Low Florida coral calcification rates in the Plio-Pleistocene

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Abstract

1

2 In geological outcrops and drill cores from reef frameworks, the skeletons of scleractinian

3 corals are usually leached and more or less completely transformed into sparry calcite because

4 the highly porous skeletons formed of metastable aragonite ($CaCO_3$) undergo rapid diagenetic

5 alteration. Upon alteration, ghost structures of the distinct annual growth bands allow often

6 for reconstructions of annual extension (= growth) rates, but information on skeletal density

7 needed for reconstructions of calcification rates is invariably lost upon alteration. This report

8 presents the bulk density, extension rates and calcification rates of fossil reef corals which

9 underwent minor diagenetic alteration only. The corals derive from unlithified shallow water

10 carbonates of the Florida platform (southeastern USA), which formed during four interglacial

11 sea level highstands dated approximately 3.2, 2.9, 1.8, and 1.2 Ma in the mid Pliocene to early

12 Pleistocene. With regard to the preservation, the coral skeletons display smooth growth

13 surfaces with minor volumes of marine aragonite cement within intra-skeletal porosity.

14 Within the skeletal structures, voids are commonly present along centers of calcification

15 which lack secondary cements. Mean extension rates were 0.44 ± 0.19 cm yr^{-1} (range 0.16 to

16 0.86 cm yr^{-1}), mean bulk density was 0.96 ± 0.36 g cm^{-3} (range 0.55 to 1.83 g cm^{-3}) and

17 calcification rates ranged from 0.18 to 0.82 g cm^{-2} yr^{-1} (mean 0.38 ± 0.16 g cm^{-2} yr^{-1}), values

18 which are 50 % of modern shallow-water reef corals. To understand the possible mechanisms

19 behind these low calcification rates, we compared the fossil calcification rates with those of

20 modern zooxanthellate-corals (z-corals) from the Western Atlantic (WA) and Indo-Pacific

21 calibrated against sea surface temperature (SST). In the fossil data, we found a widely

22 analogous relationship with SST in z-corals from the WA, i.e. density increases and extension

23 rate decreases with increasing SST, but over a significantly larger temperature window during

24 the Plio-Pleistocene. With regard to the environment of coral growth, stable isotope proxy

25 data from the fossil corals and the overall structure of the ancient shallow marine

26 communities are consistent with a well-mixed, open marine environment similar to the

2

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 localized to account also for low extension rates of Pliocene z-corals

throughout the tropical Caribbean in the WA 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 episodically moderated by

intermittent upwelling affecting the Florida platform seems to be another 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

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

The skeleton of zooxanthellate corals (z-corals) is a highly organized, porous hard tissue

formed of mineral $CaCO_3$ (aragonite). 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. One pair of these "density bands" usually represents one year of

growth (Knutson et al., 1972) and forms the basis for the calibration of internal age models

and for estimates of the extension rates, i.e. the rate of upward and outward growth of the

colony surface (Lough and Cooper, 2011). Skeletal bulk density is a measure of the volume of

pore volumes within the skeleton; the less porosity the 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 equation (1) (Lough and Cooper, 2011):

calcification rate (g cm^{-2} yr^{-1}) = annual extension rate (cm yr^{-1}) x density (g cm^{-3})   (1)

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Alternative concepts of quantifying coral skeletal growth have been reviewed by Pratchett an

co-workers (Pratchett et al., 2015). In addition to the basic calcification parameters described

above, serial chemical and isotope proxy data retrieved along the direction of maximum

skeletal extension provide independent quantitative measures of the environment. Stable

isotope ratios of the oxygen ($\delta^{18}O$) are sensitive to sea surface water temperature (SST) and

serial samples over the growth bands allow for the documentation of seasonal or interannual

SST variability on multi-annual time-scales (decade and century scale) (Felis and Pätzold,

2004; Leder et al., 1996; Swart, 1983). Limitations of the method pertain to the influence of

seawater $\delta^{18}O$ which is subject to changes due to precipitation/evaporation (i.e. salinity) and

river discharge. To overcome the problem of variable seawater $\delta^{18}O$ for SST estimates,

chemical element proxies of SST rather insensitive to evaporation/precipitation (Sr/Ca, U/Ca,

Mg/Ca) are in use in combination with skeletal $\delta^{18}O$ (Felis et al., 2004; Shen and Dunbar,

1995; Swart, 1981). Other chemical elements (Ba/Ca, Y/Ca, B/Ca) and carbon stable isotope

ratios ($\delta^{13}C$) have been shown to be recording sensitively productivity, river discharge, pH, or

also subtle diagenetic alterations (Allison et al., 2007; McCulloch et al., 2003; Sinclair et al.,

1998; Swart et al., 2010).

In the geological record, the skeletons of scleractinian corals and other sedimentary 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 (Schroeder and Purser,

1986). Although 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

4

1   withdrawn. These alterations represent growths of inorganic aragonite fiber crystals and

2   subtle dissolution phenomena within the centers of calcification (COC) (Perrin, 2004).

3   Differential diagenetic processes on crystalline phases and organic matrices also exist and

4   include aragonite – aragonite recrystallizations associated with a loss of micron-sized growth

5   information (McGregor and Gagan, 2003; Nothdurft and Webb, 2009; Perrin, 2004). In

6   contrast, in the classical freshwater diagenetic environment, the primary surface area of the

7   skeleton controls diagenetic susceptibility and rates of alteration (Constantz, 1986; Dullo,

8   1984). The freshwater effects are dominated by dissolution via moldic porosity and

9   subsequent reduction of pore spaces by cementation, or dissolution and associated

10   crystallization of blocky calcite without developing a significant moldic stage (Bathurst,

11   1975). In the latter process, ghost structures reflecting original microstructures will be

12   preserved (Flügel, 2004). More often, ghost structures of the growth bands form by subtle,

13   diffusion-controlled dissolution which preferentially starts at the COCs and continues to form

14   increasingly hollow skeletal structures (Reuter et al., 2005). The rate of skeleton-internal

15   dissolution via diffusion differs among growth bands within a specimen and responds to

16   bands of higher and lower density (Reuter et al., 2005). Given the situation where no

17   secondary addition of carbonate material has taken place, however, the hollow structures may

18   still be suitable for isotope and geochemical proxy analysis (Mertz-Kraus et al., 2009a; Mertz-

19   Kraus et al., 2008; Mertz-Kraus et al., 2009b). Following infilling by late diagenetic calcite

20   spar, this differential dissolution process leaves records of growth bands from which skeletal

21   extension can be retrieved (Brachert et al., 2006b; Johnson and Pérez, 2006; Shinn, 1966).

22   But, this process of dissolution and subsequent cementation of moldic and intra-particle

23   porosity tends to destroy all information pertaining to skeletal density. Alteration of the

24   primary skeleton along this diagenetic pathway is obvious by the presence of calcite, either

25   replacing skeletal structures or infilling skeletal porosity. While the petrographic aspect of the

26   calcite documents the type of freshwater or burial alteration environment,

cathodoluminescence analysis and geochemical data may provide further information as to the redox character of the diagenetic fluids (Flügel, 2004). Alteration of aragonite is commonly a rapid process, but in the rare event of low pore-water circulation rates, corals do escape diagenetic alteration (Anagnostou et al., 2011; Brachert et al., 2006a; Brachert et al., 2016; Denniston et al., 2008a; Gothmann et al., 2015; Griffiths et al., 2013; Mertz-Kraus et al., 2008).

In this study we present calcification data from z-corals with rather intact skeletal density 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 z-corals of the WA and Indo-Pacific (IP). According to this database, temperature generally boosts calcification rates in modern z-corals, but field studies on single species of z-coral suggest the rates to decline beyond optimum values (Carricart-Ganivet et al., 2012; Cooper et al., 2008). The non-linearity of calcification rates ($g\ cm^{-2}\ yr^{-1}$) derives from inputs of two independent variables: skeletal growth rate (extension rate, $cm\ yr^{-1}$) and skeletal density ($g\ cm^{-3}$) (Lough, 2008). The temperature effects on extension rates of *Porites* from the IP are well documented over a large temperature window and display slow increases with temperature below but sharp decreases above optimum (Cantin et al., 2010; Carricart-Ganivet et al., 2012; Lough and Barnes, 2000). The temperature responses of extension rate and density, however, are generally believed to markedly differ according to taxon and/or ocean region (Highsmith, 1979) and are further complicated by proximality trends reflecting temperature and seasonality gradients, exposure, effluxes of "inimical" bank waters, or nutrient supplies (Lough and Cooper, 2011; Manzello et al., 2015b). We discuss whether the patterns of z-coral calcification found in the fossils from the Florida Platform is a local or global signature corresponding with temperature stress or low supersaturation of the sea water

1   with respect to aragonite ($\Omega_{aragonite}$) during the Plio-Pleistocene interglacials. This study

2   complements two previous papers using sclerochronology of bivalves and z-corals for

3   reconstructions of the paleoenvironments and long-term changes of seasonality in southern

4   Florida (Brachert et al., 2016; Brachert et al., 2014) and provides a discussion of the

5   quantitative data in the context of recent global z-coral calcification patterns.

6

7   **1.2   The Florida Platform during the Plio-Pleistocene interglacials**

8   During the Plio-Pleistocene interglacials, global sea levels were up to 22 m (Miller et al.,

9   2012) or even 35 m higher (Dowsett and Cronin, 1990) and global mean temperatures 2 to

10   4°C warmer than present, whereas SSTs of the warm pools at low latitudes were ~2°C higher

11   than present (Fedorov et al., 2013; O'Brien et al., 2014). Although dramatic cooling occurred

12   in the high latitudes, long-term atmospheric pCO_2 appears to have remained rather constant

13   after the mid Pliocene climatic optimum (~3 Ma) until the present (Seki et al., 2010). During

14   and before the optimum, however, pCO_2 reached values expected for the end of this century

15   through the burning of fossil fuels (IPCC, 2013; Seki et al., 2010). Modeling of the oceanic

16   carbonate systems suggest the long-term pCO_2 changes to have had no effect on the saturation

17   state of seawater with regard to $\Omega_{aragonite}$ (Hönisch et al., 2012), but evidence exists that rates

18   of microbial carbonate precipitation and skeletal accretion of planktic foraminifera differed

19   over the last glacial / interglacial cycle, in response to changes of $\Omega_{aragonite}$ driven by pCO_2

20   (Barker, 1986; Beaufort et al., 2011; Riding et al., 2014).

21

22   The Plio-Pleistocene Florida carbonate platform represents a stack of shallow marine

23   carbonate sequences formed during sea level highstands which are separated by paleosols or

24   thin freshwater units formed during lowstands. A pronounced reef system existed along the

25   southwestern margin of the peninsula (Meeder, 1979). The single unlithified marine units

26   contain a diverse mollusk and coral fauna comparable to that of the present reef tracts and

1   back-reef systems (Meeder, 1979; Petuch and Roberts, 2007). Combined oxygen and carbon

2   stable isotope data (δ^{18}O, δ^{13}C) of diagenetically pristine mollusks and z-corals from the

3   platform sediments reflect the complexity of the depositional setting including brackish to

4   hypersaline and well-mixed, open marine environments (Brachert et al., 2014; Lloyd, 1969;

5   Tao and Grossman, 2010). The reasons for high benthic carbonate productivity by mollusks

6   during the Plio-Pleistocene is controversial, and has been suggested to be due to high nutrient

7   concentrations resulting from freshwater input (Tao and Grossman, 2010) or upwelling

8   (Allmon, 2001; Allmon et al., 1995; Brachert et al., 2016; Emslie and Morgan, 1994; Jones

9   and Allmon, 1995). Recently, SST estimates for the Pliocene and Pleistocene interglacial

10   units have been retrieved from δ^{18}O values from the reef corals *Solenastrea* and *Orbicella* and

11   assuming a modern seawater value for δ^{18}O (δ^{18}O$_{water}$) at the Florida Reef Tract (FRT). Apart

12   from low SSTs believed to be essentially the effect of upwelling, the large range of values is

13   likely in part an artifact of the uniform value for seawater δ^{18}O (δ^{18}O$_{water}$) used for the

14   calculations, irrespective of sampling locality and stratigraphic unit (Brachert et al., 2016). In

15   contrast, seasonal SST variability (~7 °C) inferred from cyclic δ^{18}O variations of the fossils is

16   independent of assumptions of δ^{18}O$_{water}$. Reconstructed seasonality is not only remarkably

17   constant within specimens and over the last 3.2 Ma, but also fits modern surface seasonality

18   along the reef tract (Brachert et al., 2016; Brachert et al., 2014). Large seasonality as

19   prevailing off North Carolina (Macintyre and Pilkey, 1969) or in inner coastal waters of

20   Florida Bay (FB) (Swart et al., 1996) has not been encountered in the data from the reef corals

21   and has also been taken for inferring a normal shallow-marine environment without unusual

22   stress from cool waters or evaporation and freshwater influxes (Brachert et al., 2014).

23

24   In southern Florida, the most extensive growth of reef corals occurs at present along the FRT

25   on the Atlantic side of the peninsula, whereas only limited z-coral growth occurs along the

1 Gulf side in the west and the shallow FB in the southeast. On the Atlantic side, coral

2 communities are characterized by diverse stands comprising abundant *Orbicella* (Lidz, 2011),

3 whereas on the Gulf side and in FB, coral growth is restricted to the two eurytopic taxa

4 *Siderastrea* and *Solenastrea* (Okazaki et al., 2013; Swart et al., 1999). Published extension

5 rates for recent *Solenastrea* inhabiting the most marine segments of FB range from 0.51 to 0.9

6 cm yr^{-1} (Hudson et al., 1989; Swart et al., 1996). Recent *Solenastrea* has also been recorded to

7 grow under rather cold water conditions along the US southeastern Atlantic coast off North

8 Carolina (Macintyre and Pilkey, 1969), but quantitative calcification data from that setting are

9 not available, leaving the question unanswered regarding the effects of low SST on extension

10 and density. Colony sizes at the northern sites similar to those of the lower latitudes have been

11 suggested to indicate similar extension and calcification rates, however (Macintyre and

12 Pilkey, 1969).

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16 **1.3   Materials**

17 Z-corals were sampled from four distinct stratigraphic units of the Florida carbonate platform

18 (USA) representing interglacial highstands of sea level subsequent to the Pliocene warm

19 period. They were dated 3.2, 2.9, 1.8 and 1.2 million years (Ma) of the mid Pliocene and early

20 Pleistocene (Fig. 1, Tab. 1) (Brachert et al., 2014). Our own sampling focused on *Solenastrea*

21 ($n = 11$) which is a common taxon in the Plio-Pleistocene shallow water carbonates of

22 southwestern Florida. This dataset was complemented by specimens of *Orbicella* ($n = 2$) and

23 *Porites* ($n = 1$) and one dataset of a *Solenastrea* taken from the literature comprising serial

24 $\delta^{18}O$ and $\delta^{13}C$ values and annual extension rates (Roulier and Quinn, 1995) (Tab. 1).

25

26 **1.4   Methods**

1   Fossil corals selected for this study were cut into <1cm thick slabs along the plane of

2   maximum growth using a conventional rock saw equipped with a water-cooled diamond

3   blade. All corals were screened for diagenetic alteration using a binocular microscope and

4   scanning electron microscope (SEM). In order to detect minimal contaminations by secondary

5   calcite, powder samples taken at random were prepared for X-ray diffraction (XRD) and

6   analysed using a Rigaku Miniflex diffractometer at angles between 20° to 60° 2θ. Only

7   skeletal areas that retained their original aragonite mineralogy (XRD), skeletal porosity and

8   microstructure without evidence for significant secondary crystal growth or dissolution

9   (microscopic and SEM observation) were accepted for further sample preparation. Coral slabs

10   of equal thickness were X-rayed using a digital X-ray cabinet (SHR 50 V) to identify potential

11   zones of diagenetic alteration (McGregor and Gagan, 2003; Reuter et al., 2005), bioerosion,

12   and to document the density bands (Knutson et al., 1972). One coral specimen (452K1) was

13   analysed geochemically using LA-ICP-MS (Böcker, 2014) with regard to concentrations of

14   environmentally sensitive elements (e.g. Sr/Ca, U/Ca, B/Ca) and following recommendations

15   for evaluating the diagenetic status of corals from strongly lithified and altered limestone

16   (Anagnostou et al., 2011; Gothmann et al., 2015). LA-ICP-MS analyses were performed at

17   the Max Planck-Institut für Chemie (Mainz, Germany) using a NewWave UP 213 laser

18   ablation system coupled to a ThermoFisher Element 2 ICP-MS.

19

20   Quantitative density measurements were made using the software CoralXDS (freeware)

21   according to Helmle and co-workers (Helmle et al., 2002). In this approach, the CoralXDS

22   software compares the gray values recorded in X-radiographs from corals with those from

23   aluminum plates having the same thickness as a background picture and an aluminum wedge

24   for density calculations. Measurements were done along transects parallel to the corallites and

25   parallel to the sampling transects for stable isotope analyses (Brachert et al., 2016). Bulk

26   skeletal density was calculated as the mean of all individual measurements taken along a

1   given transect. Calibration of the measurements was tested by measurements of standards for

2   zero density (air) and massive aragonite (slice of a *Glycimeris* bivalve shell having a thickness

3   equaling that of the coral slice). External analytical precision of the routine measurements was

4   tested by double blind measurements, and mean deviation from regression ($R^2 = 0.91$, p <

5   0.05) was found to be 0.04 ± 0.01 g cm^{-3} (range = 0.02 to 0.05 g cm^{-3}; n = 18).

6

7   As a baseline for the description and interpretation of the data from the fossils, we use

8   calcification data from recent corals reported in the literature deriving equally from tropical

9   and high latitudinal localities within the shallow-water reef belt (Baker and Weber, 1975;

10   Bessat and Buigues, 2001; Carricart-Ganivet et al., 2000; Carricart-Ganivet and Merino,

11   2001; Dodge and Brass, 1984; Dustan, 1975; Elizalde-Rendon et al., 2010; Fabricius et al.,

12   2011; Goodkin et al., 2011; Graus and Macintyre, 1982; Helmle et al., 2011; Highsmith et al.,

13   1983; Hudson et al., 1989; Lough, 2008; Mallela and Perry, 2007; Tanzil et al., 2009), and

14   one unpublished record of *Solenastrea* from FB (FB-6). We present a set of three descriptive

15   diagrams for a comparison of the patterns of calcification (extension rate, bulk density,

16   calcification rate) in the modern and fossil z-corals on the basis of linear regression. For a

17   deeper understanding of the processes, we further apply quadratic polynomial regression

18   models of experimental data calibrated with SST to account for the established non-linearity

19   of life processes.

20

21   Stable isotope data described here are the same as reported in companion publications by

22   Brachert et al. (2014, 2016) where all details of the methodology of sampling and analytical

23   procedures have been reported in detail. All carbonate values are given in per mil (‰) relative

24   to PDB according to the delta notation.

25

1   The scleractinian genus name *Orbicella* is used for corals previously assigned to *Montastraea*

2   according to the revised taxonomic classification of the reef coral family Mussidae by (Budd

3   et al., 2012). According to the same work (op. cit.), the genus *Diploria* has been split into the

4   genera *Diploria* and *Pseudodiploria*. We use the two genus names in combination as

5   *Diploria*/*Pseudodiploria*, because our database likely incorporates material from both genera

6   sensu Budd et al. (2012).

7

8   Statistical analyses were performed using the PAST paleontological statistics software

9   package (version 3.01) for education and data analysis (freeware *folk.uio.no/ohammer/past/*).

10 Variability of stable isotope data ($\delta^{18}O$, $\delta^{13}C$) was evaluated using the T-test. A linear

11 bivariate model was tested as to whether there were no statistical differences in the stable

12 isotope values in a dataset ($p > 0.05$) against the alternate hypothesis that there were

13 significant differences ($p < 0.05$). Equality of regression slopes was tested using the F-test as

14 assumed by analyses of covariance (ANCOVA). One-way analysis of variance (ANOVA)

15 tested if there were no statistical differences in the mean growth parameters (extension,

16 density, calcification) between two given coral sites ($p > 0.05$) against the alternate hypothesis

17 that there were significant differences ($p < 0.05$).

18

19 **2   Results and discussion**

20 **2.1   Preservation**

21 The metastable carbonate mineral aragonite forming the z-coral skeleton is prone to

22 modification by leaching, cementation and mineral transformation causing skeletal density to

23 be reduced or enhanced. Visual inspection of the skeletons using a binocular microscope (x 15

24 enlargement) and SEM revealed clean skeletal surfaces not covered systematically by

25 secondary cements (Fig. 2a, e), except for localized, micron-scaled patches of spherulitic

26 aragonite or patches of isopachous aragonite (Böcker, 2014). SEM observation has not

1   revealed any clear evidence for aragonite – aragonite recrystallizations (Fig. 2) but some

2   porosity within the centers of calcification (COCs, Fig. 2b). The latter does indeed imply

3   some dissolution has occurred, and therefore, subtle reductions of skeletal density, however,

4   since dissolution at the COCs has also been reported from recent specimens (Perrin, 2004),

5   this effect may also be present in the data from recent corals.

6   Secondary calcite is not documented by XRD analysis (detection limit of the method ~1%)

7   and has very rarely been observed to occur within skeletal growth porosity but never within

8   voids formed by preferential dissolution of the COCs (Fig. 2b) or microborings (Fig. 2e, f).

9   Published geochemical screenings using LA-ICP-MS for specimen 452 K1 (Böcker, 2014)

10   documented variable ratios of Sr/Ca and U/Ca which are in phase with serial $\delta^{18}O$ data. These

11   element ratios reflect SST variations consistent with reconstructions on the basis of serial

12   $\delta^{18}O$ values and recent instrumental seasonality along the FRT (Böcker, 2014). The positive

13   correlation of the Sr/Ca with U/Ca and the B/Ca ratios fluctuating between 0.3 and 0.6

14   mmol/mol is fully consistent with modern z-corals and implies little alteration has taken

15   place, especially because boron is known to be a diagenetically highly volatile element

16   (Allison et al., 2010; Böcker, 2014). According to our conviction, all these data provide no

17   critical evidence for the alteration of the original skeleton. Because of this line of reasoning

18   and low overall calcite content evident from XRD analysis (calcite below detection limits),

19   we refrained from measuring element ratios sensitive to the redox conditions of calcite

20   precipitating freshwaters or burial fluids (Fe/Ca, Mn/Ca) and other more sophisticated

21   geochemical methods as potential measures of alteration (Anagnostou et al., 2011; Gothmann

22   et al., 2015).

23

24   X-radiographs display very regular expressions of density bands, concordant with the growth

25   structures of the skeleton and stable isotope records, but no cloudy density variations or

26   patches of high (low) density as documented from diagenetically-altered specimens (Böcker,

1   2014; Brachert et al., 2006a; Mertz-Kraus, 2009). The presence of concordant density bands

2   implies the preservation of original density variations of the skeleton and, therefore, supports

3   the conclusion of a pristine state of preservation for the specimens under consideration (Fig.

4   3). It should be noted that density was measured using X-ray densitometry along transects

5   defined from visual inspection of radiographs, and measurements were taken only in segments

6   of the skeleton not affected by borings (bivalves, sponges, sipunculids) or embedded

7   encrusting biota (serpulids, bivalves). Bulk density data presented by this study and in a

8   companion publication (Brachert et al., 2016), are therefore, not influenced by the volume of

9   macroscopic biogenic borings or incrustations, although these effects may also be inherent to

10   published density data of recent corals. This is an important issue, because other approaches

11   have used "net density" (i.e. the integrative weight of carbonate laid down by the coral and

12   encrusting biota minus losses by bioerosion within a volume) for comparative calcification

13   studies (Kuffner et al., 2013). In contrast to density, extension rate is not sensitive to

14   diagenetic alterations and many data have been retrieved earlier from highly altered fossil

15   coral specimens of the WA and Mediterranean regions (Brachert et al., 2006b; Gischler et al.,

16   2009; Johnson and Pérez, 2006; Reuter et al., 2005). All of these observations and reasoning

17   suggest the z-corals selected for this calcifications study to be essentially unaltered by

18   diagenesis and X-ray densitometry to produce robust data.

19

2.2   Calcification

21   The Pliocene and Pleistocene z-corals from the Florida Platform display extension rates that

22   range from 0.16 to 0.86 cm yr^{-1} with a mean value of 0.44 $\pm$ 0.19 cm yr^{-1} ($n = 15$, $\pm$ 1σ), bulk

23   skeletal densites between 0.55 and 1.52 g cm^{-3} with a mean of 0.86 $\pm$ 0.22 g cm^{-3} ($n =14$),

24   and skeletal calcification rates from 0.18 to 0.54 g cm^{-2} yr^{-1} with a mean = 0.34 + 0.11 g cm^{-2}

25   yr^{-1} ($n =14$) (Fig. 4, Tab. 3). Annual extension rates and bulk skeletal density show a

26   significant negative correlation (R^2 = 0.329; p = 0.026), i.e. density decreases with increasing

1   extension rates. In contrast, extension rates and calcification rates display a positive

2   relationship ($R^2 = 0.484$; $p = 0.004$), which implies that calcification rates also decline with

3   increasing extension. Lastly, bulk density and calcification rate display no relationship ($R^2 =$

4   0.025; $p = 0.797$) (Fig. 4). Although no statistics were applied to the data of *Orbicella* ($n = 2$)

5   and *Porites* ($n = 1$) their calcification systematics seem to be indistinguishable from those of

6   *Solenastrea* according to visual assessment (Fig. 4). With regard to variability over geological

7   time, extension rate, bulk density and calcification rate of the three genera *Solenastrea*,

8   *Orbicella* and *Porites* from the Florida platform were plotted according to four time-slices

9   3.2, 2.9, 1.8, and 1.2 Ma (Fig. 5, Tab. 1, 2), and all calcification data were found to be

10   undistinguishable among time-slices according to ANOVA ($p > 0.05$). Published extension

11   rates of z-corals reported from various other fossil low-latitude sites of the WA region are

12   ~0.3 cm yr^{-1} in late Miocene reefs (Denniston et al., 2008b) and range from 0.3 to 0.8 cm yr^{-1}

13   in Pliocene units (Johnson and Pérez, 2006), whereas they were 0.2 and 1.0 cm yr^{-1} in the

14   Florida Reef Tract (FRT) during the late Pleistocene (0.13 Ma) (Gischler et al., 2009). As

15   such, they are all consistent with the low extension rates reported by our study (Fig. 4).

16   Importantly, skeletal density data are not available from these sites due to pervasive

17   diagenetic alterations, and therefore, skeletal density and calcification rates are unknown.

18

19   For the recent time-slice (0 Ma) we use analogue data from southern Florida published in the

20   literature and complemented in part by one new set of average values (FB-6) published here

21   for the first time (Tab. 4).

22

23   The extension rates of recent *Solenastrea* from FB range from 0.51 to 0.89 cm yr^{-1} and are

24   fully within the range found in the Pliocene and Pleistocene corals (Fig. 5). Density values

25   have not been published from FB z-corals so far; we measured a density of 1.07 g cm^{-3} (Tab.

26   2) which is compatible with fossil *Solenastrea*. The same is true for the *Orbicella* from FRT

as compared to the two fossil *Orbicella*, whereas the density records available from the FRT-*Porites* are substantially above that from the fossil *Porites* which is near the lower end of the spectrum (Fig. 5, Tab. 4). Finally, calcification rates of all three taxa of the recent z-corals in FB and FRT tend to be above the Plio-Pleistocene reconstructions (Fig. 5), and the average of all recent corals is significantly higher than the fossil average value ($p < 0.05$). From these observations the following three generalizations can be made: (1) the extension rates of the fossil z-corals are indistinguishable from those of the recent corals, and no distinction exists between FB and FRT, nearshore and offshore. (2) Bulk density is essentially the same in recent and fossil Florida z-corals, although some tendency towards higher bulk density as compared to the fossils may exist. (3) The calcification rates of the recent z-corals are all higher than those of the fossils (Fig. 5).

Stable isotope proxy data of the growth environments from the corals used here for calcification records were described and interpreted in a companion paper (Brachert et al., 2016) and will not be repeated in detail. For estimates of SSTs, an equation using skeletal $\delta^{18}O$ calibrated for *Orbicella* from FRT was applied (Leder et al., 1996) and making the assumption of a constant value of $\delta^{18}O_{water} = 1.1$ ‰ (recent FRT water) for all relevant interglacials (Brachert et al., 2016). On this basis, we found average annual SSTs between 19 and 26 °C which were likely moderated by intermittent upwelling. Reconstructed temperatures display a negative correlation with annual extension rates ($p < 0.05$) and a positive relationship with bulk density ($p < 0.05$). In contrast, no clear relation has been found between SST and calcification rate ($p > 0.05$), although visual inspection suggests an inverse correlation (Fig. 6). Making other assumptions for $\delta^{18}O_{water}$ (but keeping the value constant for all specimens) will yield other temperature values, but the range of values between minima and maxima of average annual temperatures will remain unaffected.

2.3 Significance of the calcification data

Calcification of z-corals responds to a complex array of environmental factors acting in concert as to control net calcification (Lough and Cooper, 2011). Next to water temperature, these factors include water depth, wave exposure, admixtures of "inimical waters" from carbonate bank interiors, high and low salinity or freshwater discharge, nutrient concentration, pH and aragonite saturation ($\Omega_{aragonite}$) (Cohen and Holcomb, 2009; D´Olivio et al., 2014; Ferrier-Pagès et al., 2000; Ginsburg and Shinn, 1964; Gladfelter et al., 1978; Hofmann et al., 2011; Johnson and Pérez, 2006; Klein et al., 1993; Lough and Cooper, 2011; Shinn, 1966). Thus, low calcification rates of the fossil corals can have multiple causes which are eventually hard to reconstruct. In attempting to sort out small-scale effects along environmental gradients, patterns related to taxonomy and non-linear calcification responses, we use a big picture approach beyond environmental gradients and regional acclimatization effects and compare the reconstructed growth parameters within the frame of measured systems in southern Florida, the WA and IP (see methods sections for data sources).

2.4 Environmental effects on calcification in recent and fossil z-corals from southern Florida

We use modern analogue data from southern Florida for an evaluation of the calcification rates documented here for z-corals from Pliocene and Pleistocene units of the Florida Platform. In southern Florida, environments of z-coral growth range from the salinity stressed environment of the FB where z-corals only thrive within the most marine parts, to the open settings of the FRT variably affected by the outflow of "inimical" waters from the interior bank. Within this region, the highest rates of outflow of bankwater occur in the Middle Florida Keys where also the lowest calcification rates have been observed (Manzello et al., 2015a). Negative interference by inimical bank waters with z-coral growth has been hypothesized, therefore, to be smaller in offshore reefs (>4.5 km from coast) compared to

1   inshore reefs (<4.5 km from coast). Nonetheless, long-term data averaged from several

2   *Porites* colonies (Manzello et al., 2015a) do not indicate to a measurable negative spatial

3   onshore-offshore effect on z-coral calcification. A proximality effect is also not inherent to

4   the averaged analogue data shown in figure 5: Although low calcification of *Solenastrea* in

5   FB may be considered compatible with the inimical bank water hypothesis, even lower

6   calcification rates of *Porites* from an offshore reef is clearly not. Apparently, small-scale

7   spatial stress effects reported in the literature seem to be averaged out from the big picture.

8   Because also no difference in calcification responses to environmental effects was found

9   between *Orbicella cavernosa* and *Porites astreoides* (Manzello et al., 2015a), we consider the

10   fossil data and recent analog data homogeneous entities not biased by systematic-taxonomical

11   effects. From this line of reasoning we conclude the low calcification rates of the long-term

12   fossil record from southern Florida not to reflect a restricted growth environment.

13

14   **2.5   Descriptive patterns of calcification in recent and fossil z-corals**

15   The calcification records presented by this study have been classified according to three

16   descriptive patterns: (1) A negative relationship of extension rate with density being fully

17   compatible with patterns of recent *Orbicella.* In recent *Porites*, the situation is more complex,

18   because the pattern is documented only in the IP (Lough, 2008), but not in the WA (Elizalde-

19   Rendon et al., 2010). (2) Extension rate and calcification rate showing a positive relation has

20   been described also in recent *Porites* from the WA and IP (Elizalde-Rendon et al., 2010;

21   Lough, 2008), but not in *Orbicella* from the WA which differ by a negative slope (Carricart-

22   Ganivet, 2004). This is a surprising result, because the skeletal organization of *Solenastrea*

23   closely resembles that of *Orbicella* and differs significantly from *Porites*, a pattern which was

24   expected to be reflected in the systematics of calcification. (3) The fossil *Solenastrea* and

25   recent *Orbicella* and *Porites* display deviating relationships with regard to bulk density and

26   calcification rates: while the fossil *Solenastrea* shows no relationship, it is positive in

1   *Orbicella* and WA-*Porites* but negative in IP-*Porites* (Carricart-Ganivet, 2004; Elizalde-

2   Rendon et al., 2010; Lough, 2008). When plotted against water temperatures, the three

3   calcification parameters and qualitative trends of the fossils are rather consistent with those of

4   recent *Orbicella* from the WA (Carricart-Ganivet, 2004), both, in terms of the overall effects

5   of temperature on extension rate and on bulk density. They differ, however, by the absence of

6   a temperature control on calcification rates (or the presence of a likely negative slope

7   according to visual inspection) in the fossils.

8

9   **2.6   Comparative analysis of fossil and recent z-coral calcification**

10   Calcification rates recorded by the fossil z-corals are conspicuously low as compared to recent

11   z-corals from Florida (Fig. 5) which may represent, therefore, possibly no suitable analogue

12   system. First of all, it should be noted, however, that the calcification data from the fossil

13   *Solenastrea* (plus *Orbicella* and *Porites*) appear to be from a larger window of average annual

14   temperatures (~7 °C) than covered by field studies on recent z-coral growth. Temperature

15   differences behind growth data from southern Florida are rather small, and even growth data

16   collected in the Gulf of Mexico and the Caribbean Sea both cover small gradients of average

17   annual SSTs (~1 °C) where *Orbicella* (*Orbicella annularis*) display positive calcification

18   responses with increasing SST (Carricart-Ganivet, 2004). Although calcification rates are the

19   same in both regions, average annual SSTs differ by ~2 °C and likely reflect the

20   acclimatization of the same morphological taxon to regionally different SST regimes. Thus,

21   acclimatization effects on calcification seem to play a role within rather small observational

22   scales. Within the same region, another species of the same genus (*Orbicella falveolata*),

23   however, responds with declining calcification to this subtle gradient of ~1°C of average

24   annual SST change (Carricart-Ganivet et al., 2012), either because acclimatization is not yet

25   fully accomplished, or because the SST regime is near the upper threshold of ecological

26   tolerance of *O*. *falveolata* allowing no further positive acclimatization. We assume, the latter

19

1   is more likely and, therefore, calcification responses to SST seem to be non-linear over the

2   full range of ecological tolerance of this and other taxa. This sort of non-linear responses of

3   calcification has been predicted by a modeling study on the ecological tolerance of *Orbicella*

4   over a temperature window of $3 - 4$ °C (Worum et al., 2007) and is also well documented by

5   comprehensive field studies on *Porites* from the Great Barrier Reef system (IP) (Cooper et al.,

6   2008; De'ath et al., 2013; De'ath et al., 2009). The tipping point between increases and

7   decreases of calcification rates was found to be between 26 °C and 27 °C for *Porites* and

8   *Orbicella* (Carricart-Ganivet et al., 2012; Cooper et al., 2008), or $28 - 29$ °C according to

9   modeling (Worum et al., 2007). This kind of large-scale observational data seems essential for

10   interpreting fossil calcification data and, therefore, we discuss the calcification data in the

11   context of the entire WA and IP.

12

13   2.6.1   Florida and Western Atlantic

14   Within the larger context of the WA, all parameters of calcification are higher in the recent z-

15   corals than in the fossil z-corals. The extension rates of the fossils with a mean of 0.44 ± 0.19

16   cm yr^{-1} and ranging from 0.16 to 0.86 cm yr^{-1} contrast with substantially higher mean values

17   of 0.79 ± 0.31 cm yr^{-1} and ranges between 0.28 cm yr^{-1} and 1.44 cm yr^{-1} in the recent WA

18   (Fig. 7; Tab. 3). Bulk density of the fossil z-corals displays a variability comparable to that of

19   recent z-corals but the average from all fossil specimens (0.86 ± 0.22 g cm^{-3}) is substantially

20   lower than in the recent z-corals (1.37 ± 0.24 g cm^{-3}) from the WA in our database (Fig. 7,

21   Tab. 3). Maximum values (1.22 g cm^{-3}) are lower than in the modern corals (1.94 g cm^{-3}) and

22   minimum values of 0.55 g cm^{-3} are also below minimum values of recent WA z-corals (0.78 g

23   cm^{-3}; Tab. 3). Calcification rates inferred from this set of inputs for any give extension rate

24   are ~50 % lower in fossils than those from modern z-corals.

25

1   The recent data from the WA are from the four genera (listed according to the number of data

2   available) *Orbicella, Porites, Diploria/Pseudodiploria* and *Solenastrea*, however, and some of

3   the discrepancy between fossils and recent z-corals, may therefore be an artifact of the

4   database. When compared on the taxonomical genus level, extension rates of *Porites* (range =

5   0.28 to 0.48, mean = $0.37 + 0.07$ cm yr^{-1}) and *Diploria/Pesudodiploria* (range = 0.30 to 0.40,

6   mean = $0.35 + 0.04$ cm yr^{-1}) are significantly lower than those of *Orbicella* (range = 0.38 to

7   1.44, mean = 0.91 ± 0.23 cm yr^{-1}, $p < 0.05$) but are identical with regard to density (*Porites*:

8   range =1.10 to 1.72, mean = 1.44 ± 0.20 g cm^{-3}; *Diploria/Pseudodiploria*: range = 0.97 to

9   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};

10   $p > 0.05$). *Orbicella* display a negative relationship between extension rate and bulk density

11   ($R^2 = 0.27$, $p < 0.05$), whereas no such relationship has been documented for *Porites* ($R^2 =$

12   0.30, $p > 0.05$) and *Diploria/Pseudodiploria* ($R^2 = 0.11$, $p > 0.05$) which are indistinguishable

13   in their calcification data (Fig. 7). Remarkably, *Porites* and *Diploria/Pseudodiploria* are

14   indistinguishable not only with regard to their general calcification relationship but also

15   quantitatively in terms of absolute values and clearly differ from those of *Orbicella*, whose

16   calcification rates are significantly higher at almost any given density (Fig. 7). *Solenastrea* is

17   unusual due to its low extension rates (range = 0.22 to 0.58, mean = 0.43 ± 0.19 cm yr^{-1}) and

18   low bulk density (range = 0.55 to 1.22, mean = 0.88 ± 0.22 g cm^{-3}). Like *Orbicella*, extension

19   rate and bulk density display a significant negative relationship ($R^2 = 0.23$, $p < 0.05$), whereas

20   extension rate is positively correlated with calcification rate ($R^2 = 0.47$, $p < 0.05$). Bulk

21   density, on the other hand, displays no correlation with calcification rate ($R^2 = 0.06$, $p > 0.05$).

22

23   For the relationships described above, we find no consistent patterns of the parameters of

24   calcification between recent and fossil specimens and between taxa. While the data from the

25   recent *Solenastrea* specimen is similar to the data from fossil *Solenastrea* (Fig. 7), the single

26   fossil *Porites* available is incompatible with recent *Porites* from the WA, both in terms of

1   extension rate and bulk density, but plots together with fossil *Solenastrea* (Fig. 7). Also, the

2   Pliocene *Diploria/Pseudodiploria* (only extension rates available from literature data) clearly

3   differ from their recent counterparts with significantly higher extension rates (Fig. 7). With

4   regard to *Orbicella*, bulk density of the two fossil specimens available is lower at any given

5   extension rate than in the recent *Orbicella*, but consistent with fossil *Solenastrea* (Fig. 7). In

6   extension rate vs. bulk density space, we observe a duality between recent and fossil z-corals,

7   rather than any taxonomical distinction. With regard to calcification rates, fossils also have

8   lower values at any given extension rate than recent z-corals (Fig. 7). On the other hand, no

9   clear separation exists between fossils and recent z-corals with regard to bulk density vs.

10   calcification rate because of very high extension rates of *Orbicella* compared to the other taxa

11   (Fig. 7). In contrast to field studies having demonstrated calcification systematics of reef

12   corals to differ between the genera *Orbicella* of the WA and *Porites* of the IP (Carricart-

13   Ganivet, 2004; Lough, 2008), systematics of calcification of z-corals seem, therefore, to

14   depend also on ocean regions or coral provinces.

15

16   2.6.2   Indo-Pacific

17   Extension rates of recent z-corals documented by our literature review for the WA (various

18   taxa) and IP (*Porites* only) have a broad range of values from 0.28 to 2.38 cm yr^{-1}, however,

19   z-corals of the WA have significantly lower mean extension rates (0.28 – 1.44, mean: $0.79 \pm$

20   0.31 cm yr^{-1}) than those of the IP (0.30 – 2.38, mean: 1.28 ± 0.50 cm yr^{-1}, $p < 0.05$; Tab. 3).

21   Fossil corals have lower values than the recent corals (0.16 – 0.89, mean: 0.45 ± 0.20 cm yr^{-1},

22   $p < 0.05$), including those from the WA, and some of the fossils have the smallest values

23   recorded (Fig. 8A). With regard to density, there is a broad range of values; however, no

24   significant difference exists among the WA (0.78 – 1.94, mean: 1.37 ± 0.24 g cm^{-3}) and IP z-

25   corals (1.01 – 1.90, mean: 1.30 ± 0.16 g cm^{-3}, $p > 0.05$), although the range of values is larger

26   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}; Tab. 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. 8A). 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. 8A).

Calcification rates of z-corals have a large range of values from 0.18 to 2.82 g cm^{-2} yr^{-1} (Tab. 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. 8B). 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. 8C). 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. 8B, C).

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. 8D-F, Tab. 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. 8). 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 likely

inappropriate for describing the statistics of calcification within the temperature windows

documented by the data and beyond (Fig. 8D-F) and we have alternatively applied a quadratic

function to the data. With respect to the WA 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 ($p > 0.05$), and may be an

effect of rather poor resolution of the temperature data in the database. The relationship is,

however, consistent with calcification data from regional studies (Carricart-Ganivet, 2004;

Carricart-Ganivet et al., 2012), but on a large scale.

3   Lessons from the recent analogue

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. 8). Recent z-corals from the WA display enhanced variability of bulk density

24

1   associated with low extension rates, which results from the noisy inputs of

2   *Diploria*/*Pseudodiploria* and *Porites*, whereas *Orbicella* forms a consistent population like

3   *Porites* in the IP (Fig. 7, 8). It should be noted, that the slope of linear regression is steeper in

4   WA-*Orbicella* than IP-*Porites* according to an F-test ($p < 0.05$) (Fig. 5, 7A). In contrast, the

5   Florida fossil z-corals have significantly lower extension rates and mean bulk densities than

6   all of their recent counterparts, and also have an extension rate / density relationship which

7   differs from that of all recent z-corals in the database ($p < 0.05$) (Fig. 6).

8

9   With regard to calcification rates, all recent corals display an identical relationship between

10   extension rate and calcification, irrespective of taxon or provenance, and this relationship is

11   significantly different from that of the fossils (F-test $p < 0.05$) (Fig. 8B). The relationships of

12   bulk density with calcification rate, however, significantly differ in the populations from the

13   recent WA, the IP, and the Plio-Pleistocene of Florida, respectively (Fig. 8C).

14

15   From this discussion we conclude that recent and fossil z-corals clearly differ with regard to

16   their relationships of extension rate with bulk density and that taxonomical peculiarities seem

17   not to play a significant role for the big picture (Fig. 7, 8A). We further conclude, that the

18   relationship of extension rate with calcification rate is identical in recent z-corals from all

19   ocean regions, but is significantly different between recent and fossil z-corals (Fig. 7B). Bulk

20   density and calcification rate, on the other hand, display individual traits among the recent z-

21   corals from the WA, the IP and the Plio-Pleistocene of Florida (Fig. 8C).

22

23

24   **3.1   Low calcification rates due to high nutrients or low $\Omega_{aragonite}$?**

25   Z-coral skeletal calcification is closely coupled with the saturation state of seawater with

26   respect to aragonite (Cohen and Holcomb, 2009; Gattuso et al., 1998; Langdon et al., 2000).

In the low latitudes, low $\Omega_{aragonite}$ is linked with upwelling (Furnas, 2011) which has been

documented also for the Plio-Pleistocene interglacials of Florida (Brachert et al., 2016), and 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., 2016).

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 (Brachert et al., 2016). Thus,

the latter cannot be the prime reason for the observed low calcification rates.

Furthermore, the 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 cm yr^{-1} during the Pliocene (Johnson and

Pérez, 2006), ~0.3 cm yr^{-1} in the late Miocene (Denniston et al., 2008b) and 0.2 and 1.0 cm yr^{-1} in the FRT during the late Pleistocene (0.13 Ma) (Gischler et al., 2009) (Fig. 7G). For this

reason, low extension rates recorded by the Florida fossils are representative of the entire

tropical WA at that time and were as such a large-scale regional or perhaps global

phenomenon. Globally low pH/low $\Omega_{aragonite}$ in ambient water may be sought in high

atmospheric pCO$_2$ levels. Low calcification rates of the Florida corals may, therefore, be an

effect of high pCO$_2$ during the Plio-Pleistocene interglacials. However, for the last 3 Ma after

1   the mid Pliocene climatic optimum (~3 Ma), reconstructed pCO_2 was near pre-industrial

2   levels and only during and before the climatic optimum was at the levels predicted to exist by

3   the end of this century (IPCC, 2013; Seki et al., 2010). For the long-term buffering effect of

4   the ocean, $\Omega_{aragonite}$ has been suggested to have been not significantly different from the

5   present day during the Plio-Pleistocene interglacials, however (Hönisch et al., 2012). On the

6   other hand, substantial pCO_2 changes have been documented over the glacial / interglacial

7   cycles of the Quaternary (Petit et al., 1999), concomitant with changes in calcification of

8   calcareous plankton (Barker and Elderfield, 2002; Beaufort et al., 2011). Thus, low $\Omega_{aragonite}$

9   may represent a potential driver of the observed low calcification rates.

10

11   **3.3   Low calcification rates due to heat stress?**

12   Next to $\Omega_{aragonite}$, temperature is an important control of z-coral calcification in the world

13   oceans. Given the simplification in our reconstruction of SSTs discussed above, the extension

14   rates still display a negative correlation with the average annual SST ($p < 0.05$) and bulk

15   density a positive relationship with SST ($p < 0.05$). In contrast, no clear relation has been

16   found between SST and calcification rate ($p > 0.05$), although visual inspection suggests an

17   inverse correlation (Fig. 8). This pattern is qualitatively rather consistent with recent

18   *Orbicella* (Carricart-Ganivet, 2004), however, at a substantially larger temperature window in

19   the fossil material and an absent relationship or likely negative correlation of calcification rate

20   with temperature (Fig. 6).

21

22   Over the large temperature window of 6.9 °C covered by the modern IP data, a pattern of

23   changes driven by temperature has been documented using linear regression (Fig. 8D-F). In

24   contrast, the temperature range documented by z-corals from the WA database covers only

25   2.2 °C (Fig. 8D-F) and calcification data do not display any linear relationship. Instead of a

26   linear fit, they can be approximated using a quadratic polynomial which should suggest the

27

1   present temperature window realized by recent z-corals of the WA to cover more or less the

2   ecological spectrum of this coral province. Low extension rates documented by fossil z-corals

3   from Florida and many other locations of the Caribbean, therefore, potentially document

4   temperatures either near their lower or upper levels of ecological tolerance. In our temperature

5   reconstruction using skeletal $\delta^{18}O$ values, we apply a value of $\delta^{18}O_{water}$ which likely

6   underestimates the actual SST because other methods consistently found SSTs of the WA

7   warm pool ~2 °C above present values during the last 5 Ma (Fedorov et al., 2013; O'Brien et

8   al., 2014). Low calcificartion rates in z-corals may, therefore, reflect warmer-than-present

9   SSTs during the Plio-Pleistocene interglacials. Such an interpretation is consistent with

10   concepts of nonlinear calcification responses to temperature in z-corals (Brachert et al., 2013;

11   Gischler et al., 2009; Worum et al., 2007). Correspondingly, approaches describing coral

12   calcification within temperature windows of $\leq$1 °C of annual temperature would not describe

13   z-coral calcification over the full spectrum of ecological tolerance of a given species and may

14   describe calcification near the optimum or lower / upper threshold of calcification only. In

15   application of this concept, z-coral growth in the WA was likely under significant heat stress,

16   and annual water temperatures 2 °C higher than at present were causing calcification rates 50

17   % lower than present day. It should be noted also, that upwelling has been ascribed a

18   mitigating effect on SST stresses depending on the depth of upwelling or the timing during

19   the year (Chollett et al., 2010; Riegl and Piller, 2003) and maximum extension rates /

20   minimum density of the Florida z-corals coincided with a maximum of upwelling.

21   Intermittent upwellings during the Plio-Pleistocene, therefore, seem to have created temporary

22   refuges for z-corals by episodically mitigating heat stresses (Brachert et al., 2016). This

23   finding supports notions of hot SSTs during the Eemian interglacial to have resulted in reef

24   kills at equatorial latitudes and poleward migrations of many z-coral taxa (Kiessling et al.,

25   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).

4   Conclusions

- This study presents quantitative records of calcification rates from Pliocene and Pleistocene interglacial 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 other tropical Caribbean settings at that time.

- Calcification data are undistinguishable among geological time-slices (interglacials), but bulk density and calcification rate of recent z-corals from Florida are remarkably high compared to the fossils.

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

- 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.

5

6 **Author contribution**

7 TCB designed this research; field work was carried out by TCB, MR and JSK. Laboratory analyses

8 were performed by TCB, SK and MR. KH provided calcification records from a recent *Solenastrea*

9 from Florida Bay. TCB, MR and JML wrote the paper.

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34

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

2   al. (2014).

No.	Site	Sample ID	Genus	GPS Coordinates	Lithostratigraphy	Age (Ma)
4	Palm Beach Aggregates	EP8 EP9A EP9B EP9C EP9D	*Solenastrea* *Solenastrea* *Orbicella* *Solenastrea* *Solenastrea*	N26°41´44.5" W80°21´16.2	Bermont Fm. (Holey Land Mb.)	1.2
8	Brantley Pit, Arcadia	EP6-S2	*Solenastrea*	N27°02´59.3". W81°49´36.7"	Caloosahatchee Fm. (Bee Branch Mb.)	1.8
9	DeSoto Sand and Shell LLC (site 452)	452-K1-S6* 452-K3* 452-K4 452-K5* 452-13* 452-K14 452-K15* 452-K17*	*Solenastrea* *Solenastrea* *Solenastrea* *Solenastrea* *Solenastrea* *Solenastrea* *Solenastrea* *Solenastrea*	N27° 03´35.2", W81°47´37.6"	Caloosahatchee Fm. (Bee Branch Mb.)	1.8
15	Mule Pen Quarry	EP1-S2 EP2-S2 EP3 EP5-S2	*Solenastrea* *Orbicella* *Porites* *Solenastrea*	N26° 16' 31.93", W81° 39' 55.282"	Tamiami Fm. (Golden Gate Mb.)	2.9
16	Quality Aggregates (APAC)	Coral #1**	*Solenastrea*	Not available.	Tamiami Fm. (Pinecrest Mb., unit 7)	3.2

3   * from Böcker (2014)
4   ** from Roulier & Quinn (1995)
5

6

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

Bold: minimum values. Datasets listing only extension rates not included in this table.

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[1]	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/ Pseudodiploria"[2]	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)[3]	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)[4]	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)[5]	1			0.54			1.07			0.57
Solenastrea[5] (1.2, 1.8, 2.9, 3.2 Ma)	12	0.22	0.83	0.42 ± 0.17	**0.55**	1.22	0.87 ± 0.22	0.20	0.97	0.38
Orbicella[5] (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)[5]	1			0.89			**0.60**			0.54

Data sources:

[1]: Helmle et al., 2011; Carricart-Ganivet & Merino, 2001; Carricart-Ganivet et al., 2000 (and sources therein); Highsmith et al., 1983; Mallela & Perry, 2007; Dodge & Brass, 1984

[2]: Logan & Tomascik, 1991; Mallela & Perry, 2007

[3]: Elizalde-Rendon et al., 2010; Mallela & Perry, 2007; Highsmith et al., 1983; Manzello, 2015.

[4]: Lough, 2008; Fabricius et al., 2011; Bessat & Buiges, 2001; Tanzil et al., 2009; Goodkin et al., 2011.

[5]: This work.

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. Datasets listing only extension rates not included in this table.

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[1]	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[2]	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[3]	1			0.54			1.07			0.57
Florida (USA), Plio-Pleistocene[3]	15	**0.16**	**0.86**	**0.44 ± 0.19**	**0.55**	**1.22**	**0.86 ± 0.22**	**0.18**	**0.54**	**0.34 ± 0.11**

Data sources:

[1]: Lough, 2008; Fabricius et al., 20011; Bessat & Buiges, 2001; Tanzil et al., 2009; Goodkin et al., 2011.

[2]: Logan & Tomascik, 1991; Elizalde-Rendon et al., 2010; Malella & Perry, 2007; Carricart & Merino, 2001; Carricart-Ganivet et al., 2000 (and sources therein); Highsmith et al., 1983; Dodge & Brass, 1984; Manzello, 2015.

[3]: This work

1   Table 4. Calcification data from recent z-corals, southern Florida

Taxon and site	Extension rate	Bulk density	Calcification rate	Source
Solenastrea, Florida Bay	0.89	N.A.	N.A.	(Hudson et al., 1989)
Solenastrea, FB (FB-6)	0.51	N.A.	N.A.	(Swart et al., 1996)
Porites, FRT, inshore	0.43	1.61	0.69	(Manzello et al., 2015a)
Porites, FRT, offshore	0.35	1.58	0.55	(Manzello et al., 2015a)
Orbicella, FRT	0.79	1.18	0.91	(Helmle et al., 2011)
Solenastrea, FB (FB-6)	0.54	1.07	0.58	this work

2

3
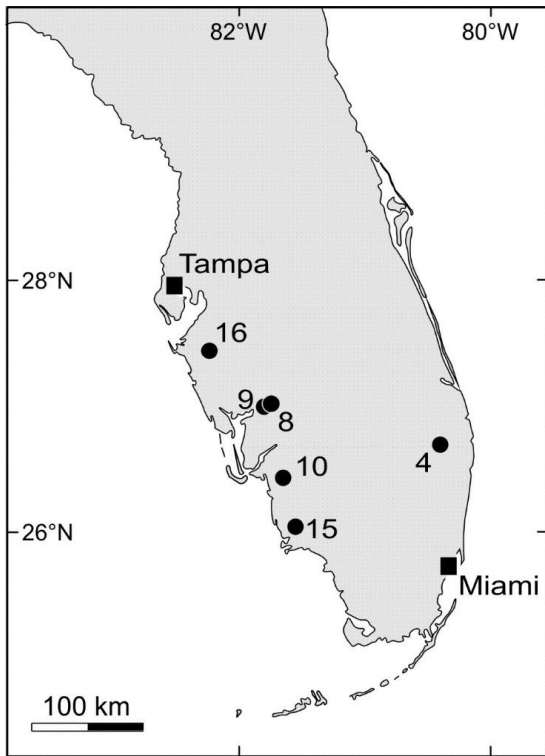
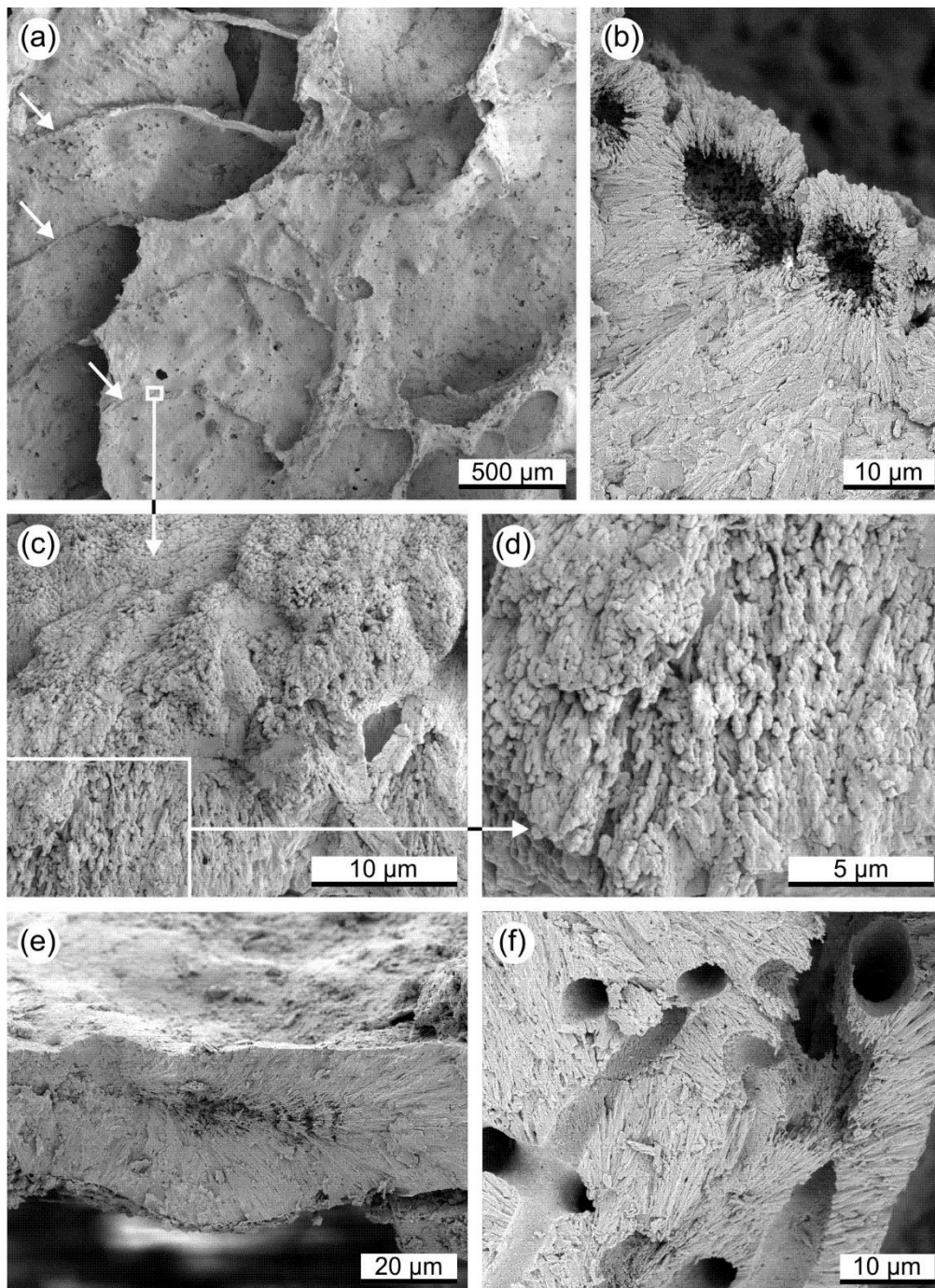# Figure 1

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 skeletons (*Solenastrea* sp.). (a): Overview of septal surfaces. Curved ridges represent the traces of broken dissepiments (arrows). (b): Cross-section of the skeleton showing the radial arrangement of aragonite fibers. Note holes at the centers of the trabecular fans which likely reflects preferential dissolution. (c) and (d): cross-section of a dissepiment composed of fans of fibers pointing downward. The individual fibers have distinct rounded edges and rounded tips. (e): Primary surface of the skeleton infested by

1 microborings. (f): Cross-section of the skeleton showing radial fiber crystals and numerous

2 microborings. The microborings are not constricted by cement or overgrowths. Note: White

3 rectangles and vertical/horizontal arrows show the position of close-ups. Sample provenance:

4 (a) – (d): *Solenastrea* sp. (EP 6), Caloosahatchee Fm., Brantley Pit, Florida/USA; (e):

5 *Solenastrea* sp. (EP 5), Tamiami Fm. (Golden Gate Mb.), Mule Pen quarry; (f) *Solenastrea*

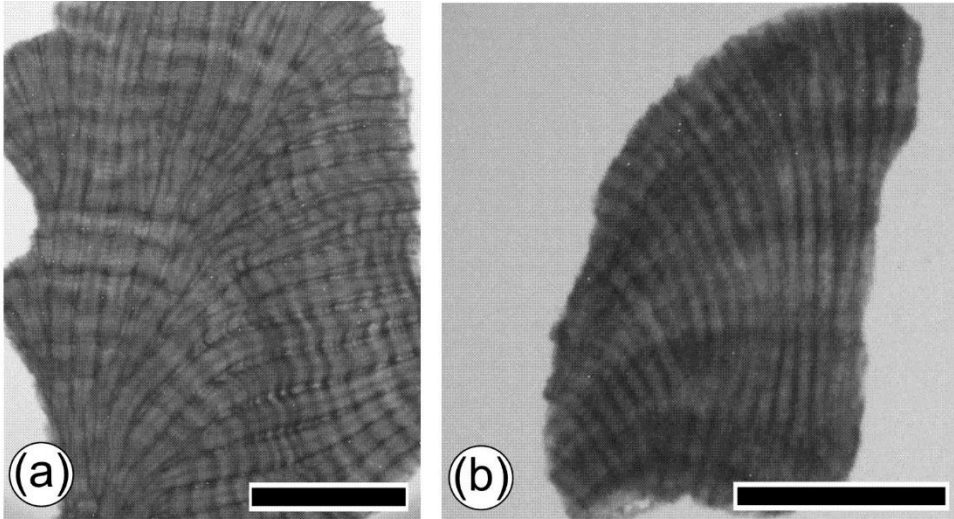6 sp. (EP 9C), Bermont Fm., Palm Beach Aggregates quarry, Florida/USA.

7

8

Figure 3

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,
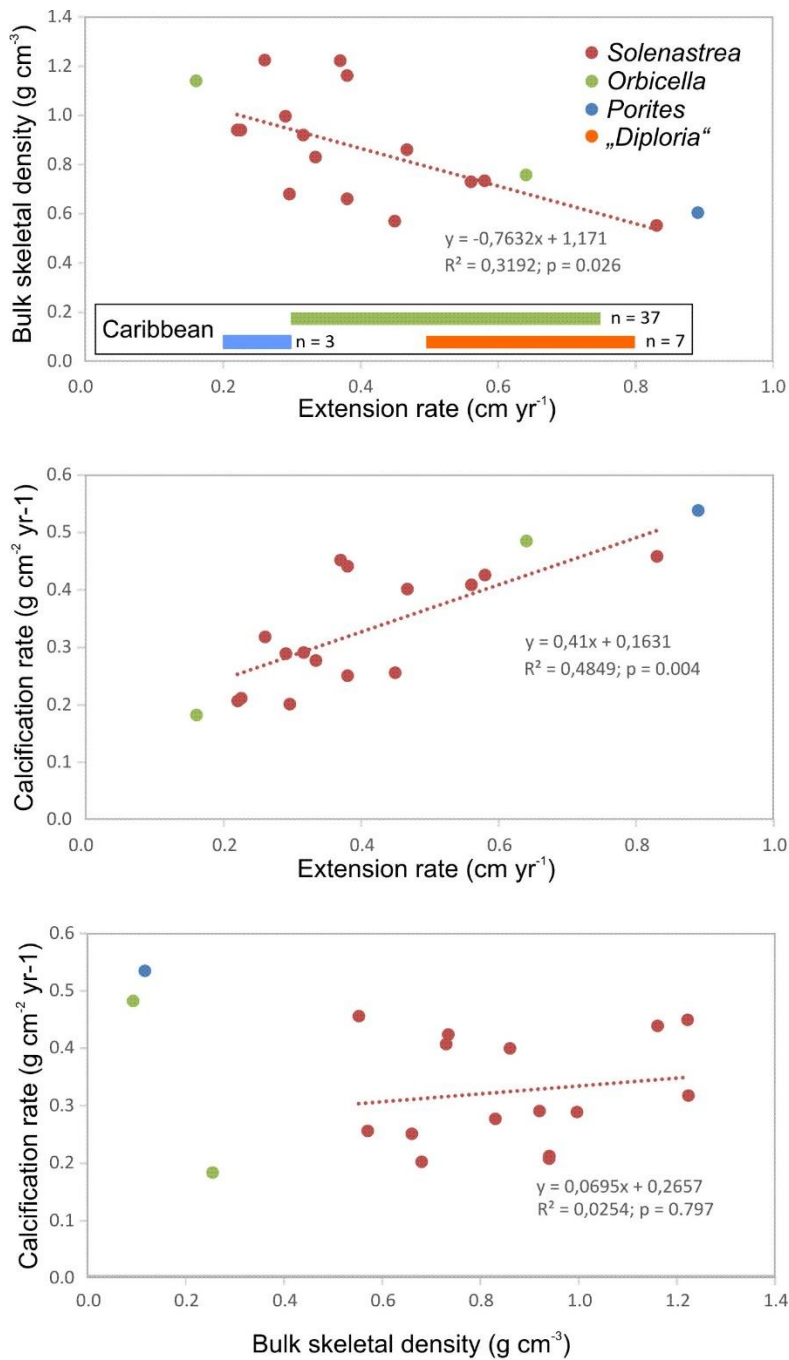Tamiami Fm., age 2.9 Ma). Scale bar 2 cm.

Figure 4

Fig. 4. Calcification systematics in three Pliocene and Pleistocene z-coral genera from the Florida Platform. Inset summarizes published extension rates from the Pliocene of the Caribbean region; corresponding density values and calcification rates are not available (Johnson and Pérez, 2006). "*Diploria*" refers to the two taxa *Diploria* and *Psedudiploria* (Budd et al., 2012).

1
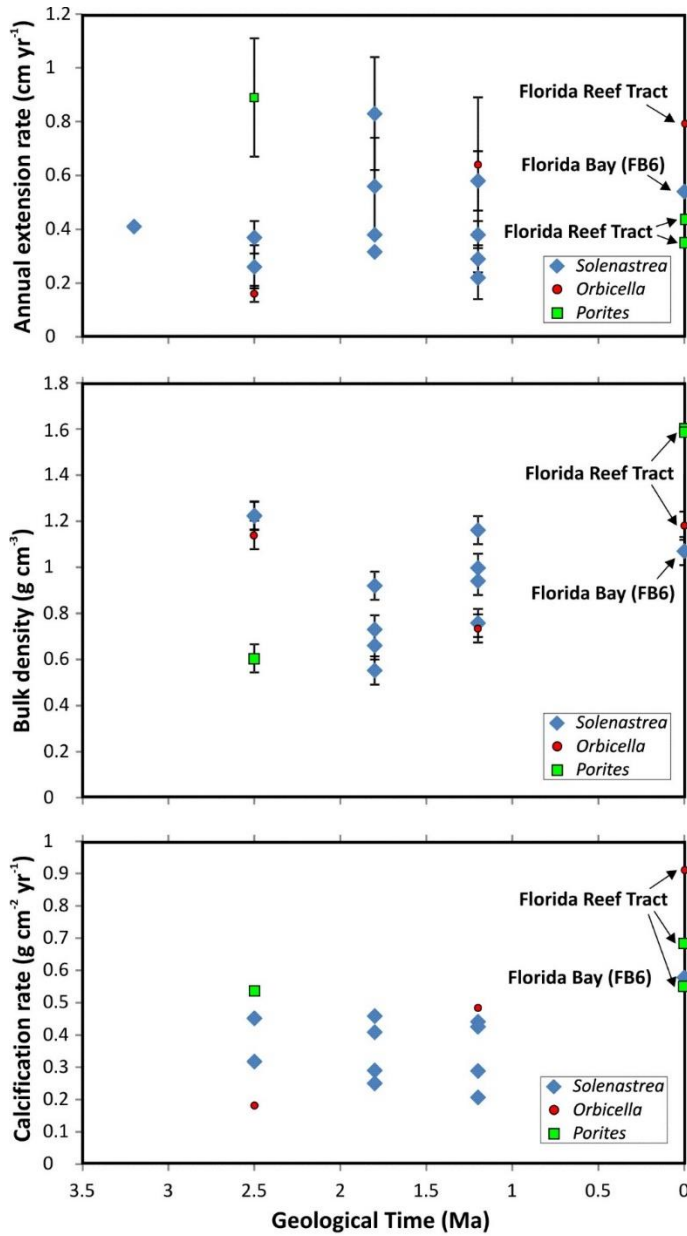
2   Figure 5

3   Figure 5. Temporal variation of the mean extension rate ($\pm$ 1σ), bulk density and mean

4   calcification rate in three z-coral genera (*Solenastrea*, *Orbicella*, *Porites*) from the Pliocene -
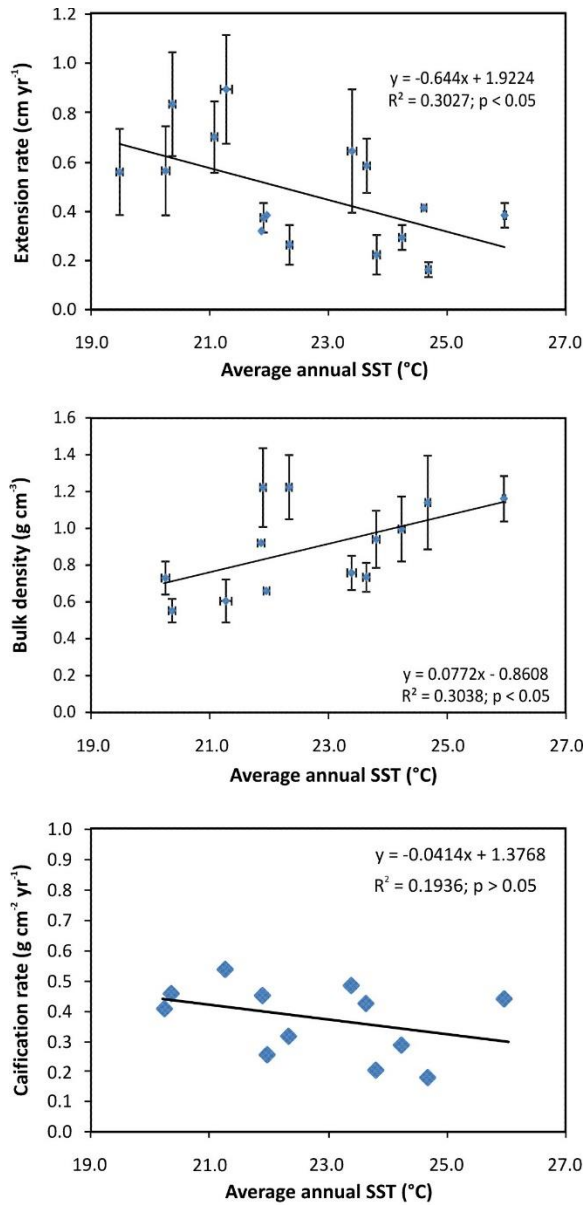
5   Pleistocene Florida platform. Recent data from (Helmle et al., 2011; Hudson et al., 1989;

6   Manzello et al., 2015a; Swart et al., 1996) and own materials (Florida Bay).
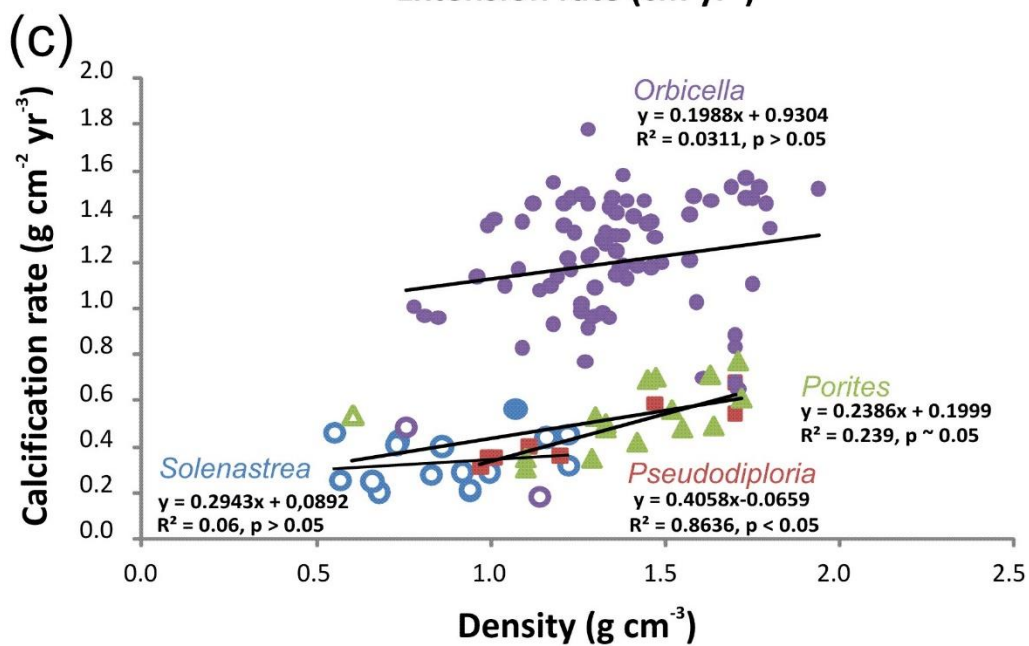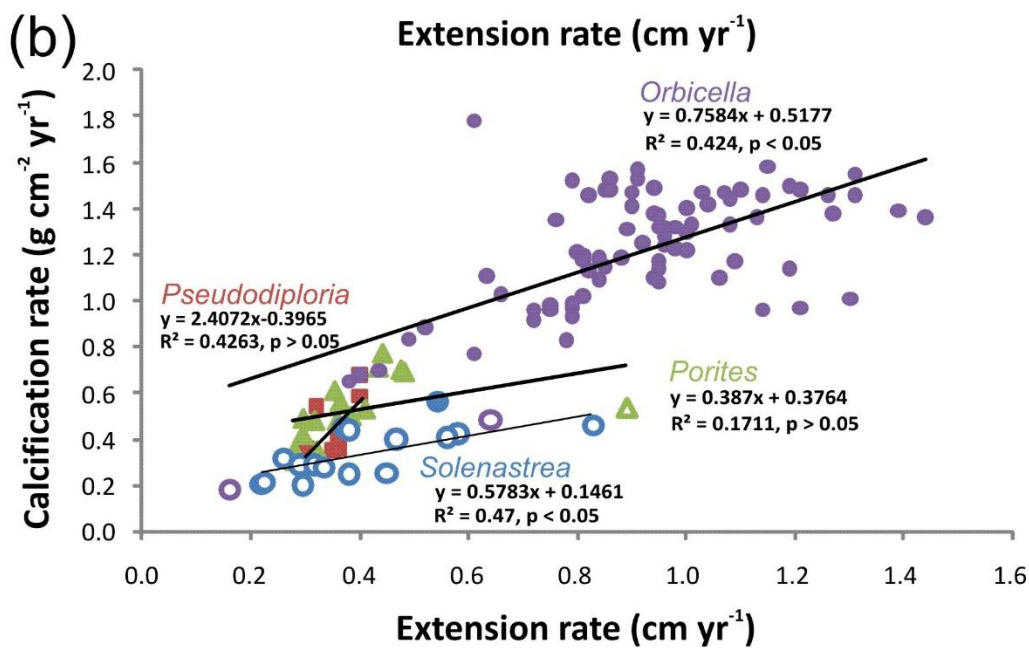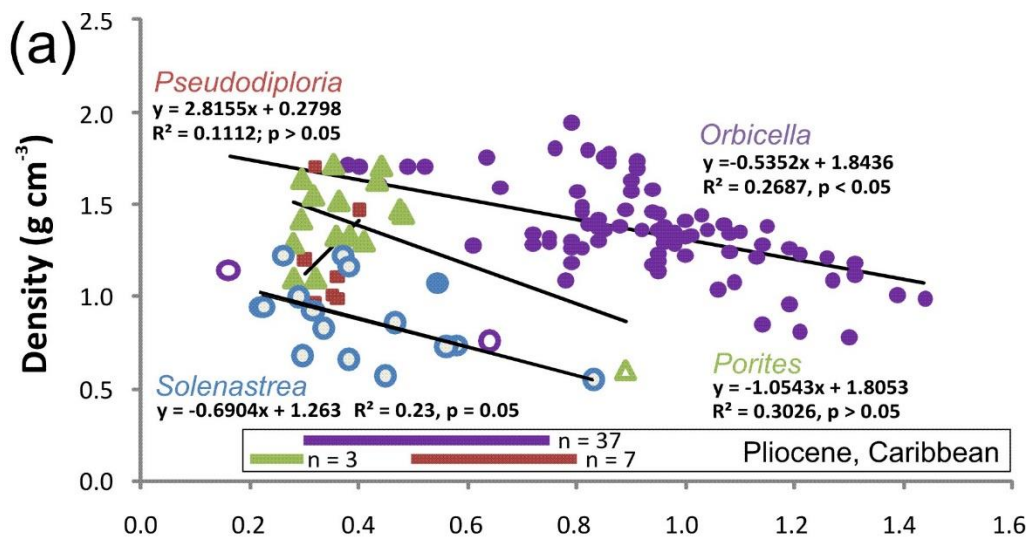
7

Figure 6. 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 δ^{18}O values (Brachert et al., 2014).

(a)

Pseudodiploria
$y = 2.8155x + 0.2798$
$R^2 = 0.1112; p > 0.05$

Orbicella
$y = -0.5352x + 1.8436$
$R^2 = 0.2687, p < 0.05$

Solenastrea
$y = -0.6904x + 1.263$ $R^2 = 0.23, p = 0.05$

Porites
$y = -1.0543x + 1.8053$
$R^2 = 0.3026, p > 0.05$

n = 37
n = 3   n = 7   Pliocene, Caribbean

Density (g cm^{-3})

Extension rate (cm yr^{-1})

(b)

Orbicella
$y = 0.7584x + 0.5177$
$R^2 = 0.424, p < 0.05$

Pseudodiploria
$y = 2.4072x - 0.3965$
$R^2 = 0.4263, p > 0.05$

Porites
$y = 0.387x + 0.3764$
$R^2 = 0.1711, p > 0.05$

Solenastrea
$y = 0.5783x + 0.1461$
$R^2 = 0.47, p < 0.05$

Calcification rate (g cm^{-2} yr^{-1})

Extension rate (cm yr^{-1})

(c)

Orbicella
$y = 0.1988x + 0.9304$
$R^2 = 0.0311, p > 0.05$

Porites
$y = 0.2386x + 0.1999$
$R^2 = 0.239, p \sim 0.05$

Solenastrea
$y = 0.2943x + 0,0892$
$R^2 = 0.06, p > 0.05$

Pseudodiploria
$y = 0.4058x - 0.0659$
$R^2 = 0.8636, p < 0.05$

Calcification rate (g cm^{-2} yr^{-3})

Density (g cm^{-3})

1 Figure 7

48

1   Figure 7. Mean extension rate, bulk skeletal density and mean calcification rate of reef corals

2   sorted according to taxon and geological time (Western Atlantic region). Magenta: *Orbicella*,

3   green: *Porites*, red: *Diploria*, blue: *Solenastrea*. Filled symbols: recent, open symbols: fossil.

4   Data on recent corals compiled from the literature (Carricart-Ganivet et al., 2000; Carricart-

5   Ganivet and Merino, 2001; Dodge and Brass, 1984; Elizalde-Rendon et al., 2010; Highsmith

6   et al., 1983; Hudson et al., 1989; Logan and Tomascik, 1991; Mallela and Perry, 2007) and

7   one unpublished record from *Solenastrea* (FB-6). Inset in uppermost panel shows range of

8   extension rates of z-corals of Pliocene age in the Caribbean region (various taxa) for

9   comparison (Johnson and Pérez, 2006). Note clustering of fossil corals at low extension rates,

10   low density and low calcification rates.

11
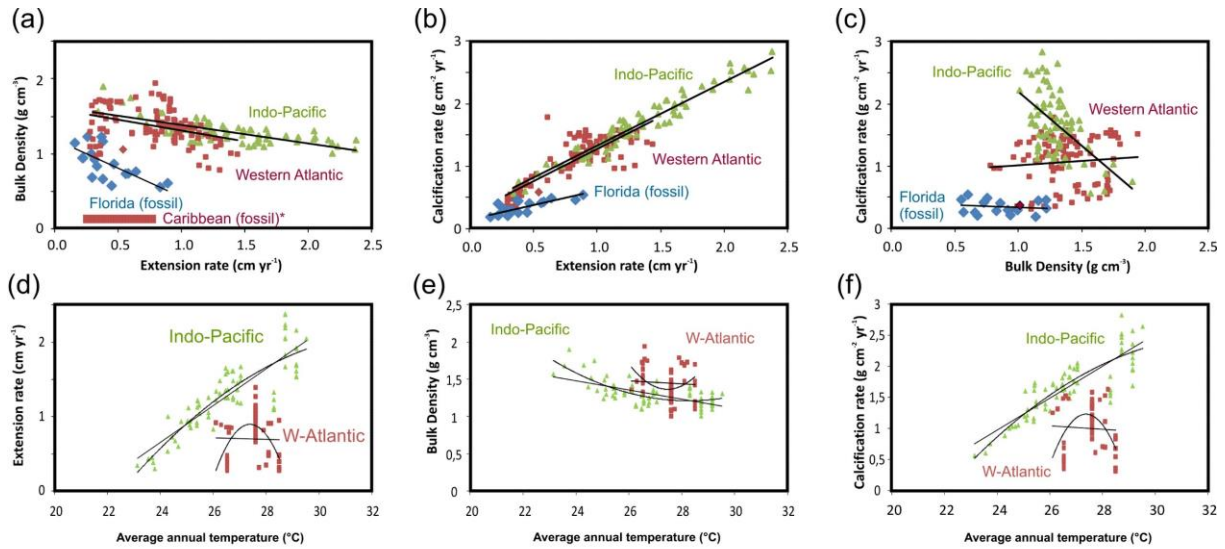
Figure 8

Figure 8. 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 figure 7A 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 $y = -0.0203x^2 + .3294x - 19.628$; $R^2 = 0.7519$; $p < 0.05$ 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 $y = 0.2566x - 5.1844$; $R^2 = 0.7322$; $p < 0.05$.