



FEATURE ARTICLE

Different calcification rates in males and females of the coral *Porites panamensis* in the Gulf of California

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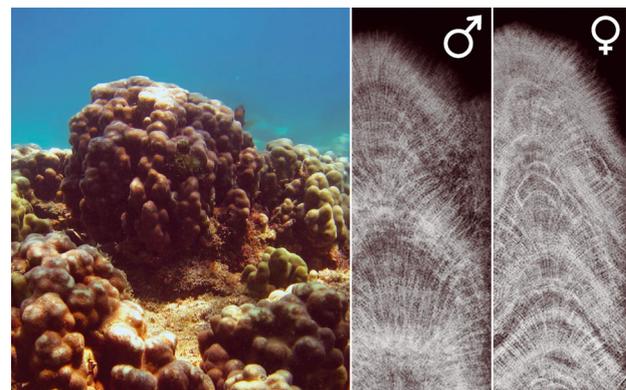
ABSTRACT: Density banding provides a record of performance of coral colonies over time and across environments, and offers 3 measurable variables: skeletal density, extension rate, and calcification rate. Skeleton formation is energetically expensive for corals and may be associated with other energy-dependent processes, such as reproduction. Egg production requires more energy expenditure than sperm production. Thus, calcification rate is hypothesized to be different for each gender. To evaluate differences in skeletal growth between males and females, we studied a gonochoric massive coral, *Porites panamensis*, from 3 regions of the Gulf of California. Colony sex was identified using histology methods, and growth parameters were measured using photo-densitometry of X-radiographs. Extension and calcification rates were significantly higher in male colonies than in females (by 18 to 23%) at 2 of our 3 study sites, while skeletal density was similar in both genders. Our results support the hypothesis of a gender bias in growth characteristics and suggest that environmental conditions may impact coral calcification differently in male and female colonies.

KEY WORDS: Coral growth parameters · Gender bias · High-latitude coral communities · Eastern Pacific

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INTRODUCTION

Sustained coral skeletal growth is a key determinant in the ecological success of scleractinian corals, as it gives corals the ability to compete for space and light



The coral *Porites panamensis* and X-radiographs of male and female colonies, from Bahía de La Paz, Gulf of California

Image: David A. Paz-García

in their natural environment and withstand the natural forces of biological and physical erosion (Lough & Barnes 2000). Measuring skeletal growth characteristics can give information about the general performance of corals over time and across different environments and regions (Lough & Barnes 2000, Lough & Cooper 2011). Skeletal growth has been measured on the basis of the annual density banding (Knutson et al. 1972). This density banding pattern (changes in bulk density, g cm^{-3}) provides historical information about 2 growth variables: annual skeletal extension rate (linear growth, cm yr^{-1}) and annual calcification rate (calcium carbonate deposition, $\text{g cm}^{-2} \text{yr}^{-1}$; Carricart-Ganivet 2007, Carricart-Ganivet & Barnes 2007). Density banding has allowed the identi-

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fication of natural variability in coral growth in relation to environmental gradients and the estimation and reconstruction of past environments and how they have affected coral growth (Barnes & Lough 1999). In addition, the thickness of the tissue layer of corals has been suggested to be a useful overall health and stress indicator of coral colonies (Barnes & Lough 1999), since it is known that it varies with sedimentation and nutrient availability (True 1995).

Coral growth is affected by environmental conditions such as sea surface temperature (SST), aragonite saturation (Ω_{ar}), sedimentation, and nutrient concentration (Lough & Cooper 2011), and measuring coral growth has become relevant as an indicator of possible degradation of coral reefs due to climate change (Kleypas et al. 1999a, Lough & Barnes 2000, Buddemeier et al. 2004, Manzello et al. 2008, Manzello 2010, Anthony et al. 2011).

In stony corals, calcification occurs in partial isolation from the surrounding seawater where corals can control the chemical conditions, including the carbonate chemistry and pH (Cohen & Holcomb 2009). Cohen & McConnaughey (2003) proposed that corals can modify their calcification region conditions due to active transportation of ions. This process pumps hydrogen ions out and transports calcium ions into the calcifying fluid, an energetically expensive process. Allemand et al. (2011) suggested that approximately 30% of a coral's energy budget is devoted to calcification. This implies that this process must be dependent on the tradeoff with other energy-demanding processes such as sexual reproduction (Leuzinger et al. 2003). For example, experiments in corals of the genus *Porites* that were exposed to steroidal estrogen hormones (associated with mass-spawning events) showed a reduction of skeletal growth rates and an increase in the thickness of the tissue layer (Tarrant et al. 2004). Thus, reproduction is hypothesized to affect growth rates, especially in coral species with a gonochoric reproductive strategy, such as *Porites* spp. (Baird et al. 2009, Kerr et al. 2010). As egg production has a higher energetic cost than sperm production (Hall & Hughes 1996), females would be expected to have lower growth rates. If this hypothesis is correct, the sensitivity and response to natural environmental changes that impact coral calcification may be different in male and female corals and could produce a bias in coral growth estimations as seen in laboratory experiments in *Astrangia poculata*, in which the growth rates of female colonies were more sensitive to environmental conditions (Holcomb et al. 2012).

The coral *Porites panamensis* has a wide latitudinal distribution along the eastern tropical Pacific, from

the upper Gulf of California (31° N) to Colombia (3° N; Reyes-Bonilla et al. 2007). This coral has extension rates from 0.4 to 1.0 cm yr⁻¹ along the Mexican Pacific and Costa Rica (Guzmán & Cortés 1989, Halfar et al. 2005). *P. panamensis* tolerates a wide range of environmental conditions, including low temperature and high-turbidity conditions that are often considered stressful for other coral species (Halfar et al. 2005). Regarding its reproductive strategy, this coral species is a known gonochoric brooder (Glynn et al. 1994, Carpizo-Ituarte et al. 2011, Rodríguez-Troncoso et al. 2011).

The Gulf of California is considered a marginal area for coral development (Kleypas et al. 1999b) due to the large seasonal temperature range, waters with high nutrients and turbidity due to upwelling events, and its naturally low pH, lower Ω_{ar} , and higher pCO₂ values than other oceanic areas (Manzello et al. 2008). These environmental variables vary along a latitudinal gradient, with more stressful conditions (i.e. higher seasonality and variability) in the northern section of the gulf (Glynn & Ault 2000, Glynn 2001).

In this study we (1) measured and compared the skeletal growth characteristics and tissue thickness in males and females of the massive coral *Porites panamensis* in 3 regions of the Gulf of California; and (2) estimated the relationships between growth parameters and environmental data of each region to assess whether the environmental influence on skeletal growth parameters is different in male and female colonies.

MATERIALS AND METHODS

Colony collection

Colonies of *Porites panamensis* were collected in 3 regions of the Gulf of California (Fig. 1): Bahía de Los Ángeles (BLA) located in the north (29° N, 113° W), Bahía Concepción (BCO) in the middle section (26° N, 111° W), and Bahía de La Paz (BLP) in the southern part (24° N, 110° W). Colonies were collected during the known reproductive period (March to July) of this species (Glynn et al. 1994, Carpizo-Ituarte et al. 2011, Rodríguez-Troncoso et al. 2011).

Ten colonies of *Porites panamensis* were collected per site (N = 30 colonies). The specimens were collected using hammer and chisel to remove the colonies from the substrate, and all colonies were sampled in water depths of 3 to 7 m. A fragment from each colony was fixed in Davison solution (Howard & Smith 1983) for subsequent histological processing and sex identification.

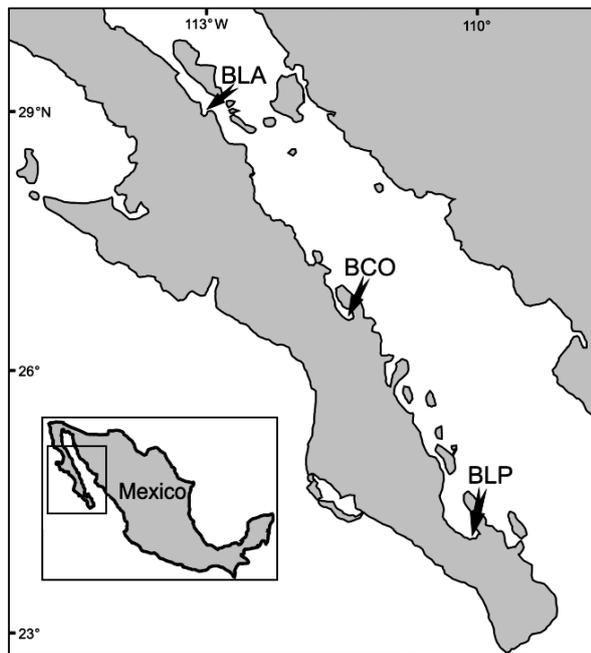


Fig. 1. Study sites on the west side of the Gulf of California. BLA: Bahía de los Ángeles, BCO: Bahía Concepción, BLP: Bahía de La Paz

Identification of sex

Histological techniques were used to identify the sex of each coral. Coral fragments were first decalcified for 24 h in a solution of 10% HCl with 0.7 g EDTA, 0.008 g sodium potassium, and 0.14 g sodium tartrate per liter (Glynn et al. 1994). The tissue was then immediately rinsed under running water until free of acid and subsequently placed in 70% ethanol until processed by conventional histological techniques (Humason 1979). Transverse sections of 8 μm thickness were obtained with a rotator manual microtome, and stained using hematoxylin and eosin. After staining, samples were observed using a microscope (Olympus BX50) to obtain descriptive records. Colonies were considered female if any planulae or oocytes were observed (regardless of their stage of development), and colonies were considered male if any spermatoocytes were observed on the slide.

Growth parameters

For each colony, 3 slices (7–8 mm thick) were cut along the major growth axis using a high-speed saw equipped with a diamond-tipped blade; 30 slices site^{-1} (i.e. 3 slices colony^{-1}) were obtained to measure growth parameters (90 slices in total). All slices were

air-dried and X-radiographed using digital mammography equipment (Senographe 600T, Senix HF, GE Healthcare). Exposures were at 36 kVp for 980 mAs and source-to-subject distance of 30 cm. An aragonite step-wedge was included on each X-radiograph as reference for the calculation of skeletal density. The step-wedge was built from 8 blocks cut from a shell of *Tridacna maxima*; each block had an area of 2.5 cm^2 and varied in thickness from 0.09 to 1.18 cm. The digitized images of the X-radiographs were used to measure growth parameters using the photodensitometry methods described by Carricart-Ganivet & Barnes (2007). Optical density tracks were measured in each slice along the vertical growth axis from digital pictures, using ImageJ 1.44 (<http://imagej.nih.gov/ij>).

Annual extension (cm yr^{-1}) was defined as the linear distance between adjacent density minima. Annual average density (g cm^{-3}) was defined as the average density of skeleton between adjacent density minima. Annual calcification rate ($\text{g cm}^{-2} \text{yr}^{-1}$) was obtained by multiplying the density value of each year by its corresponding skeletal extension (Carricart-Ganivet & Barnes 2007). All density bands were analyzed; 445 pairs of density bands (high and low density) belonged to males, and 264 pairs to females. Data from multiple slices were averaged to give average annual bands per colony ($N_{\text{total}} = 311$; 111 females, 200 males). In BLA, 134 density band pairs were analyzed (37 females, 97 males); in BCO, 74 density band pairs were measured (29 females, 45 males); and in BLP, 103 density band pairs were analyzed (45 females, 58 males).

Tissue thickness was measured in each coral slice ($n = 90$) using digital calipers. Data of tissue thickness were averaged per colony ($N_{\text{total}} = 30$). Six males and 4 females were measured in BLA; 5 males and 5 females were measured in BCO; and 6 males and 4 females were measured in BLP.

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 growth parameters between males and females. All comparisons were considered independent, and therefore no multiple comparison correction was applied to the data.

Environmental data

SST, salinity, and chlorophyll concentration (annual average, annual maximum, and annual minimum)

were obtained from the World Ocean Atlas 2009 (Boyer et al. 2009). Atmospheric CO₂ data were obtained from the Scripps CO₂ program, La Jolla, California, USA (Keeling et al. 2001). Total alkalinity was estimated using the equations proposed by Lee et al. (2006), and Ω_{ar} was calculated with the CO₂SYS computer software (Lewis & Wallace 1998). Pearson's correlation test and simple linear regressions were used to estimate relationships between mean growth parameters (skeletal extension rate, skeletal density, and calcification rate) of both sexes and environmental data. Correlations between growth data and environmental data were considered multiple comparisons tests; to avoid incurring a Type 1 statistical error, a sequential Bonferroni technique was used in all correlations (Rice 1989). The Fisher *r*-to-*z* transformation (Zar 2010) was used to assess the significance of the differences in correlation coefficients between mean growth parameters of both sexes and environmental data (average annual salinity, average annual Ω_{ar} state, average annual SST, average annual SST range, and average annual chlorophyll).

RESULTS

Coral colonies of *Porites panamensis* showed differentiated gametes, and all colonies from the 3 regions of the Gulf of California could be sexed. Sex proportions were 1:1.5 (female: male) in BLP, 1:1 in BCO, and 1:1.5 in BLA. The pooled sex ratio at each site was 1:1.3 ($\chi^2_1 = 0.4$, $p < 0.05$).

Average annual calcification and annual extension rate were significantly related in both genders. Average annual density was not significantly associated with annual average calcification or extensions rate. These relationships remained the same when data from both sexes were pooled (Table 1).

Growth parameters showed significant differences between male and female colonies when data were

Table 1. *Porites panamensis*. Correlation coefficients of female and male skeletal extension rates, calcification rates, and skeletal density. N: number of analyzed coral slices. **Bold** numbers indicate significant ($p < 0.001$) correlations after sequential Bonferroni correction

Sex/relationship	Males (N = 200)	Females (N = 111)	Both (N = 311)
Extension vs. calcification	0.98	0.97	0.97
Density vs. calcification	-0.05	-0.17	0.10
Extension vs. density	-0.18	-0.06	-0.01

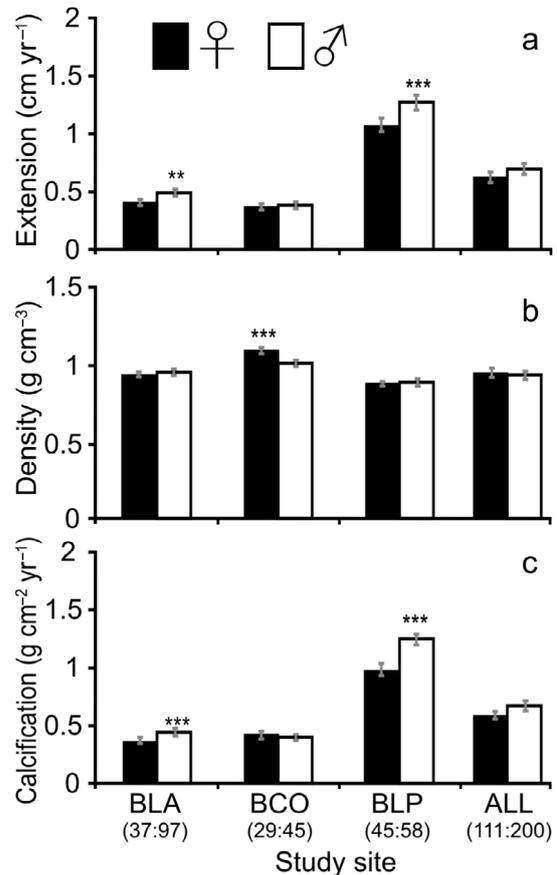


Fig. 2. *Porites panamensis*. Growth parameters at 3 locations on the west side of the Gulf of California: average annual (a) extension rate, (b) density, and (c) calcification rate. BLA: Bahía de los Ángeles, BCO: Bahía Concepción, BLP: Bahía de La Paz. Numbers in parentheses indicate pairs of density bands analyzed by site in females and males (♀:♂). Error bars are SE. ** $p < 0.01$, *** $p < 0.001$

analyzed separately at each site. Extension and calcification rates were significantly higher in male than in female colonies (by 18 to 23%), while skeletal density was similar in both sexes (Fig. 2). No differences in any of the skeletal growth parameters between males and females were found when all data were pooled ($p > 0.05$). In BLA, average skeletal extension and calcification rates were significantly higher in males than in females ($t_{133} = -3.50$, $p = 0.0006$; $t_{133} = -3.43$, $p = 0.0008$); while bulk skeletal density showed no differences between male and female colonies ($t_{133} = -0.03$, $p > 0.05$). In BCO, neither average extension rate nor calcification rate showed significant differences between genders ($t_{73} = -0.56$, $p > 0.05$; $t_{73} = 0.14$, $p > 0.05$); however, skeletal bulk density showed significantly higher values in females than in males ($t_{73} = 4.25$, $p < 0.0001$). In BLP, average

Table 2. *Porites panamensis*. Correlation coefficients between average calcification rate and environmental data for females and males. **Bold** numbers indicate significant correlations after sequential Bonferroni correction. SST: sea surface temperature

Environmental variable	Females (N = 111)		Males (N = 200)	
	r	p	r	p
Salinity	-0.96	<0.0001	-0.91	<0.0001
Aragonite saturation	0.86	0.0003	0.76	0.0003
SST	0.78	0.001	0.70	0.001
SST range	-0.76	0.002	-0.69	0.002
Chlorophyll	-0.56	0.03	-0.51	0.04
Depth	-0.45	0.12	-0.44	0.07

skeletal extension rate and calcification rate were significantly higher in males than in females ($t_{102} = -3.06$, $p = 0.002$; $t_{102} = -3.85$, $p = 0.0002$), but bulk skeletal density showed no differences between male and female colonies ($t_{102} = -0.52$, $p > 0.05$).

No significant differences in tissue thickness between males (0.46 cm) and females (0.44 cm) were found when data were pooled for all sites ($t_{29} = 0.40$, $p = 0.68$). When data were analyzed per site, no significant differences in tissue thickness between males (BLA: 0.52 cm; BCO: 0.36 cm; BLP: 0.48 cm) and females (BLA: 0.40 cm; BCO: 0.42 cm; BLP: 0.51 cm) were found (BLA: $t_9 = 2.36$, $p = 0.06$; BCO: $t_9 = -1.33$, $p = 0.22$; BLP: $t_9 = -0.57$, $p = 0.58$).

Comparison between growth parameters and environmental variables showed that calcification rate was significantly correlated (in order of importance and after sequential Bonferroni correction) with average annual salinity, Ω_{ar} , average SST, and annual range of SST (Table 2). Higher correlation values were found for females than for males. Significant correlations in both sexes were negative for salinity and SST range and positive for Ω_{ar} and SST (Table 2). Skeletal extension rate showed the same correlation trends as calcification rate. Skeletal density showed only significant correlations with average annual chlorophyll. It is important to note that Ω_{ar} covaries with SST and salinity, and therefore is correlated with these variables (Kleypas et al. 1999b).

Correlations between calcification rate and environmental variables showed that female colonies have higher correlation coefficients in comparison to their male counterparts (Table 2). However, the Fisher r -to- z transformation showed that only salinity and Ω_{ar} state correlations with calcification were significantly higher in females than in males ($z = -3.49$, $p = 0.0005$; $z = 2.48$, $p = 0.0131$).

DISCUSSION

Calcification is an energetically expensive process for corals, and approximately 30% of their energy is spent on calcification (Allemand et al. 2011). This process is affected by other events that deplete the energy available for the coral, such as reproduction (Leuzinger et al. 2003). Energy budgets of corals are not very flexible (Cohen & Holcomb 2009), and studies have suggested differences in energetic need for the production of gametes (egg versus sperm, Hall & Hughes 1996). Also, *Porites panamensis* is a brooding species, which means that larval development occurs inside the female polyps; thus, energetic costs of reproduction could be higher during brooding events because of the necessary energy diversion not only for egg production but also to secure larval development of planulae.

Based on the evidence presented above, we tested the hypothesis that corals show differences in growth rates depending on the sex of the colony and would produce lower calcification rates in females than males. In our study, growth parameters of *Porites panamensis* in the Gulf of California confirmed our hypothesis, since calcification and extension rates were lower in female than in male colonies at 2 of the 3 study sites (Fig. 2). Significant differences were not found in BCO corals. We suggest this could be because: (1) female colonies at BCO do not have the same reproductive effort as those from other sites (i.e. brief reproductive periods), giving them a wider energy budget to be able to match the extension and calcification rates of their male counterparts, or (2) environmental conditions at BCO limit the extension and calcification rates of both genders, not letting them fully develop as expected. BCO experiences several well described anoxia and upwelling conditions which lead to eutrophic waters and associated algal blooms (Mateo-Cid et al. 1993, López-Cortés et al. 2003, Ochoa 2003). These processes are known to interfere with successful coral development (Glynn & Ault 2000, Halfar et al. 2005, Lough & Cooper 2011). Differences in growth parameters between sexes were not observed when growth data were pooled for the whole region (Gulf of California). Growth parameters in corals are dependent on environmental conditions (Lough & Cooper 2011), thus, pooling different sites exposed to different environmental conditions may result in erroneous information. Therefore, further studies should consider these differences.

Variations in calcification rate were produced by variations in extension rate in both female and male

colonies (Table 1). These results indicate that *Porites panamensis* has the same growth strategy as massive *Porites* spp. in the Indo-Pacific and Atlantic Oceans, investing calcification resources into extension rather than density (Lough & Barnes 2000, Carricart-Ganivet 2007, Elizalde-Rendón et al. 2010). Sex proportions of *P. panamensis* found in this work corresponded to previously reported proportions in reproductive studies in the Gulf of California and west coast of Mexico (Rodríguez-Troncoso et al. 2011), and were also similar to those found in other areas of the eastern tropical Pacific, differing only from Costa Rica (2:1 males:females), although this proportion may be biased due to the small number of sampled colonies (Glynn et al. 1994).

Results of the Fisher *r*-to-*z* transformation showed that female colonies of *Porites panamensis* may be more sensitive to changes in salinity or Ω_{ar} of the oceans (i.e. acidification). Holcomb et al. (2012) found that under controlled laboratory conditions, elevated acidification conditions significantly reduced the relative growth (difference of buoyant weight of corals between the beginning and end of the experiment) of *Astrangia poculata* compared to growth under non-acidified conditions; the authors also found that female colonies of *A. poculata* showed slower growth and more sensitivity to acidified conditions. In our study, most female colonies grew slower and had lower calcification rates, and were more sensitive to some environmental conditions (including Ω_{ar}).

Tissue thickness was the same in both sexes at all study sites, indicating that coral colonies of both sexes were of similar health and that no evident stress conditions were affecting this parameter (Barnes & Lough 1999). Tissue thickness values were similar to the values recorded in the Great Barrier Reef (Lough & Barnes 2000) and slightly higher than those measured in other areas such as Papua New Guinea (Barnes & Lough 1999), the Gulf of Mexico, and the Caribbean (Elizalde-Rendón et al. 2010).

In order to calcify a 'healthy' skeleton, corals depend highly on their energy budget and assimilation. Corals can improve their energy assimilation by enhancing heterotrophic activity or photosynthetic activity of zooxanthellae, depending on environmental conditions (Cohen & Holcomb 2009), and thereby compensating for low calcification rates. However, this compensation ability could be restricted locally by food availability, which could also be affected by environmental conditions.

Under a hypothetical scenario of limited resilience, where scleractinean corals are exposed to increas-

ingly stressful environmental conditions, the first recognizable effect of an environmental stress would be a differential decrease in the calcification rate of corals. This would be more severe in female colonies due to different energy costs of reproduction. If stressful conditions are maintained, this could lead to a decrease in sexual reproduction of corals. Because female corals may have to adjust their energy budget to compensate for lower calcification rates, additional effects might be a decrease in the duration of reproductive periods or they could become more intermittent as seen in populations under high pollution pressure (Harrison & Wallace 1990). Finally, a change in sex proportions could be expected due to environmental selection for males, resulting in male-dominated communities as predicted by Holcomb et al. (2012).

This is the first study that provides evidence to support the hypothesis that coral calcification rate under natural environmental conditions is dependent not only on environmental variables, but also on colony sex. This phenomenon needs to be understood in order to better understand coral calcification rates and their relationship with the environment. Differences in gender responses to environmental stress should be explored to increase our understanding of coral reef ecosystems, and more research should be done to determine whether this gender bias in coral calcification rates occurs in other coral species and other relevant calcifying invertebrate groups. If gender differences in growth data are widespread across different coral genera, then it is important to note that paleo-reconstruction studies based on corals should identify colony gender at the time of core collection to help improve our understanding of paleo records.

Acknowledgements. We thank C. Rodríguez-Jaramillo and E. Meza-Chávez of CIBNOR for assisting us in the histological process. I. Fogel of CIBNOR provided editorial services. M. Cota and A. Aldana of CIBNOR assisted in the field and collection work, and C. Soto Carrasco of CIBNOR helped prepare the coral slices. We thank G. D. Danemann of Pronatura Noroeste, A.C., for his support in Bahía de Los Angeles. This manuscript was notably improved by the comments of J. Lough and 3 anonymous reviewers. This project was funded by project EP3 (CIBNOR), CT001 (CONABIO), and SEP-CONACyT (157993). R.A.C.T. (212435) and D.A.P.G. (160065) are recipients of student fellowships from CONACyT.

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*Submitted: August 17, 2012; Accepted: January 20, 2013
Proofs received from author(s): February 18, 2013*