Biogeosciences

Discussions

Open Access

EGU

Low Florida coral calcification rates in the Plio-Pleistocene

T. C. Brachert[1], M. Reuter[2], S. Krüger[3], J. S. Klaus[4], K. Helmle[5], and J. M. Lough[6]

[1]Institut für Geophysik und Geologie, Universität Leipzig, Leipzig, Germany
[2]Institut für Erdwissenschaften, Karl-Franzens-Universität Graz, Graz, Austria
[3]Institut für Geophysik und Geologie, Universität Leipzig, Leipzig, Germany
[4]Department of Geological Sciences, University of Miami, Coral Gables, USA
[5]Oceanographic Center, Nova Southeastern University, Fort Lauderdale, USA
[6]Australian Institute of Marine Science, Townsville MC, Australia

Correspondence to: T. C. Brachert (brachert@uni-leipzig.de)

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Abstract

In geological outcrops and drill cores from reef frameworks, the skeletons of scleractinian corals are usually leached and more or less completely transformed into sparry calcite because the highly porous skeletons formed of metastable aragonite ($CaCO_3$)
5 undergo rapid diagenetic alteration. Upon alteration, ghost structures of the distinct annual growth bands may be retained allowing for reconstructions of annual extension (= growth) rates, but information on skeletal density needed for reconstructions of calcification rates is invariably lost. Here we report the first data of calcification rates of fossil reef corals which escaped diagenetic alteration. The corals derive from un-
10 lithified shallow water carbonates of the Florida platform (southeastern USA), which formed during four interglacial sea level highstands dated 3.2, 2.9, 1.8, and 1.2 Ma in the mid Pliocene to early Pleistocene. With regard to the preservation, the coral skeletons display smooth growth surfaces with minor volumes of marine aragonite cement within intra-skeletal porosity. Within the skeletal structures, dissolution is minor
15 along centers of calcification. Mean extension rates were $0.44 \pm 0.19 \, \mathrm{cm \, yr^{-1}}$ (range 0.16 to $0.86 \, \mathrm{cm \, yr^{-1}}$) and mean bulk density was $0.86 \pm 0.36 \, \mathrm{g \, cm^{-3}}$ (range 0.55 to $1.22 \, \mathrm{g \, cm^{-3}}$). Correspondingly, calcification rates ranged from 0.18 to $0.82 \, \mathrm{g \, cm^{-2} \, yr^{-1}}$ (mean $0.38 \pm 0.16 \, \mathrm{g \, cm^{-2} \, yr^{-1}}$), values which are 50 % of modern shallow-water reef corals. To understand the possible mechanisms behind these low calcification rates,
20 we compared the fossil calcification with modern zooxanthellate-coral (z-coral) rates from the Western Atlantic (WA) and Indo-Pacific (IP) calibrated against sea surface temperature (SST). In the fossil data, we found an analogous relationship with SST in z-corals from the WA, i.e. density increases and extension rate decreases with increasing SST, but over a significantly larger temperature window during the Plio-Pleistocene.
25 With regard to the environment of coral growth, stable isotope proxy data from the fossil corals and the overall structure of the ancient shallow marine communities are consistent with a well-mixed, open marine environment similar to the present-day Florida Reef Tract, but variably affected by intermittent upwelling. Upwelling along the platform may

explain low rates of reef coral calcification and inorganic cementation, but is too local-ized to account for low extension rates of Pliocene z-corals recorded throughout the tropical Caribbean in the western Atlantic region. Low aragonite saturation on a more global scale in response to rapid glacial/interglacial CO_2 cyclicity is also a potential factor, but Plio-Pleistocene atmospheric pCO_2 is believed to have been broadly similar to the present-day. Heat stress related to globally high interglacial SST, only episod-ically moderated by intermittent upwelling affecting the Florida platform seems to be the most likely reason for low calcification rates. From these observations we suggest some present coral reef systems to be endangered from future ocean warming.

1 Introduction

In the geological record, the skeletons of scleractinian corals and other sedimen-tary grains composed originally of metastable aragonite ($CaCO_3$) usually form moldic porosity, or are more or less completely replaced by mosaics of blocky calcite spar. Al-though these secondary alterations generally pose no problem for classical approaches in paleoecology and taxonomy, all information stored as isotope and geochemical proxy data has been reset and makes the corals no longer available as environmental or geochronological archives. The first diagenetic alterations of the skeletons still happen at the sea floor, in deeper parts of the skeleton where the living organic tissues were previously withdrawn. These alterations represent growths of inorganic aragonite fiber crystals and subtle dissolution phenomena within the centers of calcification (Perrin, 2004). Differential diagenetic processes on crystalline phases and organic matrices also exist and include aragonite – aragonite recrystallizations associated with a loss of micron-sized growth information (McGregor and Gagan, 2003; Nothdurft and Webb, 2009; Perrin, 2004). In contrast, in the classical freshwater diagenetic environment, the primary surface area of the skeleton controls diagenetic susceptibility and rates of alteration (Constantz, 1986; Dullo, 1984). The freshwater effects are dominated by dis-solution via moldic porosity and subsequent reduction of pore spaces by cementation,

or dissolution and associated crystallization of blocky calcite without developing a significant moldic stage (Bathurst, 1975). In the latter process, ghost structures reflecting original microstructures will be preserved (Flügel, 2004). More often, ghost structures of the growth bands form by subtle, diffusion-controlled dissolution which preferentially
5 starts at the centers of calcification and continues to form increasingly hollow skeletal structures (Reuter et al., 2005). The rate of skeleton-internal dissolution via diffusion differs among growth bands within a specimen and responds to the bands of higher and lower density (Reuter et al., 2005). Given the situation where no secondary addition of carbonate material has taken place, however, the hollow structures may still be suitable
10 for isotope and geochemical proxy analysis (Mertz-Kraus et al., 2008, 2009a, b). Following infilling by late diagenetic calcite spar, this differential dissolution process leaves records of growth bands from which skeletal extension rate (= colony growth per year) can be retrieved from fully altered specimens (Brachert et al., 2006b; Johnson and Pérez, 2006; Shinn, 1966). But, this process of dissolution and subsequent cementa-
15 tion of moldic and intra-particle porosity tends to destroy all information pertaining to skeletal density. Nonetheless, in rare circumstances reef corals do escape diagenetic alteration (Brachert et al., 2006a, 2015; Denniston et al., 2008a; Griffiths et al., 2013), but no attempts have been made to date to gain information on the systematics of coral calcification from the deep geological record.
20   In this study we present calcification data from zooxanthellate corals (z-corals) from Plio-Pleistocene interglacial deposits on the Florida platform (USA; Fig. 1). We show that calcification rates were 50 % lower than they are in the present-day Western Atlantic (WA). For an understanding of the possible mechanisms behind these low calcification rates, we use modern analogue data compiled from the literature on recent
25 z-corals of the WA and Indo-Pacific (IP). According to this database, temperature generally boosts calcification rates in modern z-corals, whereas temperature effects on skeletal growth rate (extension rate) and density markedly differ according to taxon and/or ocean region. We discuss whether the pattern found is a local or global signature that may reflect a low supersaturation of the sea water with respect to arago-

nite ($\Omega_{aragonite}$) in the Plio-Pleistocene. We also discuss whether low calcification rates of the fossil z-corals are the result of either low temperatures or heat stress in the warmer-than-present world of the Plio-Pleistocene interglacials and the expression of a non-linear calcification behavior beyond the recent temperature windows at high sea surface temperatures (SSTs). This study complements two previous studies using sclerochronology of bivalves and z-corals for reconstructions of the paleoenvironments and long-term changes of seasonality in southern Florida (Brachert et al., 2014, 2015).

1.1 The Plio-Pleistocene interglacials

During the Plio-Pleistocene interglacials, global sea levels were up to 22 m (Miller et al., 2012) or even 35 m higher (Dowsett and Cronin, 1990) and global mean temperatures 2 to 4 °C warmer than present, whereas SSTs of the warm pools at low latitudes were ∼ 2 °C higher than present (Fedorov et al., 2013; O'Brien et al., 2014). Although dramatic cooling occurred in the high latitudes, long-term atmospheric $p\text{CO}_2$ appears to have remained rather constant after the mid Pliocene climatic optimum (∼ 3 Ma) and to have been of the same order of magnitude as in the pre-industrial period (Seki et al., 2010). During and before the optimum, however, $p\text{CO}_2$ reached values expected for the end of this century through the burning of fossil fuels (IPCC, 2013; Seki et al., 2010). Modeling of the oceanic carbonate systems suggest the long-term $p\text{CO}_2$ changes to have had no effect on the saturation state of seawater with regard to $\Omega_{aragonite}$ (Hönisch et al., 2012), but evidence exists that rates of carbonate precipitation and skeletal accretion differed over the last glacial/interglacial cycle, in response to changes of $\Omega_{aragonite}$ driven by $p\text{CO}_2$ (Barker, 1986; Beaufort et al., 2011; Riding et al., 2014).

The Plio-Pleistocene Florida carbonate platform represents a stack of shallow marine carbonate sequences formed during sea level highstands which are separated by paleosols or thin freshwater units formed during lowstands. A pronounced reef system existed along the southwestern margin of the peninsula (Meeder, 1979). The single unlithified marine units contain a highly diverse mollusk and coral fauna comparable

to that of the present reef tracts and back-reef systems (Meeder, 1979; Petuch and Roberts, 2007). Combined oxygen and carbon stable isotope data (δ^{18}O, δ^{13}C) of diagenetically pristine mollusks and z-corals from the platform sediments reflect the complexity of the depositional setting including brackish to hypersaline and well-mixed, open marine environments (Brachert et al., 2014; Lloyd, 1969; Tao and Grossman, 2010). The reasons for high benthic carbonate productivity by mollusks during the Plio-Pleistocene is controversial, and has been suggested to be due to high nutrient concentrations resulting from freshwater input (Tao and Grossman, 2010) or upwelling (Allmon, 2001; Allmon et al., 1995; Brachert et al., 2015; Emslie and Morgan, 1994; Jones and Allmon, 1995). Recently, SST estimates based on the reef coral *Orbicella* and modern seawater at Florida Reef Tract (Leder et al., 1996) yielded mean annual SSTs between 19.5 and 26.0 °C; the lowest temperatures occurred during episodes of maximum upwelling according to their δ^{13}C values (Brachert et al., 2015). Apart from low SSTs believed to be the effect of upwelling, the large range of values is likely in part an artifact of the uniform value for seawater δ^{18}O (δ^{18}O$_{water}$) used for the calculations, irrespective of sampling locality and stratigraphic unit (Brachert et al., 2015). In contrast, seasonal SST variability (~ 7 °C) inferred from δ^{18}O amplitudes of the fossils is independent of assumptions of δ^{18}O$_{water}$. It is not only remarkably constant within specimens and over the last 3.2 Ma, but also fits modern surface seasonality along the reef tract (Brachert et al., 2014, 2015). Large seasonality as prevailing off North Carolina (Macintyre and Pilkey, 1969) or in inner coastal waters of Florida Bay (Swart et al., 1996) has not been encountered in the data from reef corals and has also been taken to infer a normal shallow-marine environment without unusual stress from evaporation and freshwater influxes (Brachert et al., 2014).

In southern Florida, the most extensive growth of reef corals occurs at present along the reef tract on the Atlantic side of the peninsula, whereas only limited z-coral growth occurs along the Gulf side in the west and the shallow Florida Bay in the southeast. On the Atlantic side, coral communities are charaterized by abundant *Orbicella* (Lidz, 2011), whereas in the Gulf side and Florida Bay, coral growth is restricted to the two

eurytopic taxa *Siderastrea* and *Solenastrea* (Okazaki et al., 2013; Swart et al., 1999). Published extension rates for recent *Solenastrea* inhabiting the most marine segments of Florida Bay range from 0.51 to 0.9 cm yr^{-1} (Hudson et al., 1989; Swart et al., 1996). Recent *Solenastrea* has also been recorded to grow under rather cold water conditions along the US southeastern Atlantic coast (Macintyre and Pilkey, 1969), but quantitative calcification data from that setting are not available, leaving the question unanswered regarding the effects of low SST on extension and density. Colony sizes at the northern sites similar to those of the lower latitudes have been suggested to indicate similar extension and calcification rates (Macintyre and Pilkey, 1969).

1.2 Architecture of the zooxanthellate coral skeleton and systematics of skeletal calcification

The skeleton of z-corals is a highly organized, porous hard tissue formed of mineral CaCO$_3$ (aragonite). The main skeletal elements of some taxa comprise the tubular corallites were the living polyps are located, and the bulbous coenosteum between the corallites which is covered by a thin layer of soft tissue during life. The corallites are structured by radially-arranged blades (septa) and laterally fused, convex upward sheets (dissepiments) which separate the living tissue from abandoned parts of the skeleton (Fig. 2). In X-ray images of slices parallel to the axes of the corallites (axes of maximum growth), massive z-coral skeletons typically display alternations of light and dark bands (Fig. 3). These "density bands" reflect zones of cyclic changes of skeletal density concordant with former growth surfaces (Knutson et al., 1972). One pair of bands of low and high density typically represents one year of growth and forms the basis for the calibration internal age models and for estimates of the extension rates, i.e. the rate of growth of the colony surface (Lough and Cooper, 2011). Skeletal bulk density is a measure of the volume of pore volumes within the skelelton which reflects the thickness of the individual skeletal elements. The thicker and more massive the individual skeletal elements/the smaller the pores, the higher and closer will be the density to that of mineral aragonite (2.93 g cm^{-3}). Extension rate and density combine

for estimates of calcification rates according to Eq. (1) (Lough and Cooper, 2011):

$$\text{calcification rate (g cm}^{-2}\text{ yr}^{-1}) = \text{annual extension rate (cm yr}^{-1}) \times \text{density (g cm}^{-3}).$$
(1)

1.3 Materials

Z-corals were sampled from four distinct stratigraphic units of the Florida carbonate platform (USA) representing interglacial highstands of sea level subsequent to the Pliocene warm period, dated 3.2, 2.9, 1.8 and 1.2 million years (Ma) of the mid Pliocene and early Pleistocene (Fig. 1, Table 1) (Brachert et al., 2014). Sampling focused on *Solenastrea* ($n = 16$) which is by far the most common taxon in the Plio-Pleistocene shallow water carbonates of southwestern Florida. This dataset was complemented by specimens of *Orbicella* ($n = 2$) and *Porites* ($n = 1$).

1.4 Methods

Fossil corals selected for this study ($n = 18$, Table 1) were cut into <1 cm thick slabs along the plane of maximum growth using a conventional rock saw equipped with a water-cooled diamond blade. All corals were screened for diagenetic alteration using a binocular microscope and scanning electron microscopy (SEM). In order to detect minimal contaminations by secondary calcite, powder samples taken at random were prepared for X-ray diffraction (XRD) and analysed using a Rigaku Miniflex diffractometer at angles between 20 to 60° 2θ. Only skeletal areas that retained their original aragonite mineralogy (XRD), skeletal porosity and microstructure without evidence for significant secondary crystal growth or dissolution (microscopic and SEM observation) were accepted for further sample preparation. Coral slabs of equal thickness were X-rayed using a digital X-ray cabinet (SHR 50 V) to identify potential zones of diagenetic alteration (McGregor and Gagan, 2003; Reuter et al., 2005) and to document the density bands (Knutson et al., 1972). Quantitative density measurements were made using

the software CoralXDS (freeware) according to Helmle and co-workers (Helmle et al., 2002). In this approach, the CoralXDS software compares the gray values recorded in X-radiographs from corals with those from aluminum plates having the same thickness as a background picture and an aluminum wedge for density calculations. Measure-
ments were done along transects parallel to the corallites and parallel to the sampling transects for stable isotope analyses (Brachert et al., 2014). Bulk skeletal density was calculated as the mean of all individual measurements along a given transect. Cali-bration of the measurements was tested by measurements of standards for zero den-sity (air) and massive aragonite (slice of a *Glycimeris* bivalve shell having a thickness
equaling that of the coral slice). External analytical precision of the routine measure-ments was tested by double blind measurements, and mean deviation from regression ($R^2 = 0.91$, $p < 0.05$) was found to be $0.04 \pm 0.01\,\mathrm{g\,cm^{-3}}$ (range = 0.02 to $0.05\,\mathrm{g\,cm^{-3}}$; $n = 18$).

As a baseline for the description and interpretation of the data from the fossils, we
use calcification data from recent corals reported in the literature deriving equally from tropical and high latitudinal localities within the shallow-water reef belt (Baker and We-ber, 1975; Bessat and Buigues, 2001; Carricart-Ganivet et al., 2000; Carricart-Ganivet and Merino, 2001; Dodge and Brass, 1984; Dustan, 1975; Elizalde-Rendon et al., 2010; Fabricius et al., 2011; Goodkin et al., 2011; Graus and Macintyre, 1982; Helmle et al.,
2011; Highsmith et al., 1983; Hudson et al., 1989; Lough, 2008; Mallela and Perry, 2007; Tanzil et al., 2009), and one unpublished record of *Solenastrea* from Florida Bay (FB6). We present a set of three descriptive diagrams for a comparison of the patterns of calcification (extension rate, bulk density, calcification rate) in the modern and fossil z-corals on the basis of linear regression (Fig. 4). For a deeper understanding of the
processes, we further apply quadratic polynomial regression models of experimental data calibrated with SST to account for the established non-linearity of life processes.

Stable isotope data described here are the same as reported by Brachert et al. (2014, 2015), and only a short summary of the methods is given here. Sample pow-ders for stable isotope analysis were taken using a microdrill equipped with a 0.6 mm

drill bit. Prior to sampling of the corallite walls, all endothecal skeletal elements were removed. For stable isotope analysis, carbonate powders were reacted with 102 % phosphoric acid at 70 °C using a Kiel IV online carbonate preparation line connected to a MAT 253 mass spectrometer. All carbonate values are reported in per mil (‰) relative to PDB according to the delta notation. Reproducibility was checked by replicate analysis of laboratory standards and was better than ±0.04‰ (1σ) for carbon (δ^{13}C) and better than ±0.06‰ (1σ) for oxygen isotopes (δ^{18}O).

The scleractinian genus name *Orbicella* is used for corals previously assigned to the genus *Montastraea* according to the revised taxonomic classification of the reef coral family Mussidae by Budd et al. (2012).

Statistical analyses were performed using the PAST paleontological statistics software package (version 3.01) for education and data analysis (freeware folk.uio.no/ohammer/past/). Variability of stable isotope data (δ^{18}O, δ^{13}C) was evaluated using the T test. A linear bivariate model was tested as to whether there were no statistical differences in the stable isotope values in a dataset ($p > 0.05$) against the alternate hypothesis that there were significant differences ($p < 0.05$). Equality of regression slopes was tested using the F test as assumed by analyses of covariance (ANCOVA). One-way analysis of variance (ANOVA) tested if there were no statistical differences in the mean growth parameters (extension, density, calcification) between two given coral sites ($p > 0.05$) against the alternate hypothesis that there were significant differences ($p < 0.05$).

2   Results and discussion

2.1   Taxonomic systematics of calcification in WA z-corals

The calcification data presented here derive from the four genera *Orbicella*, *Diploria*, *Porites* and *Solenastrea*. While the experimental data for *Orbicella*, *Porites* and *Diploria* are essentially from recent materials, data for *Solenastrea* is, with the exception

of one specimen, retrieved entirely from Plio-Pleistocene specimens investigated during this study (Table 2). Extension rates of *Porites* (range = 0.28 to 0.48, mean = 0.37 + 0.07 cm yr^{-1}) and *Diploria* (range = 0.30 to 0.40, mean = 0.35 + 0.04 cm yr^{-1}) are significantly lower than those of *Orbicella* (range = 0.38 to 1.44, mean = 0.91 ± 0.23 cm yr^{-1}, *p* < 0.05) but are identical with regard to density (*Porites*: range = 1.10 to 1.72, mean = 1.44 ± 0.20 g cm^{-3}; *Diploria*: range = 0.97 to 1.70; mean = 1.27 ± 0.31 g cm^{-3}; *Orbicella*: range = 0.78 to 1.94, mean = 1.37 ± 0.24 g cm^{-3}; *p* > 0.05). *Orbicella* display a negative relationship between extension rate and bulk density (R^2 = 0.27, *p* < 0.05), whereas no such relationship has been documented for *Porites* (R^2 = 0.30, *p* > 0.05) and *Diploria* (R^2 = 0.11, *p* > 0.05) which are indistinguishable in their calcification data (Fig. 4). Remarkably, *Porites* and *Diploria* are indistinguishable not only with regard to their general calcification relationship but also quantitatively in terms of absolute values and clearly differ from those of *Orbicella*, whose calcification rates are significantly higher at almost any given density (Fig. 4). *Solenastrea* is unusual due to its low extension rates (range = 0.22 to 0.58, mean = 0.43 ± 0.19 cm yr^{-1}) and low bulk density (range = 0.55 to 1.22, mean = 0.88 ± 0.22 g cm^{-3}). Like *Orbicella*, extension rate and bulk density display a significant negative relationship (R^2 = 0.23, *p* < 0.05), whereas extension rate is positively correlated with calcification rate (R^2 = 0.47, *p* < 0.05). Bulk density, on the other hand, displays no correlation with calcification rate (R^2 = 0.06, *p* > 0.05).

Interpretation: No consistent relationships of the parameters of calcification exist between recent and fossil specimens and between taxa. While the data from the recent *Solenastrea* specimen is similar to the data from fossil *Solenastrea* (Fig. 4), the single fossil *Porites* available is incompatible with recent *Porites* from the WA, both in terms of extension rate and bulk density, but plots together with fossil *Solenastrea* (Fig. 4). Also, the published Pliocene *Diploria* clearly differ from their recent counterparts with distinctly higher extension rates (Fig. 4a). With regard to *Orbicella*, bulk density of the two fossil specimens available is lower at any given extension rate than in the recent *Orbicella*, but consistent with fossil *Solenastrea* (Fig. 4). In extension rate vs. bulk den-

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

|◄ | ►|

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

sity space, we observe a duality between recent and fossil z-corals, rather than any taxonomical distinction. With regard to calcification rates, fossils also have lower values at any given extension rate than recent z-corals (Fig. 4). On the other hand, no clear separation exists between fossils and recent z-corals with regard to bulk density vs. calcification rate because of very high extension rates of *Orbicella* compared to the other taxa (Fig. 4). Interestingly though, experimental studies have demonstrated calcification systematics of reef corals to differ between the genera *Orbicella* of the WA and *Porites* of the IP (Carricart-Ganivet, 2004; Lough, 2008). Apparently, in addition to some taxonomical controls, systematics of calcification of z-corals seem, therefore, to depend also on ocean regions or coral provinces.

In southern Florida, extension rates from recent *Solenastrea* inhabiting the most marine parts of Florida Bay range from 0.51 to 0.9 cm yr^{-1} (Hudson et al., 1989; Swart et al., 1996), and are fully compatible with a mean value of 0.79 cm yr^{-1} of reef corals of the entire WA (this database). Density values have not been published so far from Florida Bay corals; we measured a density of 1.07 g cm^{-3} for one specimen (FB6; Table 2) which is rather low compared to the densities recorded for *Orbicella*, but similar to that of *Porites* and *Diploria* from the WA (Fig. 4, 6a). It should be noted also, that calcification records for recent *Orbicella* from the Florida Reef Tract are not available in our database. Apart from this limitation of the dataset, low extension rates and low bulk skeletal density in the Plio-Pleistocene z-corals seems not to be an effect of stresses from high environmental variability, namely salinity changes, in an environment analogous to the recent Florida Bay.

2.2 Stratigraphic and geographic calcification patterns

Extension rate, bulk density and calcification rate of the three genera *Solenastrea*, *Orbicella* and *Porites* from the Florida platform were plotted against geological time within the five time-slices 3.2, 2.9, 1.8, 1.2, and 0 Ma (Fig. 5, Tables 1, 2). Calcification data are undistinguishable among time-slices according to ANOVA ($p > 0.05$), but both, bulk density and calcification rate in recent *Solenastrea* is strikingly near the maximum

Low Florida coral calcification rates in the Plio-Pleistocene

T. C. Brachert et al.

Title Page

Abstract	Introduction
Conclusions	References
Tables	Figures

◄◄   ►►

◄   ►

Back   Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

values of fossil z-corals. These data are similar to those of *Orbicella* and *Porites* which also supports no consistent variation with taxonomy (Fig. 5).

Extension rates of recent z-corals documented by our literature review (various taxa) for the WA and IP have a broad range of values from 0.28 to 2.38 cm yr^{-1}, however, z-corals of the WA have significantly lower mean extension rates (0.28–1.44, mean: 0.79 ± 0.31 cm yr^{-1}) than those of the IP (0.30–2.38, mean: 1.28 ± 0.50 cm yr^{-1}, $p < 0.05$; Table 3). Fossil corals have lower values than the recent corals (0.16–0.89, mean: 0.45 ± 0.20 cm yr^{-1}, $p < 0.05$), even than those from the WA, and some of the fossils have the smallest values recorded (Fig. 6a). With regard to density, there is a broad range of values; however, no significant difference exists among the WA (0.78–1.94, mean: 1.37 ± 0.24 g cm^{-3}) and IP z-corals (1.01–1.90, mean: 1.30 ± 0.16 g cm^{-3}, $p > 0.05$), although the range of values is larger in the WA. Fossil corals have a similar range but clearly have significantly lower bulk density than the recent corals ($p < 0.05$) and also have the lowest minimum values of bulk density recorded (0.55–1.22, mean: 0.86 ± 0.22 g cm^{-3}; Table 2). The recent z-corals of the WA and IP show significant negative correlations between extension rate and density with an identical slope (F test; $p < 0.05$) and intercept. While the correlation in the IP z-coral data is highly significant ($R^2 = 0.52$, $p < 0.05$) it is weaker but still significant in the WA data ($R^2 = 0.14$, $p < 0.05$; Fig. 6a). The fossil reef corals show a significant negative relationship between extension rate and bulk density defined by linear regression as well, but the slope is steeper (F test; $p > 0.05$) than in the recent corals ($R^2 = 0.43$, $p < 0.05$) (Fig. 6a).

Calcification rates of z-corals have a large range of values from 0.18 to 2.82 g cm^{-2} yr^{-1} (Table 2). In recent and fossil z-corals, there is a significant positive correlation between extension and calcification rate ($p < 0.05$). In recent WA-corals, calcification rates (0.31–1.78, mean: 1.06 ± 0.38 g cm^{-2} yr^{-1}) remain clearly below those of the IP (0.56–2.82, mean: 1.67 ± 0.49 cm^{-2} yr^{-1}) because of higher extension rates. Importantly, the slope of the relationship is identical (F test; $p < 0.05$) in the WA and IP and the relationships are highly significant ($R^2 = 0.93$ and 0.70, $p < 0.05$, respectively), whereas the slope of the relationship is smaller by ∼ 50 % (F test; $p > 0.05$) in the fossil

corals (Fig. 6b). No such simple relationships exist between density and calcification rate. In the IP, there is a significant negative relation between density and calcification ($R^2 = 0.32$, $p < 0.05$), whereas in the WA, there is no relationship ($R^2 = 0.00$, $p > 0.05$; Fig. 6c). Therefore, variations in calcification rates in the latter region are entirely driven by changes in extension rates, whereas in the IP, it is driven by both extension rates and bulk density, and decreasing density weakens the effect of increased extension on calcification. In the data from the Florida fossils no relationship of density was found with calcification rate ($R^2 = 0.02$, $p > 0.05$) which means that changes of calcification rate fully depend on variable extension and the pattern in essence resembles that of the WA (Fig. 6b, c).

Interpretation: Generally, average calcification rates display a strong link with average SST. This has been documented in a number of studies (Carricart-Ganivet, 2004; Lough, 2008) and is also reflected by our synthesis of published data (Fig. 6d–f). In the IP, extension and calcification rates significantly increase with rising temperature while bulk density decreases. In the WA, the pattern is less clear. A systematic relationship of extension rate with temperature exists under the premise of a nonlinear process, whereas no relationships can be identified of bulk density and calcification rate with temperature, respectively, even when assuming nonlinear behavior (Fig. 6d–f).

Importantly, the recent z-corals from the WA display significantly lower values and a smaller range of values of all three calcification parameters (extension rate, bulk density, calcification rate) compared to the z-corals from the IP (Fig. 6d–f, Table 2). This corresponds with different temperature windows of z-coral distribution in the database. The WA corals in the database cover a rather small range of average annual temperature between 26.4 and 28.6 °C, whereas the IP z-corals represent the spectrum of average annual water temperature between 23.0 and 29.6 °C. Within these two temperature windows, differences between the WA and IP corals also pertain to patterns: In the IP, extension rates show a marked increase but bulk density decreases which combines to present a positive relationship of calcification rate with temperature. No such relationship exists in the WA corals (Fig. 6), however, distinct temperature con-

trols on calcification have been found by experimental studies on *Orbicella* within temperature limits $< 1\,^\circ$C (Carricart-Ganivet, 2004). Within this narrow window, a negative relationship with extension rate, but positive effect of temperature on bulk density and calcification rate has been observed (Carricart-Ganivet, 2004). In this context it has been hypothesised that calcification is non-linear beyond this narrow temperature window (Worum et al., 2007) because of the established non-linearity of life processes in poikilothermic biota alike the reef corals (Goreau and Macfarlane, 1990; Grizzle et al., 2001; Townsend et al., 2008). Linear regression is, therefore, likely inappropriate for describing the statistics of calcification within the temperature windows documented by the data and beyond (Fig. 4, 6d–f) and we have alternatively applied a quadratic polynomial to the data. This procedure results in an inverted parabolic relationship of extension rate with temperature ($p < 0.05$). Corresponding parabolic regressions for density and calcification rate are not significant ($p > 0.05$), however, and may be an effect of a rather poor quality of the data in the database. Although statistically not significant in all respects, this finding seems to conform with a previous modelling study for *Orbicella* (Worum et al., 2007). It predicts extension and calcification rate to rise from a lower threshold temperature towards an optimum and then to decline again until the maximum threshold temperature of ecological tolerance is reached. In contrast, bulk density will be highest at the lowest/highest extension and minimum/maximum threshold temperatures, respectively (Brachert et al., 2013; Gischler et al., 2009).

2.3 Provincial controls on calcification

Skeletal calcification in recent reef corals from the IP and WA is remarkable uniform. Although maximum extension rates in the IP are higher than those recorded in the WA, the overall relationship with density (slope and intercept of the regression) can be regarded as identical (Fig. 6). Recent z-corals from the WA display enhanced variability of bulk density associated with low extension rates, which results from the noisy inputs of *Diploria* and *Porites*, whereas *Orbicella* forms a consistent population like *Porites* in the IP (Fig. 4, 6). It should be noted, that the slope of linear regression is steeper in WA-

Orbicella than IP-*Porites* according to an *F* test ($p < 0.05$) (Fig. 4, 6A). In contrast, the Florida fossil z-corals have significantly lower extension rates and mean bulk densities than all of their recent counterparts, and also have an extension rate/density relationship which differs from that of all recent z-corals in the database ($p < 0.05$) (Fig. 4).

5 　　With regard to calcification rates, all recent corals display an identical relationship between extension rate and calcification, irrespective of taxon or provenance, and this relationship is significantly different from that of the fossils (*F* test $p < 0.05$) (Fig. 6b). The relationships of bulk density with calcification rate significantly differ in the populations from the recent WA, the IP, and the Plio-Pleistocene of Florida, respectively 10 (Fig. 6c).

　　From this discussion we conclude that recent and fossil z-corals clearly differ with regard to their relationships of extension rate with bulk density and that taxonomical peculiarities seem not to play a significant role in the general picture (Fig. 4, 6a). We further conclude, that the relationship of extension rate with calcification rate is identical 15 in recent z-corals from all ocean regions, but is significantly different between recent and fossil z-corals (Fig. 6b). Bulk density and calcification rate, on the other hand, display individual traits among the recent z-corals from the WA, the IP and the Plio-Pleistocene of Florida (Fig. 6c).

2.4　Effects of bioerosion and diagenesis on reconstructed calcification rates

20 Our fossil z-corals display a variation of bulk density, comparable to that of recent z-corals but the average from all fossil specimens ($0.86\,\mathrm{g\,cm^{-3}}$) is substantially lower than in the recent z-corals ($1.37\,\mathrm{g\,cm^{-3}}$) from the WA (Fig. 4, Table 3). Maximum values ($1.22\,\mathrm{g\,cm^{-3}}$) are lower than in the modern ($1.94\,\mathrm{g\,cm^{-3}}$) and minimum values of $0.55\,\mathrm{g\,cm^{-3}}$ are also below minimum values of recent WA z-corals ($0.78\,\mathrm{g\,cm^{-3}}$; Ta-25 ble 3). In order to rule out that low density is not an effect of differential bioerosion, density was measured using X-ray densitometry along transects defined from visual inspection of radiographs, and measurements were taken only in segments of the skeleton not affected by visible borings. In addition to bioerosion, low density in fos-

sil specimens may also be a result of diagenesis. The aragonitic skeleton is prone to modification by leaching, cementation and mineral transformation, and thus, to have particularly low or high values, respectively. Calcite is not documented by XRD analysis (detection limit of the method $\sim 1\%$), and visual inspection of the skeletons using a binocular microscope ($\times 15$ enlargement) and SEM revealed clean skeletal surfaces not covered systematically by secondary cements, except for localized, micron-scaled patches of spherulitic aragonite or patches of isopachous aragonite visible in SEM (Böcker, 2014) (Fig. 2). Density is, therefore, not significantly enhanced by secondary cements.

Hypocalcification with regard to the low values of bulk density might be due to leaching. Visible porosity within the centers of calcification does indeed imply some dissolution has occurred (Fig. 2). Since dissolution at the centers of calcification has also been reported from recent specimens (Perrin, 2004), this effect may also be present in the data from recent corals. Also, X-radiographs display very regular expressions of density bands, concordant with the growth structures of the skeleton and stable isotope records, but no cloudy density variations or patches of high (low) density as documented from diagenetically-altered specimens (Böcker, 2014; Brachert et al., 2006a; Mertz-Kraus, 2009). The presence of density bands implies the preservation of original density variations of the skeleton and, therefore, a rather pristine state of preservation for the specimens under consideration. In contrast to density, extension rate is not affected by diagenesis and data have been retrieved successfully from highly altered specimens (Brachert et al., 2006b; Gischler et al., 2009; Johnson and Pérez, 2006; Reuter et al., 2005). Consequently, estimates of calcification (extension, density and calcification rate) in our material can be considered to approximate the original skeletal configuration.

2.5 Environmental controls on calcification

Precipitation of $CaCO_3$ in shallow water environments, both inorganically as cement and biologically in z-corals, typically increases with increasing average SST (Carricart-

Ganivet, 2004; James, 1997; Lough, 2008). In this respect, it is important to note that the Pliocene and Pleistocene z-corals from Florida have a low volume of inorganic, early diagenetic carbonate cement, which is rather atypical compared to recent z-corals from coral reefs and carbonate platforms (James, 1997; Nothdurft and Webb, 2009). Therefore, lower calcification of z-corals and precipitation of inorganic carbonate cements on Florida carbonate platform during the Pliocene and Pleistocene may have occurred in cool waters, but no clear evidence for the presence of cool-water carbonates implying winter SSTs below 18 °C has been found (Brachert et al., 2014). However, beyond temperature effects, calcification rates of recent z-corals, are known to correspond in a complex way with the growth environment. Factors other than temperature include water depth, wave exposure, salinity and freshwater discharge, nutrient concentration, pH and $\Omega_{aragonite}$ (Cohen and Holcomb, 2009; D'Olivio et al., 2014; Ferrier-Pagès et al., 2000; Gladfelter et al., 1978; Hofmann et al., 2011; Johnson and Pérez, 2006; Klein et al., 1993; Lough and Cooper, 2011). Below we discuss the saturation state of seawater with respect to aragonite and SST as the most likely causes of low calcification rates in more detail.

2.6 Low calcification rates due to high nutrients or low $\Omega_{aragonite}$?

Experimental studies on z-coral skeletal accretion found calcification rates to be closely coupled with the saturation state of seawater with respect to aragonite ($\Omega_{aragonite}$). These laboratory studies found z-corals not to acclimatize to short-term changes in $\Omega_{aragonite}$ and calcification rates decline with decreasing $\Omega_{aragonite}$ (Cohen and Holcomb, 2009; Gattuso et al., 1998; Langdon et al., 2000). Cool upwelling waters have a number of adverse effects on z-coral growth, namely low pH/low $\Omega_{aragonite}$ of ambient water (Furnas, 2011). In our fossil materials, z-coral skeletons recording maximum upwelling according to their stable isotope composition, have the smallest density values but largest values of extension rate (Brachert et al., 2015). This conforms with findings from the Galapagos upwelling system, were z-coral skeletal density is reduced under maximum upwelling stresses, but extension rate is higher than predicted from

the ambient SST (Manzello et al., 2014). In an upwelling regime, the low volumes of cements in intra-skeletal porosity of the corals and the low degree of cementation of the shallow-marine carbonates may reflect the effects of phosphate poisoning (Hallock and Schlager, 1986; Manzello et al., 2014), but the benthic assemblages and low amounts of bioerosion do not provide compelling evidence for high eutrophy. If any, these findings support intermittent upwelling which has positively interfered with z-coral calcification on the Florida platform during the Plio-Pleistocene, but clearly documents minimal calcification rates to have coincided with episodes with minimum upwelling. Thus, the latter cannot be the prime reason for the observed low calcification rates.

Furthermore, low extension rates of the Plio-Pleistocene z-corals from Florida are fully compatible with those published from fossil z-corals at various locations in the tropical WA (various taxa) which also range between 0.3 and $0.8\,\mathrm{cm\,yr^{-1}}$ during the Pliocene (Johnson and Pérez, 2006), $\sim 0.3\,\mathrm{cm\,yr^{-1}}$ in the late Miocene (Denniston et al., 2008b) and 0.2 and $1.0\,\mathrm{cm\,yr^{-1}}$ in the Florida Reef Tract during the late Pleistocene (0.13 Ma) (Gischler et al., 2009) (Fig. 6g). For this reason, low extension rates recorded by the Florida fossils must rather be a large-scale regional or global phenomenon. The saturation of the sea water with $CaCO_3$ has been shown to be an environmental factor controlling calcification rates in z-corals (Langdon et al., 2000), and causes for low pH/low $\Omega_{\mathrm{aragonite}}$ in ambient water may be sought in high atmospheric $p\mathrm{CO_2}$ levels. Substantial $p\mathrm{CO_2}$ changes have been documented over the glacial/interglacial cycles of the Quaternary (Petit et al., 1999), concomitant with changes in calcification of calcareous plankton (Barker and Elderfield, 2002; Beaufort et al., 2011). Low calcification rates of the Florida corals may, therefore, be a likely effect of high $p\mathrm{CO_2}$ during the Plio-Pleistocene interglacials. However, for the last 3 Ma after the mid Pliocene climatic optimum ($\sim 3\,\mathrm{Ma}$), reconstructed $p\mathrm{CO_2}$ was near pre-industrial levels and only during and before the climatic optimum was at the levels predicted to exist by the end of this century (IPCC, 2013; Seki et al., 2010). Nonetheless, for the long-term buffering effect of the ocean, $\Omega_{\mathrm{aragonite}}$ has been suggested to have been not significantly different from

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

|◄ | ►|

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

the present day (Hönisch et al., 2012), and may be, for these reasons not a likely driver of the observed low calcification rates.

2.7 Low calcification rates due to heat stresses?

Next to $\Omega_{aragonite}$, temperature is an important control of z-coral calcification in the world oceans. Given the shortcomings in our reconstruction of SSTs discussed above, the extension rates still display a negative correlation with the average annual SST ($p < 0.05$) and bulk density a positive relationship with SST ($p < 0.05$). In contrast, no clear relation has been found between SST and calcification rate ($p > 0.05$), although visual inspection suggests an inverse correlation (Fig. 7). This pattern is qualitatively rather consistent with recent *Orbicella* from the Gulf of Mexico (Carricart-Ganivet, 2004), however, at a substantially larger temperature window in the fossil material and an absent relationship or likely negative correlation of calcification rate with temperature (Fig. 7).

Over the large temperature window of 6.9 °C covered by the modern IP data, a pattern of changes driven by temperature has been documented using linear regression (Fig. 6d–f). In contrast, the temperature range documented by z-corals from the WA database covers only 2.2 °C (Fig. 6d–f) and calcification data do not display any linear relationship. Rather, they can be approximated using a quadratic polynomial which suggests the present temperature window realized by recent z-corals of the WA to cover more or less the ecological spectrum of this coral province. Low extension rates documented by fossil z-corals from Florida and many other locations of the Caribbean, therefore, potentially document temperatures either near their lower or upper levels of ecological tolerance. In our temperature reconstruction using skeletal δ^{18}O values, we apply a value of δ^{18}O$_{water}$ which likely underestimates the actual SST because other methods consistently found SSTs of the WA warm pool ~ 2 °C above present values during the last 5 Ma (Fedorov et al., 2013; O'Brien et al., 2014) and low extension rates in z-corals may reflect warmer-than-present SSTs during the Plio-Pleistocene interglacials. Such an interpretation is consistent with concepts of nonlinear calcification responses to temperature in z-corals (Brachert et al., 2013; Gischler et al., 2009;

20534

Worum et al., 2007). Correspondingly, experimental approaches describing coral calcification within temperature windows of $\leq 1\,^{\circ}\mathrm{C}$ would not describe z-coral calcification over the full spectrum of ecological tolerance of a given species and may describe calcification near the optimum or lower/upper threshold of calcification, respectively. In application of these concepts, z-coral growth in the WA was likely under significant heat stress, and water temperatures no more than $2\,^{\circ}\mathrm{C}$ higher than at present were already causing calcification rates 50 % lower than present day. Decreasing rates of extension and calcification have also been reported from recent *Porites* to occur at high temperatures (Cantin et al., 2010; De'ath et al., 2013). It should be noted also, that upwelling has been ascribed a mitigating effect on SST stresses depending on the depth of upwelling or the timing during the year (Chollett et al., 2010; Riegl and Piller, 2003) and maximum extension rates/minimum density of the Florida z-corals coincided with a maximum of upwelling. Intermittent upwellings during the Plio-Pleistocene, therefore, seem to have created temporary refuges for z-corals by episodically mitigating heat stresses (Brachert et al., 2015). This finding supports notions of hot SSTs during the Eemian interglacial to have resulted in reef kills at equatorial latitudes and poleward migrations of z-coral taxa (Kiessling et al., 2012). Our data also suggest recent coral reefs at equatorial latitudes to be potentially endangered from rising SSTs with ongoing climate change and ocean acidification (IPCC, 2013).

3 Conclusions

This study presents the first record of calcification rates from fossil reef corals (z-corals).

Z-coral skeletons from Pliocene and Pleistocene precursors of the modern Florida carbonate platform display pristine preservation of stable isotope signatures and calcification data.

Extension rates of Plio-Pleistocene specimens from Florida (various taxa) are remarkably low, but compatible with those of tropical Caribbean settings at that time.

Calcification data are undistinguishable among geological time-slices (interglacials), but bulk density and calcification rate of a recent *Solenastrea* from Florida Bay is remarkably high compared to the fossils and equals their maximum values.

Average calcification rates of Pliocene and Pleistocene specimens, irrespective of z-coral taxon, were only 50 % of the recent values in the WA.

Combination of the calcification records with environmental proxy data (δ^{18}O, δ^{13}C) reveals an analogous relationship of calcification with temperature: density increase vs. calcification rate decrease with increasing temperature, but no (significant) relationship of calcification rate with temperature. The analogy, however, is only valid in terms of patterns but not of quantitative data.

The reasons behind low calcification rates during the Plio-Pleistocene interglacials are not clear but a lower-than-recent saturation of seawater with aragonite or high water temperatures near the limits of ecological tolerance are likely candidates.

Author contributions. T. C. Brachert designed this research; field work was carried out by T. C. Brachert, M. Reuter and J. S. Klaus. Laboratory analyses were performed by T. C. Brachert, S. Krüger and M. Reuter. K. Helmle provided calcification records from a recent *Solenastrea* from Florida Bay. T. C. Brachert, M. Reuter and J. M. Lough wrote the paper.

References

Allmon, W. D., Spizuco, M. P., and Jones, D. S.: Taphonomy and paleoenvironment of two turritellid-gastropod-rich beds, Pliocene of Florida, Lethaia, 28, 75–83, 1995.

Allmon, W. D.: Nutrients, temperature, disturbance, and evolution: a model for the late Cenozoic marine record of the western Atlantic, Palaeogr. Palaeocl., 166, 9–26, 2001.

Baker, P. A. and Weber, J. N.: Coral growth rate: Variation with depth, Earth Planet. Sc. Lett., 27, 57–61, 1975.

Barker, S. and Elderfield, H.: Foraminiferal Calcification Response to Glacial-Interglacial Changes in Atmospheric CO_2, Science, 297, 833–836, 2002.

Barker, C. E.: Fluid inclusions in the Pleistocene Miami Limestone, southeastern Florida: potentially misleading evidence of vadose diagenesis [abs.], Geological Society of America, Abstracts with Programs, 20, A119, 1986.

Bathurst, R. G. C.: Carbonate Sediments and their Diagenesis, Elsevier Science Publ. Co., New York, 1975.

Beaufort, L., Probert, I., de Garidel-Thoron, T., Bendif, E. M., Ruiz-Pino, D., Metzl, N., Goyet, C., Buchet, N., Coupel, P., Grelaud, M., Rost, B., Rickaby, R. E. M., and de Vargas, C.: Sensitivity of coccolithophores to carbonate chemistry and ocean acidification, Nature, 476, 80–83, 2011.

Bessat, F. and Buigues, D.: Two centuries of variation in coral growth in a massive Porites colony from Moorea (French Polynesia): a response of ocean-atmoshere variability from south central Pacific, Palaeogr. Palaeocl., 175, 381–392, 2001.

Böcker, A.: Interannual and seasonal climate variability recorded by reef corals, Plio/Pleistocene (Florida) and Mio/Pliocene (Dominican Republic), Dissertation, Fakultät für Physik und Geowissenschaften, Universität Leipzig, Leipzig, 2014.

Brachert, T. C., Reuter, M., Felis, T., Kroeger, K. F., Lohmann, G., Micheels, A., and Fassoulas, C.: *Porites* corals from Crete (Greece) open a window into Late Miocene (10 Ma) seasonal and interannual climate variability, Earth Planet. Sc. Lett., 245, 81–94, 2006a.

Brachert, T. C., Reuter, M., Kroeger, K. F., and Lough, J.: Coral growth bands: A new and easy to use paleothermometer in paleoenvironment analysis and paleoceanography (late Miocene, Greece), Paleoceanography 21, PA4217, doi:10.1029/2006PA001288, 2006b.

Brachert, T. C., Reuter, M., Krüger, S., Böcker, A., Lohmann, H., Mertz-Kraus, R., and Fassoulas, C.: Density banding in corals: barcodes of past and current climate change, Coral Reefs, 32, 1013–1023, 2013.

Brachert, T. C., Reuter, M., Krüger, S., Lohmann, H., Petuch, E. J., and Klaus, J. S.: A 4.2 Million years record of interglacial paleoclimate from sclerochronological data of Florida carbonate platform (Early Pliocene to recent), Global Planet. Change, 120, 54–64, 2014.

Discussion Paper | Discussion Paper | Discussion Paper | Discussion Paper |

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

⏮ | ⏭

◀ | ▶

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Brachert, T. C., Reuter, M., Krüger, S., Kirkerowicz, J., and Klaus, J. S.: Upwellings mitigated Plio-Pleistocene heat stress for reef corals on the Florida platform (USA), Biogeosciences Discuss., 12, 16553–16602, doi:10.5194/bgd-12-16553-2015, 2015.

Budd, A. F., Fukami, H., Smith, N. D., and Knowlton, N.: Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia), Zool. J. Linn. Soc., 166, 465–529, 2012.

Cantin, N. E., Cohen, A. L., Karnauskas, K. B., Tarrant, A. M., and McCorkle, D. C.: Ocean warming slows coral growth in the central Red Sea, Science, 329, 322–325, 2010.

Carricart-Ganivet, J. P., Beltrán-Torres, A. U., Merino, M., and Ruiz-Zárate, M. A.: Skeletal extension, density and calcification rate of the reef building coral Montastraea annularis (Ellis and Solander) in the Mexican Caribbean, B. Mar. Sci., 66, 215–224, 2000.

Carricart-Ganivet, J. P. and Merino, M.: Growth responses of the reef-building coral *Montastraea annularis* along a gradient of continental influence in the southern Gulf of Mexico, B. Mar. Sci., 68, 133–146, 2001.

Carricart-Ganivet, J. P.: Sea surface temperature and the growth of the West Atlantic reef-building coral Montastraea annularis, J. Exp. Mar. Biol. Ecol., 302, 249–260, 2004.

Chollett, I., Mumby, P. J., and Cortes, J.: Upwelling areas do not guarantee refuge for coral reefs in a warming world, Mar. Ecol.-Prog. Ser., 416, 47–56, 2010.

Cohen, A. L. and Holcomb, M.: Why corals care about ocean acidification. Uncovering the mechanism, Oceanography, 22, 118–127, 2009.

Constantz, B. R.: The primary surface area of corals and variations in their susceptibility to diagenesis, in: Reef Diagenesis, edited by: Schroeder, J. H. and Purser, B. H., Springer-Verlag, New York, 1986.

De'ath, G., Fabricius, K., and Lough, J.: Yes – Coral calcification rates have decreased in the last twenty-five years!, Mar. Geol., 346, 400–402, 2013.

Denniston, R. F., Asmeron, Y., Polyak, V. Y., McNeill, D., Klaus, J. S., Cole, P., and Budd, A. F.: Caribbean chronostratigraphy constrained with U-Pb and ^{87}Sr/^{86}Sr analysis of a Miocene coral, Geology, 36, 151–153, 2008a.

Denniston, R. F., Penn, S. C., and Budd, A. F.: Constraints on Late Miocene shallow marine seasonality for the Central Caribbean using oxygen isotopes and Sr/Ca ratios in a fossil coral. In: Evolutionary stasis and change in the Dominican Republic Neogene, edited by: Nehm, R. H. and Budd, A. F., Topics in Geobiology, 30, Springer Science and business Media B.V., Heidelberg, 2008b.

Low Florida coral calcification rates in the Plio-Pleistocene

T. C. Brachert et al.

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

|◄ | ►|

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Dodge, R. E. and Brass, G. W.: Skeleton extension, density and calcification of the reef coral *Montastrea annularis*: St. Croix, U.S. Virgin Islands, B. Mar. Sci., 34, 288–307, 1984.

D'Olivo, J. P., McCulloch, M. T., Eggins, S. M., and Trotter, J.: Coral records of reef-water pH across the central Great Barrier Reef, Australia: assessing the influence of river runoff on inshore reefs, Biogeosciences Discuss., 11, 11443–11479, doi:10.5194/bgd-11-11443-2014, 2014.

Dowsett, H. J. and Cronin, T. M.: High eustatic sea level during the middle Pliocene:Evidence from the southeastern U.S. Atlantic Coastal Plain, Geology, 18, 435–438, 1990.

Dullo, W.-C.: Progressive diagenetic sequence of aragonite structures: Pleistocene coral reefs and their modern counterparts on the eastern Red Sea coast, Saudi Arabia, Palaeontographica Americana, 54, 254–160, 1984.

Dustan, P.: Growth and form in the reef-building coral *Montastrea annularis*, Mar. Biol., 33, 101–107, 1975.

Elizalde-Rendon, E. M., Horta-Puga, G., Gonzalez-Diaz, P., and Carricart-Ganivet, J. P.: Growth characteristics of the reef-building coral *Porites astreoides* under different environmental conditions in the Western Atlantic, Coral Reefs, 29, 607–614, 2010.

Emslie, S. D. and Morgan, G. S.: A Catastrophic Death Assemblage and Paleoclimatic Implications of Pliocene Seabirds of Florida, Science, 264, 684–685, 1994.

Fabricius, K. E., Langdon, C., Uthicke, S., Humphrey, C., Noonan, S., De/'ath, G., Okazaki, R., Muehllehner, N., Glas, M. S., and Lough, J. M.: Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations, Nature Climate Change, 1, 165–169, 2011.

Fedorov, A. V., Brierley, C. M., Lawrence, K. T., Liu, Z., Dekens, P. S., and Ravelo, A. C.: Patterns and mechanisms of early Pliocene warmth, Nature, 496, 43–49, 2013.

Ferrier-Pagès, C., Gattuso, J.-P., Dallot, S., and Jaubert, J.: Effect of nutrient enrichment on growth and photosynthesis of the zooxanthellate coral *Stylophora pistillata*, Coral Reefs, 19, 103–113, 2000.

Flügel, E.: Microfacies analysis of carbonate rocks. Analysis, interpretation and application, Springer Verlag, Heidelberg, 2004.

Furnas, J.: Upwelling and coral reefs. In: Encyclopedia of modern coral reefs – structure, form and process, edited by: Hopley, D., Encyclopedia of earth sciences series, Springer, Dordrecht, 2011.

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

◄ | ►I

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Gattuso, J.-P., Frankignoulle, M., Bourge, I., Romaine, S., and Buddemeier, R. W.: Effect of calcium carbonate saturation of seawater on coral calcification, Global Planet. Change, 18, 37–46, 1998.

Gischler, E., Hudson, J., and Storz, D.: Growth of Pleistocene massive corals in south Florida: low skeletal extension-rates and possible ENSO, decadal, and multi-decadal cyclicities, Coral Reefs, 28, 823–830, 2009.

Gladfelter, E. H., Monahan, R. K., and Gladfelter, W. B.: Growth rates of five reef-building corals in the northeastern Caribbean, B. Mar. Sci., 28, 728–734, 1978.

Goodkin, N. F., Switzer, A. D., McCorry, D., DeVantier, L., D. True, J. D., Hughen, K. A., Angeline, N., and Yang, T. T.: Coral communities of Hong Kong: long-lived corals in a marginal reef environment, Mar. Ecol.-Prog. Ser., 426, 185–196, 2011.

Goreau, T. J. and Macfarlane, A. H.: Reduced growth rate of *Montastrea annularis* following the 1987–1988 coralbleaching event, Coral Reefs, 8, 211–215, 1990.

Graus, R. R. and Macintyre, I. G.: Variations in growth forms of the reef coral *Montastrea annularis* (Ellis & Sollander): a quantitative evaluation of growth response to light distribution using computer simulation. In: The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, I – Structure and Communities, edited by: Rützler, K. and Macintyre, I. G., Smithsonian Contributions to the Marine Sciences No. 12, Washington, D.C., 1982.

Griffiths, N., Müller, W., Johnson, K. G., and Aguilera, O. A.: Evaluation of the effect of diagenetic cements on element/Ca ratios in aragonitic Early Miocene (~ 16 Ma) Caribbean corals: Implications for "deep-time" palaeoenvironmental reconstructions, Palaeogeogr. Palaeocl., 369, 185–200, 2013.

Grizzle, R. E., Bricelj, V. M., and Shumway, S. E.: Physiological ecology of *Mercenaria mercenaria*, in: The biology of the hard clam, edited by: Kraeuter, J. N. and Castagna, M., Developments in aquaculture and fisheries science, 31, Elsevier, Amsterdam, 2001.

Hallock, P. and Schlager, W.: Nutrient excess and the demise of coral reefs and carbonate platforms, Palaios, 1, 389–398, 1986.

Helmle, K. P., Kohler, K. E., and Dodge, R. E.: The coral X-radiograph densitometry system: CoralXDS, Nova Southeastern University, Fort-Lauderdale-Davie, 2002.

Helmle, K. P., Dodge, R. E., Swart, P. K., Gledhill, D. K., and Eakin, C. M.: Growth rates of Florida corals from 1937 to 1996 and their response to climate change, Nature Communications, 2, 215, doi:10.1038/ncomms1222, 2011.

Low Florida coral calcification rates in the Plio-Pleistocene

T. C. Brachert et al.

Highsmith, R. C., Lueptow, R. L., and Schonberg, S. C.: Growth and bioerosion of three massive corals on the Belize barrier reef, Mar. Ecol.-Prog. Ser., 13, 261–271, 1983.

Hofmann, G. E., Smith, J. E., Johnson, K. S., Send, U., Levin, L. A., Micheli, F., Paytan, A., Price, N. N., Peterson, B., Takeshita, Y., Matson, P. G., Derse Crook, E., Kroeker, K. J., Gambi, M. C., Rivest, E. B., Frieder, C. A., Yu, P. C., and Martz, T. R.: High-Frequency Dynamics of Ocean pH: A Multi-Ecosystem Comparison, PLoS ONE, 6, doi:10.1371/journal.pone.0028983, 2011.

Hönisch, B., Ridgwell, A., Schmidt, D. N., Thomas, E., Gibbs, S. J., Slujis, A., Zeebe, R., Kump, L., Martindale, R. C., Greene, S. E., Kiessling, W., Ries, J., Zachos, J. C., Royer, D. L., Barker, S., Marchitto, T. M., Moyer, R., Pelejero, C., Ziveri, P., Foster, G. L., and Williams, B.: The geological record of ocean acidification, Science, 335, 1058–1063, 2012.

Hudson, J. H., Powell, G. V. N., Robblee, M. B., and Smith III, T. J.: A 107-year-old coral from Florida Bay: barometer of natural and man-induced catastrophies?, B. Mar. Sci., 44, 283–291, 1989.

IPCC: Summary for Policymakers. In: Climate Change 2013: The Physical Science Basis, Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, edited by: Stocker, T., Qin, D., Plattner, G.-K., Tignor, M. M. B., Allen, S. K., Boschung, J., Nauels, A., Xia, Y., Bex, V., and Midgley, P. M., Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 2013.

James, N. P.: The cool water carbonate depositional realm, Society for Sedimentary Geology, Special Publication, 56, 1–20, 1997.

Johnson, K. G. and Pérez, M. E.: Skeletal extension rates of Cenozoic Caribbean reef corals, Palaios, 21, 262–271, 2006.

Jones, D. S. and Allmon, W. D.: Records of upwelling, seasonality and growth in stable-isotope profiles of Pliocene mollusk shells from Florida, Lethaia, 28, 61–74, 1995.

Kiessling, W., Simpson, C., Beck, B., Mewis, H., and Pandolfi, J. M.: Equatorial decline of reef corals during the last Pleistocene interglacial, P. Natl. Acad. Sci. USA, 109, 21378–21383, 2012.

Klein, R., Pätzold, J., Wefer, G., and Loya, Y.: Depth-related timing of density band formation in *Porites* spp. corals from the Red Sea inferred from X-ray chronology and stable isotope composition, Mar. Ecol.-Prog. Ser., 97, 99–104, 1993.

Knutson, D. W., Buddemeier, R. W., and Smith, S. V.: Coral chronometers: seasonal growth bands in reef corals, Science, 177, 270–272, 1972.

Langdon, C., Takahashi, T., Sweeney, C., Chipman, D., and Goddard, J.: Effect of calcium carbonate saturation on the calcification rate of an experimental coral reef, Global Biogeochem. Cy., 14, 639–654, 2000.

Leder, J. J., Swart, P. K., Szmant, A., and Dodge, R. E.: The origin of variations in the isotopic record of scleractinian corals: 1. Oxygen, Geochim. Cosmochim. Ac., 60, 2857–2870, 1996.

Lidz, B. H.: Florida Keys, in: Encyclopedia of modern coral reefs - structure, form and process, edited by: Hopley, D., Springer, Dordrecht, 2011.

Lloyd, R. M.: A palaeoecological interpretation of the Caloosahatchee Formation, using stable isotope methods, J. Geol., 77, 1–25, 1969.

Lough, J. M.: Coral calcification from skeletal records revisited, Mar. Ecol.-Prog. Ser., 373, 257–264, 2008.

Lough, J. M. and Cooper, T. F.: New insights from coral growth band studies in an era of rapid environmental change, Earth-Sci. Rev., 108, 170–184, 2011.

Macintyre, I. G. and Pilkey, O. H.: Tropical Reef Corals: Tolerance of Low Temperatures on the North Carolina shelf, Science, 166, 374–375, 1969.

Mallela, J. and Perry, C. T.: Calcium carbonate budgets for two coral reefs affected by different terrestrial runoff regimes, Rio Bueno, Jamaica, Coral Reefs, 26, 129–145, 2007.

Manzello, D. P., Enochs, I. C., Bruckner, A., Renaud, P. G., Kolodziej, G., Budd, D. A., Carlton, R., and Glynn, P. W.: Galapagos coral reef persistence after ENSO warming across an acidification gradient, Geophys. Res. Lett., 41, 9001–9008, 2014.

McGregor, H. V. and Gagan, M. K.: Diagenesis and geochemistry of *Porites* corals from Papua New Guinea: Implications for paleoclimate reconstruction, Geochim. Cosmochim. Ac., 67, 2147–2156, 2003.

Meeder, J. F.: A field guide with road log to "The Pliocene fossil reef of southwest Florida", Miami, 19, 1979.

Mertz-Kraus, R.: Mediterranean-type climate in the south Aegean (Eastern Mediterranean) during the Late Miocene: Evidence from isotope and element proxies, Dr. rer. nat. Dissertation, Fachbereich Chemie, Pharmazie und Geowissenschaften, Universität Mainz, Mainz, 129 pp., 2009.

Mertz-Kraus, R., Brachert, T. C., and Reuter, M.: *Tarbellastraea* (Scleractinia): A new stable isotope archive for Late Miocene paleoenvironments in the Mediterranean, Palaeogr. Palaeocl., 257, 294–307, 2008.

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

◄◄ | ►►

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Mertz-Kraus, R., Brachert, T. C., Jochum, K. P., Reuter, M., and Stoll, B.: LA-ICP-MS analyses on coral growth increments reveal heavy winter rain in the Eastern Mediterranean at 9 Ma, Palaeogr. Palaeocl., 273, 25–40, 2009a.

Mertz-Kraus, R., Brachert, T. C., Reuter, M., Galer, S. J. G., Fassoulas, C., and Iliopoulos, G.: Late Miocene sea surface salinity variability in the Eastern Mediterranean inferred from coral aragonite δ^{18}O (Crete, Greece), Chem. Geol., 262, 202–216, 2009b.

Miller, K. G., Wright, J. D., Browning, J. V., Kulpecz, A., Kominz, M., Naish, T. R., Cramer, B. S., Rosenthal, Y., Peltier, W. R., and Sosdian, S.: High tide of the warm Pliocene: Implications of global sea level for Antarctic deglaciation, Geology, 1–4, doi:10.1130/G32869.1, 2012.

Nothdurft, L. D. and Webb, G. E.: Earliest diagenesis in scleractinian coral skeletons: implications for palaeoclimate-sensitive geochemical archives, Facies, 55, 161–201, 2009.

O'Brien, C. L., Foster, G. L., Martinez-Boti, M. A., Abell, R., Rae, J. W. B., and Pancost, R. D.: High sea surface temperatures in tropical warm pools during the Pliocene, Nat. Geosci., 7, 606-611, 2014.

Okazaki, R. R., Swart, P. K., and Langdon, C.: Stress-tolerant corals of Florida Bay are vulnerable to ocean acidification, Coral Reefs, 32, 671–683, doi:10.1007/s00338-013-1015-3, 2013.

Perrin, C.: Diagenèse précoce des biocristaux carbonatés : transformations isominérales de l'aragonite corallienne, B. Soc. Géol. Fr., 175, 95–106, 2004.

Petit, J. R., Jouzel, J., Raynaud, D., Barkov, N. I., Barnola, J.-M., Basile, I., Bender, M., Chappellaz, J., Davis, M., Delaygue, G., Delmotte, M., Kotlyakov, V. M., Legrand, M., Lipenkov, V. Y., Lorius, C., Pépin, L., Ritz, C., Saltzman, E., and Stievenard, M.: Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica, Nature, 399, 429–436, 1999.

Petuch, E. J. and Roberts, C. E.: The geology of the Everglades and adjacent areas, CRC Press, New York and Boca Raton, 2007.

Reuter, M., Brachert, T. C., and Kroeger, K. F.: Diagenesis of growth bands in fossil scleractinian corals: Identification and modes of preservation, Facies, 51, 155–168, 2005.

Riding, R., Liang, L., and Braga, J.-C.: Millennial-scale ocean acidification and late Quaternary decline of cryptic bacterial crusts in tropical reefs, Geobiology, 12, 387–405, doi:10.1111/gbi.12097, 2014. 2014.

Riegl, B. and Piller, W. E.: Possible refugia for reefs in times of environmental stress, Int. J. Earth Sci., 92, 520–531, 2003.

Low Florida coral calcification rates in the Plio-Pleistocene

T. C. Brachert et al.

Title Page

Abstract	Introduction
Conclusions	References
Tables	Figures

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Seki, O., Foster, G. L., Schmidt, D. N., Mackensen, A., Kawamura, K., and Pancost, R. D.: Alkenone and boron-based Pliocene pCO2 records, Earth Planet. Sc. Lett., 292, 201–211, 2010.

Shinn, E. A.: Coral growth-rate, an environmental indicator, J. Paleontol., 40, 233–240, 1966.

5 Swart, P. K., Healy, G. F., Dodge, R. E., Kramer, P., Hudson, J. H., Halley, R. B., and Robblee, M. B.: The stable oxygen and carbon isotopic record from a coral growing in Florida Bay: a 160 year record of climatic and anthropogenic influence, Palaeogeogr. Palaeocl., 123, 219–237, 1996.

Swart, P. K., Healy, G., Greer, L., Lutz, M., Saied, A., Anderegg, D., Dodge, R. E., and Rudnick, 10 D.: The use of proxy chemical records in coral skeletons to ascertain past environmental conditions in Florida Bay, Estuarines, 22, 384–397, 1999.

Tanzil, J. T. I., Brown, B. E., Tudhope, A. W., and Dunne, R. P.: Decline in skeletal growth of the coral Porites lutea from the Andaman Sea, South Thailand between 1984 and 2005, Coral Reefs, 28, 519–528, doi:10.1007/s00338-008-0457-5, 2009.

15 Tao, K. and Grossman, E. L.: Origin of high productivity in the Pliocene of the Florida platform: Evidence from stable isotopes, Palaios, 25, 796–806, 2010.

Townsend, C. R., Begon, M., and Harper, J. L.: Essentials of Ecology, Blackwell, Oxford, 2008.

Worum, F. P., Carricart-Ganivet, J. P., Besnon, L., and Golicher, D.: Simulation and observation of annual density banding in skeletons of Montastrea (Cnidaria: Scleractinia) growing under 20 thermal stress associated with ocean warming, Limnol. Oceanogr., 52, 2317–2323, 2007.

Table 1. Sampling sites in southern Florida. The numbering follows that given by Brachert et al. (2014).

No.	Site	Sample ID	Genus	GPS Coordinates	Lithostratigraphy	Age (Ma)
4	Palm Beach Aggregates	EP8	*Solenastrea*	26°41.742′ N, 80°21.270′ W	Bermont Fm. (Holey Land Mb.)	1.2
		EP9A	*Solenastrea*			
		EP9B	*Orbicella*			
		EP9C	*Solenastrea*			
		EP9D	*Solenastrea*			
8	Brantley Pit, Arcadia	EP6-S2	*Solenastrea*	27°2.988′ N, 81°49.611′ W	Caloosahatchee Fm. (Bee Branch Mb.)	1.8
9	DeSoto Sand and Shell LLC (site 452)	452-K1-S6*	*Solenastrea*	27°3.587′ N, 81°47.627′ W	Caloosahatchee Fm. (Bee Branch Mb.)	1.8
		452-K3*	*Solenastrea*			
		452-K4	*Solenastrea*			
		452-K5*	*Solenastrea*			
		452-13*	*Solenastrea*			
		452-K14	*Solenastrea*			
		452-K15*	*Solenastrea*			
		452-K17*	*Solenastrea*			
15	Mule Pen Quarry	EP1-S2	*Solenastrea*	26°10.410′ N, 81°42.468′ W	Tamiami Fm. (Golden Gate Mb.)	2.9
		EP2-S2	*Orbicella*			
		EP3	*Porites*			
		EP5-S2	*Solenastrea*			
16	Quality Aggregates (APAC)	Coral #1	*Solenastrea*	Not available	Tamiami Fm. (Pinecrest Mb., unit 7)	3.2

* Böcker (2014)

Table 2. Extension rate, bulk density and calcification rate in recent and fossil reef corals.

Taxon	n	Minimum mean extension rate (cm yr⁻¹)	Maximum mean extension rate (cm yr⁻¹)	Mean extension rate (cm yr⁻¹)	Minimum bulk density (g cm⁻³)	Maximum bulk density (g cm⁻³)	Mean bulk density (g cm⁻³)	Minimum calcification rate (g cm⁻² yr⁻¹)	Maximum calcification rate (g cm⁻² yr⁻¹)	Mean calcification rate (g cm⁻² yr⁻¹)
Orbicella	80	0.38	1.44	0.91 ± 0.23	0.78	1.94	1.37 ± 0.24	0.65	1.78	1.22 ± 0.25
Diploria	8	0.30	0.40	0.35 ± 0.04	0.97	1.70	1.27 ± 0.31	0.31	0.68	0.45 ± 0.14
Porites (W-Atlantic)	15	0.28	0.48	0.37 ± 0.07	1.10	1.72	1.44 ± 0.20	0.31	0.77	0.53 ± 0.14
Porites (Indo-Pacific)	78	0.30	2.38	1.28 ± 0.50	1.01	1.90	1.30 ± 0.16	0.56	2.82	1.67 ± 0.49
Solenastrea (Florida Bay, recent);	1			0.54			1.07			0.57
Solenastrea (1.2, 1.8, 2.9, 3.2 Ma)	16	0.22	0.83	0.42 ± 0.17	0.55	1.22	0.87 ± 0.22	0.20	0.97	0.38
Orbicella (1.2, 2.9 Ma)	2	0.16	0.64	0.40	0.76	1.14	0.95	0.18	0.48	0.33
Porites (2.9 Ma)	1			0.89			0.60			0.54
Fossil (total)	20	0.16	0.86	0.44 ± 0.19	0.55	1.83	0.96 ± 0.36	0.18	0.82	0.38 ± 0.16

Table 3. Bulk calcification data of recent reef corals in the Indo-Pacific and Western Atlantic together with fossil reef corals from Florida (USA). Bold: minimum values.

Region with geological age	n	Extension min ($cm\,yr^{-1}$)	Extension max ($cm\,yr^{-1}$)	Extension mean ($cm\,yr^{-1}$)	Density min ($g\,cm^{-3}$)	Density max ($g\,cm^{-3}$)	Density mean ($g\,cm^{-3}$)	Calc min ($g\,cm^{-2}\,yr^{-1}$)	Calc max ($g\,cm^{-2}\,yr^{-1}$)	Calc mean ($g\,cm^{-2}\,yr^{-1}$)
Indo-Pacific, recent	78	0.30	2.38	1.28 ± 0.50	1.01	1.90	1.30 ± 0.16	0.56	2.82	1.67 ± 0.49
Western Atlantic, recent	103	0.28	1.44	0.79 ± 0.31	0.78	1.94	1.37 ± 0.24	0.31	1.78	1.06 ± 0.38
Florida Bay, recent	1			0.54			1.07			0.57
Florida (USA), Plio-Pleistocene	20	0.16	0.86	0.44 ± 0.19	0.55	1.22	0.86 ± 0.22	0.18	0.54	0.34 ± 0.11
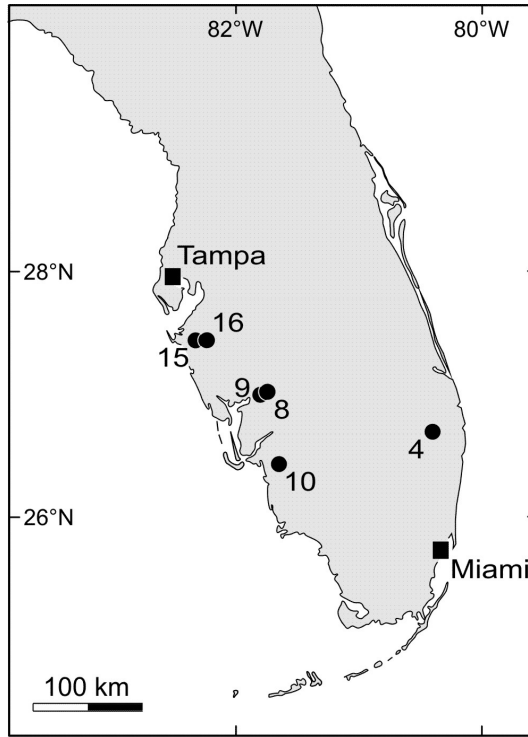
Figure 1. Sampling stations in southern Florida/USA (dots). See Table 1 for details and numbering of sampling stations.
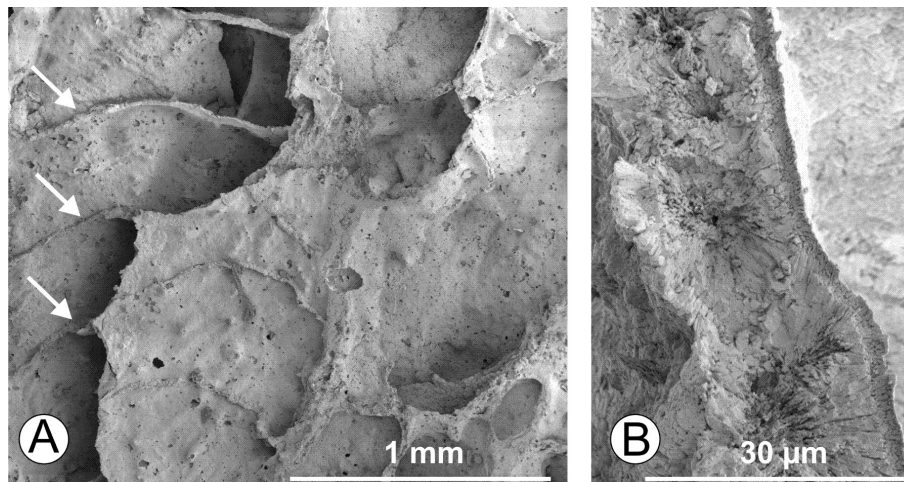
Figure 2. SEM images of fossil coral skeleton (*Solenastrea* sp. EP 6), Caloosahatchee Fm. (1.8 Ma), Brantley Pit, Florida/USA. **(a)** Overview of septal surfaces. Curved ridges represent the traces of broken dissepiments (arrows). Holes within septa are mechanical defects. **(b)** Cross-section of dissepiment showing radial fiber architecture of sclerodermites. Note minor preferential dissolution at the centers of the trabecular fans.

Figure 3. Digital X-ray photographs (positive prints) from fossil z-corals. **(a)** *Solenastrea* sp. (EP 5, Mule Pen Quarry, Tamiami Fm., age 2.5 Ma). **(b)** *Porites* sp. (EP3, Mule Pen Quarry, Tamiami Fm., age 2.9 Ma). Scale bar 2 cm.

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

|◄ | ►|

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion
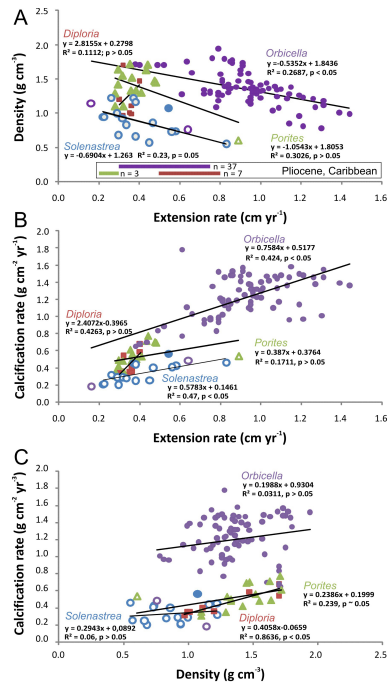
Figure 4. Extension rate, bulk skeletal density and calcification rate of reef corals sorted according to taxon and geological time (Western Atlantic region). Magenta: *Orbicella*, green: *Porites*, red: *Diploria*, blue: *Solenastrea*. Filled symbols: recent, open symbols: fossil. Data on recent corals compiled from the literature (Carricart-Ganivet et al., 2000; Carricart-Ganivet and Merino, 2001; Dodge and Brass, 1984; Elizalde-Rendon et al., 2010; Highsmith et al., 1983; Hudson et al., 1989; Mallela and Perry, 2007) and one unpublished record from *Solenastrea* (FB6). Inset in A shows range of extension rates of z-corals of Pliocene age in the Caribbean region (various taxa) for comparison (Johnson and Pérez, 2006). Note clustering of fossil corals at low extension rates, low density and low calcification rates.
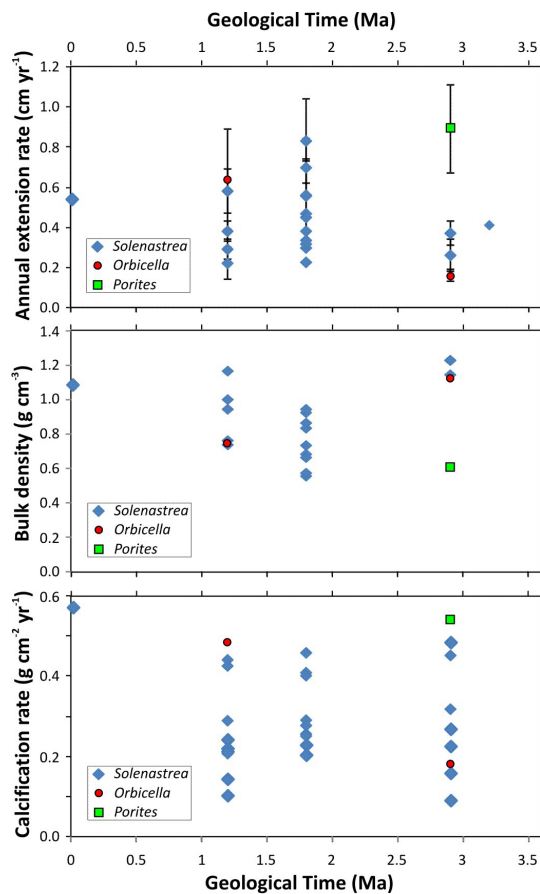
Figure 5. Temporal variation of extension rate (±1σ), bulk density and calcification rate in three z-coral genera (*Solenastrea*, *Orbicella*, *Porites*) from the Florida platform.

Figure 6. Experimental data of extension rate, density and calcification rate of recent and fossil z-corals. Indo-Pacific (green triangles), Western Atlantic (red squares) and Florida fossils (blue diamonds). **(a–c)** Descriptive diagrams for relationships of extension rate, density, and calcification rate within the temperature windows shown in **(d–f)** for modern corals. Recent corals compiled from literature (Carricart-Ganivet et al., 2000; Carricart-Ganivet and Merino, 2001; Dodge and Brass, 1984; Elizalde-Rendon et al., 2010; Highsmith et al., 1983; Hudson et al., 1989; Lough, 2008; Mallela and Perry, 2007; Tanzil et al., 2009). Red horizontal bar in Fig. 5a summarizes published extension rates of z-corals of Pliocene age in the Caribbean region (various taxa) for comparison (Johnson and Pérez, 2006). **(d–f)** Extension rate, bulk density and calcification rates as a function of average annual temperature. Results of linear and quadratic polynomial regression are as follows: **(a)** Western Atlantic $y = -0.2958x + 1{,}6072$; $R^2 = 0.1399$, $p < 0.05$. Indo-Pacific $y = -0.2499x + 1.6358$; $R^2 = 0.5167$, $p < 0.05$. Florida (fossils) $y = -0.7607x + 1.2774$; $R^2 = 0.4297$, $p < 0.05$. **(b)** Western Atlantic $y = 1.0235x + 0.2545$; $R^2 = 0.6956$, $p < 0.05$. Indo-Pacific $y = 1.0212x + 0.3064$; $R^2 = 0.9327$, $p < 0.05$. Florida (fossils) $y = 0.4961x + 0.1648$; $R^2 = 0.3171$, $p < 0.05$. **(c)** Western Atlantic $y = 0.1428x + 0.868$; $R^2 = 0.0084$, $p > 0.05$. Indo-Pacific $y = -1.7219x + 3.9122$; $R^2 = 0{,}3204$, $p < 0.05$. Florida (fossils) $y = -0.0779x + 0.4058$; $R^2 = 0.0233$, $p > 0.05$. **(d)** Western Atlantic $y = -0.3747x^2 + 20.525x - 280.21$; $R^2 = 0.3524$; $p < 0.05$ and $y = -0.0104x + 0.9913$; $R^2 = 0.0006$; $p > 0.05$. Indo-Pacific $y = -0.0203x^2 + 1.3294x - 19.628$; $R^2 = 0.7519$; $p < 0.05$ and $y = 0.2472x - 5.282$; $R^2 = 0.7376$; $p < 0.05$. **(e)** Western Atlantic $y = 0.1588x^2 - 8{,}7235x + 121.16$; $R^2 = 0.1128$; $p > 0.05$ and $y = -0.0193x + 1.9758$; $R^2 = 0.0036$; $p > 0.05$. Indo-Pacific $y = 0.0206x^2 - 1.1664x + 17.691$; $R^2 = 0.5101$; $p < 0.05$ and $y = -0.0613x + 2.9539$; $R^2 = 0.3885$; $p < 0.05$. **(f)** Western Atlantic $y = -0.4333x^2 + 23.722x - 323.44$; $R^2 = 0.2699$; $p < 0.05$ and $y = -0.0282x + 1.7778$; $R^2 = 0.0025$; $p > 0.05$. Indo-Pacific $y = -0.0223x^2 + 1.4534x - 21.144$; $R^2 = 0.7476$; $p < 0.05$ and $y = 0.2566x - 5.1844$; $R^2 = 0.7322$; $p < 0.05$.
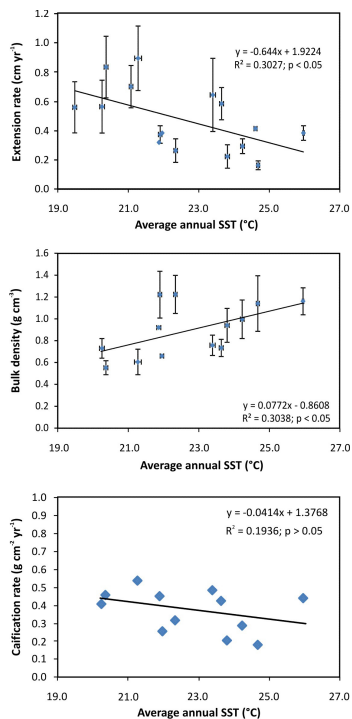
Figure 7. Diagrams showing annual extension rate ($cm\,yr^{-1}$), bulk density ($g\,cm^{-3}$) and annual calcification rate ($g\,cm^{-2}\,yr^{-1}$) with water temperature inferred from published $\delta^{18}O$ values (Brachert et al., 2014). For temperature estimates we used the stable isotope composition of modern seawater along the Florida reef tract ($\delta^{18}O_{water} = 1.1‰$ SMOW) and the temperature equation by Leder et al. (1996). The reconstructed SSTs are likely noisy because the corals analysed derive from different locations and stratigraphic units. This reconstruction likely underestimates Plio-Pleistocene temperatures due to the assumption of modern $\delta^{18}O_{water}$ and are intended to be relative estimates only.

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

|◄ | ►|

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion