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Seasonality and zooid size variation in Panamanian encrusting bryozoans

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A model describing the positive correlation between variation in zooid size within bryozoan colonies and the amount of seasonal variation in temperature is tested in Panamanian encrusting bryozoans from contrasting seasonal regimes. Results reveal that in a natural setting the model provides accurate estimates of the level of seasonality experienced by the colonies.

INTRODUCTION

Zooid size within colonies of cheilostome Bryozoa has been shown to vary inversely with ambient temperature. Evidence demonstrates that this phenomenon occurs across a variety of bryozoan growth forms and is neither phylogenetic nor taxon-specific (Hunter & Hughes, 1994; O'Dea & Okamura, 1999, 2000; O'Dea & Jackson, 2002 and references therein). As zooids are budded sequentially throughout the growth of a bryozoan colony, an increase in the amount of seasonal variation in temperature that a colony experiences results in an increase in the amount of variation in zooid size within that colony. This theory has been tested; by analysing over 150 recent colonies of both encrusting and erect cheilostome species from widely differing seasonal environments, the positive correlation between mean coefficient of variance (CV) of zooid frontal area (b) and the mean annual range of temperature (MART) experienced by the bryozoans has been formulated algebraically into $\mathrm{MART}=-3+0.745(\mathrm{b})$ (O'Dea & Okamura, 2000). Consequently, this model has been developed as a tool for investigating levels of seasonality in ancient environments. By applying zooid size data in fossil bryozoans to the model, absolute data on the level of seasonality can be estimated. In the present study this approach is tested using recent encrusting bryozoans from environmentally contrasting seasonal environments on either side of the Isthmus of Panama.

The seas around Panama are well suited to investigating the morphological responses of animals to varying seasonal environments. The Isthmus of Panama is a geologically young land bridge; previous to its formation Pacific and Caribbean waters were connected across the Central American region. As a result, closely related yet distinct marine species can be found on both coasts. In addition, pronounced environmental differences occur across the isthmus (D'Croz & Robertson, 1997) (Figure 1). For example, seasonal upwelling in the Gulf of Panama from January to May results in strong seasonal shifts in temperature, nutrients and productivity. High levels of mud, rocky shores and low coral diversity dominate the Pacific coast. In contrast, the Caribbean coast experiences little seasonal variation in temperature, the seas are oligotrophic and considerably less productive. Here the coasts are generally carbonate rich and dominated by diverse coral growth and mangrove.

The two contrasting coasts of Panama thereby provide an unparalleled opportunity with which to further test the zooid size MART approach. This opportunity has already been exploited to demonstrate the validity of the approach in free-living cheilostomes from either side of the Isthmus of Panama (O'Dea & Jackson, 2002). The present study extends the test to include encrusting bryozoans. Comparisons are made between species from the seasonal Gulf of Panama in the Pacific and the aseasonal San Blas in the Caribbean (Figure 1).

For the Gulf of Panama, five species (*Membranipora annae* (Osburn, 1953), *Onychocella* cf. *angulosa*, *Hippopodina feegeensis* (Busk, 1884), *Parasmittina crosslandii* (Hastings, 1930) and *Conopeum reticulum* (Linnaeus, 1767)) encrusting bivalves and

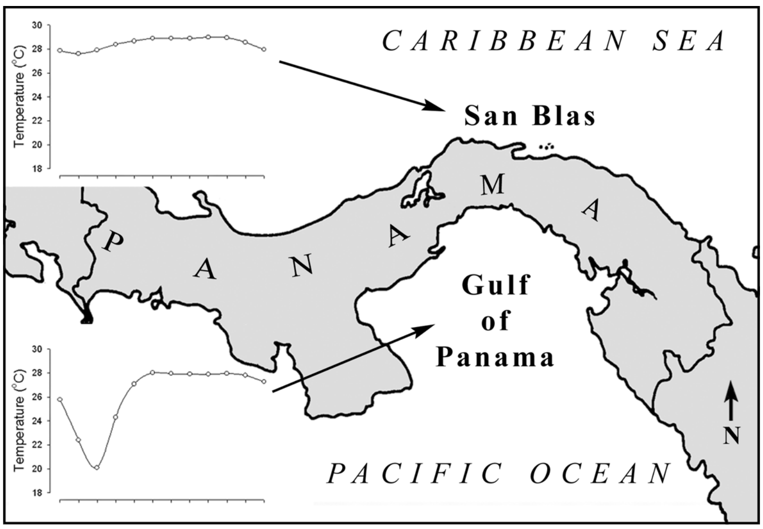

Figure 1. Location and typical seasonal trends in temperature of the sites used in this study. Temperature data from D'Croz & Robertson (1997).

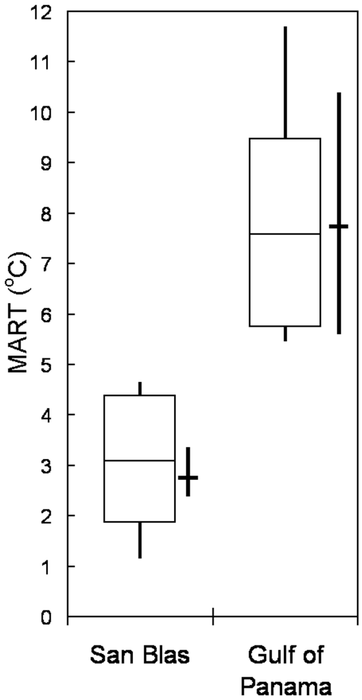

Figure 2. Comparing estimated and actual MARTs between the two sites. Box plots represent estimated MARTs, with mean (horizontal line), SD (extent of box), and ranges (extent of whiskers). Adjacent lines represent actual MART with mean (horizontal line) and interannual ranges (extent of whiskers).

small rocks were collected from subtidal localities around the islands of Naos, Taboga and Contadora in the Gulf of Panama. For the San Blas region, two species (*Stylopoma spongites* (Pallas, 1766) and *Steginoporella magnilabris* (Busk, 1854)) were collected on the undersides of coral at a depth of 0–40 m.

For each species five colonies were analysed. Thus, the study comprised 25 colonies from the Gulf of Panama and ten colonies from the San Blas. For each colony 20 randomly selected zooids were measured for maximum length and width. For each zooid, length multiplied by width provided an index of zooid frontal area. For each colony the CV in zooid area was calculated and applied to the model to estimate the MART. Detailed procedures for data collection and analysis are described in O'Dea & Okamura (2000). The mean, variance and ranges of the estimated MARTs could then be compared with actual environmental data.

Difference in intracolony CV of zooid area was tested using analysis of variance. Values were $\log_{10}$ transformed to correct for inequality of variances.

Intracolony CV of zooid area was found to be significantly greater in the Gulf of Panama (N=25, μ=14.3, SD=2.5) than the San Blas (N=10, μ=8.2, SD=1.9) (F=47.28, $P<0.001$), demonstrating an increase in intracolony variation in zooid size within bryozoan colonies from the more seasonal of the two environments.

For each colony CV of zooid area was applied to the model to estimate the MART experienced by the colonies. Figure 2 compares the estimated and actual MARTs experienced by the bryozoans from the two sites. The average estimated MART from the Gulf of Panama was 7.7°C (SD=1.9) and ranged from 5.5 to 11.7°C while the actual MART from this region is 7.8°C and ranges, year to year, from approximately 5.7 to 10.4°C. This wide range in the level of seasonality between years reflects the generally unstable seasonal environment typical of the Gulf of Panama and is somewhat related to the suppression of upwelling that occasionally occurs along the whole of the Pacific coast (El Niño).

Colonies from the San Blas region estimated an average MART of 3.1°C (SD=1.3) and ranged from 1.2 to 4.6°C while the actual MART is 2.7°C and ranges from around 2.4°C and 3.3°C (Figure 2). This low level of interannual variation in seasonality typifies the thermal stability of the Caribbean. Estimated values of MARTs strongly mirror actual levels of seasonality, demonstrating that the model developed by O'Dea & Okamura (2000) is applicable to encrusting cheilostomes in Central America. Furthermore, the variation in seasonality across years is represented in the data, a particularly significant result given the unstable climate typical of the Gulf of Panama.

The precise mechanism behind temperature-mediated zooid size changes in cheilostomes is not currently fully understood (O'Dea & Okamura, 1999). Concerns that food availability may account for some of the size changes observed have so far been shown to be untenable given that all empirical evidence shows a clear link between zooid size and temperature but not food availability (see O'Dea & Jackson, 2002). The extremely close-tie between the estimated and actual MARTs shown in this study provides yet further evidence that temperature is an important correlate of zooid size.

Despite the currently unclear mechanism which links zooid size and temperature, the data presented here demonstrate, once again, that zooid size analysis can function as an accurate environmental proxy. Provided replicate data are employed, the approach supplies both an absolute estimate of seasonality and an index of the degree of interannual stability and can, with confidence, be applied to bryozoans from ancient marine environments. Given the numerous problems associated with more traditional techniques of investigating palaeoseasonality (see O'Dea & Okamura, 2000) the development of this approach should be seen as highly desirable. Furthermore, seasonality plays such an important yet currently under-appreciated role in both the understanding of palaeoceanography and the biology and evolution of fossil organisms, that corroborative techniques of this sort will become highly valuable and of broad significance.

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