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REPORT

Gender-related differences in the apparent timing of skeletal density bands in the reef-building coral *Siderastrea siderea*

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Abstract Density banding in skeletons of reef-building corals is a valuable source of proxy environmental data. However, skeletal growth strategy has a significant impact on the apparent timing of density-band formation. Some corals employ a strategy where the tissue occupies previously formed skeleton during as the new band forms, which leads to differences between the actual and apparent band timing. To investigate this effect, we collected cores from female and male colonies of *Siderastrea siderea* and report tissue thicknesses and density-related growth parameters over a 17-yr interval. Correlating these results with monthly sea surface temperature (SST) shows that maximum skeletal density in the female coincides with low winter SSTs, whereas in the male, it coincides with high summer SSTs. Furthermore, maximum skeletal densities in the female coincide with peak Sr/Ca values, whereas in the male, they coincide with low Sr/Ca values. Both results indicate a 6-month difference in the apparent timing of density-band formation between genders. Examination of skeletal extension rates also show that the male has thicker tissue and extends faster, whereas the female has thinner tissue and a denser skeleton—but both calcify at the same rate. The correlation between extension and calcification, combined with the fact that density banding arises from thickening of the skeleton throughout the depth reached by the tissue layer, implies that *S. siderea* has the same growth strategy as massive *Porites*, investing its calcification resources into linear extension. In addition, differences in tissue thicknesses suggest that females offset the greater energy requirements of gamete production by generating less tissue, resulting in differences in the apparent timing of density-band formation. Such gender-related offsets may be common in other corals and require that environmental reconstructions be made from sexed colonies and that, in fossil corals where sex cannot be determined, reconstructions must be duplicated in different colonies.

Keywords Extension rate · Calcification rate · Proxy environmental records · Sr/Ca

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Introduction

Knutson et al. (1972) discovered that the skeletons of some massive scleractinian corals show alternating high-density (HD) and low-density (LD) bands under X-radiography and that these two bands represent the corals' annual growth. Given that sea surface temperature (SST) is an important driver of calcification (e.g., Wórum et al. 2007), HD bands are associated with summer and LD bands are associated with winter. Nevertheless, annual density banding is dependent on the corals' growth strategy and skeletal architecture (Carricart-Ganivet 2007). In corals that have plocoid and solid skeletons, such as *Montastraea* and *Diploria*, density banding results from different amounts of thickening deposited over skeletal structures laid down at different times of the year, and HD-band deposition is immediate forming during the summer (Dodge et al. 1992; Helmle et al. 2000; Dávalos-Dehullu et al. 2008). However, in corals with porous skeletons, such as *Porites*, the coral tissue layer penetrates the previously formed skeleton, and the density banding arises from thickening of the skeleton throughout this layer. As a consequence, there is a difference between the actual and apparent timing of HD-band formation, which depends on the thickness of the tissue layer and extension rate, causing conflicting reports of seasonal-band dating (Taylor et al. 1993; Barnes and Lough 1996). In colonies of *Porites*, Barnes and Lough (1993) found a difference in the apparent timing of HD-band formation with an average 3 months, ranging from 1 to 8 months.

Understanding the strategies employed by corals and quantifying the apparent timing of density-band formation is important because the skeletal carbonate produced by these organisms contains a wealth of historical proxy climate and environmental information (Lough 2010). Proxy environmental data from corals are particularly important since other proxy recorders such as tree rings and ice cores poorly represent the tropics (Barnes and Lough 1993, 1996). Also, skeletal density banding provides historical information about mean annual skeletal density (bulk density; $gCaCO_3\ cm^{-3}$), annual extension rate (linear growth rate; $cm\ yr^{-1}$) and annual calcification rate (calcium carbonate deposition rate; $gCaCO_3\ cm^{-2}\ yr^{-1}$). The annual calcification rate is expected to be high when environmental conditions are optimal for skeletal accretion of $CaCO_3$.

This study investigates gender-related differences in the apparent timing of density-band formation in *Siderastrea siderea* (Ellis and Solander, 1786). This coral has recently been used to reconstruct past environments (e.g., Saenger et al. 2009; Castillo et al. 2011; Vásquez-Bedoya et al. 2012) because it has several qualities, such as low growth rates (1–8 mm yr^{-1}) and high longevity (>100 yrs), which make it a valuable resource as environmental proxy (Guzmán and Jarvis 1996; Guzmán and Tudhope 1998). It is a gonochoric reef-building species that spawns during summer (Szmant 1986) and inhabits shallow-reef environments around the Caribbean (Veron 2000). Forming dome-shaped colonies up to 2 m in diameter, the corallites of this species are cerioid with fenestrated theca that makes the skeleton porous (Cairns 1982). The results show that depending on gender, there is a ~6-month difference in the apparent timing of HD-band formation in *S. siderea*—a situation that could cause invalid interpretations of the proxy climate and environmental data contained within their skeletons.

Materials and methods

Sampling site and sex determination

Small tissue fragments (~2 cm^2) were broken from two adjacent colonies of *S. siderea* growing in ~3 m of water in Puerto Morelos Reef, northeast coast of the Yucatán Peninsula in the State of Quintana Roo, Mexico (20°50′N; 86°52′W). Histological techniques were used to determine the gender of each coral colony (Glynn et al. 1991). Fragments were fixed in 10 % buffered formalin and then decalcified in 5 % buffered formic acid. The tissue samples were dehydrated in a series of reagent alcohols (75, 85, 95 and 100 %), cleared in reagent grade xylene and infiltrated in paraffin. The tissue samples were sectioned longitudinally at 5 microns and mounted on positively charged glass microscope slides. The sections were then deparaffinized in xylene and brought to distilled water through a series of alcohols (100, 95, 85, 75 %) and then stained with the standard hematoxylin and eosin stain method and coverslipped. Sex determination of both colonies was made at Mass Histology Service, Inc., using microscopic differentiation of oocytes (female) and spermaries (male).

Bulk density

On August 6, 2009, cores were collected along the growth axis of the same colonies which were sampled for gender determinations, using a submersible underwater hydraulic drill fitted with a 7-cm-diameter, 60-cm-long diamond-bit core barrel. From the two cores, a 7-mm-thick slice was obtained using a rock saw equipped with diamond-tipped blade. The two slices were rinsed with freshwater, dried at 80 °C in a laboratory oven and X-radiographed using a conventional CGR X-ray source. X-ray films were digitized with a Kodak® DirectView Classic CR System at 75-dpi resolution. Included on X-radiographs, with each coral slice, was an aluminum bar, placed along the anode–cathode axis of the X-ray machine to correct for the heel effect, and an aragonitic wedge, cut from a shell of the giant clam *Tridacna maxima*. Along a track placed in the vertical growth axis observed in the digital X-radiograph of each slice, density was measured pixel-by-pixel (i.e., each 0.30 mm) using ImageJ 1.41 free software (http://rsbweb.nih.gov/ij/). A data series of absolute density versus distance was generated and dated backwards until 1993 for each slice following the densitometry from digitized images of X-radiographs methodology (Carricart-Ganivet and Barnes 2007).

Modeled coral-year density

Assuming that the coral-year starts in August (the month with the highest SST in the sampling site, i.e., from midsummer to the next midsummer; see Hudson et al. 1976), maximum and minimum density values for each year from 1993 to 2009 were identified on each density series. After that, interpolated data between maximum and minimum density values were calculated in order to get monthly density values for each year (assuming a constant sub-annual extension rate). Then, a cross-correlation analysis was conducted to assess whether there was a difference in the apparent timing of HD-band formation between both studied colonies. Finally, average monthly density values were calculated and a modeled coral-year density was achieved for each cored colony.

Sr/Ca

To confirm a difference in the apparent timing of HD-band formation between colonies, Sr/Ca measurements were conducted as follows: cores were further cut into sheets and cleaned in an ultrasonic bath and washed with milli-Q water. From 2003 to 2007 in both cores, a Merchantek micromill was used to remove point samples (i.e., not a continuous time series) from the exothecal wall associated with density peaks and troughs, along the growth axis in both density series cores (i.e., associated with the maximum and minimum density values for each year). For each density peak or trough, approximately 100 mg of powder was split into aliquots of ~70 mg for Sr/Ca analyses. Sr/Ca ratios were analyzed using a ThermoFinnigan Element II inductively coupled plasma mass spectrometer (ICP-MS) following the method of Rosenthal et al. (1999) at the mass spectrometry facility of the Department of Geology and Geophysics of Woods Hole Oceanographic Institution. The Sr and Ca measurements were done in parallel, and one standard solution was applied to correct matrix effects related to the interference of the different concentrations of calcium, according to the methodology of Schrag (1999). Precision for Sr/Ca measurements was ± 0.02 mmol mol^{-1} based on replicate standard analyses ($n = 73$). Each measured Sr/Ca value was positioned on its corresponding absolute density series (i.e., on the corresponding coral slice) coupling the distance from the top of the core to the point where each value was obtained.

Growth parameters and tissue thickness

With the information obtained from the cross-correlation analysis and the absolute density series, successive density maxima or minima were dated backwards from the time of collection. Annual linear extension was defined as the linear distance between adjacent density maxima or minima, and average annual density was defined as the average density of skeleton between adjacent density maxima or minima. For each sampled coral, measurements of mean annual density and annual extension rate were then made for each coral year from 1994 to 2008. The annual calcification rate was calculated as the product of the annual extension rate and the average density of skeleton deposited in making that extension (Dodge and Brass 1984). A *t* test for independent samples was used to assess statistical differences in density, extension rate and calcification rate between the two specimens.

The thickness (mm) of the living tissue layer was randomly measured at 10 positions along the outer edge of each slice with a caliper (Mitutoyo® Absolute Digimatic, 0.01 mm precision). A *t* test for independent samples was used to assess statistical differences in tissue thickness between the two specimens.

Sea surface temperature

A monthly mean SST data series from August 1993 to August 2009 was generated by the Meteorology and Oceanography Service of the Reef System Unit, ICMyL, UNAM, with near-daily measurements at a depth ~2.5 m, following the CARICOMP level I protocol (see Rodríguez-Martínez et al. 2010). Taking into account the month when the corals were cored, the SST series was superimposed on the two generated absolute density series from the coral slices in order to assess whether there was an offset of SST peaks and density peaks. From the entire SST series, averaged monthly SST was calculated and then superimposed on the modeled coral-year density of each slice.

Results

Microscopic observations revealed that both colonies of *S. siderea*, regardless of their developing stage, showed differentiated reproductive structures (oocytes and spermaries) and could be sexed. One of the cored colonies was a female and the other one, a male.

The contact print of the female specimen shows a low-density annual growth band at its apex; meanwhile, the male specimen shows a high-density annual growth band (Fig. 1). The absolute density series obtained from the female coral show that the maximum density values coincide with low SSTs, implying that the apparent timing of HD-band formation is in winter (Fig. 2a), whereas in the male, maximum density values coincide with high SSTs, implying that the apparent timing of HD-band formation is in summer (Fig. 2b). The difference of the apparent timing of HD-band formation between the female and male corals is confirmed by the cross-correlation analysis (Fig. 3a), which shows a 180-degree rotation between the two density series, denoting a ~6-month difference in the apparent timing of HD-band formation between the female and male

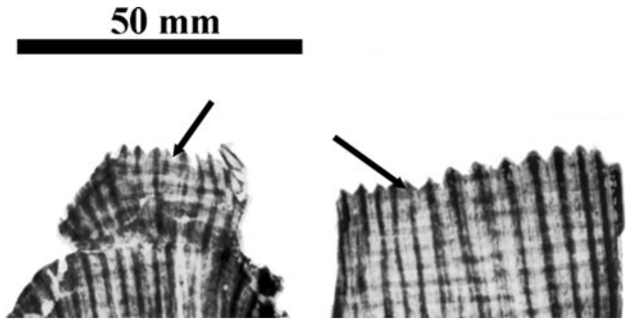


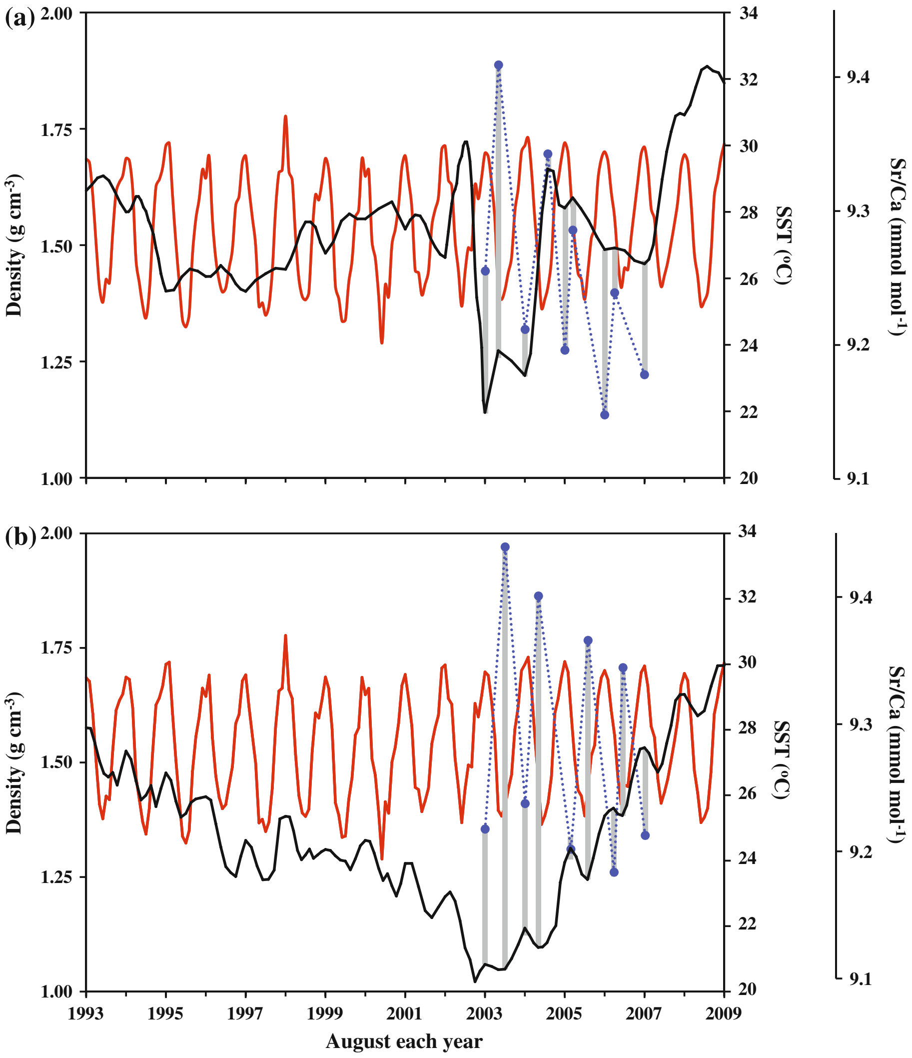
Fig. 1 Mammographic X-radiograph positives (contact prints) of the top of the *S. siderea* female (*left*) and male (*right*). Note that the female presents a low-density band at its apex, and the male, a high-density band (*arrows*). Contrast between high- and low-density bands in the contact prints was enhanced with Adobe Photoshop (Adobe Systems Incorporated, USA

($r = 0.79$, $P < 0.0001$). This is also visually evident when comparing the modeled coral-year density between the female and male (Fig. 3b).

A difference between male and female colonies was also found in the Sr/Ca data: the Sr/Ca value of each maximum density value in the female is higher than the adjacent minimum density values, whereas in the male, the Sr/Ca value of each maximum density value is lower than the adjacent minimum density values (Fig. 2).

Given these gender-related differences in apparent timing of HD-band formation, annual values of extension rate, density and calcification rate from 1994 to 2008 were compared between male and female colonies. Annual extension rate was significantly lower in the female than in the male (2.11 ± 0.65 and 2.88 ± 0.42 mm yr^{-1}, respectively; $t_{24} = 3.81$, $P < 0.0008$), mean density was significantly higher in the female than in the male (1.50 ± 0.10 and 1.32 ± 0.14 g cm^{-3}, respectively; $t_{25} = -4.06$, $P = 0.0004$), and there was no significant difference in annual calcification rate between both genders (0.32 ± 0.10 and 0.38 ± 0.08 g cm^{-2} yr^{-1} in the female and male, respectively; $t_{26} = 1.82$, $P = 0.08$). Thus, males extend faster whereas females form a denser skeleton, but they

Fig. 2 Absolute density series (*black lines*) and Sr/Ca sub-annual point values (*blue circles* connected by a *dotted line*) obtained from the *S. siderea* **a** female and **b** male, and monthly sea surface temperatures (*red lines*) from August 1993 to August 2009. Note that in the female, high-density bands coincide with low SSTs, whereas in the male, they coincide with high SSTs. *Vertical gray lines* connect the Sr/Ca values with maximum and minimum density values for each year between 2003 and 2007 (see text for details)



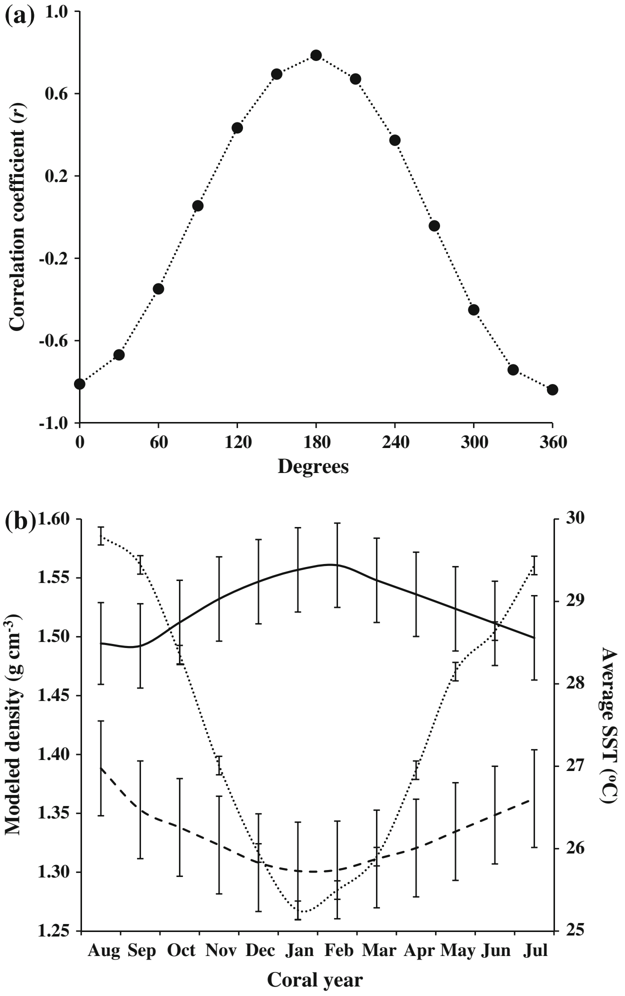


Fig. 3 **a** Correlation coefficient (*r*) values resulting from the cross-correlation analysis between the density series of the *S. siderea* female and male as a function of degree rotation. Note that 360° are equivalent to a coral year (i.e., from August to following August). **b** Modeled coral-year density of the *S. siderea* female (*continuous line*) and male (*dashed line*). Note the 6-month difference between the maximum density value in the female (February) and that in the male (August), which correspond with low- and high-average monthly sea surface temperatures (*dotted line*), respectively. *Error bars* are standard errors of the mean

both calcify at the same rate. A difference between genders also occurs in the tissue thickness (Fig. 4; Table 1), which is significantly lower in the female than in the male (4.27 ± 0.29 and 5.66 ± 0.30 mm, respectively; $t_{18} = 10.6$, $P < 0.0001$).

Regression relationships and correlation coefficients for these data (Fig. 5; Table 2) show that there is no significant correlation between extension rate and density (Fig. 5a; Table 2), and although there is a significant correlation between calcification rate and density in the female and male (28 and 70 %, respectively), its significance was not maintained when all data were pooled together (Fig. 5b; Table 2). There is a significant correlation, however, between calcification rate and extension rate in the two colonies of *S. siderea* when examined separately, with a high percentage of the variability explained for the data from the female and the male (98 and 81 %, respectively), as well as for all data pooled together (85 %, Fig. 5c; Table 2). In addition, coefficients of variability (SD as % of the mean, i.e., = [SD × 100]/mean) for extension rate were 15 and 31 %, and for calcification rate, 22 and 33 %, for the female and male, respectively. In all of these results, density was the most conservative variable in both the female and male, with coefficients of variability of 11 and 7 %, respectively (Table 1).

Discussion

The 6-month difference in the apparent timing of HD-band formation between male and female colonies found in this study is the first report of gender-related differences in skeletal density banding in reef-building corals. The fact that the two colonies of *S. siderea* grew next to each other implies that environmental variability is unlikely to be the cause of these results. It would be useful, however, to reproduce them experimentally or by collection of more colonies. Nevertheless, the gender-related differences in the point values of Sr/Ca data confirm that this 6-month difference is real and not a growth-related artifact (Fig. 2). It should be noted that these Sr/Ca values are not useful in deriving SST series or trends, since they are not a continuous time series (i.e., they are point samples of the HD and LD bands).

In massive *Porites*, Barnes and Lough (1993) and Taylor et al. (1993) concluded that differences in the apparent timing of HD-band formation depend on the depth reached by the living tissue layer in the skeleton (i.e., tissue thickness) and its extension rate. This is consistent with our findings in *S. siderea*, where both tissue thickness and extension rate were significantly lower in the female than in the male colonies (Table 1, Fig. 4). Given that density is more conservative than extension and calcification rates in both the female and male (Table 1), and that calcification and extension rates are significantly highly correlated (Fig. 5c; Table 2), it seems likely that *S. siderea* has the same growth strategy as massive *Porites* and invests its calcification resources into linear extension. It is widely reported that temperature is an important control in coral calcification rate (Clausen and Roth 1975; Vago et al. 1997; Marshall and Clode 2004; Edmunds 2005) and that calcification rate responds to the annual SST cycle, being higher in summer than in winter (Dodge and Brass 1984; Carricart-Ganivet 2007; Wórum et al. 2007). It follows that if calcification resources are invested into linear extension in *S. siderea*,

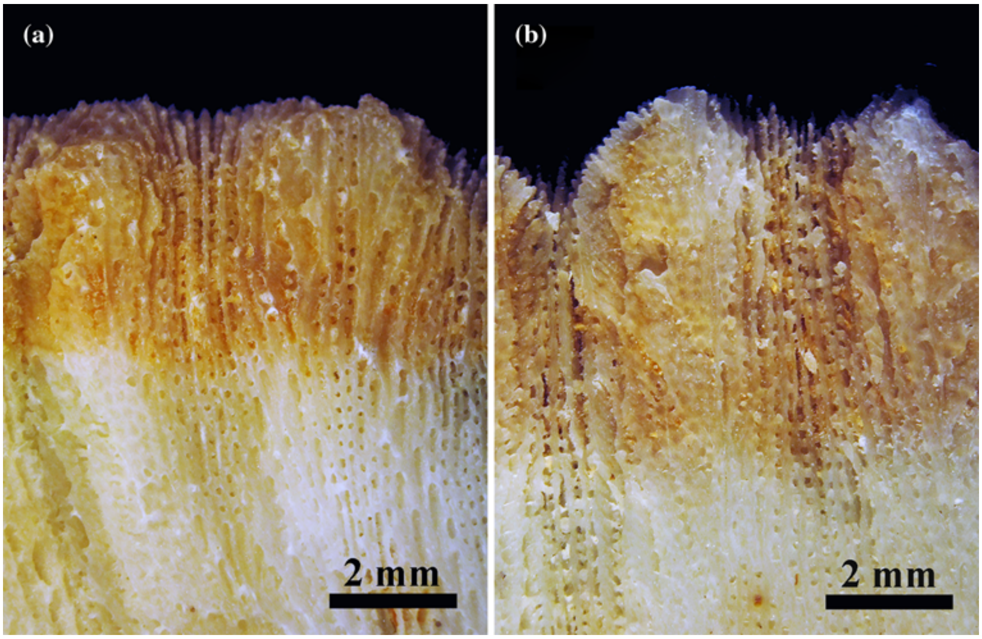


Fig. 4 Photographs of the longitudinal section of the core slices of *S. siderea* **a** female and **b** male. Note deeper penetration of living tissue layer (i.e., tissue thickness) in the male skeleton

Table 1 Extension rate, density and calcification rate per year, and mean tissue thickness in the female and male specimens of *S. siderea*

Years	Female			Male		
	Extension rate (mm yr^{-1})	Density (g cm^{-3})	Calcification rate (g cm^{-2} yr^{-1})	Extension rate (mm yr^{-1})	Density (g cm^{-3})	Calcification rate (g cm^{-2} yr^{-1})
1994	2.47	1.62	0.40	3.21	1.51	0.48
1995	2.35	1.53	0.36	3.21	1.46	0.47
1996	1.76	1.43	0.25	2.85	1.42	0.41
1997	2.82	1.43	0.40	2.83	1.33	0.37
1998	1.41	1.43	0.20	2.47	1.30	0.32
1999	2.82	1.51	0.43	3.53	1.32	0.47
2000	1.76	1.54	0.27	2.82	1.30	0.37
2001	1.06	1.56	0.17	3.18	1.27	0.40
2002	2.82	1.52	0.43	2.12	1.22	0.26
2003	2.73	1.53	0.42	2.82	1.12	0.32
2004	1.06	1.22	0.13	2.12	1.07	0.23
2005	2.47	1.49	0.37	3.18	1.15	0.36
2006	2.63	1.55	0.41	2.47	1.30	0.32
2007	1.41	1.48	0.21	3.18	1.44	0.46
2008	2.13	1.64	0.35	3.18	1.56	0.49
Mean ± SD	2.11 ± 0.65	1.50 ± 0.10	0.32 ± 0.10	2.88 ± 0.42	1.32 ± 0.14	0.38 ± 0.08
C.V. (%)	14.7	10.7	21.6	30.8	6.7	32.7
Mean tissue thickness ± SD (mm)	4.27 ± 0.29			5.66 ± 0.30		

SD standard deviation, *C.V.* coefficient of variability

extension rate must also vary during the year due to the SST cycle. As a consequence of this and of the porosity structure of its skeleton, it is probable that density banding in this species arises the same way as in massive *Porites*: from thickening of the skeleton throughout the depth reached by the living tissue layer.

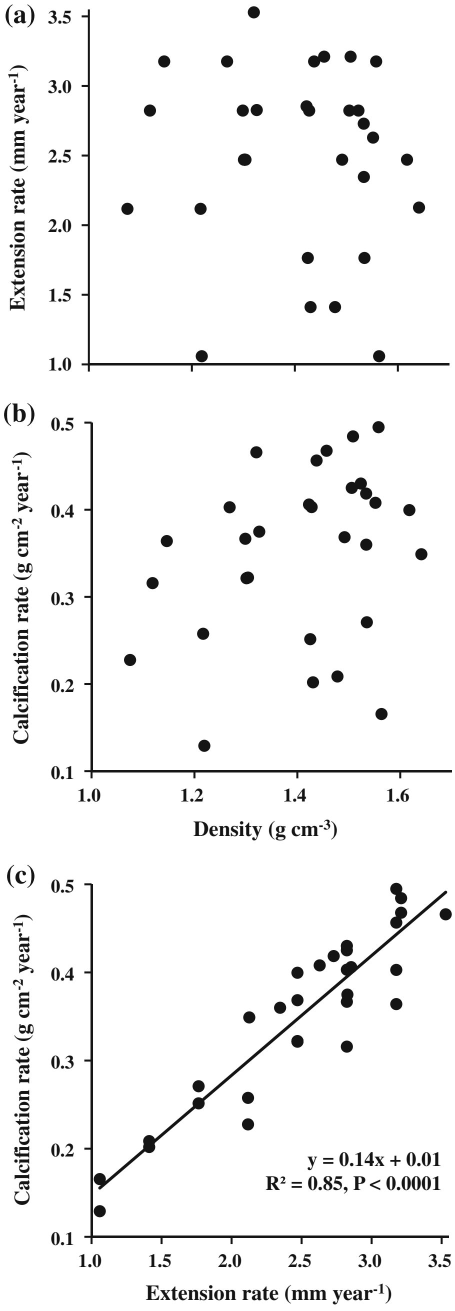


Fig. 5 Relationships between the three growth variables in *S. siderea*. **a** Extension rate versus density, **b** calcification rate versus density and **c** calcification rate versus extension rate. Regression line is shown for calcification rate versus extension rate since these are the only two growth variables significantly related

For massive *Porites*, Barnes and Lough (1993) conjectured that thickening at any point of the skeleton would be a function of the annual temperature cycle over the time the tissue resided at that point (which itself is a function of extension rate) and that the peaks and troughs generated in the annual density cycle would therefore correspond to high and low seasonal density banding. They calculated that the distance of a density peak or trough below the skeletal surface is half the depth of the tissue layer, and the apparent time difference (ATD) in months between the surface and the position of a peak or trough in skeletal density is given as follows:

$$\mathrm{ATD} = 12(0.5 \times \mathrm{TT}/\mathrm{ER}).$$

where 12 = number of months of a year, 0.5 = half-depth assumption, TT = tissue thickness, ER = extension rate.

Assuming that *S. siderea* has the same growth strategy and that the density-banding pattern in this species arises the same way as in massive *Porites*, Barnes and Lough's (1993) equation can be applied to the tissue thickness and mean extension-rate values for the female and male colonies of *S. siderea* studied herein. For the female colony, the ATD is 9 months, whereas in the male, it is 16 months, giving a 7-month difference. This difference is close to the 180-degree rotation, or 6-month difference, in the apparent timing of HD-band formation between the female and male density series (Fig. 3).

Although the female *S. siderea* colony had a lower extension rate and a higher density than the male colony, the results show there was no gender-related difference in calcification rate (Table 1). This is unexpected given that reproduction reduces energy available for calcification (Leuzinger et al. 2003) and that egg production needs more energy than sperm production (Hall and Hughes 1996). Nevertheless, several results are consistent with the finding of equal calcification between genders. First, a lower tissue thickness of the female *S. siderea* colony (Table 1) implies lower energy expenditure, and energy requirements of tissue production are known to be equivalent to gamete production (Leuzinger et al. 2003). Second, it is known that energetic costs of reproduction are lower in gonochoric broadcaster species, such as *S. siderea*, 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 gender-related differences in calcification in gonochoric brooding corals, such as some massive *Porites* (which can be broadcasters or brooders; Glynn et al. 1994), and the resulting differences in the apparent timing of HD-band formation. For example, Cabral-Tena et al. (2013) found that calcification rate is lower in females than in males of *P. panamensis*, a massive gonochoric brooder.

The consequence of such gender-related differences in the apparent timing of HD-band formation is particularly significant for environmental proxies derived from coral skeletal banding (see Barnes et al. 1995; Barnes and Lough 1996, for a detailed discussion). For example, it is known that Sr/Ca has a negative correlation with temperature (e.g., Shen et al. 1996) and that Sr/Ca paleothermometry overestimates changes in SST because their records are

Table 2 Correlation coefficients between extension rate, density and calcification rate of the cored female and male colonies of *S. siderea*

Growth parameter/gender	Female $n = 15$	Male $n = 15$	Both together $n = 30$
Density versus extension rate	0.41 (0.13)	0.52 (0.05)	−0.08 (0.69)
Density versus calcification rate	0.53 (0.04)	0.84 (0.0001)	0.30 (0.10)
Extension rate versus calcification rate	0.99 (<0.0001)	0.90 (<0.0001)	0.92 (<0.0001)

Probability values (P) in parenthesis

attenuated during skeletogenesis within the living tissue layer (Gagan et al. 2012). The fact that the apparent timing of HD-band formation also differs between gender in *S. siderea* and potentially other coral species adds a new factor that must be taking into account when reconstructing paleoenvironmental proxies using coral skeletons. For example, in the case of Sr/Ca time series performed on coral species with gender-related differences in apparent timing of density-band formation, such as in *S. siderea*, incorrectly assuming that the HD band corresponds to high temperatures in females (i.e., to summer) would result not only in an increased overestimation of SST in males, but in a positive correlation with temperature in females. This becomes particularly problematic in fossil colonies where gender determination is not possible and requires that records be collected from more than one coral.

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