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Sex-associated variations in coral skeletal oxygen and carbon isotopic composition of *Porites panamensis* in the southern Gulf of California

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Abstract

Coral $\delta^{18}\text{O}$ variations are used as a proxy for changes in near sea surface temperature and seawater isotope composition. Skeletal $\delta^{13}\text{C}$ of coral is frequently used as a proxy for solar radiation because most of its variability is controlled by an interrelationship between three processes: photosynthesis, respiration, and feeding. Coral growth rate is known to influence the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ isotope record to a lesser extent. Recent published data show differences in growth parameters between female and male coral; thus, skeletal $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ are hypothesized to be different in each sex. To assess this difference, this study describes changes in the skeletal $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ record of four female and six male *Porites panamensis* coral collected in Bahía de La Paz, whose growth bands spanned 12 years. The isotopic data were compared to SST, precipitation, PAR, chlorophyll *a*, and skeletal growth parameters. *Porites panamensis* is a known gonochoric brooder whose growth parameters are different in females and males. Splitting the data by sexes explained 81 and 93 % of the differences of $\delta^{18}\text{O}$, and of $\delta^{13}\text{C}$, respectively, in the isotope record between colonies. Both isotope records were different between sexes. $\delta^{18}\text{O}$ was higher in female colonies than in male colonies, with a 0.31 ‰ difference; $\delta^{13}\text{C}$ was lower in female colonies, with a 0.28 ‰ difference. A difference in the skeletal $\delta^{18}\text{O}$ implies an error in SST estimates of $\approx 1.0^\circ\text{C}$ to $\approx 2.6^\circ\text{C}$. The $\delta^{18}\text{O}$ records showed a seasonal pattern that corresponded to SST, with low correlation coefficients (-0.45 , -0.32), and gentle slopes ($0.09\text{‰}^\circ\text{C}^{-1}$, $0.10\text{‰}^\circ\text{C}^{-1}$) of the $\delta^{18}\text{O}$ –SST relation. Seasonal variation in coral $\delta^{18}\text{O}$ represents only 52.37 and 35.66 % of the SST cycle; 29.72 and 38.53 % can be attributed to $\delta^{18}\text{O}$ variability in seawater. $\delta^{13}\text{C}$ data did not correlate with any of the environmental variables; therefore, variations in skeletal $\delta^{13}\text{C}$ appear to be driven mainly by metabolic effects. Our results support the hypothesis of a sex-associated difference in skeletal $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ signal, and suggest that environmental conditions and coral growth parameters affect skeletal isotopic signal differently in each sex.

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1 Introduction

Coral are useful as recorders of oceanic conditions because their growth is affected by environmental variables, and the calcareous material is deposited in annual density bands that allow for the determination of events over time (Druffel, 1997; Gagan et al., 2000; Grottoli and Eakin, 2007; Lough and Barnes, 2000; Lough and Cooper, 2011). This memory of oceanographic conditions at the time of calcification, record variations at the intra-annual, inter-annual, inter-decadal, and sometimes centennial timescale of El Niño-Southern Oscillation changes (ENSO), the Pacific Decadal Oscillation (PDO), and pre- and post-industrial climate events (Grottoli and Eakin, 2007). Skeletal growth, isotope composition, and minor and trace element ratios in coral skeletons vary in a predictable way from environmental variations in temperature, salinity, precipitation, cloud cover, fresh water discharge, upwelling, and pH (Dunbar and Wellington, 1981; Bernal and Carriquiry, 2001; Hönisch et al., 2004; Grottoli and Eakin, 2007). Among the proxies used in coral skeletons (trace element ratios, $\delta^{18}\text{O}$, $\delta^{13}\text{C}$, $\delta^{11}\text{B}$, $\delta^{15}\text{N}$), skeletal $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ are the most common measurements because they are relatively easy to estimate and interpret (Dunbar et al., 1994; Linsley et al., 1994; Swart et al., 1996a; Tudhope et al., 1996; Charles et al., 1997; Schrag, 1999).

Most of the variability in skeletal $\delta^{18}\text{O}$ in calcifying organisms, including coral, results from a combination of temperature-induced isotopic fractionation of local sea-water $\delta^{18}\text{O}$ ($\delta^{18}\text{O}_{\text{sw}}$) that depends on changes in precipitation and oceanic evaporation, which affect salinity (Epstein et al., 1953). Depletion in carbonate $\delta^{18}\text{O}$ occurs as temperature increases in inorganic and biogenic carbonates (Allison et al., 1996). In tropical and subtropical oceans, variations in salinity caused by evaporation, rainfall, or river run-off affect skeletal $\delta^{18}\text{O}$ and need to be considered when establishing a skeletal $\delta^{18}\text{O}$ -SST relationship (Cole and Fairbanks, 1990; Carriquiry et al., 1994; Al Rousan et al., 2007; Sazzad et al., 2010).

Variations of skeletal $\delta^{13}\text{C}$ are controlled mainly by an interrelationship between photosynthesis, respiration, and feeding. During high photosynthesis, zooxanthellae

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et al., 1996; Barnes et al., 1995; Cohen and Hart, 1997). Skeletal growth parameters in coral have sex-based differences in some gonochoric species (Cabral-Tena et al., 2013; Carricart-Ganivet et al., 2013), so it is possible for the sex of a coral colony to be another cause of deviation in oxygen and carbon isotope fractionation. The influence of metabolic effects, such as reproduction, is another factor affecting the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ signal in skeletons (Kramer et al., 1993; Gagan et al., 1994; Barnes et al., 1995; Taylor et al., 1995; Allison et al., 1996; Cohen and Hart, 1997; Lough et al., 1996; Swart et al., 1996b).

The stony coral *Porites panamensis* has a wide distribution along the eastern tropical Pacific, from Mexico to Ecuador, and tolerates a wide range of environmental conditions, including low temperature and high-turbidity that are often stressful to other coral species (Halfar et al., 2005; Reyes-Bonilla et al., 2007). This coral has extension rates ranging from 0.4 to 1.2 cm yr^{-1} , along the coast of Mexico and Costa Rica (Guzmán and Cortés, 1989; Halfar et al., 2005; Cabral-Tena et al., 2013), where extension and calcification rates are different in males and females (Cabral-Tena et al., 2013). *P. panamensis* is a gonochoric brooder with reproductive activity throughout the year (Glynn et al., 1994; Carpizo-Ituarte et al., 2011; Rodríguez-Troncoso et al., 2011).

This study describes changes in the skeletal isotopic oxygen and carbon record of six male and four female *P. panamensis* coral, collected in Bahía de La Paz, with growth density banding covering 12 years. Oxygen and carbon isotope recording was used to assess a possible sex-associated variation in the coral skeletal $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ signal related to differences in the “vital effect” of colonies between sexes. The isotopic record was compared to surface seawater temperature (SST), rainfall, photosynthetically active radiation (PAR), concentration of chlorophyll *a*, and skeletal growth data.

sity tracks were placed in the maximum growth axis in the digital X-radiography of each slice; density was measured using the ImageJ 1.44 image processing program (<http://imagej.nih.gov/ij>). A data series of absolute density vs. distance was generated and dated backwards for each slice, using photodensitometry (Carricart-Ganivet and Barnes, 2007). The coral year starts in the summer, with the highest SST at the sampling site (Hudson et al., 1976). The maximum and minimum density for each year (1993 through 2009) were identified in each density series.

2.3 Isotope analysis

After the skeletal growth analysis, one slice covering the most extensive chronological extension of each of the ten colonies was selected for isotope analysis. Continuous samples of aragonite powder were collected along each coral's maximum growth axis using a drill with a 0.1 mm bit. Each sample was ~ 1 mm apart.

Aragonite powder was analyzed using an isotope ratio mass spectrometer (Delta V Plus, Thermo Scientific, Waltham, MA) with an automated system for carbon analysis in an acid bath (Finnigan Gas Bench II, Thermo Electron, Madison, WI). Each isotope sample had < 0.05‰ error. Reference NBS-19 (International Atomic Energy Agency, Vienna, Austria) was used as the isotope standard. The seasonal pattern of $\delta^{18}\text{O}$ was used to establish chronology. This is supported by the consistent pattern of annual density-band pairs described for *Porites* by Lough and Barnes (2000). Chronologies were established by designating the minimum $\delta^{18}\text{O}$ value in a year equal to summer (consistent with maximum SST). To eliminate the effects of different sampling resolutions on the calculation of mean coral $\delta^{18}\text{O}$ values, the results were interpolated to create four equally spaced values per year. Normality and homoscedasticity of the data were tested using Kolmogorov–Smirnov and Bartlett tests, respectively. Student's *t* test for independent samples with uneven variance was used to assess statistical differences in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ between sexes. Pearson's correlation test and simple linear regressions were used to estimate relationships between mean skeletal extension rate, skeletal density, and calcification rate with isotope data of both sexes. An

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ANCOVA test was used to assess the differences between slopes and the y intercept of lineal equations of $\delta^{13}\text{C}$ vs. $\delta^{18}\text{O}$ plots of the results of male and female data.

2.4 Environmental data

SST, PAR, and concentration of chlorophyll a data were obtained from the NOAA live access server (<http://las.pfeg.noaa.gov/oceanWatch/oceanwatch.php>), and in situ thermograph temperature data (2003–2007) from the Marine Observatory for the Mexican Pacific region (Sicard-González et al., 2012). This information was used to compare satellite and in situ temperature data. Both temperature records (satellite and in situ measurements) from Bahía de La Paz showed the same seasonal signal and a close fit ($r = 0.90$, $p < 0.05$). This result supports the use of satellite SST data for coral skeletal $\delta^{18}\text{O}$ calibration. Rainfall data were obtained from the Servicio Meteorológico Nacional (<http://smn.cna.gob.mx/>). Some sea surface salinity data was obtained from previous published data in the study area (Obeso-Niebla, 2007). $\delta^{18}\text{O}_{\text{sw}}$ was calculated from the $\delta^{18}\text{O}$ relationship with the salinity equation for the Eastern Pacific (Fairbanks et al., 1997). Pearson's correlation test and simple linear regressions were used to estimate relationships between environmental data and isotope data of both sexes. Regime shift index for environmental and isotope data were calculated with the Sequential Regime Shift Detection Software (Rodionov, 2004).

3 Results

3.1 Skeletal growth

All specimens were collected in March, a period of low SST in Bahía de La Paz. All X-radiographs had a low-density annual growth band in the apex of the slice. This means that *P. panamensis* form a low-density band in winter. Annual growth bands in each colony were dated and the sampling resolution for isotope analysis was determined.

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The average yearly extension rate was $1.05 \pm 0.04 \text{ cm yr}^{-1}$ for female colonies, and $1.27 \pm 0.04 \text{ cm yr}^{-1}$ for male colonies. The average skeletal density was $0.94 \pm 0.01 \text{ g cm}^{-3}$ for females, and $0.95 \pm 0.01 \text{ g cm}^{-3}$ for males. The average calcification rate was $0.97 \pm 0.04 \text{ g cm}^{-2} \text{ yr}^{-1}$ for females, and $1.24 \pm 0.03 \text{ g cm}^{-2} \text{ yr}^{-1}$ for males.

3.2 Skeletal isotope composition and environmental data

The $\delta^{18}\text{O}$ records of female and male coral colonies show a seasonal pattern (Fig. 1) that was strongly correlated between sexes ($r = 0.45$, $p > 0.000\,001$). $\delta^{18}\text{O}$ in female colonies, was higher than in male colonies (Fig. 1). The overall average $\delta^{18}\text{O}$ in female colonies was -2.89 ± 0.33 , and $-3.20 \pm 0.37\text{‰}$ in male colonies (Table 1). Overall, the $\delta^{18}\text{O}$ average of females is significantly higher than that of males ($t_{498} = 9.34$, $p > 0.000\,001$). $\delta^{18}\text{O}$ data of all colonies showed a “regime shift” of the mean in 2004, from -2.75 to -3.14‰ , with a regime shift index (RSI) of -0.69 ($p = 0.008$) in female colonies, and from -3.08 to -2.42‰ with a RSI of -0.65 ($p = 0.003$) in male colonies. This coincides with a regime shift in the rainfall mean of 2003, changing from 15.76 to 30.25 mm, with a RSI of 0.30 ($p = 0.01$).

$\delta^{13}\text{C}$ showed a cyclic pattern in female and male colonies (Fig. 2), that was correlated between both genders ($r = 0.19$, $p = 0.005$). The skeletal $\delta^{13}\text{C}$ of female colonies was lower than the skeletal $\delta^{13}\text{C}$ of male colonies (Fig. 2). The overall average of $\delta^{13}\text{C}$ in female colonies was -1.66 ± 0.38 , and $-1.38 \pm 0.37\text{‰}$ in male colonies (Table 1). The overall average of $\delta^{13}\text{C}$ in females is significantly lower than in males ($t_{498} = -8.01$, $p > 0.000\,001$). No regime shift was found in the $\delta^{13}\text{C}$ data of either sex.

The $\delta^{18}\text{O}$ skeletal data series corresponds to the SST (Fig. 1). Table 2 shows correlation coefficients between the $\delta^{18}\text{O}$ isotope data of coral colonies and environmental variables. The correlation coefficient between the isotope average time series data and SST was -0.45 ($p = 0.000\,003$) for female colonies, and -0.32 ($p = 0.000\,05$) for male colonies; the r to Z transformation showed that both correlation coefficients are equally strong ($Z = -1469$; $p = 0.07$). No significant correlation was found between the

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$\delta^{18}\text{O}$ skeletal data sets and the rainfall data. The $\delta^{13}\text{C}$ skeletal data series did not significantly correlate to any of the environmental data variables in any of the colonies (Table 3).

The relationship between $\delta^{18}\text{O}$ and satellite-derived SST for 13 years (1997–2009) was calibrated. The linear regression (Fig. 3) equations for $\delta^{18}\text{O}$ dependence on temperature were:

$\text{SST} = 7.0889 - 5.7193(\delta^{18}\text{O})(r^2 = 0.23, p = 0.00003)$ for female coral, and

$\text{SST} = 14.739 - 2.9246(\delta^{18}\text{O})(r^2 = 0.10, p = 0.00007)$ for male coral.

The annual range of $\delta^{18}\text{O}$ was the difference between the highest $\delta^{18}\text{O}$ measurement in January–March, and the lowest in July–September (1997–2008). The colonies had a small seasonal variation. The average amplitude was $0.37 \pm 0.15\%$ in female colonies, and $0.28 \pm 0.72\%$ in male colonies. Satellite data of SSTs had an average amplitude cycle of $7.85 \pm 0.77^\circ\text{C}$, and rainfall had an average annual amplitude of 3.55 ± 16.07 mm. Using the calculated gradients of $0.09\% \text{ } ^\circ\text{C}^{-1}$ for female colonies, and $0.10\% \text{ } ^\circ\text{C}^{-1}$ for male colonies, the average seasonal variation of $\delta^{18}\text{O}$ would reflect a temperature change of 4.11°C in female colonies, and 2.80°C in male colonies. This is 52.37% in female colonies, and 35.66% in male colonies of the seasonal range of the SST. The expected variation of approximately 0.11% of $\delta^{18}\text{O}$ in seawater (0.43 psu) is 29.72% in female colonies, and 38.53% in male colonies of the average seasonal variation in $\delta^{18}\text{O}$.

The departure from isotope equilibrium of our samples was estimated with the equations by Grossman and Ku (1986), for $\delta^{18}\text{O}$, and Romanek et al. (1992) for $\delta^{13}\text{C}$. We found that the theoretical $\delta^{18}\text{O}$ value of coral aragonite that precipitates at equilibrium with seawater is -0.65% , which means that our samples of coral have an average departure from isotope equilibrium of $\sim 3.54\%$ in females, and $\sim 3.80\%$ in males. For $\delta^{13}\text{C}$, we found a theoretical value of -1.15% for coral aragonite that precipitates at equilibrium with seawater. This means that average departure from isotope equilibrium is $\sim 2.81\%$ in females, and $\sim 2.53\%$ in males.

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3.3 Skeletal isotopic composition and skeletal growth

The analysis showed that high density bands are depleted in ^{18}O and ^{13}C , which are deposited during summer; low density bands are enriched in ^{18}O and ^{13}C , which are deposited during winter. In female colonies, a strong negative correlation between the mean annual coral $\delta^{18}\text{O}$ and skeletal density was found (Table 4; $r = -0.78$, $p = 0.001$) (Table 4). This suggests that denser skeletons are more depleted in $\delta^{18}\text{O}$, compared to less dense skeletons, and no significant correlation was found between $\delta^{18}\text{O}$ and other skeletal growth parameters in female colonies; no significant correlations between mean annual coral $\delta^{13}\text{C}$ and any growth parameters were found. In male colonies, there was a strong negative correlation between mean annual coral $\delta^{18}\text{O}$ and the linear extension and calcification rates (Table 4; $r = -0.50$ and -0.44 , $p = 0.045$ and 0.0008). This suggests that faster growing and calcifying colonies are more depleted in $\delta^{18}\text{O}$. No significant correlation was found between $\delta^{18}\text{O}$ and skeletal density in male colonies; no significant correlation between any coral growth parameter and mean annual coral $\delta^{13}\text{C}$ was found.

4 Discussion

Our isotope data showed a significant dependency of skeletal $\delta^{18}\text{O}$ on SST, with a low r (-0.45 in female coral, and -0.28 in male coral), and a gentle slope of the $\delta^{18}\text{O}$ –SST calibration equations ($0.09\text{‰}\cdot\text{°C}^{-1}$ F; $0.11\text{‰}\cdot\text{°C}^{-1}$ M; Fig. 3), compared with slopes ($> 0.20\text{‰}\cdot\text{°C}^{-1}$) in *Porites* spp. in other areas of the Pacific: the Great Barrier Reef (Gagan et al., 1994), Costa Rica (Carriquiry, 1994), Panama (Wellington and Dunbar, 1995), and the Galapagos Archipelago (McConnaughey, 1989). These studies show high correlation coefficients (better than -0.80) of $\delta^{18}\text{O}$ and SST. Our results are similar to studies reporting small correlation coefficients of $\delta^{18}\text{O}$ and SST (less than -0.70) and a gentle slope ($< 0.17\text{‰}\cdot\text{°C}^{-1}$) of the $\delta^{18}\text{O}$ –SST calibration equations, such as at

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Clipperton Atoll (Linsley et al., 1999), Fiji (Le Bec et al., 2000), and Guam (Asami et al., 2004).

Asami et al. (2004) suggest that the low correlation coefficient between $\delta^{18}\text{O}$ and SST, and the gentle slope in the $\delta^{18}\text{O}$ –SST calibration equations are related to small seasonal variations in SST ($< 3^\circ\text{C}$), or the greater influence of $\delta^{18}\text{O}_{\text{sw}}$. The seasonal variation in SST of our study area is $7.85 \pm 0.77^\circ\text{C}$, and the variation in $\delta^{18}\text{O}$ accounts for only 52.37% in female coral, and 35.66% in male coral, of the seasonal range, so the seasonal variation of SST is not likely to be the cause. Variations in $\delta^{18}\text{O}_{\text{sw}}$ represent 29.72% in female coral, and 38.53% in male coral, of the average seasonal $\delta^{18}\text{O}$ variation. We found a significant regime shift ($p < 0.01$) in the $\delta^{18}\text{O}$ data of colonies of both genders, that coincides with a regime shift ($p = 0.01$) in rainfall (which changes the $\delta^{18}\text{O}_{\text{sw}}$). We think that a greater influence of $\delta^{18}\text{O}_{\text{sw}}$ is the most likely source of our findings. This means that the $\delta^{18}\text{O}$ of coral in Bahía de La Paz is influenced more by the $\delta^{18}\text{O}_{\text{sw}}$ than in other places in the Pacific.

We found a positive relationship between skeletal $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ in our data, where $r = 0.42$ in females, and $r = 0.58$ in males. Swart et al. (1996b) suggest that this means that the maximum photoperiod in Bahía de La Paz occurs during winter (high $\delta^{18}\text{O}$ = low SST, high $\delta^{13}\text{C}$ = high photosynthesis). When the SST peaks in the summer and surface seawater generally becomes depleted of nutrients, zooxanthellae disperse (Hoegh-Guldberg, 1999; Barton and Casey, 2005). Hence, photosynthesis might be less intense until the nutrient-rich waters of winter promote the growth of zooxanthellae and restore photosynthesis intensity (Jokiel, 2004; Franklin et al., 2006).

Skeletal $\delta^{13}\text{C}$ (Fig. 2) was higher in both genders, between November and January (lowest SST and PAR), and lower from June through August (highest SST and PAR), suggesting a positive relationship between $\delta^{13}\text{C}$ and photosynthesis, and a dominant role of light-induced photosynthesis on seasonal changes of $\delta^{13}\text{C}$ in coral. Still, the $\delta^{13}\text{C}$ –PAR regressions and correlations were not significant, meaning that photosynthesis was not stimulated or inhibited by light, and remained near its maximum efficiency during the whole year, according to Sun et al. (2008), in *Porites* in southern

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China. They suggest that other factors may be affecting photosynthesis in addition to light, such as abundance of dissolved nutrients. High concentrations of chlorophyll *a* occurred during periods of relative enrichment of ^{13}C in the coral skeleton (November through January), when fixation by algae of the isotopically lighter carbon enriches $\delta^{13}\text{C}$ in coral skeletons (Allison et al., 1996); however, the correlations of skeletal $\delta^{13}\text{C}$ and chlorophyll *a* were not significant in any case.

Trends in coral skeletal $\delta^{13}\text{C}$ reflect seasonal variations in metabolic effects, that is, modifications of photosynthesis to respiration ratios in the $\delta^{13}\text{C}$ pool of coral. Higher coral respiration reduces coral $\delta^{13}\text{C}$ (McConnaughey, 1989; McConnaughey et al., 1997). Respiration normally increases with temperature and lowers ^{13}C in coral skeletons, which is reflected in our results, high SST = low $\delta^{13}\text{C}$. No other environmental variables considered in this work explained this pattern in coral $\delta^{13}\text{C}$, driven mainly by metabolic effects as described by Sun et al. (2008) in *Porites* coral of the South China Sea.

We found a negative correlation ($r = -0.78$, $p = 0.001$) between $\delta^{18}\text{O}$ and the skeletal density in female colonies, i.e. more dense skeletons are depleted in $\delta^{18}\text{O}$. This is not consistent with studies that have observed that coral skeletal high-density bands are enriched in ^{18}O (Klein et al., 1992; Al-Rousand, 2007). This may be due to a difference in timing of skeletal density bands in different *Porites* coral species, as described by Lough and Barnes (2000). In male coral, we found a negative correlation between the $\delta^{18}\text{O}$ and linear extension and calcification rates ($r = -0.50$, $p = 0.045$ and $r = -0.44$, $p = 0.0008$), meaning that the faster a colony grows and calcifies, the more it is depleted in $\delta^{18}\text{O}$. This is consistent with the observations of other authors of *Porites* spp. coral (McConnaughey, 1989; Felis et al., 2003). In *Porites* corals, SST is a dominating control of variations in growth parameters and of $\delta^{18}\text{O}$; the skeletal extension and calcification rate increases with SST, while skeletal density decreases (Lough and Barnes, 2000), so the growth parameters of both sexes and $\delta^{18}\text{O}$ behave as expected; that is, an increase in SST = a decrease in density = $\delta^{18}\text{O}$ enrichment in females, and an increase in SST = an increase in extension and calcification rate =

$\delta^{18}\text{O}$ enrichment in males. No significant correlation was found between skeletal $\delta^{13}\text{C}$ and skeletal growth parameters in either males or females, meaning that regardless of the skeletal extension rate, density or calcification rate, *P. panamensis* deposited a widely varying $\delta^{13}\text{C}$, as reported by Allison et al. (1996) in *Porites* coral from South Thailand, and by Swart et al. (1996b) in *Montastrea annularis* in Florida, USA.

General consensus states that all coral skeletons contain appreciable amounts of carbon and oxygen in isotopic disequilibrium, and are depleted in ^{18}O and ^{13}C because of kinetic variations due to differences in coral growth. Larger isotopic disequilibrium occurs when coral grows faster (Land et al., 1975; McConnaughey, 1989; Aharon, 1991). McConnaughey (1989) named this phenomenon “Vital effect”. We found this to be true for all sampled coral (disequilibrium = 3.54‰ F, 3.80‰ M in $\delta^{18}\text{O}$; 2.81‰ F, 2.53‰ M in $\delta^{13}\text{C}$). McConnaughey (1989) considers kinetic depletion as a constant in coral with fast extension rates ($> 0.5 \text{ cm yr}^{-1}$). The average yearly extension rates of all sampled coral were fast (1.05 cm yr^{-1} for females, and 1.27 cm yr^{-1} for males). Thus, we assume kinetic disequilibrium is constant in all coral.

All $\delta^{18}\text{O}$ ratios of female colonies are more enriched in ^{18}O than the ones in male colonies, with an average difference of ~ 0.31 ‰ (female average minus male average). Female $\delta^{13}\text{C}$ values were lower than the $\delta^{13}\text{C}$ of male colonies, with an average difference of ~ 0.28 ‰. All coral colonies in our study grew and calcified in the same environmental conditions (SST, $\delta^{18}\text{O}_{\text{sw}}$, PAR, chlorophyll *a*, etc.). Thus, differences in the isotope record between coral growing in the same environment are attributed to differences in the “Vital effect” of each colony (Linsley et al., 1999; Felis et al., 2003).

Linsey et al. (1999) found differences of 0.4‰ in the $\delta^{18}\text{O}$ records of six *Porites lobata* coral living in nearly identical environments (2 km of each other), in the Clipperton atoll. Felis et al. (2003) found a 1.28‰ difference in the $\delta^{18}\text{O}$ records of 11 coral of several *Porites* species (not detailed by the authors), in three sites in the northern part of the Gulf of Aqaba. None of the mentioned works considered the sex of the colony as a factor explaining differences in the “Vital effect” of coral colonies. If we pool the isotopic data of both sexes together, the differences between our isotopic records are

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duction in gonochoric spawners are lower than in gonochoric brooding species where energy is required not only for egg production, but also for larval development (Szmant, 1986). This implies that there should be sex-associated variations in the coral skeletal isotope data of other gonochoric brooding coral, as some massive *Porites* (which can be spawners or brooders; Glynn et al., 1994; Baird et al., 2009).

Considering $\delta^{18}\text{O}$ of coral skeletons is used to estimate SST in different sites and conditions, the next part of the discussion seeks to exemplify what would a difference in $\delta^{18}\text{O}$ between sexes would represent in terms of errors in SST estimation. Using the widely accepted paleotemperature equations for calcite (Epstein et al., 1953) and aragonite (Grossman and Ku, 1986), a $\sim 0.31\text{‰}$ difference between sexes would represent an error in SST estimates of $\sim 1.47\text{°C}$ and $\sim 1.33\text{°C}$. Using accepted SST–coral $\delta^{18}\text{O}$ relationships from different regions of the Pacific, derived from *Porites* spp., the $\delta^{18}\text{O}$ difference between sexes would represent an error of $\sim 1.75\text{°C}$ (Red Sea; Al-Rousand et al., 2003), $\sim 1.71\text{°C}$ (Great Barrier Reef; Gagan et al., 1994), $\sim 1.31\text{°C}$ (Costa Rica; Carriquiry, 1994), $\sim 1.39\text{°C}$ (Central and Eastern Tropical Pacific; Druffel, 1985), $\sim 1.47\text{°C}$ (The Galapagos; McConnaughey, 1989), and $\sim 1.47\text{°C}$ in SST estimates, for the commonly admitted paleotemperature calibration in coral ($0.21\text{‰}\text{°C}^{-1}$).

$\delta^{13}\text{C}$ of coral skeletons has been used as a proxy for the photosynthetic activity of zooxanthellae (mainly driven by light). Until now, no general rule applies to how much $\delta^{13}\text{C}$ means how much radiance (like the dependence of $\delta^{18}\text{O}$ to SST resulting in paleotemperature equations), but a difference of $\sim 0.28\text{‰}$ in coral $\delta^{13}\text{C}$ between sexes should be taken into account for this kind of applications, since it may influence the descriptions of the variability in $\delta^{13}\text{C}$ of coral skeletons. $\delta^{13}\text{C}$ of coral skeletons is also used to correct the $\delta^{18}\text{O}$ data when estimating the SST at which coral grew, by using the regression line equations obtained from the $\delta^{13}\text{C}$ vs. $\delta^{18}\text{O}$ plots (Smith et al., 2000). When we compared the regression line equations obtained from the $\delta^{13}\text{C}$ vs. $\delta^{18}\text{O}$ plots of both sexes, the ANCOVA showed that both the slope ($F_{498} = 9.619$, $p = 0.002$) and the y intercept ($F_{498} = 222.5$, $p < 0.00001$) are different between equations (Fig. 4.). Also, Fisher's r to z transformation ($z = -2.34$, $p = 0.01$) showed that the

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$\delta^{13}\text{C}$ vs. $\delta^{18}\text{O}$ correlation coefficients are significantly different between sexes, i.e. the relationship in $\delta^{13}\text{C}$ vs. $\delta^{18}\text{O}$ is different in both sexes; this has important implications because it could add a variability source to the use of the $\delta^{13}\text{C}$ vs. $\delta^{18}\text{O}$ regression line as corrector for $\delta^{18}\text{O}$ data, if the sex of the colony is not taken into account in the analysis.

This study provides evidence of sex-associated variations in coral skeletal $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of *P. panamensis*. This has some implications and has to be considered when climate conditions are estimated based on comparisons of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of gonochoric coral genera, if sex identification is not taken into account when possible.

Author contributions. R. A. Cabral-Tena and E. F. Balart conceived and designed the study; R. A. Cabral-Tena, A. H. Ruvalcaba-Díaz and A. Sánchez processed isotopically the material. R. A. Cabral-Tena, A. Sánchez, H. Reyes-Bonilla and E. F. Balart analyzed the data. All authors discussed the results and wrote the manuscript.

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Table 1. Summary of the overall average extension rate, skeletal density, calcification rate, $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of *Porites panamensis* colonies from Bahía de La Paz, Gulf of California.

Colony	Sex	Avg Ext (cm yr^{-1})	Avg Den (g cm^{-3})	Avg Cal ($\text{g cm}^{-2} \text{ yr}^{-1}$)	Avg $\delta^{18}\text{O}$ (‰)	Avg $\delta^{13}\text{C}$ (‰)
BLP32	F	1.06 ± 0.32	0.87 ± 0.04	0.88 ± 0.25	-2.94 ± 0.35	-1.66 ± 0.38
BLP33	F	0.94 ± 0.22	0.98 ± 0.01	0.93 ± 0.22	-2.88 ± 0.32	-1.65 ± 0.39
BLP36	F	1.05 ± 0.31	0.93 ± 0.04	1.03 ± 0.29	-2.89 ± 0.33	-1.67 ± 0.38
BLP40	F	1.10 ± 0.19	0.94 ± 0.02	1.03 ± 0.17	-2.87 ± 0.31	-1.66 ± 0.39
BLP31	M	1.21 ± 0.61	0.90 ± 0.08	1.21 ± 0.44	-3.19 ± 0.38	-1.39 ± 0.37
BLP34	M	1.35 ± 0.30	0.98 ± 0.04	1.33 ± 0.29	-3.25 ± 0.38	-1.37 ± 0.37
BLP35	M	1.59 ± 0.31	0.95 ± 0.01	1.61 ± 0.28	-3.19 ± 0.37	-1.39 ± 0.37
BLP37	M	1.28 ± 0.34	0.96 ± 0.03	1.23 ± 0.34	-3.21 ± 0.39	-1.39 ± 0.38
BLP38	M	0.83 ± 0.36	0.88 ± 0.02	0.75 ± 0.33	-3.19 ± 0.37	-1.39 ± 0.38
BLP39	M	1.39 ± 0.40	1.00 ± 0.02	1.40 ± 0.40	-3.18 ± 0.37	-1.38 ± 0.37
Avg F	F	1.05 ± 0.04	0.94 ± 0.01	0.97 ± 0.04	-2.89 ± 0.33	-1.66 ± 0.38
Avg M	M	1.27 ± 0.04	0.95 ± 0.01	1.24 ± 0.03	-3.20 ± 0.37	-1.38 ± 0.37

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Table 2. Correlation coefficients between skeletal $\delta^{18}\text{O}$ of *Porites panamensis* colonies and: Sea surface temperature, precipitation, photosynthetically active radiation and chlorophyll *a* from Bahía de La Paz. Bold numbers indicate significant ($p < 0.05$) correlations.

Colony	Sex	SST		Precipitation		PAR		chlorophyll <i>a</i>	
		<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
BLP32	F	-0.36	0.007	0.10	0.44	-0.41	0.02	-0.08	0.55
BLP33	F	-0.35	0.01	0.07	0.58	-0.40	0.03	-0.11	0.44
BLP36	F	-0.37	0.006	0.08	0.55	-0.42	0.02	-0.11	0.42
BLP40	F	-0.38	0.006	0.08	0.54	-0.41	0.02	-0.11	0.43
BLP31	M	-0.28	0.04	0.05	0.68	-0.36	0.05	-0.06	0.64
BLP34	M	-0.26	0.06	0.06	0.65	-0.31	0.09	-0.08	0.53
BLP35	M	-0.29	0.03	0.06	0.67	-0.36	0.05	-0.06	0.65
BLP37	M	-0.28	0.04	0.06	0.65	-0.34	0.06	-0.07	0.60
BLP38	M	-0.29	0.03	0.06	0.67	-0.36	0.04	-0.05	0.68
BLP39	M	-0.28	0.04	0.05	0.69	-0.36	0.05	-0.06	0.64

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Table 3. Correlation coefficients between skeletal $\delta^{13}\text{C}$ of *Porites panamensis* colonies and: Sea surface temperature, precipitation, photosynthetically active radiation and chlorophyll *a* from Bahía de La Paz. Bold numbers indicate significant ($p < 0.05$) correlations.

Colony	Sex	SST		Precipitation		PAR		chlorophyll <i>a</i>	
		<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
BLP32	F	0.19	0.17	−0.07	0.62	−0.11	0.54	0.10	0.45
BLP33	F	0.17	0.22	−0.04	0.73	−0.12	0.51	0.11	0.43
BLP36	F	0.17	0.22	−0.06	0.63	−0.16	0.38	0.09	0.51
BLP40	F	0.15	0.28	−0.07	0.62	−0.11	0.54	0.08	0.52
BLP31	M	0.005	0.97	−0.01	0.89	−0.33	0.07	0.24	0.08
BLP34	M	0.03	0.79	−0.02	0.86	−0.35	0.05	0.25	0.07
BLP35	M	0.01	0.93	−0.02	0.84	−0.35	0.06	0.26	0.05
BLP37	M	0.01	0.92	−0.01	0.93	−0.32	0.08	0.25	0.07
BLP38	M	0.003	0.98	−0.01	0.93	−0.32	0.09	0.25	0.07
BLP39	M	0.02	0.88	−0.02	0.88	−0.33	0.07	0.24	0.09

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Table 4. Correlation coefficients between skeletal extension rate, skeletal density and calcification rate, and skeletal $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of *Porites panamensis* colonies from Bahía de La Paz. Bold numbers indicate significant ($p < 0.05$) correlations.

Colony	Sex	Ext vs. $\delta^{18}\text{O}$		Den vs. $\delta^{18}\text{O}$		Cal vs. $\delta^{18}\text{O}$		Ext vs. $\delta^{13}\text{C}$		Den vs. $\delta^{13}\text{C}$		Cal vs. $\delta^{13}\text{C}$	
		r	p	r	p	r	p	r	p	r	p	r	p
BLP32	F	0.34	0.24	-0.81	0.001	0.31	0.23	0.42	0.14	-0.20	0.53	0.43	0.14
BLP33	F	0.37	0.22	-0.85	0.001	0.40	0.19	0.45	0.12	-0.11	0.71	0.39	0.23
BLP36	F	0.34	0.21	-0.78	0.003	0.41	0.17	0.41	0.11	-0.07	0.80	0.45	0.13
BLP40	F	0.40	0.18	-0.73	0.008	0.40	0.18	0.39	0.23	-0.09	0.74	0.37	0.26
BLP31	M	0.61	0.018	-0.13	0.69	-0.51	0.008	-0.26	0.35	-0.35	0.25	-0.38	0.21
BLP34	M	0.62	0.018	-0.19	0.53	-0.54	0.005	-0.28	0.35	-0.36	0.21	-0.33	0.24
BLP35	M	0.67	0.009	-0.16	0.63	-0.49	0.011	-0.30	0.29	-0.41	0.15	-0.32	0.29
BLP37	M	0.55	0.021	-0.20	0.48	-0.48	0.019	-0.38	0.21	-0.36	0.21	-0.29	0.34
BLP38	M	0.60	0.023	-0.15	0.58	-0.47	0.001	-0.24	0.35	-0.35	0.21	-0.24	0.34
BLP39	M	0.63	0.011	-0.24	0.39	-0.51	0.008	-0.25	0.34	-0.36	0.21	-0.28	0.35

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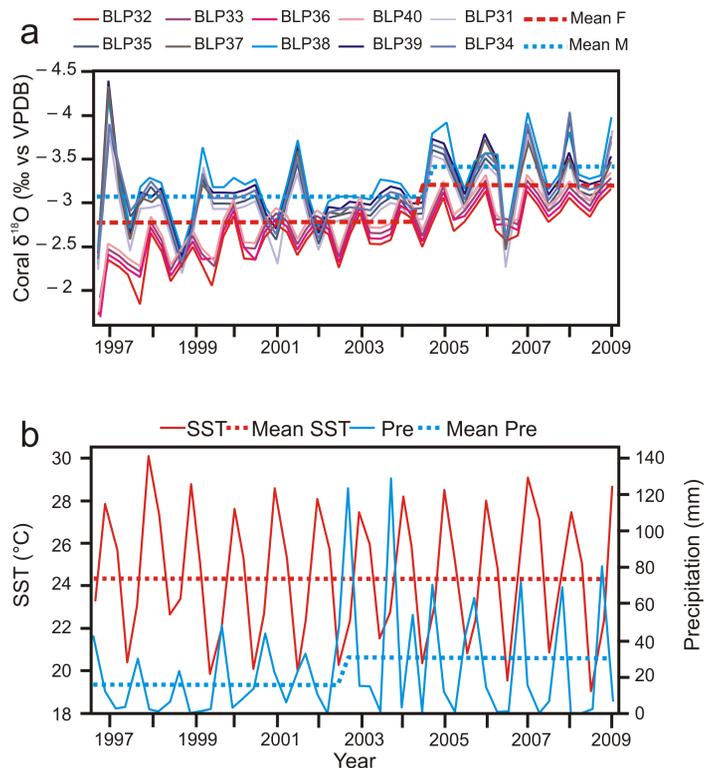


Figure 1. (a) Seasonal variation in $\delta^{18}\text{O}$ composition (VPDB) from *Porites panamensis* coral colonies along the major growth axis. Blue lines represent male colonies; Red lines represent female colonies; red dotted line female colonies' regime mean; blue dotted line, male colonies' regime mean. (b) Satellite sea surface temperature and precipitation (1997–2009) records. Sea surface temperature (red line; $^{\circ}\text{C}$), mean sea surface temperature (dotted red line; $^{\circ}\text{C}$), precipitation (blue line; mm), mean precipitation (dotted blue line; mm).

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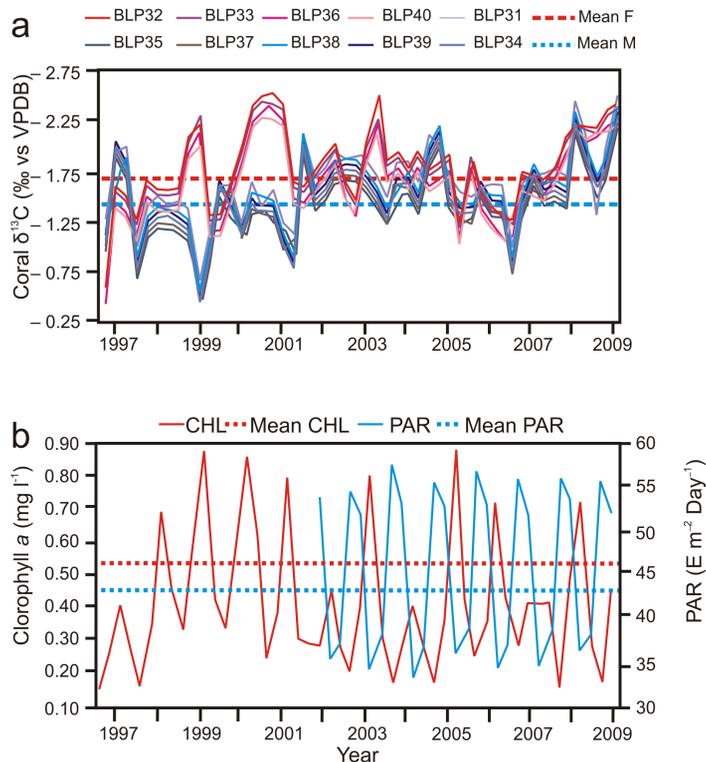


Figure 2. (a) Seasonal variation in $\delta^{13}\text{C}$ composition (VPDB) from *Porites panamensis* coral colonies along the major growth axis. Blue lines represent male colonies; Red lines represent female colonies; red dotted line female colonies' regime mean; blue dotted line, male colonies' regime mean. (b) Satellite chlorophyll a and PAR (1997–2009) records. Chlorophyll a (red line; mg L^{-1}), mean chlorophyll a (dotted red line; mg L^{-1}), photosynthetically active radiation (blue line; $\text{E m}^{-2} \text{ day}^{-1}$), photosynthetically active radiation (dotted blue line; $\text{E m}^{-2} \text{ day}^{-1}$).

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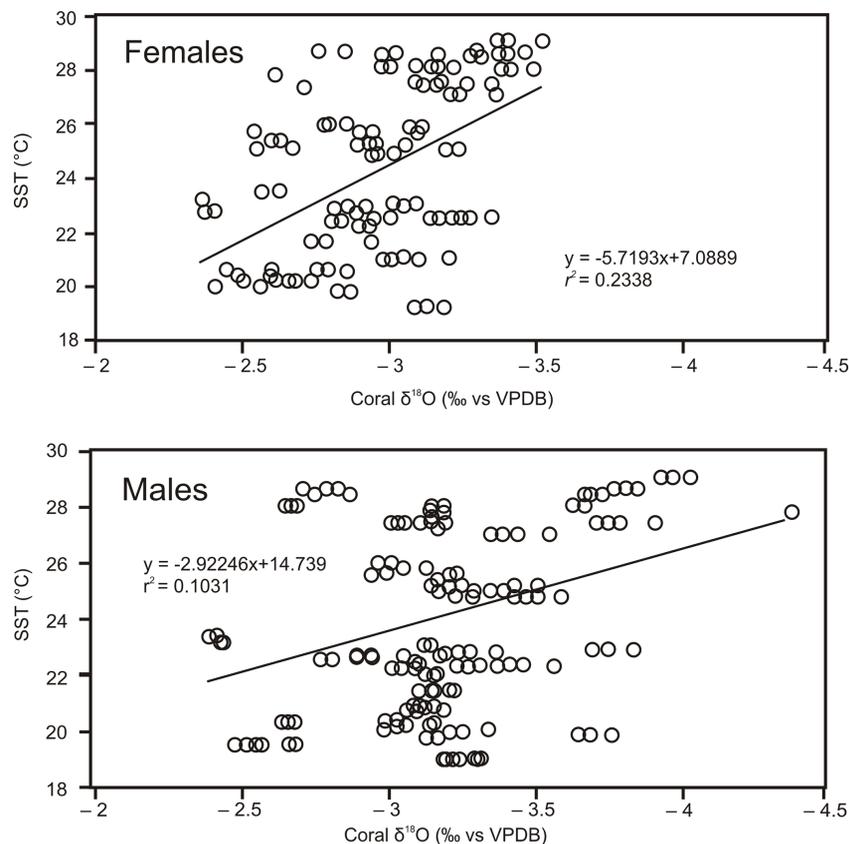


Figure 3. Linear regressions between satellite derived sea surface temperature (°C) and skeletal $\delta^{18}\text{O}$ (VPDB) of female, and male *Porites panamensis* coral from Bahía de La Paz. Line equations and coefficients are shown.

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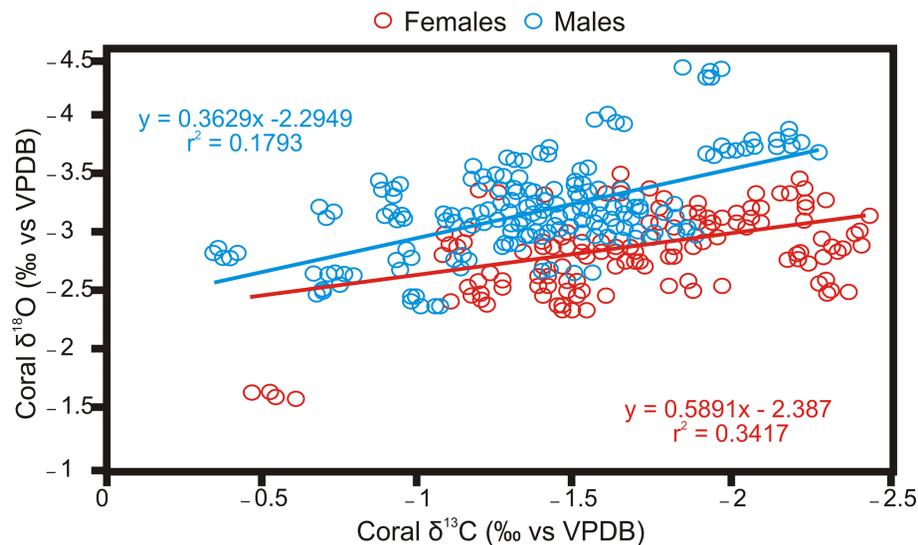


Figure 4. Plot of $\delta^{13}\text{C}$ vs. $\delta^{18}\text{O}$ of female (red dots), and male (blue dots) *Porites panamensis* coral from Bahía de La Paz. Line equations and coefficients (red represents females; blue represents males) are shown.

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