook, P.L., Chimonides, P.J., 1983. A short history of lunulite Bryozoa. *Bull. Mar. Sci.* 33, 566–581.
- D'Croz, L., Robertson, D.R., 1997. Coastal oceanographic conditions affecting coral reefs on both sides of the Isthmus of Panama. *Proc. 8th Int. Coral Reef Symp.* 2, 2053–2058.
- D'Croz, L., Del Rosario, J.B., Gomez, J.A., 1991. Upwelling and phytoplankton in the Bay of Panama. *Rev. Biol. Trop.* 39, 233–241.
- D'Croz, L., Robertson, D.R., Martinez, J.A., 1999. Cross-shelf distribution of nutrients, plankton, and fish larvae in the San Blas Archipelago, Caribbean Panama. *Rev. Biol. Trop.* 47, 203–215.
- Feldman, G.C., Kuring, N.A., Ng, C., Esaias, W.E., McClain, C.R., Elrod, J.A., Maynard, N., Endres, D., Evans, R., Brown, J., Walsh, S., Carle, M., Podesta, G., 1989. Ocean color: Availability of the Global Data Set. *EOS* 70, 634–641.
- Glynn, P.W., Maté, J.L., 1997. Field guide to the Pacific reefs of Panama. *Proc. 8th Int. Coral Reef Symp.* 1, 145–166.
- Greeley, R., 1967. Natural orientation of lunulitiform bryozoans. *Geol. Soc. Am. Bull.* 78, 1179–1182.
- Hageman, S.J., 1995. Observed phenotypic variation in a Paleozoic bryozoan. *Paleobiology* 21, 314–328.
- Hageman, S.J., Bayer, M.M., Todd, C.D., 1999. Partitioning phenotypic variation: genotypic, environmental and residual components from bryozoan skeletal morphology. *J. Nat. Hist.* 33, 1713–1735.
- Håkansson, E., Thomsen, E., 2001. Asexual propagation in cheilostome Bryozoa: evolutionary trends in a major group of colonial animals. In: Jackson, J.B.C., Lidgard, S., McKinney, F.K. (Eds.), *Evolutionary Patterns*. University of Chicago Press, Chicago, IL, pp. 326–347.
- Herrera-Cubilla, A., submitted. Preliminary report on the systematics of Tropical American Cupuladriidae from opposite sites of the Isthmus of Panama. *Proc. 12th International Bryozoology Association Conference*, Dublin.
- Hunter, E., Hughes, R.N., 1994. The influence of temperature, food ration and genotype on zooid size in *Celleporella hyalina* (L.). In: Hayward, P.J., Ryland, J.S., Taylor, P.D. (Eds.), *Biology and Palaeobiology of Bryozoans*. Olsen and Olsen, Fredensborg.
- Jackson, J.B.C., Cheetham, A.H., 1990. Evolutionary significance of morphospecies: A test with cheilostome Bryozoa. *Science* 248, 579–583.
- Jackson, J.B.C., D'Croz, L., 1997. The ocean divided. In: Coates, A.G. (Ed.), *Central America: A Natural and Cultural History*. Yale University Press, New Haven, CT, pp. 38–71.
- Jackson, J.B.C., Herrera-Cubilla, A., 2000. Adaptation and constraint as determinants of zooid and ovicell size among encrusting ascophoran cheilostome Bryozoa from opposite sides of the Isthmus of Panama. In: Herrera-Cubilla, A., Jackson, J.B.C. (Eds.), *Proc. 11th International Bryozoology Association Conference*. Smithsonian Tropical Research Institute, Balboa.
- Jones, D.S., 1998. Isotopic determination of growth and longevity in fossil and modern invertebrates. In: Norris, R.D., Corfield, R.M. (Eds.), *Isotope Paleobiology and Paleocology*. Paleontological Society Papers, Vol. 4.
- Keigwin, L.D., Jr., 1982. Isotopic paleoceanography of the Caribbean and east Pacific: Role of Panama uplift in Late Neogene time. *Science* 217, 350–352.
- Knowlton, N., 1993. Sibling species in the sea. *Annu. Rev. Ecol. Syst.* 24, 189–216.
- Kwiecinski, B., Chial, B., 1983. Algunos aspectos de la oceanografía del Golfo de Chiriquí, su comparación con el Golfo de Panamá. *Rev. Biol. Trop.* 31, 323–325.
- Lessios, H., 1990. Adaptation and phylogeny as determinants of egg size in echinoderms from the two sides of the isthmus of Panama. *Am. Nat.* 135, 1–13.
- Malmgren, B.A., Kennet, J.P., 1978. Late Quaternary palaeoclimatic applications of mean size variations in *Globigerina bulloides* d'Orbigny in the southern Indian Ocean. *J. Palaeontol.* 52, 845–854.
- Marcus, E., Marcus, E., 1962. On some lunulitiform Bryozoa. *Univ. São Paulo Bol. Fac. Philos. Sci. Letr. Zool.* 3, 111–153.
- McKinney, F.K., Jackson, J.B.C., 1989. *Bryozoan Evolution*. Unwin Hyman, Boston, MA.
- Menon, N.R., 1972. Heat tolerance, growth and regeneration in three North Sea bryozoans exposed to different constant temperatures. *Mar. Biol.* 15, 1–11.
- Morris, P.A., 1976. Middle Pliocene temperature implications based on the Bryozoa *Hippothoa* (Cheilostomata-Ascophora). *J. Paleontol.* 50, 1143–1149.
- O'Dea, A., 1999. *Environmental Inferences using Recent and Fossil Bryozoans*. Ph.D. Thesis, University of Bristol, Bristol.
- O'Dea, A., Okamura, B., 1999. Influence of seasonal variation in temperature, salinity, and food availability on module size and colony growth in the estuarine bryozoan, *Conopeum seurati*. *Mar. Biol.* 135, 581–588.
- O'Dea, A., Okamura, B., 2000. Cheilostome bryozoans as indicators of seasonality in the Neogene epicontinental seas of Western Europe. In: Herrera-Cubilla, A., Jackson, J.B.C. (Eds.), *Proc. 11th International Bryozoology Association Conference*. Smithsonian Tropical Research Institute, Balboa, pp. 74–86.
- O'Dea, A., Okamura, B., 2000b. Intracolony variation in zo-

- oid size in cheilostome bryozoans as a new technique for investigating palaeoseasonality. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 162, 319–332.
- O'Dea, A., Okamura, B., 2000c. Life history and environmental inferences through retrospective morphometric analysis of bryozoans: a preliminary study. *J. Mar. Biol. Assoc.* 80, 3596–3599.
- Okamura, B., 1987. Seasonal changes in zooid size and feeding activity in epifaunal colonies of *Electra pilosa*. In: Ross, J.R.P. (Ed.), *Bryozoa: Present and Past*. Western Washington University, Bellingham, WA, pp. 197–203.
- Okamura, B., Bishop, J.D.D., 1988. Zooid size in cheilostome bryozoans as an indicator of relative palaeotemperature. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 66, 145–152.
- Okamura, B., Partridge, J.C., 1999. Suspension feeding adaptations to extreme flow environments in a marine bryozoan. *Biol. Bull.* 196, 205–215.
- Pätzold, J., Ristedt, H., Wefer, G., 1987. Rate of growth and longevity of a large colony of *Pentapora foliacea* (Bryozoa) recorded in their oxygen isotope profiles. *Mar. Biol.* 96, 535–538.
- Podestá, G.P., Glynn, P.W., 1997. Sea surface temperature variability in Panamá and Galápagos: Extreme temperatures causing coral bleaching. *J. Geophys. Res.* 102, 15749–15759.
- Poluzzi, A., Coppa, M.G., 1991. Zoarial strategies to win substratum space in *Calpensia nobilis* (Esper). In: Bigey, F.P., d'Hondt, J. (Eds.), *Bryozaires Actuels et Fossiles (Bryozoa Living and Fossil)*. Société des Sciences Naturelles de l'Ouest de la France, Nantes. *Bull. Soc. Sci. Nat. Ouest de la France, Mém. HS 1*, pp. 337–360.
- Ryland, J.S., 1963. The species of *Haplopoma* (Polyzoa). *Sarsia* 10, 9–18.
- Sadler, J.C., Lander, M.A., Hori, A.M., Oda, C.K., 1987. *Tropical Marine Climatic Atlas, Part 1: Indian Ocean and Atlantic Ocean*. Department of Meteorology, University of Hawaii, Honolulu, HI.
- Sebens, K.P., 1979. The energetics of asexual reproduction and colony formation in benthic marine invertebrates. *Am. Zool.* 19, 683–697.
- Sebens, K.P., 1982. The limits to indeterminate growth: an optimal size model applied to passive suspension feeders. *Ecology* 63, 209–222.
- Silén, L., Harmélin, J.-G., 1976. *Haplopoma sciaphilum* sp.n., a cave living bryozoan from Skagerrak and the Mediterranean. *Zool. Scr.* 5, 61–66.
- Strauch, F., 1968. Determination of Cenozoic sea-temperatures using *Hiatella arctica* (Linné). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 5, 213–233.
- Taylor, P.D., Furness, R.W., 1978. Astogenetic and environmental variation of zooid size within colonies of Jurassic *Stomatopora* (Bryozoa, Cyclostomata). *J. Paleontol.* 52, 1093–1102.
- Teranes, J.L., Geary, D.H., Bemis, B.E., 1996. The oxygen isotopic record of seasonality in Neogene bivalves from the Central American isthmus. In: Jackson, J.B.C., Budd, A.F., Coates, A.G. (Eds.), *Evolution and Environment in Tropical America*. Chicago University, Chicago, IL, pp. 21–56.
- van Voorhies, W.A., 1996. Bergmann size clines: A simple explanation for their occurrence in ectotherms. *Evolution* 50, 1259–1264.
- Winston, J.E., 1988. Life histories of free-living bryozoans. *Natl. Geogr. Res.* 4, 528–539.
- Winston, J.E., Håkansson, E., 1989. Molting by *Cupuladria doma*, a free-living bryozoan. *Bull. Mar. Sci.* 44, 1152–1158.