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SPECIALTY SECTION

This article was submitted to
Coral Reef Research,
a section of the journal
Frontiers in Marine Science

RECEIVED 14 November 2022

ACCEPTED 07 April 2023

PUBLISHED 25 April 2023

CITATION

Jordán-Garza AG, Blanchon P,
Carricart-Ganivet JP and
Jordán-Dahlgren E (2023) Lower skeletal
extension in Pleistocene *Orbicella*
(*Montastraea*) corals than in their modern
counterparts.

Front. Mar. Sci. 10:1098430.

doi: 10.3389/fmars.2023.1098430

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Lower skeletal extension in Pleistocene *Orbicella* (*Montastraea*) corals than in their modern counterparts

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Introduction: Despite warmer conditions during the Last Interglacial, coral colonies of *Orbicella* were abundant and reached large sizes on many Caribbean reefs, including the extinct *O. nancyi*.

Methods: To explore variation in growth rates, we examined the yearly mean linear extension of growth bands in two fossil *Orbicella* species and compared them with two modern species of the same genus from shallow waters of the wider Caribbean. We measured the linear extension of corals exposed in a fossil reef and their modern counterparts, from both *in situ* colonies and coral slab X-rays.

Results: Few coral colonies showed autocorrelation or a linear trend on their linear-growth time series. A Bayesian ANOVA showed lower linear-extension rates of fossils compared to modern colonies and similar or lower than other fossil corals from the Pleistocene. Growth rates and growth form contribute significantly to the amount of tissue and size of coral colonies and can be a decisive trait for inter and intra specific competition.

Discussion: It is unlikely that temperature or interspecific competition explain modern coral extension rates and the low rates of the fossils data, which seem to be controlled instead by past habitat conditions.

KEYWORDS

Pleistocene, coral reef, fossil corals, *Orbicella nancyi*, coral extension rates

1 Introduction

Each year, corals of the Western Atlantic genus *Orbicella* (formerly *Montastraea*) deposit a skeletal band composed of high and low-density portions of calcium carbonate (Highsmith, 1979; Barns and Lough, 1993). The width of each band (linear extension) varies between years and is sensitive to natural and anthropogenic environmental changes (Buddemeier et al., 1974; Carilli et al., 2010; Rico-Esenaro et al., 2019). For example, changes in time series of the linear extension of *Orbicella annularis* at various sites in Puerto Rico correlated positively with water temperature (Dodge, 1981), and at the East Flower Gardens Bank, *O. annularis* extension rates varied inversely with annual discharge of the Atchafalaya river (Dodge and Lang, 1983). Mean linear extension value and variability depend on (i) the size of the coral colony and the length of the sampled time series, (ii) genetic differences between colonies (Osinga et al., 2011), and (iii) acclimation to the environment (Castillo et al., 2011; Groves et al., 2018). Furthermore, under moderately adverse conditions, species of *Orbicella* avoid a loss in linear extension by decreasing skeletal density (Dodge and Brass, 1984; Carricart-Ganivet and Merino, 2001). However, if conditions are severe enough, the mean linear extension is depressed (Dodge and Thomson, 1974; Dodge and Brass, 1984). The mean linear extension of *Orbicella* spp. can decrease with increasing temperature (Carricart-Ganivet, 2004), low light due to water turbidity and depth (Hubbard and Scaturo, 1985; Huston, 1985), sedimentation (Dodge et al., 1974; Torres, 2001; Carilli et al., 2009) and water quality (Dodge and Brass, 1984).

Several studies have examined the mean linear extension of fossil corals and made ecological and environmental inferences. For example, Gischler et al. (2009) reported a lower-than-present mean linear extension in massive Pleistocene *Orbicella* corals from lagoonal environments in Florida. They mentioned higher temperature as a probable cause during the Last Interglacial (LIG) which lasted ~10 ka (~130 to 120 ka). This interval was characterized by enhanced summer insolation that forced large polar deglaciation, leading to a reduced latitudinal temperature gradient and a higher sea level (Stirling et al., 1998; Denton et al., 2010). These conditions favored the extensive development of coral reefs as tropical waters expanded polewards and warm seas transgressed further across shallow shelves (Greenstein and Pandolfi, 2008; O’Lear et al., 2008; Blanchon, 2010; Kiessling et al., 2012). At that time, species richness in the Caribbean was slightly higher than present (Budd et al., 1994; Budd, 2000) and the *Orbicella annularis* species complex included three extant species, as well as a columnar form, and the organ-pipe *Orbicella nancyi* (Pandolfi, 2007). *O. nancyi* was widely distributed in shallow waters of San Andrés, Barbados, Lesser and the Greater Antilles, and Curaçao (Geister, 1977; Pandolfi and Jackson, 2001; Pandolfi et al., 2002). Pandolfi et al. (2002) proposed that the now-extinct *O. nancyi* had a high linear extension and that other species of *Orbicella* reduced their linear growth when this coral was present.

To investigate the extent to which environmental or ecological factors control on linear extension, we compared rates in massive and columnar species of *Orbicella* from a 125 kyr-old reef deposit at Xcaret, Quintana Roo, México (Jordán-Dahlgren, 1997; Blanchon et al., 2009; Blanchon, 2010), with two modern *Orbicella* species from shallow

habitats of the wider Caribbean. We assess autocorrelation and linear trends of the coral’s time series and mean differences within and between fossil species in Xcaret and modern *O. faveolata* and *O. annularis*.

2 Materials and methods

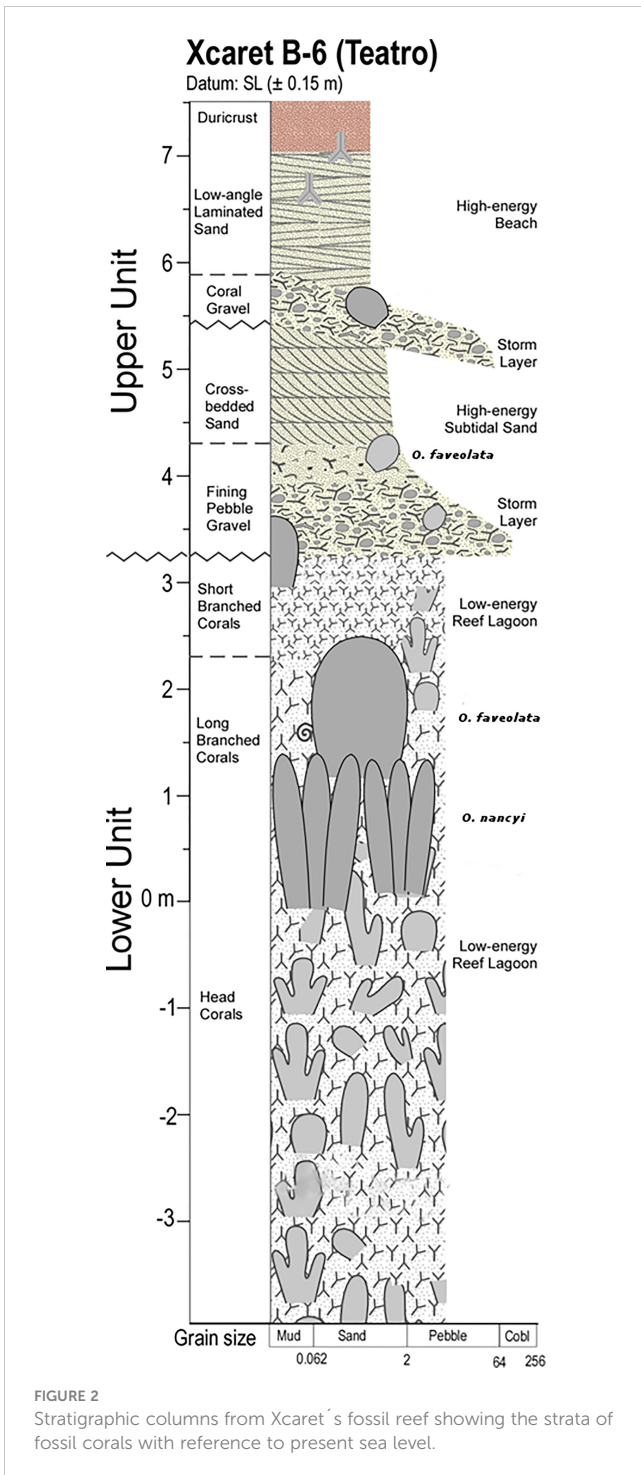
2.1 Reef location

After the LIG high stand, sea level fell as glaciation proceeded, leaving fossil reefs elevated above the present sea level (Potter and Lambeck, 2004). Our study site is along the east coast of the Yucatán Peninsula, which is a karstic platform (Ward et al., 1985) where dissolution during sea-level lowstands has formed some of the largest known underground rivers (Steinich et al., 1996). At Xcaret, a tourist attraction located south of Playa del Carmen, México (Figure 1), one of these underground rivers has been artificially enlarged and provides unparalleled exposure of a fossil fringing reef (Jordán-Dahlgren, 1997; Blanchon, 2010). We worked on an area that corresponds to the proximal back-reef (Blanchon et al., 2009; Blanchon, 2010), which has a rich scleractinian assemblage that is mainly in growth position including, among others: *Orbicella* spp., *Siderastrea* spp., *Pseudodiploria* spp., *Montastraea cavernosa* and *Pocillopora* spp. (Figure 2). Fossil colonies of *O. faveolata* form the walls of Xcaret’s tunnels and removing them would have caused significant damage; instead three large colonies were measured *in situ*. Elsewhere branches of *O. nancyi* could be easily detached and columns from three colonies were collected and examined by X-radiographs.

To compare these fossils with modern corals, we used core slabs from colonies of *Orbicella faveolata* and *O. annularis* collected from the Gulf of Mexico and the Caribbean. Extension rates came from 14 colonies of *O. annularis* and 16 colonies of *O. faveolata* from Cayo Arcas, collected by Jordán-Dahlgren and Jordán-Garza in 2008. In addition, we used data from five colonies of *O. annularis* and three colonies of *O. faveolata* from Puerto Morelos (Carricart-Ganivet et al., 1994; Carricart-Ganivet et al., 2000 and Carricart-Ganivet and Merino, 2001). All modern coral colonies



FIGURE 1
Location of the study sites (black circles). Fossil corals were located at Xcaret recreational park, Quintana Roo, México. The map was created in QGIS 2.4.0 (<http://qgis.osgeo.org>) using Natural Earth free vector and raster map data @naturalearthdata.com.



were living in shallow (2 to 10 m) environments, which are comparable to the paleo-water depth (2-7 m) of fossil corals in the proximal back-reef zone of Xcaret (Blanchon, 2010).

2.2 Linear extension rates of fossil and modern corals

Linear extension data of fossil corals were collected from three organ-pipe colonies (*Orbicella nancyi*, Pandolfi, 2007) and three colonies with massive morphotypes (most closely resembling

modern *O. faveolata*) found in growth position in the back-reef zone behind the upper reef tract at Xcaret, México (Figures 2, 3). Although the fossil corals were not dated, they came from the same site and stratigraphic level (0 to +2.3 m above mean sea level) as the corals that Blanchon et al. (2009) used for dating. According to these authors, the approximate age of this reef ranges between ~117 and ~127 ky ago, which corresponds to the last interglaciation and marine isotope stage 5e (Blanchon, 2010; Dahl-Jensen et al., 2013).

Samples from the organ pipe corals were sectioned with a rock saw for X-ray analysis (Knutson et al., 1972), and the slabs were digitized using a flat-bed scanner (Figure 3). The width of the growth bands was measured with the program Coral XDS (Helmle et al., 2002). Growth analysis was feasible *in situ* for the massive morphotype, as colonies had been sectioned during cave excavations for tourism. The colonies were found encased in the fossil-reef framework in apparent growth positions and showed corallites with vertical orientations typical of living corals. In these colonies, the growth bands could be clearly distinguished due to diagenetic alteration (Weil and Knowlton, 1993). We measured linear extension directly on these colonies using a vernier caliper (minimum scale 0.05 cm, Figure 3). We then compared the Xcaret fossil corals with modern members of the same species complex from shallow water habitats (Figure 1). The methods for obtaining coral-band widths were similar in all modern cases: X-radiographs from core slices from different coral colonies (Figure 4). Although the vernier and X-radiographs methods differ, both are directly measuring the width of the growth bands with a precision.

2.3 Data analysis

For each coral's time series, we estimated lag autocorrelation using a function that compares the covariance sequence at time t (c_t) to the original's time series covariance (c_0) using the autocorrelation function (acf) in R (R Core Team, 2022). In addition, a linear trend of each coral's time series was established by estimating the slope of a generalized least squares model using package "nlme" in R (Pinheiro et al., 2022). Linear extension measurements from all colonies were grouped by species (*O. nancyi*, *O. faveolata*, and *O. annularis*) and location (Gulf of Mexico, the Caribbean, and Pleistocene Caribbean). To test for mean differences in linear extension for each species and location as fixed factors and with the coral colony as a random factor, we used a Bayesian ANOVA (Supplementary Data) employing a normal prior and accounting for heteroscedasticity between groups (McCarthy, 2008). Comparisons were made between all groups, and differences were assessed with the 95% credible intervals of the unstandardized effect sizes (the difference between group means), not including 0 (Nakagawa and Cuthill, 2007).

Given that vital rates (like survival and reproduction) in modular organisms like corals are linked to colony size (Hughes and Connell, 1987; Hughes et al., 1992; Rodríguez-Martínez et al., 2011) and ultimately to the surface of living tissue (Weil et al., 2009), we highlight the importance of even small differences in growth rates using a simple growth model of massive (like *O. faveolata* or *O. annularis*) and columnar (like *O. nancyi*, see Pandolfi, 2007):

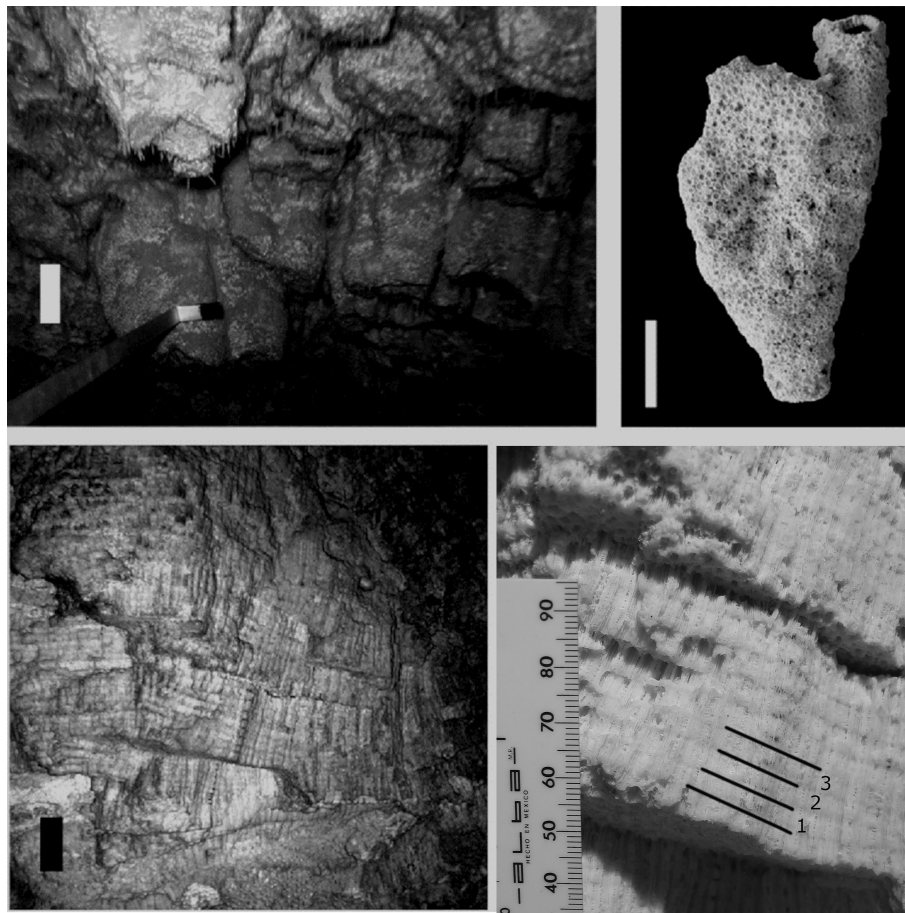


FIGURE 3
 Organ-pipe colonies (*Orbicella nancyi*) were reachable via the underground river (top left, scale 10 cm) and columns were detached by hand. The columns were club-shaped and all covered by intact corallites (top right, scale 1.5 cm); the massive colonies (*O. faveolata*) were exposed on cave walls (bottom left, scale 5 cm) and growth characteristics were measurable *in situ* with the width of 3 bands shown in black (bottom right).

$$(dt SA massive)/dt = 2 \cdot \pi \cdot (r + GR \cdot t)^2;$$

$$(dt SA columnar)/dt$$

$$= NC \cdot ((r + (GR \cdot dr \cdot t))^2 + (h + (GR \cdot t)) \cdot (2 \cdot \pi \cdot (r + (GR \cdot dr \cdot t))^2));$$

with SA = surface area of living tissue in cm² for massive and columnar growth forms; r = initial radius (0.5 cm) of the coral colony or column in cm; t = time in years and GR = growth rate in cm/y, h = initial column height (0.5 cm), NC = number of columns, and dr = damping rate (0.5) to account for a columnar form that increases in diameter at half the rate than in height.

3 Results

Neither modern nor fossil corals show consistent lag-1 autocorrelation on their linear extension time series. As shown in Table S1, of the 44 colonies sampled, only 11% showed lag-1 autocorrelation. Similarly, no consistent linear trends were found. Only 25% of the coral colonies showed significant trends, with three

modern corals showing a positive trend, five showing a negative trend, and two fossil corals showing positive linear trends (Table S1). More interestingly, results show that fossil colonies of *Orbicella* have linear extension rates that are ~40% lower than modern corals (Figure 5, Table 1). The mean linear extension rate in fossil corals from Pleistocene Xcaret vary between 0.52 (0.48 to 0.56) for the fossil *O. faveolata* and 0.66 (0.58 to 0.74) cm/year for *O. nancyi* (mean and 95% credible intervals, Figure 4). In contrast, the mean linear extension rates in modern corals are similar for *O. annularis* and *O. faveolata* and vary between 0.87 (0.84 to 0.89) at the Gulf of Mexico and 0.99 (0.94 to 1.06) cm/year at the Mexican Caribbean. The mean extension rate is slightly higher in the Caribbean (Car) than the Gulf of Mexico (GoM) (mean effect size: GoM vs Car. -0.099 (-0.15 to -0.04) cm/year) and higher in both modern seas compared to Pleistocene Caribbean (PCar) (mean effect size: GoM vs PCar 0.377 (0.32 to 0.42) cm/year and Car vs PCar 0.47 (0.4 to 0.54) cm/year).

Differences in the mean linear extension exist between the fossil corals with *O. faveolata* having credibly lower linear extension than *O. nancyi* with a mean effect size of 0.14 (0.05 to 0.23) cm/year. Compared to their modern counterparts, the corals *O. nancyi* and fossil *O.*

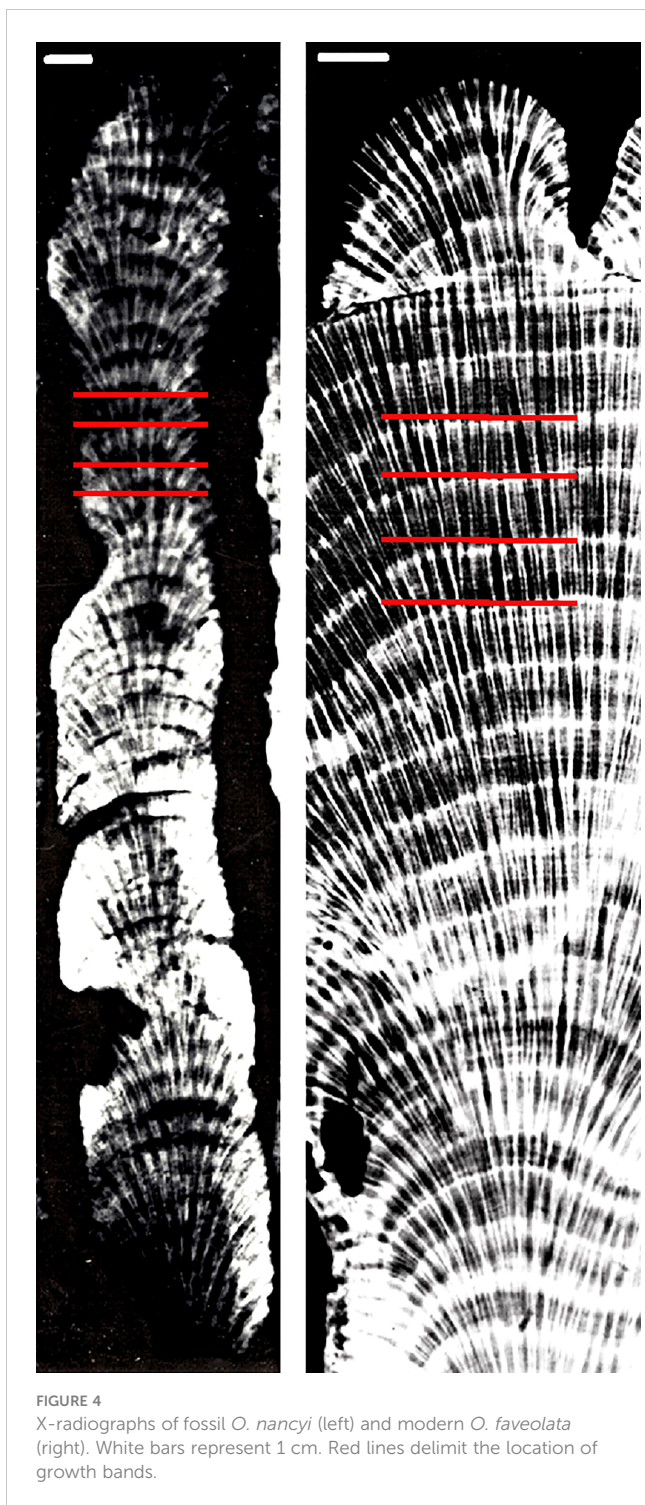


FIGURE 4
X-radiographs of fossil *O. nancyi* (left) and modern *O. faveolata* (right). White bars represent 1 cm. Red lines delimit the location of growth bands.

faveolata have lower extension rates (Figure 5). In general, modern coral species showed no significant differences in their growth rates or had small effect sizes (Table 2). However, the effect sizes of the differences in growth rates are large between modern and fossil corals and intermediate between the two fossil species at Xcaret (Table 1). Compared to other Atlantic coral fossils of the same genus or species, Xcaret’s *O. nancyi* shows a lower mean linear extension and massive forms show a range from 0.5 to 0.9 cm/year (Table 3).

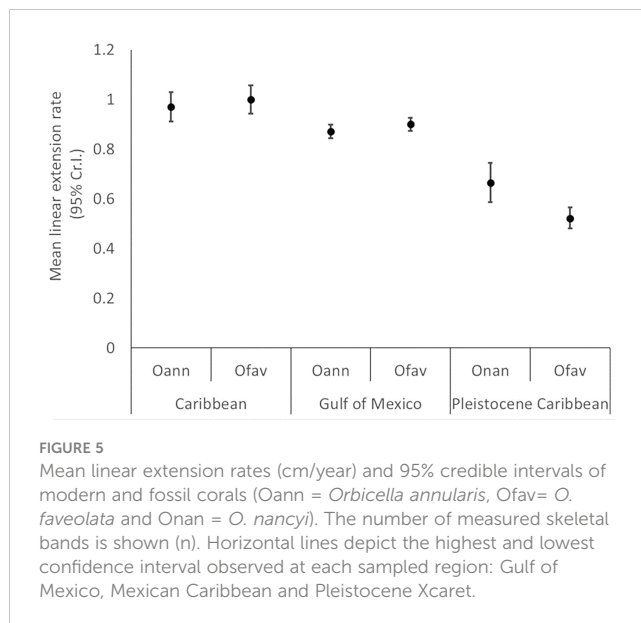


FIGURE 5
Mean linear extension rates (cm/year) and 95% credible intervals of modern and fossil corals (Oann = *Orbicella annularis*, Ofav = *O. faveolata* and Onan = *O. nancyi*). The number of measured skeletal bands is shown (n). Horizontal lines depict the highest and lowest confidence interval observed at each sampled region: Gulf of Mexico, Mexican Caribbean and Pleistocene Xcaret.

Small differences in mean linear extension can, in a few years, have a significant effect on the colony size in terms of the amount of tissue grown; in addition, a columnar growth form like *O. nancyi*’s has an even more significant effect on the rapid growth of living tissue (Figure 6).

4 Discussion

The fossil coral at Xcaret with the highest linear extension was *O. nancyi*, followed by *O. faveolata* (Figure 5). Although *O. nancyi* has a higher linear extension than fossil *O. faveolata*, both species have a mean linear extension that is ~0.5 cm lower than expected (~50% less) when compared to modern corals and the fossil *O. nancyi* from Barbados (Tomascik, 1990; Holcomb et al., 2004). Slow growing fossil corals have also been reported elsewhere, including massive forms in Florida (Gischler et al., 2009), columnar forms in Barbados (Holcomb et al., 2004) and organ pipe forms in Curaçao (del Valle, 2012). By contrast some *Orbicella* spp. fossils show high growth rates (> 0.8 cm/year), including massive forms from Curaçao (Johnson and Pérez, 2006), and organ pipe forms from Curaçao and Barbados (Holcomb et al., 2004; del Valle, 2012). Both fast and slow-growing fossil corals come from paleo-habitats that were less than 6 m deep.

Two possible explanations have been given for low extension rates on fossil corals. First, Gischler et al. (2009), working with massive *Orbicella* from the LIG in Florida, considered temperature as a possible environmental factor inhibiting linear extension. Second, Pandolfi et al. (2002) and Pandolfi (2007) proposed that the linear extension of Pleistocene *Orbicella* corals sympatric with *O. nancyi* was depressed through competition for space and light. According to this competition hypothesis, the extinction of *O. nancyi* at ~82 kyr caused a character release in the *O. annularis* species complex, partly because *O. nancyi* was a fast grower and, through competition, suppressed the growth of sympatric *Orbicella* spp. Upon extinction, *O. nancyi* released the extant species from the

TABLE 1 Mean linear extension and standard deviation for each fossil corals colony (Col.).

	Fossil <i>O. faveolata</i>			<i>O. nancyi</i>		
	Col. 1	Col. 2	Col. 3	Col. 1	Col. 2	Col. 3
Mean	0.55	0.51	0.47	0.71	0.68	0.65
SD	0.11	0.06	0.07	0.17	0.16	0.16

TABLE 2 Multiple comparisons of mean linear extension rate between modern and fossil corals from a Bayesian ANOVA.

Region		Caribbean		Gulf of Mexico		Pleistocene Caribbean
Species		Mann	Mfav	Mann	Mfav	Mnan
Caribbean	Mann	#				
	Mfav	-0.03 (-0.06 to 0.007)	#			
Gulf of Mexico	Mann	0.09952 (0.04 to 0.15)	0.069 (-0.0001 to 0.14)	#		
	Mfav	0.06974 (0.0001 to 0.14)	0.099 (0.04 to 0.15)	-0.03 (-0.06 to 0.007)	#	
Pleistocene Caribbean	Mnan	0.3049 (0.2 to 0.4)	0.33 (0.23 to 0.43)	0.2 (0.12 to 0.28)	0.23 (0.15 to 0.31)	#
	Mfav	0.4477 (0.37 to 0.5)	0.47 (0.4 to 0.54)	0.34 (0.29 to 0.39)	0.37 (0.32 to 0.42)	0.14 (0.05 to 0.23)

Differences were determined based on the credible intervals of group differences not containing 0 and are shown in bold.

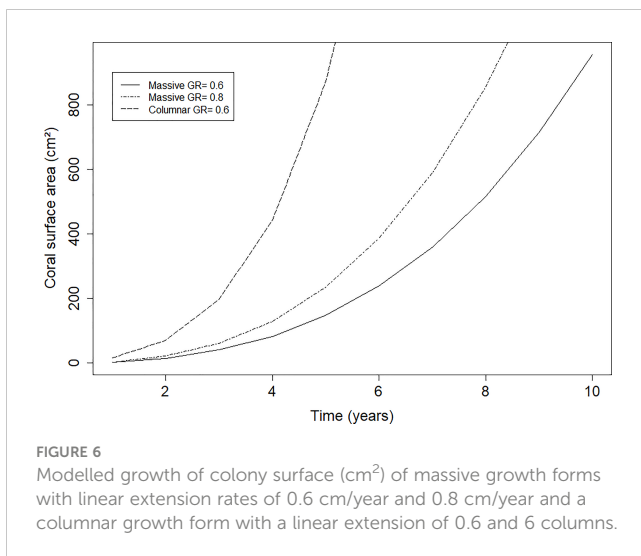
TABLE 3 Mean linear extension rates for fossil *Orbicella* spp. Corals for 125kyr and 82kyr Pleistocene at different localities in the Caribbean.

Period	Locality	Morph (Species)	Depth	Linear extension (cm/year)	SD/range (cm/year)	Sample size	Study
125 kyr	Curaçao	Massive	shallow<5m	0.91	0.75 to 1.25	11 colonies	Johnson and Pérez, 2006
125 kyr	Key Largo, Florida	Massive	shallow patch reef	0.52	0.1	17 colonies, 1429 bands	Gischler et al., 2009
125 kyr	Curaçao	Organ pipe(<i>O. nancyi</i>)	windward	1.1	0.6 to 1.5	6 cores	del Valle, 2012
125 kyr	Curaçao	Organ pipe(<i>O. nancyi</i>)	leeward	0.8	0.5 to 1.1	18 cores	del Valle, 2012
82 kyr	Barbados	Columnar form	shallow back reef<5m	0.54	0.13	27 colonies	Holcomb et al., 2004
82 kyr	Barbados	Organ pipe(<i>O. nancyi</i>)	shallow back reef<5m	1.26	0.21	30 colonies	Holcomb et al., 2004

competition, and linear extension rates increased presumably to modern values.

Neither of these hypotheses, however, sufficiently explains differences in the linear extension data between Xcaret and modern corals. Our modern *O. faveolata* and *O. annularis* extension data occur in two regions with different temperature regimes: the Mexican Caribbean Sea, which has a higher (~1.3° C) mean sea surface temperature than the Gulf of Mexico (Carricart-Ganivet, 2004). This temperature difference is like the estimated higher sea temperature of the LIG (Otto-Bliesner et al., 2006), and yet differences in linear extension between modern corals in both regions are not as large compared to fossil and modern corals.

Modern temperature differences between the regions are likely within the acclimation capacities of these corals (Dodge and Brass, 1984; Carricart-Ganivet and Merino, 2001; Carricart-Ganivet, 2004). In addition, Helmle et al. (2011) showed a recent increase in linear extension for *O. faveolata* that made coral growth tolerant to the ongoing increase in temperature due to climate change. In fact, *Orbicella* corals can exhibit a positive correlation between linear extension and temperature (Dodge, 1981), yet higher water temperatures can lead to reduced rates of skeletal extension (Gischler et al., 2009). This suggests that there may be a temperature threshold beyond which coral extension is negatively impacted. The exact mechanisms behind the threshold are not fully understood



but might be related to the physiology of the coral. Under moderate stress *Orbicella* avoids a loss in linear extension by decreasing skeletal density (Carricart-Ganivet and Merino, 2001), but Mendes and Woodley (2002) showed a decrease in extension rate of *O. annularis* after a bleaching event possibly related to an impairment in reproduction, the effect was harsher the longer the extreme water temperature lasted. Maintaining high linear extension rates might be advantageous to the corals to compete for light and space but at high physiological cost (Rinkevich, 1996).

Nevertheless, competition could have the opposite effect. Corals compete using various mechanisms (Richardson et al., 1979) and their growth rates have been shown to decrease in the presence of macroalgae (Lirman, 2001), turf algae (Quan-Young and Espinoza-Avalos, 2006) and other corals (Tanner, 1997; Lapid and Chadwick, 2006). As a consequence, colony growth rates can influence community structure and development through competition (Maguire and Porter, 1977). Comparing the extant *Orbicella* species, interspecific ecological interactions show that *O. annularis* is the least aggressive, followed by *O. faveolata* and *O. franksi* (Weil and Knowlton, 1993). This aggressiveness between competing species can result in tissue mortality and sometimes the suppression of mean linear growth rates, with faster-growing species escaping competition by size (Sebens, 1982; Tanner, 1997; Cruz-Piñon et al., 2003). For our modern corals, which share the same habitat, we found no evidence that the stronger competitor, *O. faveolata*, had systematically higher linear extension rates (Figure 5, Table 1). This finding is consistent with Cruz-Piñon et al. (2003), who reported higher skeletal extension rates in *O. faveolata* than in *O. annularis*, whereas Tomascik (1990) reported a reverse trend in the same corals from Barbados, and Van Veghel and Bosscher (1993) found no significant differences between the two species. This lack of consistency in species linear extension differences is likely due to interspecific competition being rare on modern reefs (van Woosik, 2002), and the large variability in reef environments and growth plasticity in species of *Orbicella* (Foster, 1979). Given that Xcaret's *O. nancyi* shows a lower extension rate than modern and fossil corals in other locations, it is possible that other characteristics, such as growth form (Figure 5), made *O. nancyi* a stronger competitor (Pandolfi et al., 2002). Despite being in the same

stratigraphic unit and level, it is uncertain if these coral species were cohorts that lived together. However, the clear facies on the deposit point to similar environmental conditions during the time the corals grew (Figure 2). Also, members of the *Orbicella* complex seem to have coexisted at different locations and periods of the Pleistocene (see Pandolfi et al., 2002) and it is likely that this also occurred at Xcaret.

The lack of a consistent temperature or species effect on extension rates implies that the lower linear extension rates of fossil *Orbicella* at both Xcaret and Florida (Gischler et al., 2009) is more likely to have resulted from deleterious habitat conditions. Data from *O. nancyi* samples collected by del Valle (2012), showed lower extension rates on the leeward side of Curaçao. Lower extension rates in back-reef corals from Xcaret are consistent with those of lagoonal corals reported by Gischler et al. (2009). Corals at both of these sites grew in or adjacent to large lagoons that resulted from extensive coastal inundation during a sea-level highstand at least 6 m higher than present (Blanchon et al., 2009). As a result, the lagoons and adjacent back reef environments must have been subject to high sediment flux and were associated with the development of sediment-tolerant biota (Blanchon, 2010). If coral growth in and near these lagoons was indeed depressed by sedimentation, then the same species from different habitats should show higher extension rates, which seems to be the case. More growth data from Pleistocene corals in different paleohabitats are required to test this hypothesis and better understand their response to changing environments.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

AJ-G, EJ-D collected data. AJ-G, EJ-D performed the statistical analysis. AJ-G, PB, EJ-D, JC-G analysed the results and wrote the manuscript. All authors contributed to reviewing and editing the manuscript. All authors contributed to the article and approved the submitted version.

Funding

This work was supported by CONACyT grant 1043508 to PB.

Acknowledgments

We want to thank the Xcaret administration, who allowed unrestricted access to the park to work on the fossil reef. We also thank J.M. Pandolfi for his help in identifying the fossil species *O. nancyi*, R.E. Rodríguez-Martínez for her editorial comments.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer GHP declared a shared affiliation with the authors PB, JPCG and EJD to the handling editor at the time of review.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2023.1098430/full#supplementary-material>

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