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Uncertainty and variability of extension rate, density and calcification rate of a hermatypic coral (*Orbicella faveolata*)

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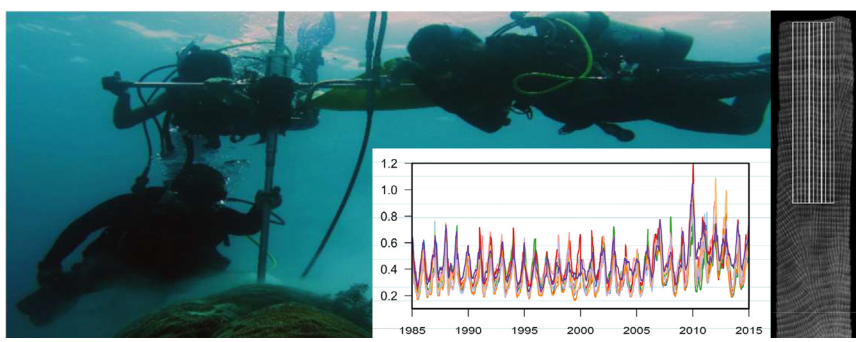
HIGHLIGHTS

- Hermatypic corals are widely used to reconstruct past environmental conditions.
- Uncertainties of all measurements were considered to calculate growth variables.
- The measurement uncertainty was small (<2%).
- Band variability was half of the overall variability (~30%).
- Coral growth variability must be considered for environmental reconstructions.

GRAPHICAL ABSTRACT



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ABSTRACT

Skeleton growth variables of hermatypic corals, such as extension rate, density and calcification rate, are widely used to study coral response to environmental stressors, establish chronological age models and reconstruct the evolution of key climate variables. In this work, we addressed methodological aspects of the measurement of coral growth variables and the implications of their variability. A core of *Orbicella faveolata* was collected from the Puerto Morelos coral reef, in the Mexican Caribbean, and we measured and analysed 10 parallel transects of a core slab, covering 30 years. Density calibration was performed by measuring a high-quality and well-characterised wedge of *Tridacna maxima*, and the interval of interest was adjusted to the measured coral optical densities. The measurement uncertainties of extension rate, density and calcification rate were 0.011%, 1.1% and 1.6%, respectively. However, for density and calcification rate, overall variability was 29% and 33%, respectively, of which about half was attributed to intra-band growth variability. The intra-band variability of extension rate was only 0.68%, indicating the suitability of extension rate as a precise environmental proxy. These results likely differ by coral species, environments and experimental conditions, such as the exact location of the core within the colony and the method used to determine density. Uncertainties of coral growth variables should be carefully considered when reconstructing past environmental conditions.

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1. Introduction

Hermatypic corals are colonial organisms, formed by polyps, that build aragonitic exoskeletons (Goreau and Goreau, 1959). The high density bands (HDB) of massive hermatypic corals are related to the warmer season, and their study allows us to obtain descriptors of skeleton growth, such as linear extension (Knutson et al., 1972; Barnes and Lough, 1993; Carricart-Ganivet et al., 2000). Hermatypic coral growth bands usually provide a clear chronological framework, and growth variables (extension rate, density and calcification rate) have been used to reconstruct the evolution of key environmental variables (Lough and Cooper, 2011), such as sea surface temperature (SST) (Lough and Barnes, 1997; Saenger et al., 2009; Vásquez-Bedoya et al., 2012), and identifying the response of corals to environmental stressors (De'ath et al., 2009). In *Orbicella*, banding and geochemical information contained in bands have been used to study past environmental changes (Dodge et al., 1993), mainly SST (Kilbourne et al., 2008; DeLong et al., 2011; Flannery et al., 2018), although the absence of long instrumental time series in tropical coasts complicates the interpretation of coral-based environmental records (Helmle et al., 2011).

The determination of coral growth variables, such as calcification rate, is commonly performed by sclerochronology based on X-ray images (Carricart-Ganivet and Barnes, 2007). Much work has been carried out to study the relation of coral growth with i) environmental variables such as SST, light, latitude, depth and distance to the coast (see the extensive dataset by Lough et al., 1999), and ii) biological characteristics such as colony, size, sex, morphology and species (Tortolero-Langarica et al., 2016a).

The uncertainties of coral growth variables are usually not well constrained, and should be considered to interpret coral-derived environmental records. In order to consider the inherent variability of the X-ray images, owing to the irregular shape and distribution of the corallites, many authors measure coral density along three different tracks (Tortolero-Langarica et al., 2016b), but the variability is seldom reported. To the best of our knowledge, this variability has not yet been quantified in most coral species. In this work, we carefully estimate measurement uncertainties of X-ray densitometry, and assess the variability of coral growth along multiple parallel transects in the same core. The proposed methodology is also useful to study the variability of coral growth in other colonies, species and environmental conditions.

2. Material and methods

2.1. Sampling

The Puerto Morelos reef is part of the Mesoamerican Coral Reef, in the Western Caribbean Sea and northeastern Yucatan peninsula (Fig. S1a), Mexico, and since 1998 it is a protected national park (Instituto Nacional de Ecología, 2000). The fringing reef conforms a coastal reef lagoon, rich in seagrasses (Rodríguez-Martínez et al., 2010). The lagoon (Fig. S1b) has an average depth of 3–4 m (maximum = 8 m) and has two connections to the open ocean: La Bocana to the north (length = 300 m, depth = 6 m), and a south navigational channel (width = 400 m, depth = 8 m; Coronado et al., 2007). The climate is tropical wet and dry savanna (Aw; Kottek et al., 2006), with a dry winter and wet summer. The region is prone to hurricanes during June–November. The mean monthly SST in the lagoon (1 m depth) showed minimum and maximum values of 24 and 31 °C, respectively (SAMMO-UNAM, 2018).

A core (2.3 m total length) of a single *O. faveolata* colony (BOC2) was collected in June 2016 from La Bocana (Fig. S1c, 20° 52.5′ N, 86° 51.0′O) by using a pneumatic underwater drill Tech 2000™, with a 10 cm diameter and 1 m length corer, following the maximum growth axis. In this site, *O. faveolata* is the most common species, with a mean coral coverage of 11% and 4 m mean height (CONANP, 2015). At the time of sampling, the colony top was at 6 m water column depth. The four coral core pieces retrieved were marked and immediately carried to the laboratory, washed with distilled water, carefully assembled and high quality digital images of the whole core were obtained (Canon PowerShot G13, at 1.3 m distance).

2.2. Sample preparation and analysis

A ~1 cm thick slab was cut with a rock saw from the core center, of which BOC2-L3 was selected for this work. The slab was exposed to X-rays (exposure parameters: 81 kV, 32 mA, 0.2 s) with a GE Hungay Rt. Medical Systems X-ray device at the Cancun Radiological Center. An aragonite wedge, of known dimensions and density, carefully prepared from a *Tridacnia maxima* shell, was also radiographed serving as a standard for density measurements (Fig. 1). The wedge was carefully built with flat surfaces and a constant slope, and its density was measured by the buoyancy method ($\rho = 2.826$ g cm^{-3}, reported by Carricart-Ganivet and Barnes (2007). The dimensions of the wedge, measured with a Vernier Calibrator (Mitutoyo CD-6″ CS), were length (l_0) = 10.713 cm and maximum height (h_0) = 1.380 cm, thus slope was 0.1288, corresponding to an angle of 7.340°. Wedge dimension uncertainties were <0.1% and were not considered in this work.

To correct for the X-ray intensity heterogeneity due to spherical spreading and heel effect, X-ray images were processed following the digital detrending method developed by Duprey et al. (2012). Growth variables were determined based on the optical densitometry technique (Carricart-Ganivet and Barnes, 2007). Optical density (OD) values were calculated with the open source image processing program ImageJ (Schneider et al., 2012). The OD values of the aragonite wedge standard were used to construct a calibration function, whose uncertainties were used to estimate density and calcification rate uncertainties. Growth variability was assessed by measuring OD along 10 parallel transects of the top core piece, which covered the last 30 years (1985–2015; Fig. 1). In this work, uncertainties are defined as 1 standard deviation.

2.3. Growth variables

Extension rates (X, cm yr^{-1}) were measured as the distance between HDB. Coral densities (D, g cm^{-3}) were calculated as the ratio of mass depth (M, g cm^{-2}), obtained through calibration with the aragonite wedge, and the measured slab thickness (T, cm) as:

$$D = \frac{M}{T} \tag{1}$$

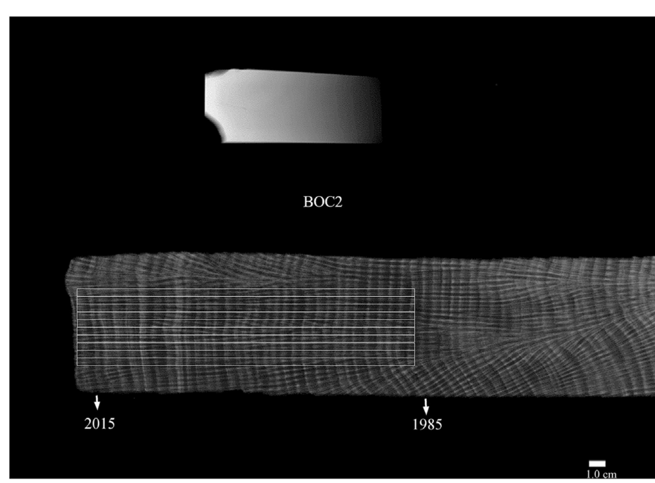

Fig. 1. Tracks selected for X-ray sclerochronology in core BOC2-L3, *O. faveolata*, La Bocana, Puerto Morelos, Mexico. Dark and light shading represents low and high density bands, respectively.

Finally, calcification rates (G, g cm^{-2} yr^{-1}) were calculated as the product of extension rates and densities. In terms of measured or calibrated magnitudes, calcification rates were calculated as:

$$G = \frac{X\,M}{T} \quad (2)$$

2.4. Measurement uncertainty and variability

In order to estimate growth variability, we first determined the measurement uncertainties of variables related to distance (extension rate and slab thickness), then derived wedge calibration uncertainties, and calculated density and calcification rate uncertainties with a Monte Carlo method. Finally, we analysed coral growth variability, based on the statistical analysis of 10 parallel measurement tracks on the core.

HDB were used both to establish the age model and to measure extension rates. OD plots were used to determine maximum OD, assumed to correspond to summer calcification (Dodge and Brass, 1984; Carricart-Ganivet, 2007), and annual extension was determined as the distance between two OD maxima. Thickness was carefully measured at each 1 cm along the mid track of the coral slice with a digital micrometer (Mitutoyo, IP65), with a nominal instrumental resolution of 1 μm.

Mass depths were calculated through calibration with the *T. maxima* wedge. Density and calcification rate uncertainties were estimated with a Monte Carlo method (with 5×10^5 iterations).

Growth variability was estimated from the statistical analysis of 10 parallel tracks along the measured slab with ImageJ (Fig. 1). The slab thickness was interpolated for each measured interval. The measured variables for each track and interval were the distance from an arbitrary origin and OD. The uncertainties of coral growth measurements caused by the variable coral structures and measurement uncertainties, were estimated for each measured interval (11,515 measurements).

In order to estimate the variability of density and calcification rates, we assumed that the extension rate was constant along each year. We calculated the ages of each measurement by dividing interval positions by the annual extension rate. Slab thickness was estimated from interpolation between bands, and the relative uncertainty was assumed to be constant. For each measurement interval (circa 10 days), we calculated mass depth with the wedge calibration (Eq. (4)), and estimated densities (Eq. (1)) and calcification rates (Eq. (2)). Uncertainties for these variables at all intervals were calculated with a Monte Carlo method (5×10^4 iterations per interval).

2.5. Extension rate and slab thickness uncertainties

The interval used to measure OD was 0.018 cm, which was assumed to be the instrumental resolution r of each measurement, which is equivalent to an uncertainty of $u = r/2\sqrt{3} = 0.005$ cm (ISO, 1993). Therefore, as the extension rate is the difference between to positions, the total uncertainty of X is $\sqrt{2}\,u = 0.007$ cm yr^{-1}. The mean annual extension rate in BOC2-L3 of 0.628 cm (300 measurements) corresponds to a 1.1% uncertainty, close to the uncertainties reported by Barnes and Devereux (1988) for *Porites* spp. An unknown uncertainty source for the extension rate is whether maximum calcification always occurs at the same time of the year, and further research is needed in this direction.

In order to estimate the thickness uncertainty, we measured 10 times the thickness of 20 bands along 2 tracks (40 bands, 400 measurements), and the mean relative uncertainty was 0.64%. This value is about 200 times larger than the instrument uncertainty, owing to the irregular geometry of the coral slab, and emphasises the need to estimate realistic uncertainties for thickness measurements. This value is sensibly lower than the uncertainty reported for *P. lobata* (>3%, Barnes and Lough, 1989).

2.6. Wedge calibration

We defined the wedge position origin ($x_0 = 0\,cm$) at the thick end of the wedge, so its height at a position x was:

$$h = h_0 - x\ \tan\left(\frac{h_0}{l_0}\right) \quad (3)$$

Wedge OD were calculated with the ImageJ software, and wedge mass depths were calculated as $M = D\ T$ (from Eq. (1)). As OD in BOC2-L3 ranged from 14 to 85, corresponding to wedge positions 6.1–10.1 cm, we constrained the calibration analysis to the positions 5.0–10.5 cm. X-ray images may show significant saturation at high mass depths, but this was not the case for this wedge at the irradiation conditions used. Although mass depth versus OD showed a significant linear relationship, a better fit was observed with a quadratic function ($R^2 = 0.995$, $p < 2.2 \times 10^{-16}$; Fig. S2) (Carricart-Ganivet and Barnes, 2007; Duprey et al., 2012), and the use of more complex functions was not deemed necessary. The small deviation from a perfect linear fit might be due to non-linearity of OD at high exposure or small wedge inhomogeneities. The calibration equation for the mass depth M was:

$$M\ (g\ cm^{-2}) = a + b\ OD + c\ OD^2$$
$$a = -(1.69 \pm 0.03)\ 10^{-1};\ \ b = (2.63 \pm 0.01)\ 10^{-2}; c = -(5.4 \pm 0.1)\ 10^{-5} \quad (4)$$

where all coefficients were highly significant ($p < 2 \times 10^{-16}$) and uncertainties are 1σ.

2.7. Density uncertainty

In order to estimate the density measurement uncertainty along the core, we used the mean OD observed in slab BOC2-L3 (OD = 30.5). This value was used to obtain the mass depth M (Eq. (4)), and then density D (Eq. (1)), with a mean slab thickness of 0.910 ± 0.006 cm. By using a Monte Carlo method (with 5×10^5 iterations) for the wedge calibration and slab thickness, the mean density was 0.640 ± 0.007 g cm^{-3}, i.e. only a 1.1% relative uncertainty. This small uncertainty is the result of adjusting the wedge calibration to the region of interest, and should be estimated for each X-ray image, as it depends on X-radiation sources, irradiation conditions and image quality. This value is lower than most reported density measurement uncertainties, which range from 2.4–5.0 (Barnes and Devereux, 1988; Duprey et al., 2012; Deveaux et al., 2017).

2.8. Calcification rate uncertainty

Calcification rate (G, Eq. (2)) can also be seen as the product of extension rate (X) and density (D). By using a Monte Carlo method, which now included the mean extension rate for BOC2-L3 (0.628 ± 0.007 cm), the mean G was 0.402 ± 0.006 g cm^{-2} yr^{-1}, i.e. a relative uncertainty of only 1.6% (Fig. S3). This number should be considered as a reasonable estimate of the measurement uncertainty of our methodology for a single point measurement, as it does not include the expected variability of OD for real coral samples. Also, G uncertainty depends on the specific details of each experiment, such as image quality, calibration and slab thickness determination. This uncertainty is lower than that obtained by gamma ray densitometry (Deveaux et al., 2017).

2.9. Variability of coral growth

The most common approach to study coral calcification is to use annual values of the variables, which are more reliable as HDB allow estimating with reasonable confidence annual extension rates, and thus the temporal framework. Optical density (OD) annual means were used to calculate mass depths, and these were used to calculate annual densities and calcification rates. Annual OD uncertainties were estimated as the standard deviation of measurements within each band for each track (mean number of measurements = 38 per year and track). The mean OD uncertainty was large (21%), owing to the variability of coral density within each year. Uncertainties of annual mass depths, densities and calcification rates were calculated with a Monte Carlo method (5 $\times$ 10^5 iterations). To show the variability and long-term trends, values were smoothed with a local polynomial regression fit (Cleveland et al., 1992; R Core Team, 2017).

3. Results

Densities and calcification rates for 10 parallel tracks along the BOC2 core are shown in Fig. 2. The overall 30 yr variability of these high time resolution records for density and calcification rates was 29% and 33%, respectively. The annual variability of density and calcification rates was 15% and 20%, respectively. These values were significantly larger than those corresponding to a single point measurement (1.1% and 1.6% for density and calcification rate, respectively), where OD variability was not considered, but logically lower than the high-resolution record, which included the inter-annual variability. Therefore, we estimated that the intra-band variability (i.e. that caused by the irregularities of single bands) was 12% for density and 16% for calcification rate, almost half of the overall variability.

The evolution of annual mean densities and calcification rates over the 30 years period are shown in Fig. 3. Density showed a significant but small increasing trend (slope = 0.0030 ± 0.0006 g cm^{-3} yr^{-1}, $p < 2\ 10^{-6}$), with fluctuations of non-well defined periodicity, and two maxima at the end of the record (2007 and 2013). Calcification rate showed values increasing since 2005, and a clear maximum in 2011–2012. A secondary maximum was observed in 2007, in agreement with the first density maximum at the end of the record.

4. Discussion

The use of coral exoskeletons as environmental archives requires a good knowledge of the uncertainties before sound interpretations can

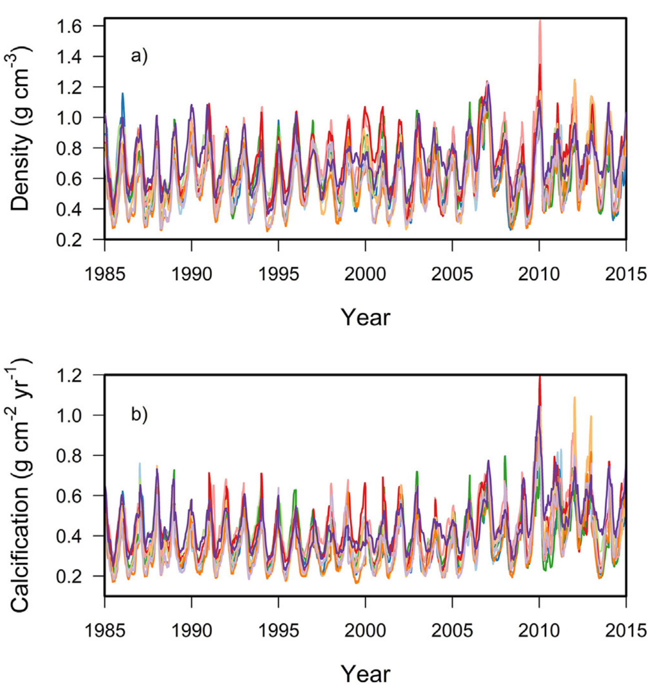

Fig. 2. Densities (a) and calcification rates (b) of 10 tracks in coral core BOC2-L3, *O. faveolata*, Puerto Morelos, Mexico. Time resolution is circa 10 days.

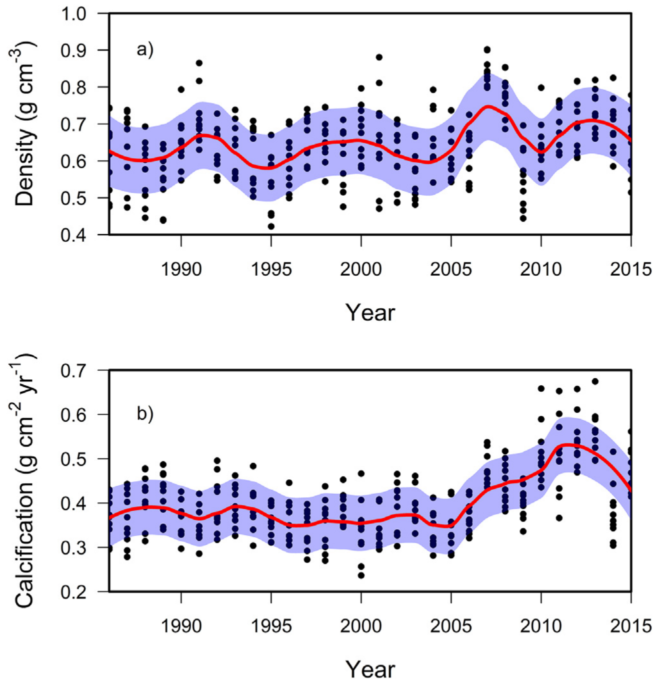

Fig. 3. Annual mean densities (a) and calcification rates (b) of 10 tracks in coral core BOC2-L3, *O. faveolata*, Puerto Morelos, Mexico. The red line is a local polynomial regression fitting, and the shaded area covers the 95% confidence interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

be provided. While the uncertainties of most geochemical proxies are rather well-constrained, this is not usually the case for coral growth variables, such as density, extension and calcification rate. By using the described procedure, the measurement uncertainty of extension rate, density and calcification rate was only 0.011%, 1.1% and 1.6%, respectively. These values are lower than those reported by Duprey et al. (2012; 3.32% for density), likely because of the different species studied (*Porites* sp. and *Siderastrea siderea*, with *T. squamosa* wedges) and overall experimental setup and conditions.

In BOC2-L3, the overall variability of density and calcification rates (Fig. 2), calculated from the analysis of 10 adjacent tracks parallel to the growth axis (Fig. 1), was high (29% and 33%, respectively) (Fig. 2). This variability could be attributed to a large number of causes, including environmental changes and the micro and macro-structure of the specific species and colony studied. A great deal of information on environmental processes can be obtained from such high temporal resolution records, which will be subject to further investigation.

Annual extension rates were directly determined and annual records of density and calcification rates were also obtained for the 10 studied tracks. A fundamental question is whether the selection of different tracks for measurement can bias the results and, consequently, the record interpretation. The mean variability of extension rates was only 1.1%, suggesting that the selection of contiguous tracks did not affect this variable in our core, and could be and excellent proxy of environmental processes. When annual means were considered, the variabilities of density and calcification rates were only 15% and 20%, respectively. Therefore, we concluded that the variability of density and calcification attributable to band irregularities was 12% and 16%, respectively, i.e. almost half of the overall variability. These values can be compared with laboratory measurements for *Pocillopora* spp., which were found to be similar for density (11%) and larger for calcification rate (17–23%; Tortolero-Langarica et al., 2017b).

Intra-band variability reflects the observed variability in the X-ray images of the skeleton structures, notably the individual corallites. One must bear in mind that variability largely depends on species, colony, site and the experimental conditions used, as also observed in computer tomography (DeCarlo, 2017). Intra-band variability should be taken into account when growth variables are used to study past environmental conditions. The use of multiple tracks (or the extension of the surface of the analysed image) is recommended to significantly reduce the variability inherent to band inhomogeneities. Whether OD measurements of individual corallites would improve the uncertainties of density and calcification rates, should be further investigated.

The observed large intra-band variability does not preclude to successfully reconstruct and quantify past environmental processes, such as those that could be inferred from Fig. 3, with a maximum value at the end of the period. In fact, the high resolution record of density and calcification rates (Fig. 2) is certainly consistent, and a careful examination might lead to inferences of density and calcification rates changes, likely linked to changing environmental conditions and biological factors. However, statistical analysis used to make inferences should always include an estimation of coral growth variability, for example along a horizontal track of each slab. Although individual coral cores might provide somewhat different records than those of neighboring colonies, we believe that major features and trends should be recorded in different cores from a particular location, or even region (Tortolero-Langarica et al., 2017a).

5. Conclusions

We described the methodology used to measure extension rates, densities and calcification rates in a core of *O. faveolata* collected from the Puerto Morelos coral reef, Mexico, with emphasis on the estimation of uncertainties and variability, which are usually poorly constrained. The measurement uncertainty for extension rate, density and calcification rate were low (0.011%, 1.1% and 1.6%, respectively). Overall variabilities of density and calcification rates estimated from 10 parallel tracks of the same core were much higher (29% and 33%, respectively), of which nearly half can be attributed to intra-band variability. The variability of density and calcification rate is dominated by OD variability, inherent to the X-ray image variability caused by the coral macro and microstructures. Further investigation is needed to reduce this uncertainty, such as working with larger analysis surfaces of each coral slab.

Skeleton growth uncertainties should be taken into account when performing environmental reconstructions from coral cores. Although coral growth variability should not preclude the successful reconstruction of past environmental conditions, it should be carefully considered when making statistical inferences.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.08.397.

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