

STABLE ISOTOPE PROFILING IN MODERN MARINE BRYOZOAN COLONIES ACROSS THE ISTHMUS OF PANAMA

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ABSTRACT

In the tropics, upwelling of cold, deep water is the principal source of major seasonal fluctuations in temperature. Along the tropical eastern Pacific (TEP) coast of the Isthmus of Panama, seasonal upwelling induces corresponding drops in temperature. Upwelling does not occur along the southwestern Caribbean (SWC) coast of the isthmus. Our goal was to use these oceanographic differences to test the use of stable isotope profiles of free-living modern cupuladriid bryozoans as a method for quantifying paleo-seasonality. We determined O and C stable isotope values from micromilled carbonates profiled along the growth axis in three colonies of *Cupuladria exfragminis* Herrera-Cubilla, Dick, Sanner and Jackson, 2006 from the upwelling Gulf of Panama in TEP and three colonies of *Cupuladria surinamensis* Cadée, 1975 from the non-upwelling Bocas del Toro Archipelago in SWC. Pacific colonies had inter-colony $\delta^{18}\text{O}_{\text{carb}}$ values ranging from -2.1‰ to -0.2‰ on the international Vienna Pee Dee Belemnite scale, whereas SWC colonies ranged from -1.7‰ to -0.6‰ . Pacific colonies consistently reveal cyclical trends in $\delta^{18}\text{O}_{\text{carb}}$ that are absent in the Caribbean colonies. Based on published measurements of temperature, salinity, and $\delta^{18}\text{O}_{\text{sw}}$, the ≤ 2.5 yrs of cyclicity seen in the Pacific colonies reflects a combination of seasonal freshening and seasonal upwelling of colder water. This preliminary study suggests the potential for more exploration of bryozoans as a source of paleoclimate proxies.

Revealing changes in Earth's past climate helps refine models of future environmental change (UN's Intergovernmental Panel on Climate Change: Randall et al. 2007). Although predictive models are increasingly sophisticated and incorporate greater temporal and spatial resolution (e.g., Randall et al. 2007), they are most robust at predicting mean annual temperature (e.g., Jansen et al. 2007). This is despite the fact that the amount of seasonal variation in climate plays an important role in characterizing the environment of a region and determines the distribution, life histories, and growth of species. A significant milestone will be to incorporate better constraints on seasonality into the next generation of models (Flückiger et al. 2008, McGlone et al. 2010); thus, there is a pressing need to reconstruct how seasonality has changed through Earth's history. Several techniques exist to do so, principally owing to the fact that many organisms that grow by accretion fossilize well and, therefore, record a time series of environmental information (e.g., tree rings, coral colonies, mollusc shells, fish otoliths, mammal teeth) either in morphology or chemistry.

One of the most productive methods for extracting environmental information from animal skeletons is stable isotope sclerochemistry (see review by Gröcke and Gillikin 2008). This involves measuring stable isotope ratios in the mineralized skeleton of an organism, parallel to its growth axis. Since the pioneering work of Epstein and Lowenstam (1953), the field has expanded and its methods matured (Rhoads and Lutz 1980, Schöne and Surge 2005). The temporal resolution of the preserved

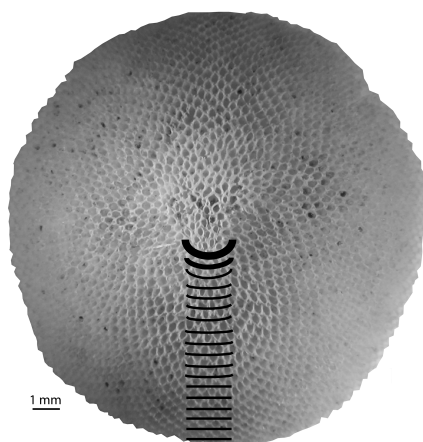


Figure 1. Frontal surface of *Cupuladria exfragminis* colony GP3 showing schematic micromilling paths. See Table 1 for collection and locality information.

environmental conditions is a function of the growth rate of the animal's skeleton and the spatial resolution of the sampling (Wefer and Berger 1991). The spatial resolution of sampling technologies continues to improve (Arnold and Jones 2007, Schöne and Nunn 2010).

Of specific relevance to this project is the use of O and C stable isotope profiles in testing for seasonal upwelling, mostly in molluscs, but also corals and fish otoliths (Andrus et al. 2002, Tao and Grossman 2010, Ahmad et al. 2011, Sadler et al. 2012). This sub-annual sampling technique has also been utilized to document seasonal growth patterns in bryozoans (Pätzold et al. 1987, Brey et al. 1998, 1999, Bader 2000, Smith and Key 2004, Bader and Schäfer 2005, Knowles et al. 2010). Ours is the first study to construct O and C stable isotopic profiles from bryozoan skeletons to infer seasonal upwelling cycles.

The goal of the present study was to develop a proxy using the O and C stable isotope ratios from the skeletons of free-living bryozoans to explore marine paleo-seasonality. Bryozoans are colonial, mostly marine, invertebrate animals that secrete a carbonate skeleton. Most bryozoans form sessile colonies made of asexually replicated individual modules called zooids (Ryland 1970, McKinney and Jackson 1989). In contrast, cupuladriids (Fig. 1) form small (<30 mm in diameter), unattached (free-living), and motile cone-shaped colonies that are able to unbury themselves after burial and move across the substrate with their elongate setae belonging to polymorphic zooids called vibracula (O'Dea 2009). In theory, these two species are motile, but the speeds of movement measured in aquaria are <2 mm d⁻¹ (O'Dea 2009). Assuming an average colony age of 3 yrs (O'Dea and Jackson 2002), over the course of a colony's lifetime it would travel laterally approximately 2 m (O'Dea 2009). Colony migration into shallower or deeper waters with different temperatures and salinities is therefore not a realistic concern for our study.

Reproduction occurs by sexual (presumably asexual) reproduction of planktonic larvae that settle to form new colonies or by asexual (clonal) fragmentation (O'Dea et al. 2008). Once settlement occurs, growth of the colony is by radial budding of zooids away from the proximal part of the colony creating a cap-shaped colony (Fig. 1; O'Dea and Jackson 2002). Cupuladriid colonies grow through the iterative budding

of zooids. Colonies under observation for >3 yrs tend to maintain a growing edge around the entire circumference of the colony suggesting that growth is constant. Nonetheless, accretionary growth of the colony almost certainly increases at times of increased food availability as has been shown almost universally in other cheilostomes (see review in Hageman et al. 2009). Growth is typically slow with a maximum measured radial accretion of $25 \mu\text{m d}^{-1}$, but typically much slower at about $4 \mu\text{m d}^{-1}$ (O'Dea and Jackson 2002, O'Dea 2006, O'Dea unpubl data). Each zooid generation is a function of zooid length, which on average is approximately 0.3 (SD 0.06) mm long in these cupuladriids.

Bryozoans are under-utilized biogenic proxy recorders of past climate change. Here, we test their utility with modern bryozoans from both sides of the Isthmus of Panama. If successful, this approach will provide an independent method for quantifying seasonal upwelling across the isthmus and help constrain hypotheses regarding the geological and biological evolution of tropical America.

SETTING

Since the rise of the Central American Isthmus in the Miocene resulted in the closure of the Central American Seaway in the Late Pliocene (O'Dea et al. 2007, Schmidt 2007), the oceanic conditions of the SWC and TEP have been distinctly different. The SWC is warmer, more saline, and is more nutrient-poor, with less primary planktonic productivity, less of a daily tidal range, and minimal seasonal variation in temperature and salinity due to the absence of upwelling. In contrast, the TEP, especially the Gulf of Panama, is less saline and has more dissolved nutrients/higher primary planktonic productivity, a greater daily tidal range, and more seasonal variation in temperature and salinity due to seasonal upwelling (D'Croz and Robertson 1997, D'Croz et al. 2005, D'Croz and O'Dea 2007, 2009).

The sea surface salinity contrast across the isthmus is due to the westward transport of fresh water across the Isthmus of Panama (Benway and Mix 2004). The seasonality contrast across the isthmus is due to seasonal upwelling in the Gulf of Panama that is lacking on the Caribbean side. Modern marine conditions along the Pacific coast of Central America typically are dominated by the eastern Pacific warm pool with sea surface temperatures of 27°C or more (Fiedler and Talley 2006). The warm North Equatorial Counter Current terminates along the Pacific coast of Central America creating the eastern Pacific warm pool (Wang and Enfield 2001). This structured water column breaks down with the seasonal migration of the Inter-Tropical Convergence Zone (ITCZ, defined by the convergence of the northeast and southeast trade winds) that overlies the highest sea surface temperatures (Rodríguez-Rubio et al. 2003).

From May through December, the ITCZ is in its northernmost position, over or slightly north of Panama, and light winds with variable directions dominate across Panama during the rainy season. This switches beginning in December when the ITCZ retreats southward, and in the boreal winter intense northeast trade winds from the Atlantic blow over the region forming wind-jets where gaps in the cordilleran elevation permit (Fig. 2). From January to March, this wind pushes the warm coastal surface waters of the Gulf of Panama offshore and reduces the sea surface temperatures due to wind-driven turbulent mixing (Liang et al. 2009) and upwelling (Schaefer et al. 1958, Forsbergh 1969, D'Croz et al. 1991, D'Croz and Robertson 1997,

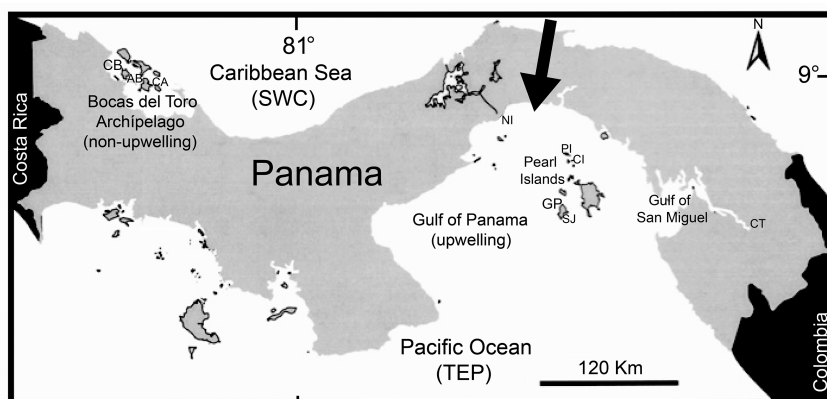


Figure 2. Map of Panama showing sampling localities. CB = Caribbean Sea locality in Almirante Bay (AB), Bocas del Toro Archipelago, southwest Caribbean (SWC). GP = Gulf of Panama locality near San José Island (SJ), Pearl Islands, tropical eastern Pacific (TEP). Other localities mentioned in text are CA = Cayo Agua, NI = Naos Island, PI = Pacheca Island, CI = Contadora Island, and CT = Chucunaque-Tuira River system. Black arrow indicates O'Dea et al.'s (2012) location of upwelling-inducing wind jet through topographic gap in Cordillera. Modified from D'Croz et al. (2001).

Rodríguez-Rubio et al. 2003, O'Dea et al. 2012). The upwelling occasionally starts as early as December and can last into April (Smayda 1966, Curry et al. 1983). Deeper, more nutrient-rich, saltier, and cooler waters then well up to replace the expelled surface water. The thermocline temporarily shoals, cooling the sea surface and driving phytoplankton growth until the trans-isthmian winds weaken, the thermocline deepens and sea surface waters revert to the typical warm nutrient-poor conditions (Smayda 1966, D'Croz and Robertson 1997, D'Croz and O'Dea 2007).

MATERIALS AND METHODS

Cupuladriid bryozoan colonies were collected by bottom dredge sampling from the Smithsonian Tropical Research Institute's R/V URRACÁ from both sides of the isthmus (Table 1). Each dredge sample was sieved at 2 mm, and all cupuladriid colonies and fragments of colonies picked. Colonies were dried and bleached, cleaned, and identified. We avoided colonies with any evidence of zooecial damage/repair that could have signaled a growth hiatus. We chose colonies that were sexually produced from larvae as opposed to asexually fragmented colonies that may have resulted in missing zooid generations. Three large colonies (CB1–3) of *Cupuladria surinamensis* Cadée, 1975 (var. *gigante*) were selected from 10 to 23 m water depth in Almirante Bay, Bocas del Toro Archipelago on Panama's northwestern coast in the SWC (Fig. 2). Three large colonies (GP1–3) of *Cupuladria exfragminis* Herrera-Cubilla, Dick, Sanner and Jackson, 2006 were selected from 19.7 m water depth off San José Island, Pearl Islands, Gulf of Panama on Panama's southeastern coast in the Panama Bight of the TEP (Fig. 2). Colonies from the SWC averaged 21.5 mm in diameter, 7.3 mm high, and weighed 0.43 g (Table 1). TEP colonies averaged 16.3 mm in diameter, 5.3 mm high, and weighed 0.25 g (Table 1). The colonies were not necessarily alive when collected, so death dates cannot be assigned.

Epibionts on the colonies were either removed or avoided during sampling to minimize contamination. Colonies were cleaned for 5 min by ultrasonic vibration in deionized water to remove as many sediment grains trapped in autozooecial apertures as possible (e.g., black grains in Fig. 1). We also avoided sediment grains located in the apex of the colony on the basal side upon which the original larval settlement occurred.

Table 1. Specimen and locality information for *Cupuladria surinamensis* (var. *gigante*) from Almirante Bay, Bocas del Toro Archipelago, the southwest Caribbean; and *Cupuladria exfragminis* from San José Island, Pearl Islands, Gulf of Panama, the tropical eastern Pacific.

Specimen ID	Species	Colony metrics			Date of collection	Water depth (m)	Latitude (°N)	Longitude (°W)
		Diameter (mm)	Height (mm)	Weight (g)				
CB1	<i>C. surinamensis</i> (var. <i>gigante</i>)	21.6	8.0	0.44	12–20 October, 2005	10.0	9.304300	82.19970
CB2	<i>C. surinamensis</i> (var. <i>gigante</i>)	21.4	6.6	0.42	12–20 October, 2005	10.0	9.304300	82.19970
CB3	<i>C. surinamensis</i> (var. <i>gigante</i>)	33.0*	1.6*	0.07*	8 October, 1998	23.0	9.421700	82.34000
GP1	<i>C. exfragminis</i>	16.8	4.6	0.23	9 April, 2004	19.7	8.291420	79.10316
GP2	<i>C. exfragminis</i>	16.6	6.3	0.31	9 April, 2004	19.7	8.291420	79.10316
GP3	<i>C. exfragminis</i>	15.6	5.0	0.20	9 April, 2004	19.7	8.291420	79.10316

*Incomplete colony; triangular fragment with 16.5 mm radius.

Powders for stable isotope analysis were micromilled (sensu Wurster et al. 1999) with New Wave Research's Merchantek MicroMill™ automated micro-sampler using a 0.5 mm Brassler carbide dental drill bit. Consecutive micromilling paths were oriented parallel to the colony growth increments (i.e., each generation of zooids). Thus, a time series profile was serially created from the edge of the colony (i.e., the youngest part) toward the center of the colony (i.e., the oldest part where the founding larva metamorphosed into the ancestrula) along the growth axis (Fig. 1). Sampling was performed along the longest radius of each colony to maximize the spatio-temporal resolution of micromilling. Powder was collected with a razor blade at the end of each pass. Between passes, any remaining powder was removed from the colony, drill, and stage with compressed air.

Based on colony size and budget constraints, a total of 100 paths were micromilled across the six colonies. There was an average of 17 paths per colony (range: 11–21 paths per colony; SD 5 paths per colony). The path widths ranged from 0.07 to 1.87 mm (mean: 0.59 mm, SD 0.32 mm). The micromill paths generally became wider as micromilling progressed from the colony margin toward the center. This was in response to the corresponding decrease in colony perimeter length. As a result, the temporal resolution of the sampling decreased across each colony.

Carbonate samples were heated in a vacuum oven at 200 °C for 1 hr to remove water and volatile organic contaminants that may confound stable isotope values of carbonates. Stable isotope values were obtained using a Finnigan Kiel-IV carbonate preparation device directly coupled to the dual inlet of a Finnigan MAT 253 isotope ratio mass spectrometer. A range of 20–50 µg of carbonate was reacted at 70 °C with 3 drops of anhydrous phosphoric acid for 420 s. The CO₂ evolved was then cryogenically purified before being passed to the mass spectrometer for analysis. Isotope ratios were corrected for acid fractionation and ¹⁷O contribution using the Craig (1957) correction. Isotope ratios are reported in per mil notation (‰) relative to the international Vienna Pee Dee Belemnite (VPDB) scale using the standard δ notation where: $\delta_{\text{sample}} = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \times 10^3$. R is ¹⁸O/¹⁶O or ¹³C/¹²C ratio. Using the standard correction of Kim et al. (2007), the δ¹⁸O_{carb} values reflect the aragonite-calcite difference in isotopic fractionation during acidification. Data were directly calibrated against Friedman et al.'s (1982) NBS-19 standard that is by definition δ¹⁸O_{carb} = -2.2‰ VPDB and δ¹³C_{carb} = 1.95‰ VPDB. Precision/accuracy of data were monitored through routine analysis of NBS-19 and in-house check standards which have been stringently calibrated against NBS-19. The precision/accuracy of δ¹⁸O_{carb} and δ¹³C_{carb} are 0.11‰ and 0.05‰ VPDB, respectively.

Of the 100 powder samples collected, only 86 yielded usable results. Six samples had too little powder to generate the minimum signal intensity of 100 mV to return a value from the mass spectrometer. Eight samples had too little powder to generate the minimum signal intensity of 450 mV to return a dependable value from the mass spectrometer. These lost

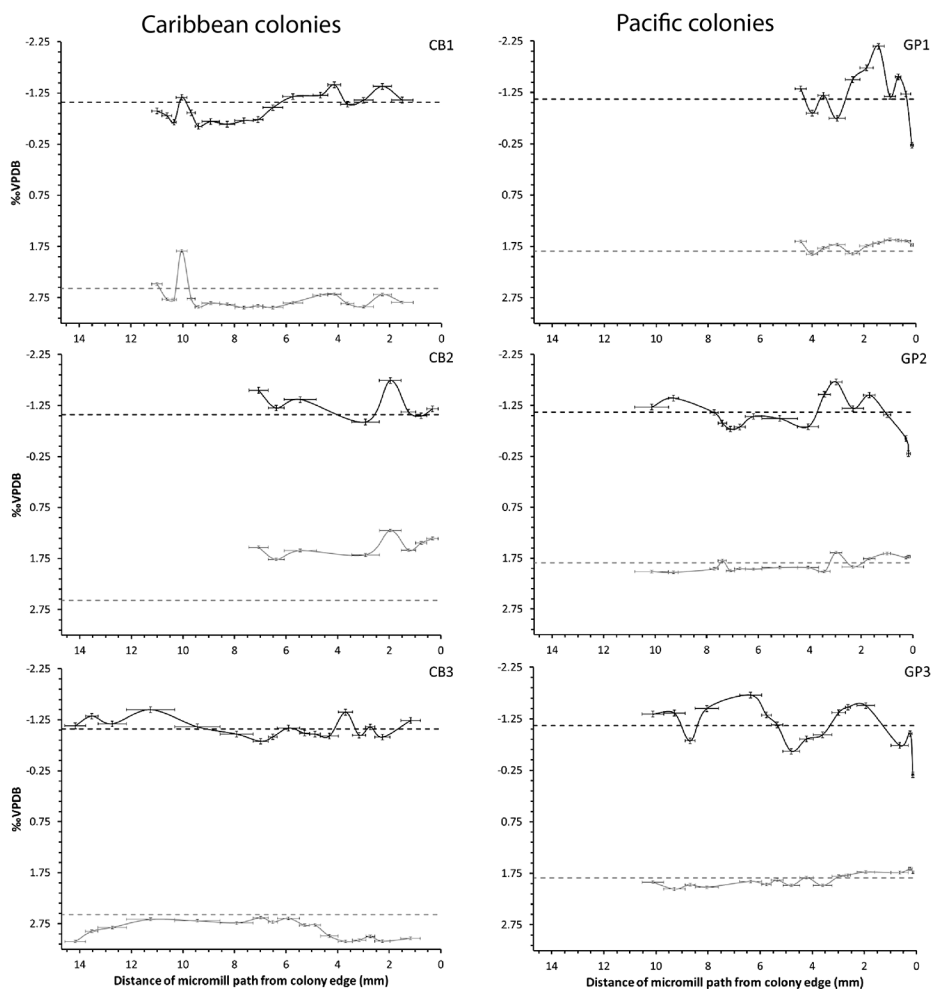


Figure 3. O and C stable isotope profiles from colonies from the Caribbean (CB1–3) and Pacific (GP1–3) sides of the Isthmus of Panama. Dashed lines indicate the mean values for the three colonies on each side of the isthmus. Horizontal error bars indicate the micromill path width. Vertical error bars indicate the analytical error of mass spectrometer.

samples are a function of the methodological challenge of balancing the need for obtaining enough carbonate powder to get a reliable result from the mass spectrometer (i.e., >20 μg) and minimizing the width of each micromill path so as to not include multiple zooid generations. This is a shortcoming of the methodology.

RESULTS

We plotted the O and C isotope ratios the conventional way on the vertical axis with more negative values at the top vs distance of micromill path from the colony edge on the horizontal axis to produce colony age profiles of $\delta^{18}\text{O}_{\text{carb}}$ and $\delta^{13}\text{C}_{\text{carb}}$ for each colony (Fig. 3). In SWC colonies, $\delta^{18}\text{O}_{\text{carb}}$ values vary from -1.7‰ to -0.6‰ VPDB (mean: -1.1‰ VPDB, SD: 0.3‰ VPDB). In TEP colonies, $\delta^{18}\text{O}_{\text{carb}}$ values vary from -2.1‰ to -0.2‰ VPDB (mean: -1.1‰ VPDB, SD: 0.4‰ VPDB). Thus the range

in $\delta^{18}\text{O}_{\text{carb}}$ values is 75% more in TEP colonies (2.0‰ VPDB) than in SWC colonies (1.1‰ VPDB).

There is a marked cyclicity in $\delta^{18}\text{O}_{\text{carb}}$ values of TEP colonies that is responsible for this greater variation. A cycle was defined by the $\delta^{18}\text{O}_{\text{carb}}$ curves (Fig. 3) relative to the mean value for the three colonies on each side of the isthmus. A cycle must have two or more consecutive data points on one side of the mean, followed by two or more consecutive data points on the opposite side of the mean, followed by two or more consecutive data points on the original side of the mean. Based on this definition, the Pacific colonies show 1.0–2.5 cycles, whereas the SWC colonies show none. The same pattern holds if a two point running average is used instead of the curve in Figure 3. The same pattern holds if the midpoint of the maximum and minimum value of each colony is used instead of the mean value for the three colonies on each side of the isthmus.

In contrast, $\delta^{13}\text{C}_{\text{carb}}$ values display greater variation in SWC colonies and no cyclicity on either side of the isthmus. In SWC colonies, $\delta^{13}\text{C}_{\text{carb}}$ values range from 1.2‰ to 3.1‰ VPDB (mean: 2.6‰ VPDB, SD 0.6‰ VPDB). In TEP colonies, $\delta^{13}\text{C}_{\text{carb}}$ values range from 1.6‰ to 2.1‰ VPDB (mean: 1.8‰ VPDB, SD: 0.1‰ VPDB). Thus the range in $\delta^{13}\text{C}_{\text{carb}}$ values is more than three times higher in SWC colonies (1.9‰ VPDB) than in TEP colonies (0.4‰ VPDB). Much of the variation in $\delta^{13}\text{C}_{\text{carb}}$ values of SWC colonies comes from colony CB2 which has values closer to the TEP colonies. There is an apparent subtle covariation between $\delta^{18}\text{O}_{\text{carb}}$ and $\delta^{13}\text{C}_{\text{carb}}$ values in colonies CB1 and CB2 (Fig. 3), but it is not significant (linear regression: $P > 0.05$) in these or any of the colonies.

DISCUSSION

ESTIMATED COLONY AGES.—Not only are $\delta^{18}\text{O}_{\text{carb}}$ time series with a cyclic pattern useful for inferring upwelling and freshening, they can also be used to estimate colony age. If the above cycles are interpreted as annual upwelling- and freshening-induced seasonal cycles, then the age of each colony can be inferred by counting the number of annual cycles in the TEP colonies. Thus, colony GP1 died at approximately 1.0 yrs, colony GP2 at approximately 1.5 yrs, and GP3 approximately 2.5 yrs (mean: 1.7 yrs, SD: 0.62 yrs). This range in ages suggests that either there is intraspecific variation in growth rates as the colonies are similar sizes, or the micromilling may have missed a seasonal cycle, especially in colony GP1. The latter is more likely as these colony ages are slightly less than those of other bryozoan species from the Gulf of Panama determined by O’Dea and Jackson (2002; Table 1) using mean annual range in temperature (MART) analysis. MART analysis is based on the inverse relationship between temperature and zooid size in bryozoans which results in an empirical relationship between MART and the coefficient of variation of zooid size (O’Dea and Okamura 2000). They reported *Cupuladria exfragminis* (then referred to as *C. aff. biporosa*) had a mean age at collection of 3.4 (SD 0.55) yrs, and *Discoporella cookae* Herrera-Cubilla, Dick, Sanner and Jackson, 2008 (then referred to as *D. aff. umbellata*) had a mean age at collection of 2.5 (SD 0.58) yrs. As discussed above, our colony ages are minimum ages as our methodology is more likely to undercount seasonal cycles due to overly coarse micromilling and resulting time averaging. Based on these colony age estimates, our micromilling approach yielded an average temporal resolution of 1.2 mo per sample.

The lack of cyclicity in the SWC colonies prohibits a direct estimate of colony age, so their lack of cyclicity could simply be due to shorter colony life spans and not recording as long a record of seasonal variation. O'Dea and Jackson (2002) used MART analysis to infer colony ages in TEP. On the TEP side, they live on average 3.4 yrs, but it is not possible to derive colony age estimates for SWC colonies using MART analysis due to the lack of seasonal temperature variation (O'Dea and Jackson 2002). No estimates on the rate of growth for SWC *Cupuladria* species currently exist with which to infer colony ages, although circumstantial evidence from size-frequency histograms of *Cupuladria* colonies from Florida suggests a growth rate of approximately 1–5 mm yr⁻¹ (fig. 7 in Winston 1988, O'Dea and Jackson 2002). Applying these growth rate estimates to our SWC colonies suggests a minimum colony age of 4 yrs, more than enough time to indicate seasonal cycles. In addition, the SWC colonies are larger (mean diameter: 21.5 mm) than the TEP colonies (mean diameter: 16.3 mm). Assuming they have similar growth rates as they are congeneric species, the SWC colonies are probably as old if not older than the TEP colonies. Therefore, it is more likely that the lack of seasonal cyclicity in the SWC colonies is not due to sub-annual life spans but is due to the reduced seasonal variation in temperature and salinity in the SWC discussed below.

OXYGEN ISOTOPE VALUES.—Our $\delta^{18}\text{O}_{\text{carb}}$ values are similar to those predicted by previous studies based on temperature and salinity. For the SWC, Geary et al. (1992) predicted a SWC seasonal range in $\delta^{18}\text{O}_{\text{carb}}$ values of -1.3‰ to -1.5‰ VPDB and for TEP -0.5‰ to -2.9‰ VPDB. Tao et al. (2013) predicted a SWC seasonal range in $\delta^{18}\text{O}_{\text{carb}}$ values of -0.1‰ to -1.4‰ VPDB (Fig. 4C, site CB) and for TEP (20 m water depth in Gulf of Panama) 0.5‰ to -2.1‰ VPDB (Fig. 4C, sites GP1 and GP2).

The oxygen isotope value of biogenic carbonate ($\delta^{18}\text{O}_{\text{carb}}$) is a function of both the temperature and the oxygen isotope value of the seawater ($\delta^{18}\text{O}_{\text{sw}}$) in which the organism grew (Epstein and Lowenstam 1953 and references therein). Our $\delta^{18}\text{O}_{\text{carb}}$ values will be discussed first in relation to temperature, and $\delta^{18}\text{O}_{\text{sw}}$ second.

There are three time series of temperature data from or near Almirante Bay in Bocas del Toro close to our SWC site. The first is data logger-based from 1999 to 2004 with temperature measured hourly at 1–20 m depth, 15 km from our SWC sites (Kaufman and Thompson 2005). They recorded a maximum temperature range of 5.8 °C (25.6–31.4 °C) with a range in monthly means of 2.4 °C (27.3–29.7 °C, mean: 28.6 °C). The second time-series is also data logger-based from 2000 to 2007 with temperature measured daily at 4 m depth at Cayo Agua in Bocas del Toro (Fig. 2), 15 km from Almirante Bay. It recorded a maximum temperature range of 5.1 °C (25.9–31.0 °C, mean: 28.7 °C; Fig. 5). The third was derived from the historical database of the World Ocean Atlas 2001 offshore sites at 20 m depth <10 km from our SWC sites (Fig. 4A, site CB). It shows a range in monthly mean temperatures of 5.1 °C (23.6–28.7 °C, mean: 26.5 °C).

There are five temperature time series from the Pearl Islands in the Gulf of Panama close to our TEP site. The first is a data logger-based data set for 14 mo from 1978 to 1979, which recorded temperature weekly at 3–10 m depth off Contadora Island in the Pearl Islands (Fig. 2), 40 km from our TEP site (Dunbar and Wellington 1981). This time series recorded a maximum temperature range of 12 °C (18–30 °C) with a range in monthly means of 7 °C (21.5–28.5 °C, mean: 26.1 °C). The second is data logger-based for 7 mo in 2003 with temperature measured every 30 min, 1–7 m depth off Contadora Island, Pearl Islands, 37 km from our TEP site (Matthews et al. 2008).

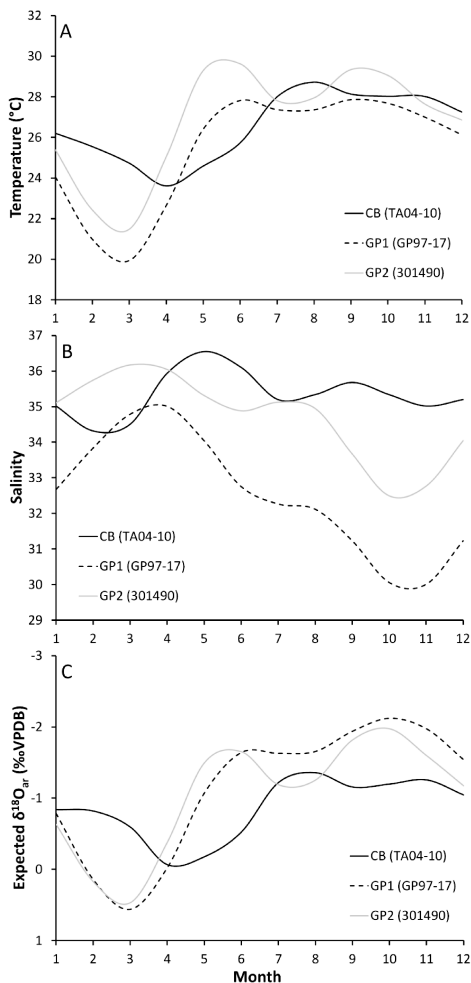


Figure 4. Temperature (A) and salinity (B) profiles at 20 m depth and the resulting estimated $\delta^{18}\text{O}_{\text{ar}}$ profiles (C) for the three localities closest to our study sites from the Ocean Data View World Atlas 2001 database (Conkright et al. 2002). CB is from the Caribbean side at Bocas del Toro at Lat. 9.45°N , Long. 82.32°W . GP1 is from the Pacific side in the Gulf of Panama at Lat. 7.99°N , Long. 79.25°W . GP2 is from the Pacific side in the Pearl Islands in the Gulf of Panama at Lat. 8.27°N , Long. 78.91°W . Modified from Tao et al. (2013).

They recorded a monthly mean temperature range of 10°C ($19\text{--}29^{\circ}\text{C}$) with a range in upwelling to non-upwelling seasonal means of 4.3°C ($23.8\text{--}28.1^{\circ}\text{C}$). The third is also data logger-based from 1995 to 2008 with temperature measured daily at 12 m depth off Pacheca Island in the Pearl Islands (Fig. 2), 20 km from our TEP site. It recorded a maximum temperature range of 14.1°C ($15.7\text{--}29.8^{\circ}\text{C}$, mean: 26.9°C ; Fig. 5). The fourth and fifth were derived from the historical database of the World Ocean Atlas 2001 offshore sites at 20 m deep for two sites 20–30 km from our TEP site (Fig. 4A, sites GP1 and GP2). They recorded a range in monthly mean temperatures of 7.9 and 8.1°C , respectively ($19.9\text{--}27.9^{\circ}\text{C}$, $21.5\text{--}29.6^{\circ}\text{C}$, mean: 25.4°C , 26.8°C , respectively).

As the mean temporal resolution of our sampling was 1.2 mo, it is best to compare monthly mean ranges than maximum ranges. Based on the above review of published time series temperature data near our study sites, the seasonal range in monthly mean temperature is less at the SWC site (mean temperature range: 3.7°C) than the TEP site (mean temperature range: 8.5°C).

In contrast to temperature, $\delta^{18}\text{O}_{\text{sw}}$ varies in response to the effects of evaporation (i.e., ice volume and salinity). This can vary on a range of spatial and temporal scales from global glacial-interglacial terrestrial ice volume cycles (Shackleton 1967,

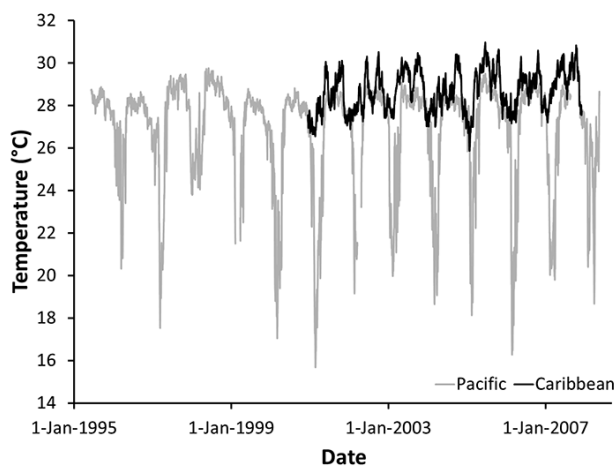


Figure 5. Daily temperature records from both sides of the Isthmus of Panama from Smithsonian Tropical Research Institute data loggers in the Caribbean (4 m depth at Cayo Agua in Bocas del Toro) and Pacific (12 m depth at Pacheco Island, Pearl Islands, Gulf of Panama). Modified from Tao et al. (2013).

Zachos et al. 2001), to regional inter-annual cycles in response to El Niño–Southern Oscillation events (Carré et al. 2005a), to local annual cycles in salinity in response to rainfall, river runoff, and/or upwelling (Lachniet and Patterson 2006, Lachniet 2009, McConnell et al. 2009). In the present study with a minimal temporal duration, the main influence on $\delta^{18}\text{O}_{\text{sw}}$ is assumed to be seasonal variation in salinity due to freshening.

There are two time series of salinity data from Almirante Bay in Bocas del Toro close to our SWC site. The first is data logger–based from 1999 to 2004, which measured salinity daily at 0.5 m depth, 15 km from our SWC sites (Kaufman and Thompson 2005). It recorded a maximum salinity range of 14 (20–34) with a range in monthly means of 3 (30.5–33.5, mean: 32). The second was derived from the historical database of the World Ocean Atlas 2001 offshore sites at 20 m depth, <10 km from our SWC sites (Fig. 4B, site CB). It shows a range in monthly mean salinities of 2.2 (34.3–36.5, mean: 35.3).

There are four salinity time series from the Pearl Islands in the Gulf of Panama, close to our TEP site. The first is data logger–based for 14 mo from 1978 to 1979 which recorded salinity monthly at 3–10 m depth off Contadora Island in the Pearl Islands, 40 km from our TEP site (Dunbar and Wellington 1981). They recorded a maximum salinity range of 12 (23–35) with a range in monthly means of 8 (27–35, mean: 30.5). The second is also data logger–based for 7 mo in 2003 with salinity measured every 3 d, 1–7 m depth off Contadora Island, Pearl Islands which is 37 km from our TEP site (Matthews et al. 2008). They recorded a monthly mean salinity range of 7 (28–35) with a range in upwelling to non-upwelling seasonal means of 4.1 (30.8–34.9). The third and fourth were derived from the historical database of the World Ocean Atlas 2001 offshore sites for 20 m deep for two sites 20–30 km from our TEP site (Fig. 4B, sites GP1 and GP2). They show a range in monthly mean salinities of 5.0 and 3.7, respectively (30.0–35.0, 32.5–36.2, mean: 32.5, 34.7, respectively).

Based on the above review of published time series of salinity data near our study sites, the seasonal range in monthly mean salinity is less at the SWC site (mean

salinity range: 2.5) than the TEP site (mean salinity range: 5.7). These differences are reflected in the measured $\delta^{18}\text{O}_{\text{sw}}$ values.

There have been few studies on the seasonal variation in $\delta^{18}\text{O}_{\text{sw}}$ values in the Gulf of Panama. Dunbar and Wellington (1981) made five measurements from surface waters at Naos Island Marine Laboratory (80 km north of our TEP site; Fig. 2) and found a seasonal range in $\delta^{18}\text{O}_{\text{sw}}$ values of -0.2‰ to -0.8‰ VSMOW. Matthews et al. (2008) measured $\delta^{18}\text{O}_{\text{sw}}$ every 3 d in 2003 over the upwelling and non-upwelling seasons from 1 to 7 m depth off of Contadora Island, Pearl Islands. This is 37 km north of our TEP study site. Matthews et al.'s (2008) $\delta^{18}\text{O}_{\text{sw}}$ values were measured relative to VPDB and were converted to Vienna Standard Mean Ocean Water (VSMOW) following Coplen (1988). Their mean upwelling $\delta^{18}\text{O}_{\text{sw}}$ value was 0.31‰ VSMOW, and the mean non-upwelling $\delta^{18}\text{O}_{\text{sw}}$ value was -0.46‰ VSMOW. Tao et al. (2013) twice-weekly measured $\delta^{18}\text{O}_{\text{sw}}$ near the Naos Island Marine Laboratory in the Gulf of Panama, and from March 2011 through August 2012 they recorded a monthly mean range from -0.08‰ to -1.76‰ VSMOW (range: 1.68‰ VSMOW, SD: 0.53‰ VSMOW). Thus, based on these previous studies, $\delta^{18}\text{O}_{\text{sw}}$ values in the Gulf of Panama range on average from 0‰ VSMOW during the dry upwelling season to -1‰ VSMOW during the rainy non-upwelling season.

Across the isthmus in the SWC, the only time series of $\delta^{18}\text{O}_{\text{sw}}$ data available are from Tao et al. (2013) who twice-weekly measured $\delta^{18}\text{O}_{\text{sw}}$ near the Galeta Island Marine Laboratory. From March 2011 through August 2012 they recorded a monthly mean range from 0.24‰ to 0.92‰ VSMOW with a mean of 0.65‰ VSMOW (range: 0.67‰ VSMOW, SD: 0.18‰ VSMOW). This reduced variation in $\delta^{18}\text{O}_{\text{sw}}$ values in Almirante Bay compared to the Pearl Islands is due to less coastal freshwater runoff in the former.

Most freshwater runoff into the Gulf of Panama occurs in May and June, and the least is in February and March during the dry season, coinciding with the upwelling season (Forsbergh 1969). This rain was largely evaporated from the Caribbean Sea and has low $\delta^{18}\text{O}$ values due to progressive rainout and orographic distillation as it passes over the Cordillera before falling on the Pacific coast of Panama (Lachniet and Patterson 2006, Lachniet et al. 2007, Lachniet 2009).

Our Pacific site, off San José Island, is 80 km from the mouth of Panama's largest estuary, the Gulf of San Miguel (Fig. 2). The estuary captures 45% of the precipitation from the Gulf of Panama's watershed, and it contains Panama's largest river, the Chucunaque-Tuira River system (Fig. 2), that annually discharges $29 \times 10^8 \text{ m}^3$ (Suman 2007). This is the likely cause of the greater seasonal variation in salinity and $\delta^{18}\text{O}_{\text{sw}}$ values in the Pearl Islands compared to Almirante Bay.

In response to these differences in temperature and salinity, the SWC colonies have a smaller range in $\delta^{18}\text{O}_{\text{carb}}$ values (mean: 0.7‰ VPDB, SD: 0.1‰ VPDB) than those from TEP colonies (mean: 1.6‰ VPDB, SD: 0.2‰ VPDB). We define the range as the difference between the maximum and minimum value in each colony. If the range is calculated using the maximum and minimum value from each side of the isthmus, as opposed to the colony means, the maximum range in SWC colonies is 1.1‰ VPDB and 2.0‰ VPDB for TEP colonies.

Thus, the variation in $\delta^{18}\text{O}_{\text{carb}}$ values is a function of varying degrees of upwelling-induced temperature changes and freshening-induced salinity changes (Tao et al. 2013). Using coral skeletons from the Gulf of Panama, Dunbar and Wellington (1981) estimated that 30% of the variation in $\delta^{18}\text{O}_{\text{carb}}$ is due to salinity-influenced $\delta^{18}\text{O}_{\text{sw}}$

Table 2. Comparison of seasonal range in $\delta^{18}\text{O}_{\text{carb}}$ values between previous and current studies. SWC = southwest Caribbean, TEP = tropical eastern Pacific.

Water depth, location	Source of isotope values (total # of specimens)	Seasonal range in $\delta^{18}\text{O}_{\text{carb}}$ values (‰ VPDB)	Reference
Non-upwelling SWC			
<10 m, San Blas Islands	1 gastropod sp. (1)	1.5	Geary et al. (1992, fig. 5)
11–16 m, San Blas Islands and Bocas del Toro Archipelago	2 gastropod sp. (4)	1.1	Tao et al. (2013, fig. 5)
<24 m, coast of Colón and east of Panama Canal	2 bivalve sp. (2)	0.9	Bemis and Geary (1996, table 3)
24 m, east of Panama Canal	1 bivalve sp. (1)	0.7	Teranes et al. (1996, table 5.1)
		\bar{X} : 1.0 (SD 0.3)	
10–23 m, Almirante Bay, Bocas del Toro Archipelago	1 bryozoan sp. (3)	0.7	Present study
Upwelling TEP			
<10 m, Venado Beach, Panama City	1 gastropod sp. (1)	4.5	Geary et al. (1992, fig. 4)
10–17 m, Pearl Islands	4 gastropod sp. (5)	2.6	Tao et al. (2013, fig. 5)
<45 m, Pearl Islands and Parita Bay	4 bivalve sp. (4)	2.5	Bemis and Geary (1996, table 3)
20 m, Parita Bay	1 bivalve sp. (1)	2.8	Teranes et al. (1996, table 5.1)
1–4 m, Contadora Island, Pearl Islands	1 coral sp. (7)	2.5	Dunbar and Wellington (1981, fig. 1c,d,2)
7 m, Contadora Island, Pearl Islands	3 coral sp. (15)	1.1	Matthews et al. (2008, fig. 5D–F)
		\bar{X} : 2.7 (SD 1.1)	
19.7 m, San José Island, Pearl Islands	1 bryozoan sp. (3)	1.6	Present study

variation, the rest temperature. This is supported by the greater seasonal temperature variation in the TEP compared to the seasonal salinity variation.

Our seasonal ranges in $\delta^{18}\text{O}_{\text{carb}}$ values from both sides of the isthmus are less than those found in previous studies from similar localities, but using different organisms. The seasonal range in our SWC bryozoan $\delta^{18}\text{O}_{\text{carb}}$ values (mean: 0.7‰ VPDB) is slightly less than that found in previous studies (mean: 1.0‰ VPDB, Table 2) using gastropods (mean: 1.3‰ VPDB; Geary et al. 1992, Tao et al. 2013) and bivalves (mean: 0.8‰ VPDB; Bemis and Geary 1996, Teranes et al. 1996). The seasonal range in our SWC bryozoan $\delta^{18}\text{O}_{\text{carb}}$ values is also less than that predicted from temperature and salinity values by Tao et al. (2013) (Fig. 4). They predicted $\delta^{18}\text{O}_{\text{carb}}$ values to have a seasonal range of 1.3‰ VPDB for their site TA04-10 at 20 m depth in Almirante Bay, 20 km from our SWC sites.

The seasonal range in our TEP bryozoan $\delta^{18}\text{O}_{\text{carb}}$ values (mean: 1.6‰ VPDB) is less than that found in previous studies (mean: 2.7‰ VPDB, Table 2) using gastropods (mean: 3.5‰ VPDB; Geary et al. 1992, Tao et al. 2013), bivalves (mean: 2.7‰ VPDB; Bemis and Geary 1996, Teranes et al. 1996), and corals (1.8‰ VPDB; Dunbar and Wellington 1981, Matthews et al. 2008). The seasonal range in our TEP bryozoan $\delta^{18}\text{O}_{\text{carb}}$ values is also less than that predicted from temperature and salinity values by Tao et al. (2013) (Fig. 4). They predicted $\delta^{18}\text{O}_{\text{carb}}$ values to have a seasonal range of 2.7‰ VPDB for their site GP97-17 at 20 m depth in the Pearl Islands 20 km from

ours and 2.4‰ VPDB for their site 301490 at 20 m depth in the Pearl Islands 30 km from ours.

The lower-than-predicted seasonal range in $\delta^{18}\text{O}_{\text{carb}}$ values has several possible explanations. (1) Less replication as our study included only two bryozoan species, whereas the previous studies totaled 20 species spanning two groups of molluscs and corals. (2) Cupuladriids may fractionate O isotopes differently during biomineralization, but in general this is less common for O relative to C (Wefer and Berger 1991) and as discussed below has not been documented in *Cupuladria*. (3) Differing spatial and temporal hydrologies, particularly with respect to depths and sampling during ENSO years. As the colonies were not necessarily alive when collected and, as indicated in Table 1, the SWC colonies were collected in different years (1998 and 2005) from the TEP colonies (2004), absolute dates were not assigned to the colonies. Only one of the colonies (CB3) was potentially impacted by an El Niño year (1997–1998; Wolter and Timlin 2011). Even this was unlikely as El Niño conditions in Boca del Toro generally affect only cloud cover, not temperature or other measures (Kaufmann and Thompson 2005), so this is an unlikely explanation. (4) Cessation of growth in cupuladriids, although colonies of *C. exfragminis* from the Gulf of Panama show year-round growth in ambient water conditions of the Gulf of Panama (O’Dea et al. 2007, O’Dea 2009, O’Dea unpubl data). (5) Micromilled samples have a lower temporal resolution than instrument-based temperature data, and our data miss maximum and minimum isotope values due to either time averaging or ephemeral peaks in upwelling.

We suggest that the micromilling methodology best explains the lower than predicted values. Each micromilled sample represents on average 1.2 mo, which is coarse enough to moderate the ephemeral peaks in temperature and salinity that are observed in the region. Time averaging should be partly offset by the inverse relationship between zooid size in these bryozoans and environmental temperature (O’Dea and Jackson 2002) and the fact that growth rate of *C. exfragminis* increases during upwelling times (O’Dea et al. 2007), but nonetheless it would be unexpected to reflect the full range at the resolution of our sampling.

On the SWC side, there is minimal seasonality in precipitation-induced freshening and upwelling-induced cooling resulting in no cyclicity in the $\delta^{18}\text{O}_{\text{carb}}$ profiles. In contrast, on the TEP side, there is more seasonal variation in precipitation-induced freshening and upwelling-induced cooling which is reflected in the cyclic $\delta^{18}\text{O}_{\text{carb}}$ profiles. Maximum $\delta^{18}\text{O}_{\text{carb}}$ values represent the late boreal winter to early boreal spring season of upwelling of cooler, normal (33–34) salinity waters in the Gulf of Panama. Minimum $\delta^{18}\text{O}_{\text{carb}}$ values represent the rainy season when upwelling ceases and warmer, lower salinity, meteoric water with lower $\delta^{18}\text{O}$ values flows into the Gulf of Panama. Similar results were found using the same methodology in the same general locations using gastropods (Geary et al. 1992, Tao et al. 2013) and bivalves (Bemis and Geary 1996, Teranes et al. 1996).

Our interpretation is supported by a corresponding morphological pattern in similar cupuladriid bryozoans from the same environments (O’Dea and Jackson 2002). O’Dea and Jackson (2002) documented seasonal variation in zooid size in response to temperature fluctuations in the Gulf of Panama that was lacking in their Caribbean colonies. Teusch et al. (2002) also reported a similar correspondence between the isotopic and morphologic signal of upwelling in gastropods off Chile.

Higher $\delta^{18}\text{O}_{\text{carb}}$ values typically are due to upwelling of colder, deeper water. The cyclicity of the $\delta^{18}\text{O}_{\text{carb}}$ signal is driven both by colder water temperatures during the drier, saltier, upwelling season (i.e., higher $\delta^{18}\text{O}_{\text{carb}}$ values), as well as increased freshwater runoff during the wetter, fresher, non-upwelling season (i.e., lower $\delta^{18}\text{O}_{\text{carb}}$ values). This is because organisms incorporate more ^{18}O into their skeletons in colder water (i.e., leading to higher $\delta^{18}\text{O}_{\text{carb}}$ in colder water), and because evaporation preferentially removes ^{16}O , saltier water has a higher $\delta^{18}\text{O}_{\text{sw}}$ than fresher water. Thus in the TEP, temperature and salinity are generally unsynchronized with the higher salinity water coming with the lowest temperatures during upwelling and lower salinities and higher temperatures during the non-upwelling season (Geary et al. 1992, Teranes et al. 1996, Tao et al. 2013).

In contrast, in the SWC, salinity and temperature are more synchronous with the higher salinity waters generally occurring with the highest temperatures when evaporation is highest (Geary et al. 1992, Teranes et al. 1996, Tao et al. 2013). As a result of this positive correlation between salinity and temperature in the SWC, their effects on $\delta^{18}\text{O}_{\text{carb}}$ may serve to partially cancel each other out. Elevated temperatures result in lower $\delta^{18}\text{O}_{\text{carb}}$ values, but elevated temperatures also result in higher salinity that results in higher $\delta^{18}\text{O}_{\text{carb}}$ values (Geary et al. 1992, Teranes et al. 1996, Molnar 2008).

CARBON ISOTOPE VALUES.—Controls on $\delta^{13}\text{C}_{\text{carb}}$ values are more complicated than those on $\delta^{18}\text{O}_{\text{carb}}$ (e.g., Gillikin et al. 2006). Influences on $\delta^{13}\text{C}_{\text{carb}}$ include environmental conditions [e.g., seawater temperature, freshwater runoff, phytoplankton productivity, and dissolved inorganic carbon content (DIC) of the seawater] and biological effects (e.g., metabolically produced CO_2 , diet, growth rate, organismal age; see review in Sadler et al. 2012). Typically, upwelling yields lower $\delta^{13}\text{C}_{\text{carb}}$ values as photosynthetic activities by planktonic organisms in surface waters selectively remove ^{12}C from the ambient DIC reservoir. When these planktonic organisms die, they carry carbon with low $\delta^{13}\text{C}_{\text{org}}$ values to deeper waters. Oxidation of this organic debris at depth releases relatively large amounts of ^{12}C (Kroopnick 1974, 1980), so that during upwelling, cooler water with lower $\delta^{13}\text{C}_{\text{DIC}}$ values is brought to the surface (Killingley and Berger 1979, Curry et al. 1983, Geary et al. 1992, Jones and Allmon 1995). The higher nutrient availability also causes faster calcification at a higher respiration rate, which involves more respired CO_2 with lower $\delta^{13}\text{C}_{\text{carb}}$ values (Wurster and Patterson 2003). But freshwater runoff can also introduce isotopically light carbon into coastal settings (Tao and Grossman 2010) due to the input of decayed terrestrial vegetation (e.g., Diefendorf et al. 2008).

The higher $\delta^{13}\text{C}_{\text{carb}}$ values in the SWC colonies is likely due to terrestrial organic matter influencing the $\delta^{13}\text{C}_{\text{DIC}}$ more in the Gulf of Panama than Almirante Bay. The Pacific side may be receiving more dissolved organic carbon and particulate organic carbon from terrestrial sources, both of which influence the $\delta^{13}\text{C}_{\text{DIC}}$ once they transfer into that part of the carbon cycle.

Matthews et al. (2008) measured $\delta^{13}\text{C}_{\text{carb}}$ in corals from 1 to 7 m depth off Contadora Island, Pearl Islands, 37 km north of our TEP study site. They measured seawater $\delta^{13}\text{C}_{\text{DIC}}$ every 3 d in 2003 over the upwelling and non-upwelling seasons. They found no significant difference in seawater $\delta^{13}\text{C}_{\text{DIC}}$ between the seasons and suggested this was the cause of the lack of seasonal variation in $\delta^{13}\text{C}_{\text{carb}}$ values. This may also explain the lack of cyclicity in our $\delta^{13}\text{C}_{\text{carb}}$ values.

The lighter $\delta^{13}\text{C}_{\text{carb}}$ values of colony CB2 may be due to locally lighter $\delta^{13}\text{C}_{\text{DIC}}$ values. CB2 was collected in Almirante Bay which is fringed by mangroves (Guzmán et al. 2005). Mangroves have $\delta^{13}\text{C}_{\text{carb}}$ values as low as -28‰ VPDB (Tue et al. 2012). The locally common red mangrove (*Rhizophora mangle* Linnaeus) has $\delta^{13}\text{C}$ values of -25‰ VPDB (Smallwood et al. 2003). These mangroves can lower the local water $\delta^{13}\text{C}_{\text{DIC}}$ value considerably if their dissolved organic carbon and particulate organic carbon transfer into that part of the carbon cycle (Patterson and Walter 1994).

LACK OF COVARIATION BETWEEN O AND C ISOTOPE VALUES.—The classic O and C stable isotope pattern associated with upwelling are higher $\delta^{18}\text{O}_{\text{carb}}$ values and lower $\delta^{13}\text{C}_{\text{carb}}$ values (Killingley and Berger 1979). Only colony GP1 showed any kind of inverse relationship between $\delta^{18}\text{O}_{\text{carb}}$ and $\delta^{13}\text{C}_{\text{carb}}$ values (i.e., some of the peaks and troughs line up in Fig. 3), but it is not statistically significant (linear regression: $P > 0.05$) in this or any of the other colonies. Even though $\delta^{18}\text{O}_{\text{carb}}$ values from the Pacific colonies show evidence of seasonal variation in freshening and upwelling of cooler water, most studies have found results similar to ours with a robust cyclic $\delta^{18}\text{O}_{\text{carb}}$ pattern but without the classic (Killingley and Berger 1979) 180° -out-of-phase $\delta^{13}\text{C}_{\text{carb}}$ values (Geary et al. 1992, Jones and Allmon 1995, Bemis and Geary 1996, Teranes et al. 1996, Carré et al. 2005b, Nützel et al. 2010). Tao et al. (2013) suggest that freshening during the rainy, non-upwelling season masks the expected, negatively covarying pattern.

CONCLUSIONS

O stable isotope values along growth axes of the skeletons of cupuladriid marine bryozoan colonies from opposite sides of the Isthmus of Panama reveal greater variation in colonies from the Pacific compared to the Caribbean.

Variation in O stable isotope values along growth axes of the skeletons of cupuladriid marine bryozoan colonies is cyclic on the Pacific side, but not on the Caribbean side, a finding attributed to the presence of both seasonal upwelling and freshening on the Pacific side and their relative absence on the Caribbean side.

The higher $\delta^{13}\text{C}_{\text{carb}}$ values in the SWC colonies are likely due to terrestrial organic matter influencing the $\delta^{13}\text{C}_{\text{DIC}}$ more in the Gulf of Panama than Almirante Bay. The Pacific side may be receiving more dissolved organic carbon and particulate organic carbon from terrestrial sources.

Our preliminary study suggests the potential of bryozoans as a source of paleoclimate proxies. Stable isotope profiling in cupuladriid bryozoan skeletons can record seasonal upwelling and freshening conditions.

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