<u>Calcification response of reef corals to seasonal upwelling in the</u> <u>northern Arabian Sea</u> <u>Nutrients attenuate the negative effect of</u> ocean acidification on reef coral calcification in the Arabian Sea <u>upwelling zone</u> (Masirah Island, Oman)

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Tropical shallow-water reefs are the most diverse ecosystem in the ocean. Its persistence rests upon adequate calcification rates of the reef building biota, such as reef corals. The calcification mechanism of reef corals performs best Optimum

- 15 calcification rates of reef corals occur in oligotrophic environments with high seawater saturation states of aragonite (Ω_{sw}), <u>leadingwhich leads</u> to <u>anits</u> increased vulnerability to anthropogenic ocean acidification and eutrophication. <u>The calcification</u> response of reef corals on rapid changes in Ω_{sw} and seawater nutrient concentrations is currently under discussion in coral <u>science</u>The calcification response of reef corals to this changing environment is largely unknown, however. <u>Here we present</u> <u>Porites</u> calcification records from the northern Arabian Sea upwelling zone and investigate the coralir calcification response
- 20 to low Ω_{sw} and high nutrient concentrations associated to seasonal due to seasonal upwelling. Calcification rates were was determined from the product of skeletal extension and bulk density-derived from X ray densitometry. Skeletal Ba/Ca and Li/Mg proxy data allowed to enabled identificationidentify-of skeletal portions calcified during upwelling and non-upwelling seasons, respectively, and to reconstruction of growth temperatures. With regard to sub-annual calcification patterns, our results demonstrate compromised that the compromised calcification rate-is compromised during the upwelling season. This
- 25 is due to declining extension rate, which we attribute to light dimming caused by high primary production. because of slow al growth [BT1] that we attribute to the light dimming effect of turbid waters Interestingly, skeletal density shows no relationship with remains unaffected by temporally low Ω_{sw} during upwelling. This-and, suggestsing relatively constant, high year-round saturation states of aragonite at the site of calcification (Ω_{cf}) independent of external variability of Ω_{sw} . Although upwelling does not affect seasonal density variability, exceptionally low mean annual density Lmean-annual-implies permanent Ω_{cf}
- 30 <u>adaptationjustment of the calcification mechanism towards the lowest sub-annual ly occurring Ω_{sw} (e.g., upwelling) [BT2] [BT3]. In the Arabian Sea upwelling zone, mean annual calcification rate is similar to *Porites* from non-upwelling regions because</u>

low skeletal density is compensated by high extension growth. During the calcification process, smallcontribution of [BT4]to calcification rate issWe anticipate maintenance of adequate reef coral calcification rate under global change is largely reliant on extension rates, which we variable responses to nutrients may either compensate or exacerbate negative effects of

35 <u>diminished skeletal density associated with ocean acidification. Here, we present annually and sub annually resolved records of calcification rates (n=3) of the coral *Porites* from the nutrient rich and low Ω_{sw}. Arabian Sea upwelling zone (Masirah Island, Oman). Calcification rates were determined from the product of skeletal extension and bulk density derived from X-ray densitometry.</u>

Compared to a reference data set of coral skeletons from typical reef environments (Great Barrier Reef, Hawaii), mean annual

- 40 skeletal bulk density of *Porites* from Masirah Island is reduced by 28 %. This density deficit prevails over the entire year and probably reflects a year round low saturation state of aragonite at the site of calcification (Ω_{ef}), independent of seasonal variations in Ω_{sw} (e.g. upwelling). Mean annual extension rate is 20 % higher than for the reference data set. In particular, extension rate is strongly enhanced during the seasons with the lowest water temperatures, presumably due to a high PO₄³⁻ /NO₃⁻ ratio promoting rapid upward growth of the skeleton. Enhanced annual extension attenuates the negative effect of low
- 45 density on calcification rate from 25 % to 11 %, while sub annual calcification rates during the cool seasons even exceed those of the reference corals. We anticipate optimal nutrient environments (e.g. high PO₄³/NO₃⁻ ratios) to have significant potential to compensate the negative effect of ocean acidification on reef coral calcification, thereby allowing to maintain adequate rates of carbonate accumulation, which are essential for preserving this unique ecosystem.

1 Introduction

- 50 <u>Tropical coral reefs are the most diverse aquatic ecosystem on the planet (Hughes et al., 2017).</u> Their basic building blocks are the calcareous (aragonite) skeletons of symbiotic zooxanthellate scleractinian corals (reef corals) are the basic building blocks of tropical shallow water reefsa, the most diverse ecosystem in the ocean (Hughes et al., 2017). and sustained precipitation of skeletal carbonate (calcification) is fundamental for maintaining their structure and function (Perry et al., 2012Howells et al., 2018). The persistence of reefs habitats rests upon coralline aragonite precipitation (calcification), which counteracts natural
- 55 reef degradation due to erosion and dissolution determines [RM5] the delicate balance between reef build up and natural destruction [RM6]. Optimum calcification of reef corals is found in oligotrophic water masses of temperatures between 21 °C to 29.5 °C and a saturation state of seawater with respect to aragonite >3.3 ($\Omega_{sw}\Omega_{sw}$) (Kleypas et al., 1999). Anthropogenic greenhouse gas emissions threaten reef coral calcification by increasing sea surface temperature (SST) and by causing ocean acidification. In addition, land use, sewage disposal discharge of waste-water and fish farming turn the near-shore shallow-
- 60 marine environments towards more eutrophic conditions. The responses of reef coral calcification on this the rapidly changing environment are highly variable and remains contemporarily a matter of debate_intense research (Cornwall et al., 2021; Guan et al., 2020; Hall et al., 2018).

Coral calcification rate (g cm⁻² yr⁻¹) is the product of linear extension rate (cm yr⁻¹) measured along the axis of maximum growth and bulk density (g cm⁻³) of an annual skeletal growth increment [BT7] (Dodge and Brass, 1984). Linear extension rate

- 65 in reef corals is linked to efficiency of photosynthesis in symbiotic maicro-algae-symbionts, providing energy to the host for skeletal-upwards growth of the skeleton (Muscatin et al., 1981; Sun et al., 2008). Availability of light and water temperature are the main drivers controlling photosynthetic efficiency and thus also-positively related to the extension rate (Al-Rousan, 2012; Logan and Tomascik, 1991; Lough and Barnes, 2000). ArBT8Jt certain taxon-specific threshold temperatures, however, extension rate declines rapidly due to thermal stress offor the micro-algae symbionts (Cantin et al., 2010). Due to sub-annual
- 70 variations in extension rates, skeletal portions of high and low density are formed, with high-density bands (HDBs) coinciding with low extension rates (and vice versa for low-density bands = LDBs) (DeCarlo and Cohen, 2017; Highsmith, 1979; Klein and Loya, 1991; Knutson et al., 1972). Bulk density within an annual increment is spatially not uniform, and portions of elevated density (high density bands = HDBs) reflect biomineralization at less optimal high and low growth temperatures (Highsmith, 1979; Klein and Loya, 1991). While on an annual time scale, extension rate and calcification rate is positively.
- 75 related to SST, skeletal bulk density is negatively related to SST (Fabrizius et al., 2011; Lough, 2008; Lough and Barnes, 2000). These inverse linear relations of extension rate and skeletal density at increasing temperature turn over at a certain, taxon specific, threshold temperature, when extension rates rapidly decline due to increasing thermal stress (Cantin et al., 2010). In addition to temperature, the aragonite saturation of the calcifying fluid (Ω_{cf}) determines bulk skeletal density (Mollica et al., 2018). Ω_{cf} is approximately five times higher than the aragonite saturation of the external seawater (Ω_{sw}) and long-term
- 80 changes in Ω_{sw} due to ocean acidification lead to declining Ω_{cf} (McCulloch et al., 2017; D'Olivo et al., 2019). On an i<u>l</u>ntraannual<u>ly-basis, however</u>, corals are, <u>however</u>, able to maintain relatively stable levels of Ω_{cf} largely independent of short term variations in Ω_{sw} by upregulating their internal pH_{cf} and DIC_{cf} pool (McCulloch et al., 2017; DeCarlo et al., 2018; D'Olivo and McCulloch, 2017, Ross et al., 2019a). With regard to climate models for the end of the 21st century, McNeil et al. (2004) stated a general increase in calcification rate as the effect of ocean warming far outweighs deficits due to decreases in seawater
- 85 aragonite saturation.

Near-shore coral reefs are increasingly exposed to anthropogenic eutrophication induced by land use, fish farming and sewavage disposal (Lapointe and Clark, 1992; Chen et al., 2019; Chen and Yu, 2011). Eutrophication can have both beneficial as well as detrimental effects on coral growth, however (Tomascik and Sander, 1985; Tomascik, 1990)The effects of nutrients on coral reefs appear to be versatile, however. In general, rReef corals are highly adapted to oligotrophic waters with micro-

- 90 algae symbionts to because symbiosis with phototrophic zooxanthellae allows an efficient use of essential nutrients and to outcompete other fast-growing biota on a reef whose growth is inhibited by the undersupply of nutrients (Vermeij et al., 2010; BarFott and Rohwer, 2012). Strong eutrophication disturbs this adaptive advantage, leading to harmful algal blooms followed by reef coral mass mortality (Al Shehhi et al., 2014) and reef destruction due to the increasing abundance of bioeroders (Hallock, 1988). On the other hanHoweverd, moderate increases of certain nutrients such as ortho-phosphate (PO₄³⁻) have been
- 95 shown to promote linear extension rates but to inhibit skeletal thickening, thus having a negative effect on skeletal density

(Bucher and Harrison, 2001; Dunn et al., 2012; Koop et al., 2001; Dunn et al., 2012; Bucher and Harrison, 2001). The opposite effect is reported for nitrate (NO₃⁻), even though the calcification response is less pronounced compared to PO_4^{3-} (Koop et al., 2001). Increasing eutrophy is considered to explain <u>increasingenhanced</u> coral calcification rates along an offshore – inshore gradient where the effect of temperature is negligible (D'Olivo et al., 2013; <u>Risk and Sammarco[BT9]</u>, 1991; Manzello et al., 2015).

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Understanding how coral calcification responds to rapid changes in seawater nutrient conditions and Ω_{sw} is critical for more accurate predictions on the persistence of reef habitats under the influence of global change The versatile effect of nutrients in interaction with the impeding effect of low aragonite saturation on coral calcification remains largely unknown. Tropical upwelling Study areas are well suited for this kind of research are those affected by upwelling, since as the upwelling deep

- 105 water masses are rich in nutrients but cool-and low in Ω_{sw} . This allows these regions to serve as natural laboratories to investigate the calcification response of reef corals to these multiple environmental stressors that are likely to affect global coral reefs in the near future (Camp et al., 2018; Wizemann et al., 2018). PUpwelling areas are heralded as possible refuges for tropical coral species in times of globally rising temperatures due to the potential to mitigate high SSTs (Riegl & Piller, 2002; Chollett et al., 2010). Furthermore, the calcification response of reef corals from upwelling zones could provide
- 110 important implications regarding the survival of tropical coral reefs, which are increasingly threatened by human caused ocean acidification and eutrophication. Published calcification data <u>of athe majorof a major</u> reef-building coral <u>genus (Porites)</u> spp. genus from the Indo Pacific (Porites) growing within regions affected by <u>seasonal</u> upwelling are generally sparse and only available from three Pacific reef sites (Manzello et al., 20145; Mollica et al., 2018). In the here presented this study, we report the first calcification data (calcification rate, extension rate, skeletal bulk density) of six Porites coral specimens from the so
- 115 far unexplored region of the northern Arabian Sea upwelling zone (Masirah Island, Oman). Three out of the six samples that were considered representative for the site under studiedy were selected for further geochemical analysis (Li/Mg, Ba/Ca). This facilitated the establishment of a detailed sub-annual chronology yielding monthly resolved records of calcification. This approach enablesallowed uss for an unprecedented comparison of sub-annual calcification performance between the upwelling and non-upwelling season. In this way, this study improves the general knowledge on seasonal and annual patterns of reef
- 120 coral calcification under exposure to variable Ω_{sw} and nutrient concentrations, thereby contributes to more accurate predictions on the persistence of reef habitats under the influence of global change.
 (Manzello et al., 2015; Mollica et al., 2018). Only two records of extension rate and skeletal density are available from the eastern Pacific upwelling zones (Manzello et al., 2015; Mollica et al., 2018).
- 125 (Montone, 2010; Tudhope et al., 1996; Watanabe et al., 2017). In the here presented study, we report the first annually and monthly resolved calcification records (extension rate, skeletal bulk density, calcification rate) of three *Porites* coral specimens from the Arabian Sea upwelling zone (Masirah Island, Oman). The results are discussed with regard to environmental controls on calcification (SST, Ω_{swī} nutrients) and compared to coral calcification data reported in the literature from typical reef

environments (warm, oligotrophic). This study contributes to assessing changes in patterns of reef coral calcification in the

130 context of ongoing global change (ocean acidification and eutrophication) and contributes to the identification of regions deserving high conservation priority due to favourable environmental conditions for the persistence of tropical shallow water reefs.

1.1 Arabian Sea climate and oceanography

The northwestern portion of the Indian Ocean between India and the Arabian Peninsula is the Arabian Sea. Its coastline against

- 135 the Arabian Peninsula forms a straight line running towards the northeast up to the Cape Ras al Hadd where it turns almost at right angles to the northwest into the Gulf of Oman (Fig. 1). The regional climate of the Arabian Sea is characterised by a semi annual alternation of the prevailing wind directions (Beal et al., 2013). During northern hemisphere summer, strong winds of the Southwest Monsoon (SWM) cross the Arabian Sea in the direction of the low pressure system above the Tibetan Plateau (Findlater, 1969). During winter, prevailing winds from the northeast cause the Northeast Monsoon (NEM) (Hastenrath
- 140 and Greischar, 1991). Low wind speeds without preferred orientation typically occur during the two intermonsoon seasons (spring intermonsoon = SIM; autumn intermonsoon = AIM) (Beal et al., 2013; Lee et al., 2000). Surface wind fields are the driving force behind the upper hydrospheric structure and the seasonal variation of the oceanic surface current system (Swallow and Bruce, 1966). During summer, southwest monsoonal winds cause a strong coastal current (Oman Coastal Current) which runs northward parallel to the coast of the Arabian Peninsula and induces rigorous upwelling (Currie et al., 1973; Currie, 1992,
- Smith and Bottero, 1977). Increased nutrient supply during southwest monsoonal upwelling is associated with an increased primary productivity in the cuphotic zone (Anderson et al., 1992; Bauer et al., 1991) (Fig. 2). Compared to equatorial upwelling regions of the castern Pacific, the northern Arabian Sea upwelling is characterized by a high phosphate to nitrate ratio (Kleypas et al., 1999). But although nutrient supply is linked to upwelling, concentrations of PO₄² and NO₃² remain on a high level throughout the year, because of a prevailing iron limitation of the primary production (Mother Earths Iron Experiment) (Smith, 2001). Southwest monsoonal upwelling furthermore causes a drop in surface water pH, causing seawater aragonite saturation (Ω_{sw}) to decrease temporally from 3.5 4 during non-upwelling season to 2.5 during the upwelling season, which is well below critical values assumed to be required for coral growth (Kleypas et al., 1999; Omer, 2010).



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Figure 1: General map of the castern Arabian Peninsula and the adjacent seas showing the reef sites (red) and coral reef provinces off Oman (yellow) [(1) Marbat, (2) Kuria Muria Islands, (3) Masirah Island and Barr al Hikman, (4) Capital Area (5) Daymaniyat Islands and (6) Musandam (Salm, 1993; Burt et al., 2016)]. The black asterisk marks the sampling site at the southern tip of Masirah Island. Black arrows indicate the Omani current of the southwest monsoon season. The hatched area delimitates the region of maximum upwelling inferred from August sea surface temperatures <25 °C (1995 – 2005 monthly averages; WOA18, Locarnini et al., 2018). The blue shading displays water depth gradients (dark blue = shallow, light blue = deep).



Figure 2: Ocean climatological data estimated from daily SSTs (JPL MUR) and monthly seawater phosphate (PO4³) and nitrate (NO2) concentrations (WOA18) at the sampling site. The blue shaded area represents the deviation (1 σ) from averages of daily SSTs within the period 2003 – 2018.

1.2 Coral growth at Masirah Island

Coral growth off Oman occurs within six demarcated provinces, including Marbat, the Kuria Muria Islands, Masirah Island and Barr al Hikman, the Capital Area, the Daymaniyat Islands and Musandam (Fig. 1; Burt et al., 2016). Sheltered from the open ocean, coral growth at Masirah Island occurs to the west (Strait of Masirah) and southwest (Barr al Hikman) of the island

170 (Salm, 1993). Compared to the other coral reef provinces of Oman, the reefs to the southwest of Masirah Island represent the largest area of spatially continuous coral cover, but have the lowest coral diversity (Salm, 1993; Coles, 1996). Fast growing cabbage and brain corals such as *Montipora* and *Platygyra* are the dominant genera, but massive *Porites* are also present (Coles, 1996).

2 Material and methods

175 2.1 Arabian Sea climate and oceanography

<u>The Arabian Sea is the northwestern partortion of the Indian Ocean between India and the Arabian Peninsula (Fig. 1) is the</u> <u>Arabian Sea.</u> <u>The Arabian Sea coastline of southern OmanIts coastline against the Arabian Peninsula formsextends a straight</u> <u>line running from Dhofar in the southwest towards the northeast up to the Cape Ras al Hadd in the northeast of the sultanate,</u> <u>where it turns almost at right angles to the northwest into the Gulf of Oman (Fig. 1)</u>. The regional climate of the Arabian Sea

- 180 is characterised by a semi-annual alternation of the prevailing wind directions (Beal et al., 2013). During northern hemisphere summer, strong winds of the sSouthwest mMonsoon (SWM) cross the Arabian Sea in the direction of the low pressure system above the Tibetan Plateau (Findlater, 1969). During winter, reversal of the atmospheric pressure system prevailing winds from the northeast-causes the nNortheast mMonsoon (NEM) (Hastenrath and Greischar, 1991). Low wind speeds without preferred orientation typically occur during the two intermonsoon seasons (spring intermonsoon = SIM; autumn intermonsoon = AIM)
- 185 (Beal et al., 2013; Lee et al., 2000). Surface wind fields are the driving force behind the upper hydrospheric structure and the seasonal variation of the oceanic surface current system (Swallow and Bruce, 1966). During summer, southwest monsoonal winds cause a strong coastal current (Oman Coastal Current), which runs northward parallel to the coast of the Arabian Peninsula and induces rigorous upwelling (Currie et al., 1973; Currie, 1992, Smith and Bottero, 1977). Increased nutrient supply during southwest monsoonal upwelling is associated with an increased primary productivity in the euphotic zone
- 190 (Anderson et al., 1992; Bauer et al., 1991; Quinn and Johnson, 1996) (Fig. 2). Compared to equatorial upwelling regions of the eastern Pacific, the northern Arabian Sea upwelling is characterized by a high phosphate to nitrate ratio (Kleypas et al., 1999). But although nutrient supply is linked to upwelling, concentrations of $PO_4^{3^2}$ and NO_3^{-1} remain on a high level throughout the year, because of a prevailing iron limitation of the primary production (Mother Earths Iron Experiment) (Smith, 2001). Southwest monsoonal upwelling furthermore causes a drop in surface water pH, causing seawater aragonite saturation (Ω_{sw})
- 195 to decrease temporally from 3.5 4 during non-upwelling season to 32.5 during the upwelling season, which is well below

2014) (Fig.2).



 Figure 1: General map of the eastern Arabian Peninsula and the adjacent seas showing the reef sites (red) and coral reef provinces

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 off Oman (yellow) [(1) Marbat, (2) Kuria Muria Islands, (3) Masirah Island and Barr al Hikman, (4) Capital Area (5) Daymaniyat

 Islands and (6) Musandam (Salm, 1993; Burt et al., 2016)]. The black asterisk marks the sampling site at the southern tip of Masirah

 Island. Black arrows indicate the Omani current of during the southwest monsoon-season. The hatched area delimitates the region

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 et al., 2018). The blue shading displays water depth gradients (dark blue = shallow, light blue = deep).

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Figure 2: Ocean climatological data estimated from daily SSTs (JPL MUR), <u>-ond-monthly seawater phosphate (PO4³⁻) and nitrate</u> (NO3⁻) concentrations (WOA18) <u>-(Garcia et al., 2019) and aragonite saturation state ($\Omega_{aragonite}$) (Takahashi et al., 2014) at the sampling site. The blue shaded area represents the deviation (1 σ) from averages of daily SSTs within the period 2003-2018.</u>

Seasonal abbreviations: 5 Seasons are shown as NEM (northeast monsoon), SIM (spring intermonsoon), SWM (southwest monsoon), und[RM10] AIM (autumn intermonsoon).

21.2 Coral growth and sample collection at Masirah Island

- 215 Coral growth off Oman occurs within six distinctemarcated provinces, including Marbat, the Kuria Muria Islands, Masirah Island and Barr al Hikman, the Capital Area, the Daymaniyat Islands and Musandam (Fig. 1; Burt et al., 2016; Salm et al., 1993). The occurrence of corals at Masirah Island is limited to very shallow water depths of 1-4 metres (Glynn, 1993). Sheltered from the open ocean, coral growth at Masirah Island corals growth occurs to the west in the [RM11](Strait of Masirah) to at the western coast of Masirah Island RM12](and at Barr al Hikman[RM13] to the southwest (Barr al Hikman[RM14]) of the
- 220 <u>island (Salm, 1993). Compared to the other coral reef provinces of Oman, the reefs to the southwest of Masirah Island represent</u> <u>the largest area of spatially continuous coral cover, but have the lowest coral diversity (Salm, 1993; Coles, 1996).</u> Fast growing <u>cabbage and brain corals such as *Montipora* and *Platygyra* are the dominant genera, but massive *Porites* are also present <u>(Coles, 1996).</u></u>
- In March 2018, <u>dead coral material from sixthree massive Porites_-colonies (Sample identifier: 5.9; 5.10; 5.13; 5.15; 5.21; 5.22)</u> were-was collected at the southernmost tip of Masirah Island <u>from the uppermost part of the shore (20.16N, 58.64E)</u> (Fig. 1). <u>This coral occurrence e sampling position at the uppermost part of the shore represents a storm deposit attribute</u>related to Because the sampling position on the uppermost part of the shore is not affected by common high tides, the corals must have been washed ashore during a high energy storm or tsunami event. The last significant storm event was cyclone Gonu in
- 230 2007 (Fritz et al., 2010). with maximum wind speeds of 260 km/h. However, no immediate devastation caused by this storm was reported from Masirah Island, since most intense landfalls of the storm occurred at Ras al Hadd (Fig. 1) and further to the northwest in the Gulf of Oman (Fritz et al., 2010). In contrast, the second strongest cyclonic event reported for the Arabian Peninsula occurred in 1977, causing severe damage at Masirah Island by south westerly winds with speeds of up to 185 km/h (Membery, 2002).

235 2.3 Methodology

Coral samples were cut to slices of 6 mm thickness parallel to the axis of maximum growth using a rock saw at lowest tournament speed and equipped with a water-cooled diamond blade. Subsequent usage of a CNC mill ensured co-planarity with maximum deviations of 1____3 % over the entire slab. The slabs were ultrasonically cleaned in deionized water and dried overnight at 40 °C. Coral slabs were X-rayed using a digital X-ray cabinet (SHR 50 V) to document alternating growth bands of high (HDB) and low density (LDB) (Knutson et al., 1972), biogenic borings, encrustations, and cementation. Sampling

- 240
 - 40 of high (HDB) and low density (LDB) (Khutson et al., 1972), biogenic borings, encrustations, and cementation. Sampling transects for all further analyses were carefully selected so as not to be affected by bioerosion and encrustations but normal to HDBs and LDBs following trajectories of maximum linear extension (for the positioning of individual sampling transects see supplementary material, Fig. S1). Density measurements were performed using X_--ray densitometry based on CoralXDS

software (Helmle et al., 2002, 2011). Grey-scale <u>–</u> density calibrations were verified by measurements of standards for zero density (air, $\rho = 0$ g/cm⁻³) and massive aragonite (*Tridacna* shell, $\rho = 2.93$ g/cm⁻³) having the same thickness as the coral slabs. Maximum target deviations were 0.02 ± 0.01 g cm⁻³ for zero density (air) and 0.03 ± 0.06 g cm⁻³ for massive aragonite (Tridacna shell). Width of density measurement transects were set to 4 mm, including a representative mixture of approximately 12 corallites (4 x 6 mm). <u>Annual extension rate was estimated from the distance between two HDBs of</u> maximum grey scale intensity on the radiographs. The mean annual skeletal density was calculated from the mean of all

250 <u>individual measurements along the transect and within one annual growth increment.</u> <u>Adjacent to the density measurement transects of coral 5.10, 5.13 and 5.21, skeletons were sampled for Li/Mg and Ba/Ca ratios (Fig. S1).</u>

Li/Mg thermometry was used for estimating absolute growth temperatures (Montagna et al., 2014; Cuny Guirriec et al., 2019, Ross et al., 2019b, Harthone et al., 2013; Fowell et al., 2016; D'Olivo et al., 2018; Zinke et al., 2019). Li/Mg — SST relationships were shown to be site dependent, however, and similar Li/Mg ratios produce differences in SST estimations of ~2 °C between inter reef (Hathorne et al., 2013) and intra reef settings (Fowell et al., 2016). Such spatial variability in Li/Mg SST relationships is likely due to poorly constrained effects of extension rate and seawater pH on skeletal Li/Mg ratios (Fowell et al., 2016; Inoue et al., 2007; Tanaka et al., 2015). For this reason, we use a separate calibration of the Li/Mg thermometer for Masirah Island corals in order to overcome misleading SST estimates resulting from local seawater pH and extension rate effects associated with upwelling.

ETrace and minor element concentrations were determined at the Institute for Geosciences, Johannes Gutenberg University Mainz (Germany), using an Agilent 7500ce inductively coupled plasma-mass spectrometer (ICP-MS) coupled to an ESI NWR193 ArF excimer laser ablation (LA) system equipped with a TwoVol2 ablation cell. The ArF LA system was operated at a pulse repetition rate of 10 Hz and an energy density of ca. e-3 J cm⁻². Ablation was carried out under a He atmosphere and 265 the sample gas was mixed with Ar before entering the plasma. Measurement spots with a beam diameter of 120 µm were aligned along transects in spot mode with a midpoint distance of 250 µm following discrete skeletal elements. Backgrounds were measured for 15 s prior to each ablation. Ablation time was 30 s, followed by 20 s of wash out. The isotopes monitored were ⁷Li, ²⁵Mg, ⁴³Ca and ¹³⁸Ba. Signals were monitored in time-resolved mode and processed using an in-house Excel spreadsheet (Jochum et al., 2007). Details of the calculations are given in Mischel et al. (2017). NIST SRM 610 and 612 were 270used as calibration material, applying the reference values reported in the GeoReM database (http://georem.mpchmainz.gwdg.de/, Application Version 27;- Jochum et al., 2005; Jochum et al., 2011) to calculate the element concentrations of the sample measurements. During each run, basaltic USGS BCR-2G, synthetic carbonate USGS MACS-3 and a nano-powder pellet of biogenic carbonate JCp-1 (Garbe-Schönberg and Müller, 2014) were analyzed analyzed repeatedly as quality control materials (OCM) to monitor precision and accuracy of the measurements as well as calibration strategy. All reference materials 275 were analyzed analyzed at the beginning and at the end of a sequence and after ca. 40 spots on the samples. For all materials ⁴³Ca was used as internal standard applying for the USGS BCR-2G and MACS-3 the preferred values reported in the GeoReM

database, for JCp-1 38.18 wt.% (Okai et al., 2002) and for the samples a Ca content of 39 wt.% (Mertz-Kraus et al., 2009).

Resulting element concentrations for the QCMs together with reference values are provided in the supplementary material

(Table S1). Element concentrations for the samples are converted into molar ratios of Ca, i.e., Li/Ca, Mg/Ca, Ba/Ca as well as Li/Mg.

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Li/Mg thermometry was used for estimating absolute growth temperatures (Montagna et al., 2014; Cuny-Guirriec et al., 2019, Ross et al., 2019b, Harthone et al., 2013; Fowell et al., 2016; D'Olivo et al., 2018; Zinke et al., 2019). Li/Mg - SST relationships were shown to be site dependent, however, and similar Li/Mg-ratios produce differences in SST estimations of ~2 °C between inter-reef (Hathorne et al., 2013) and intra-reef settings (Fowell et al., 2016). Such spatial variability in Li/Mg - SST

285 relationships is likely due to poorly constrained effects of extension rate and seawater pH on skeletal Li/Mg ratios (Fowell et al., 2016; Fowell, 2017; Inoue et al., 2007; Tanaka et al., 2015). For this reason, we use a separate calibration of the Li/Mg thermometer for Masirah Island corals in order to overcome misleading SST estimates resulting from local seawater pH and extension rate effects associated with upwelling.

Ba/Ca ratios were used to identify skeletal portions calcified under upwelling conditions (Lea et al., 1989; Tudhope et al.,
 1996). Elevated Ba/Ca ratios in coral skeletons reflect high seawater Ba concentrations associated with upwelling deep waters, which are also nutrient-rich and acidic (Fallon et al., 1999; Montaggioni et al., 2006).

Daily Sea surface temperatures (SST_{rem}) were extracted from JPL MUR (v4.1) available from https://podaac.jpl.nasa.gov. The JPL MUR data range used for this study covers the period 2003___2018 and has a spatial resolution of 0.01° degrees (Grid cell: N19.90, E58.60). SSTs of equal calendar dates of consecutive years were averaged receiving one generalized annual record of mean daily SSTs for the period 2003___2018 (Fig. 2). Reliability of the remote sensed data was confirmed by daily

295 record of mean daily SSTs for the period 2003–2018 (Fig. 2). Reliability of the remote sensed data was confirmed by daily in-situ observed SSTs (SST_{in-situ}) recorded at the southern tip of Masirah Island (water depth: 5 m) between October 2001 and September 2002 (Wilson, 2007). Annual mean SSTs were in excellent accordance to each other (SST_{rem} = 25.79 °C; SST_{in-situ} = 25.54 °C) and daily SSTs were strongly correlated ($r^2 = 0.79$, p < 0.0001).

Monthly <u>S</u>eawater phosphate and nitrate concentrations <u>were-extracted_come</u> from the World Ocean Atlas 2018 (WOA18) available on https://www.nodc.noaa.gov/OC5/woa18/woa18data.html (<u>Grid cell: N19.5, E58.5, water depth: 5 m; Fig. 2</u>). The WOA18 nutrient data is a generalized interpolation of all available in-situ observations performed within individual months at certain depth levels within each 1° square (Garcia et al., 2018).

Monthly interpolated seawater aragonite saturation states for the northern Arabian Sea (Grid cell: N16.0, E57.5; Fig.2) were extracted from https://www.ldeo.columbia.edu/res/pi/CO2/carbondioxide/pages/global ph.html (Takahashi et al., 2014).

305 Annual mean nutrient concentrations were extracted for Masirah Island as well as for upwelling sites from where published coral calcification data was available (Table 1). Monthly values were solely extracted for Masirah Island (Grid cell: N19.5, E58.5, water depth: 5 m; Fig. 2).

Table 1: Mean annual seawater phosphate (PO4³⁻) and nitrate (NO3⁻) concentrations (±1σ) of Masirah Island as well as of

 310
 upwelling sites from where published coral calcification data is available (WOA18). Numbers (n) indicate the quantity of observations used for the calculation of an average concentration for each grid square.

Location	Grid cell	Water depth [m]	₽⊖₄ ³⁻ {µmol L ⁻¹ }	n	NO ₃⁻ [µmol L⁻¹]	n	₽0 4 ³⁻ / NO3 ⁻
Masirah Island (this study)	58.5E ; 19.5N	5	0.741 ± 0.616	11	4 .790 ± 6.257	2	0.155
Marbat (Tudhope et al., 1996)	54.5E ; 16.5N	5	0.478 ± 0.302	6	2.513 ± 1.558	3	0.190
Kuria Muria (Montone, 2010)	56.5E ; 19.5N	5	0.472 ± 0.074	9	2.356 ± 0.163	7	0.200
Bandar Khayran (Watanabe et al., 2017)	59.5E ; 23.5N	5	0.473 ± 0.060	11	1.606 ± 0.50 4	10	0.295
Galapagos (Manzallo et al., 2014)	92.5W ; 1.5S	5	0.858 ± 0.283	5	7.288 ± 1.875	5	0.118
Saboga (Mollica et al., 2018)	78.5W ; 6.5N	5	0.229 ± 0.148	18	2.341 ± 1.597	15	0.098

For the evaluation of measured coral calcification data (extension rate, bulk density and calcification rate), we used a reference 315 data set for *Porites* from Indo Pacific reefs including 14 reefs from Hawaii (Grigg, 1981) and 29 reef sites from the Great Barrier Reef (Lough and Barnes, 2000). Each site represents mean annual calcification data of 6 – 15 coral records and annual mean SSTs (1903 – 1994, GOSTAPlus). For this dataset, we assume an oligotrophic growth habitat and calcification of these corals to be largely controlled by ambient SSTs, while an effect of nutrients and seawater acidification is negligible. The relationship between SST and the calcification parameters within these two regions was used to develop linear calibrations for

320 predictions of skeletal density, extension rate and calcification rate from ambient SST. Slopes and intercepts of the calibrations slightly differ from those reported by Lough and Barnes (2000), because we confine the reference sites to Hawaii and the Great Barrier Reef. The resulting calibrations are as follows:

Bulk density [g cm ⁻³]	$= -0.1185 \times \text{SST} + 4.4158$	$(r^2 = 0.49; p < 0.0001)$	Eq. 1
Extension rate [cm yr^{-1}]	= 0.3113 × SST + 6.8994	$(r^2 = 0.90; p < 0.0001)$	Eq. 2
Calcification rate $[g cm^{-2} yr^{-1}]$	= 0.3342 × SST + 7.1554	$(r^2 = 0.82; p < 0.0001)$	Eq. 3

2.41 Data matching and age model development

Records of skeletal density and element concentrations of corals 5.10, 5.13 and 5.21 were matched with optical microscope images allowing for the correlation of ablated spots from LA-ICP-MS with distinctive features on X-radiographs. Internal Slight variations-offsets between the x-axis of the LA-ICP-MS record and the density records can occur, because to some extent the LA-ICP-MS sampling paths were not ultimately straight due to following discrete corallites and avoiding bioerosion traces and incrustations. To overcome this, the chronologies of the density records inferred from straight transects orientated parallel to the direction of growth were applied to the LA-ICP-MS records using AnalySeries software (Paillard et al., 1996). Age models are based on Li/Mg-ratios in combination with Ba/Ca-ratios. Li/Mg is inversely related to temperature, which allows to identify the two warm (inter-monsoon) and two cool (monsoon) seasons (Harthone et al., 2013). In order to identify the upwelling season (SWM) among the two cool monsoons seasons SWM and NEM, we use Ba/Ca ratios as proxy (Tudhope et al., 1996) (Fig. 3). The individual coral records comprise three full years for coral 5.10 and five full years for coral 5.13 and 5.21, respectively. A detailed chronological frame for the Li/Mg records was established with the aid of the generalized annual

record of remote sensing SST data (JPL MUR, daily averaged 2003 – 2018) (Fig. 2). Dates of seasonal SST extremes as well as dates of inflection points between consecutive seasons were assigned to corresponding data points of the Li/Mg records (see supplementary material, Fig. S2). —A detailed chronological frame for the Li/Mg records was established with the aid of the generalized annual record of remote sensing JPL MUR data (daily averaged 2003 – 2018) (Fig. 2), demonstrating average calendar dates of seasonal extremes to occur on 31.05. (SIM), 15.08. (SWM), 25.10. (AIM) and 06.02. (NEM). Average dates

- 340 calendar dates of seasonal extremes to occur on 31.05. (SIM), 15.08. (SWM), 25.10. (AIM) and 06.02. (NEM). Average dates of inflection points between consecutive seasons from JPL MUR data were 18.03. (NEM SIM), 25.06. (SIM SWM), 30.09. (SWM AIM) and 10.12. (AIM NEM). This methodology allows tuning the age models to a total of eight tie-points per year (two per season). Dates between tie-points were interpolated linearly and the entire time axis was resampled to monthly intervals using AnalySeries software (Paillard et al., 1996). Accuracy of the age model was checked by comparing the timing
- of seasonal remote sensing SST maxima and minima of individual years with dates of the generalized annual record (daily averages 2003_22018) and was found to be ± 4 weeks during NEM, ± 3 weeks during SIM and SWM, and ± 1.5 weeks during AIM.

3 Results

350 3.1 SST calibration of Li/Mg recordsCoral Ba/Ca and Li/Mg records

Multi-year monthly means of the Ba/Ca records show pronounced maxima within one annual cycle, which have been used in establishing the age model to determine the southwest monsoonal upwelling season (Fig.3) (Tudhope et al., 1996; Lea at al., 1989). Peak intensities vary considerably between samples, with coral 5.13 showing the lowest and coral 5.21 the highest Ba/Ca ratios during upwelling. All individual Ba/Ca records are positively related with WOA18 seawater phosphate and nitrate data (5.10: r² (PO₄³) = 0.68, p = 0.0009; r² (NO₃^{*}) = 0.74, p = 0.0003; 5.13: r² (PO₄³) = 0.84, p < 0.0001; r² (NO₃^{*}) = 0.94, p < 0.0001; r² (PO₄³) = 0.77, p = 0.0002; r² (NO₃^{*}) = 0.84, p < 0.0001) (Garcia et al., 2018).



Figure 3: Multi-year monthly means in Ba/Ca and Li/Mg of three Masirah corals (blue, orange, yellow). The grey shaded area represents uncertainty (1σ) between equal months of consecutive years. Seasonal abbreviations: ;, Seasons are shown as NEMNEM (northeast monsoon), SIM (spring intermonsoon), SWM (southwest monsoon), und AIM (autumn intermonsoon).

All multi-year monthly means of the Li/Mg records show pronounced patterns of two maxima and two minima within one annual cycle (Fig. 3). Li/Mg maxima coincide with peaks in Ba/Ca during summer-southwest monsoonal upwelling (SWM)
(Tudhope et al., 1996), while a second, maximum of Li/Mg is reached during winter (NEM). Minima occur during the intermonsoon seasons (SIM, AIM).-<u>All Monthly individual Li/Mg</u> records exhibit the typical inverse relationship with monthly remote sensing SST_{rem} data (JPL MUR) (5.10: r² = 0.65, p = 0.0016; 5.13: r² = 0.75, p = 0.0003; 5.21: r² = 0.91, p < 0.0001). Multi coral monthly means in Li/Mg are used for the calibration of the Li/Mg thermometer with mean monthly SSTs_{rem} (averages of 2003_-2018, JPL MUR) (Fig. 4). 83 % of the intra-annual multi coral monthly Li/Mg variation is explained by temperature and the resultant SST-calibration is estimated as:

Li/Mg [mmol mol⁻¹] =
$$-0.083 (\pm 0.012) \times SST + 4.029 (\pm 0.305)$$
 (r² = 0.83; p < 0.0001) Eq. 14



Figure 3: Multi-year monthly means in Li/Mg of the three Masirah corals (blue, orange, yellow). The grey shaded area represent
 uncertainty (1σ) between equal months of consecutive years. Regular peaks in Ba/Ca (dotted line) associated to upwelling indicate the southwest monsoonal season (Tudhope et al., 1996).



Figure 4: Multi coral calibration of the Li/Mg thermometer with SSTs_{rem} (monthly means 2003_2018, JPL MUR). Horizontal error
 bars (1σ) represent <u>SST</u> uncertainty between <u>equal mean-monthsly SSTs</u> of consecutive years (2003_2018) and vertical error bars (<u>1σ</u>) represent uncertainty of multi-year monthly mean Li/Mg ratios between the three Masirah corals. The grey shaded area indicates the 95 % confidence interval of the linear regression.

 Table 1: Mean seasonal SSTs (± 1σ) inferred from multi-year monthly mean Li/Mg ratios of individual corals from Masirah Island.

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 Uncertainty (1σ) represents variability between equal seasons of consecutive years. Seasonal abbreviations: NEM (northeast monsoon), SIM (spring intermonsoon), SWM (southwest monsoon), AIM (autumn intermonsoon).

	<u>5.10</u>	<u>5.13</u>	<u>5.21</u>
	<u>Li/Mg-SST</u> [<u>°C]</u>	<u>Li/Mg-SST</u> [<u>°C]</u>	<u>Li/Mg-SST</u> [°C]
<u>SIM</u>	<u>27.03 ± 0.45</u>	$\underline{27.85\pm0.88}$	<u>29.00 ± 1.25</u>
<u>SWM</u>	<u>23.03 ± 0.95</u>	24.79 ± 0.74	<u>24.36 ± 1.25</u>
AIM	<u>25.00 ± 1.28</u>	<u>26.08 ± 0.48</u>	$\underline{28.49 \pm 0.80}$
<u>NEM</u>	24.13 ± 0.42	$\underline{24.88\pm0.57}$	<u>25.72 ± 1.19</u>

3.2 Pattern of calcification

Mean annual skeletal density, extension rate and calcification rate as well as the number of record years investigated within
 each of the six individual coral specimens is shown in Table 2. Sub-annually resolved patterns of calcification of coral 5.10,
 5.13 and 5.21 are expressed as multi-year monthly means (Fig.5). The variability in monthly calcification rate within all three specimens is strongly determined by extension rate (5.10: r² = 0.94, p < 0.0001; 5.13: r² = 0.77, p < 0.0002; 5.21: r² = 0.81, p < 0.0001). Coral 5.13 and 5.21 show three distinct peaks of highest extension rate in March, June and October. Reduced linear growth occurs during SWM, NEM as well as in-between April and May. Coral 5.10 slightly deviates from the pattern of the two other specimens due toby the lack of elevated a lower growth rate during June, leading to two peaks of maximum extension

in February/March and October. In this specimen, a decrease in linear growth starts in SIM and reaches its minimum during SWM.

<u>Sub-annual variability in skeletal bulk density of coral specimens 5.10 and 5.13 show a pattern of two distinct high density</u> bands (HDBs) between two bands of low density (LDB) within one annual growth increment (Fig.5). Skeletal portions of low

400 density were deposited during SIM and AIM, high density portions formed during SWM and NEM. This alternating pattern of HDBs and LDBs causes skeletal density variation in coral 5.10 and 5.13 to be significantly inversely related to monthly reconstructed Li/Mg-SSTs (5.10: $r^2 = 0.87$, p < 0.0001; 5.13: $r^2 = 0.34$, p < 0.05) (Fig.6c). This is not the case for coral 5.21, as a well expressed LDB equivalent with AIM is lacking. Rather, it shows one wide LDB with density increasing from SWM to NEM.

405 Mean annual extension rate of

<u>Table 2: Mean annual skeletal bulk density, linear extension rate and calcification rate $(\pm 1\sigma)$ of all six coral specimens from Masirah</u> <u>Island. Uncertainty (1 σ) represents variability between consecutive record years.</u>

	Record years	Bulk density	Extension rate	Cacification rate
	<u>[n]</u>	[g cm ⁻³]	[cm yr-1]	[g cm ⁻² yr ⁻¹]
<u>5.9</u>	<u>6</u>	1.03 ± 0.04	$\underline{1.19\pm0.16}$	1.22 ± 0.15
<u>5.10</u>	<u>3</u>	$\underline{1.02\pm0.02}$	$\underline{1.43\pm0.05}$	$\underline{1.45\pm0.08}$
<u>5.13</u>	<u>5</u>	0.91 ± 0.06	1.17 ± 0.12	$\underline{1.03\pm0.07}$
<u>5.15</u>	<u>3</u>	$\underline{1.07\pm0.04}$	1.07 ± 0.16	$\underline{1.14\pm0.14}$
<u>5.21</u>	<u>5</u>	0.99 ± 0.07	1.53 ± 0.11	$\underline{1.49\pm0.10}$
<u>5.22</u>	<u>4</u>	$\underline{0.95 \pm 0.05}$	1.47 ± 0.13	$\underline{1.38\pm0.08}$

the coral specimens is 1.43 ± 0.05 cm yr⁴, 1.17 ± 0.12 cm yr⁴ and 1.53 ± 0.11 cm yr⁴ for coral 5.10, 5.13 and 5.21 respectively

(Fig. 5). Corals 5.13 and 5.21 show three peaks of highest extension rates in March, June and October. Reduced linear growth

- 410 <u>occurs during SWM, NEM as well as in between April and May. Coral 5.10 slightly deviates from the pattern of the two other specimens due to the lack of elevated growth rates during June, leading to two peaks of maximum extension in February/March and October. In this specimen, a decrease in linear growth starts in SIM and reaches its minimum during SWM. Mean annual bulk density of the coral samples is 1.02 ± 0.02 g cm⁻³ (n = 3), 0.91 ± 0.06 g cm⁻³ (n = 5) and 0.99 ± 0.07 g cm⁻³ (n = 5) for coral 5.10, 5.13 and 5.21 respectively (Fig. 5). Two out of the three coral specimens (5.10 and 5.13) show a pattern of two</u>
- 415 distinct high density bands (HDBs) between two bands of low density (LDB) within one annual growth increment. Skeletal portions of low density were deposited during SIM and AIM, high density portions formed during SWM and NEM. Coral sample 5.21 is similar to 5.10 and 5.13 but differs by lacking a well expressed LDB equivalent with AIM. Rather, it shows one wide LDB with density increasing from SWM to NEM. Mean annual extension rate of the coral specimens is 1.43 ± 0.05 cm yr⁴, 1.17 ± 0.12 cm yr⁴ and 1.53 ± 0.11 cm yr⁴ for coral 5.10, 5.13 and 5.21 respectively (Fig. 5). Corals 5.13 and 5.21 show
- 420 three peaks of highest extension rates in March, June and October. Reduced linear growth occurs during SWM, NEM as well as in between April and May. Coral 5.10 slightly deviates from the pattern of the two other specimens due to the lack of elevated growth rates during June, leading to two peaks of maximum extension in February/March and October. In this

specimen, a decrease in linear growth starts in SIM and reaches its minimum during SWM. Monthly mean calcification is mainly determined by linear extension rates, showing an equal inter-annual pattern for all three corals studied. Net calcification rate is 1.45 ± 0.08 g cm⁻² yr⁻¹, 1.03 ± 0.07 g cm⁻² yr⁻¹ and 1.49 ± 0.10 g cm⁻² yr⁻¹ for coral 5.10, 5.13 and 5.21 respectively (Fig. 5).

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430 Figure 5: Results of multi-year monthly means in-of calcification rate, extension rate and skeletal density, extension rate and calcification rate-of-_three corals from Masirah Island_(blue, orange, yellow). The grey shaded area represents uncertainty (1σ) between equal months of consecutive years. Seasonal abbreviations: -Seasons are shown as NEM (northeast monsoon), SIM (spring intermonsoon), SWM (southwest monsoon), and AIM (autumn intermonsoon).



Figure 6: Multi-year monthly means inof (a) calcification rate, (b) extension rate and (c) skeletal bulk density and associated Li/Mg-SSTs of three corals from Masirah Island (blue, orange, yellow). The coloured shaded polygons combine monthly data that belong to the same season. Seasonal abbreviations:; with NEM (northeast monsoon), SIM (spring intermonsoon), SWM (southwest monsoon), und AIM (autumn intermonsoon).

Calcification rate during SWM is only 51 %, 96 % and 78 % of that observed during NEM (for coral 5.10, 5.13 and 5.21, respectively) (Table 3; Fig.6a). This difference in seasonal calcification rate is related to low extension rate during southwest monsoonal upwelling, which is 49 %, 71 % and 91 % relative to that observed during NEM (for coral 5.10, 5.13 and 5.21, respectively). Interestingly, monthly extension rate during SWM exhibit a strong negative correlation with skeletal density

445 across all three specimen ($r^2 = 0.88$, p = 0.0002), which is not the case during NEM ($r^2 = 0.04$, p = 0.60) (Fig.7). According to individual SWM extension rates, this produces varying density patterns across the three specimens, with corals 5.13 and 5.10 having the lowest SWM extension rate showing the highest intra-annual skeletal density during this season (Table 3; Fig.5). Coral 5.21 that shows relatively fast SWM extension growth compared to all other specimens only reveals a moderate increase in skeletal density, which remains below those observed during the NEM.

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Table 3: Mean	<u>n seasonal skele</u>	tal bulk den	<u>sity, linear e</u>	extension ra	ite ar	nd calcification	on rate	$(\pm 1\sigma)$ of t	hree corals from	m Masi	<u>rah Island.</u>
Uncertainty ((1σ) represents	variability	between ec	ual season	s of	consecutive	years.	Seasonal	abbreviations:	NEM	(northeast
monsoon) SI	M (snring inter	monsoon) S	WM (south	west monsc	on)	AIM (autum	n inter	monsoon)			

		5.10			5.13		5.21			
	Bulk density [g cm ⁻³]	Extension rate [cm yr ⁻¹]	Cacification rate	Bulk density [g cm ⁻³]	Extension rate [cm yr ⁻¹]	Cacification rate [g cm ⁻² yr ⁻¹]	Bulk density [g cm ⁻³]	Extension rate [cm yr ⁻¹]	Cacification rate [g cm ⁻² yr ⁻¹]	
<u>SIM</u>	<u>0.94 ± 0.04</u>	$\underline{1.26\pm0.23}$	<u>1.18 ± 0.20</u>	0.81 ± 0.07	<u>1.25 ± 0.34</u>	<u>1.02 ± 0.25</u>	$\underline{0.80\pm0.1}$	<u>1.83 ± 0.30</u>	<u>1.47 ± 0.33</u>	
<u>SWM</u>	<u>1.10 ± 0.01</u>	$\underline{0.87 \pm 0.06}$	<u>0.95 ± 0.06</u>	$\underline{1.15\pm0.08}$	<u>0.90 ± 0.18</u>	<u>1.02 ± 0.18</u>	0.94 ± 0.05	<u>1.31 ± 0.23</u>	<u>1.24 ± 0.28</u>	
AIM	<u>0.99 ± 0.03</u>	<u>1.83 ± 0.28</u>	<u>1.81 ± 0.33</u>	0.83 ± 0.07	<u>1.25 ± 0.27</u>	<u>1.03 ± 0.21</u>	$\underline{1.09\pm0.06}$	<u>1.55 ± 0.20</u>	1.65 ± 0.19	
<u>NEM</u>	1.05 ± 0.01	1.79 ± 0.17	1.88 ± 0.17	$\underline{0.85\pm0.05}$	1.26 ± 0.31	<u>1.06 ± 0.26</u>	1.12 ± 0.1	<u>1.44 ± 0.20</u>	1.58 ± 0.11	



Figure 7: Multi-year monthly means in extension rate versus skeletal bulk of the three corals from Masirah Island (blue, orange, yellow). The coloured shaded polygons combine monthly data that belong to the same season. Seasonal abbreviations:; with NEM (northeast monsoon), SIM (spring intermonsoon), SWM (southwest monsoon), und AIM (autumn intermonsoon).

4 Discussion

460 4.1 Ba/Ca records

Multi-year monthly means in skeletal Ba/Ca are in excellent agreement with WOA18 nutrient data. This confirms Ba/Ca to be an appropriate It isan appropriate proxy for intra-annual variability in seawater nutrient concentrations (Fallon et al., 1999; Montaggioni et al., 2006). Ebecauseeffects of terrestrial-riverine input on the skeletal Ba/Ca record arecan be excluded due to the absence of fluvial regimesrivers in the arid regions of north-eastern Oman (Alibert et al., 2003; Jiang et al., 2017). This

465 <u>allows intra-annual variability in Ba/Ca to be fully attributed to upwelling (Tudhope et al., 1996; Lea et al., 1989). Variable Ba/Ca ratios across specimens during southwest monsoonal upwelling season (SWM) are likely to result from spatial heterogeneous seawater bBarium distribution within the reef.</u>

4.21 Li/Mg thermometry records

SST reconstructions based upon the calibration of the Li/Mg thermometer described above (Eq. 41) reproduce the monthly curse of the SST_{rem} data ($r^2 = 0.83$, p < 0.0001) as well as observed SST_{in-situ} variations at Masirah Island ($r^2 = 0.93$, p < 0.0001) 470 (Wilson, 2007). Temperature sensitivity of the Li/Mg----thermometer deduced from reconstructed seasonality is in good agreement with the majority of proxy calibration studies from the literature (Hathorne et al., 2013; Ross et al., 2019b; Cuny-Guirriec et al., 2019; Montagna et al., 2014; Fowell et al., 2016 (Forereef)). The intercept of the linear Li/Mg_-SST calibration of the Masirah corals, however, is 4-58 °C higher-than reported in the literature (Fig. 86). Analytical uncertainties that 475 noticeably bias the Li/Mg ratio are unlikely as a source for high Li/Mg ratios, because systematic measurement discrepancies deduced from the JCp-1 QCM for Li/Ca and Mg/Ca would rather tend to underestimate the Li/Mg ratios (Li/Ca: +4.44 %; Mg/Ca: +7.37 %; Table S1). In contrast, In addition to temperature, seawater pH also has shown to bias the skeletal Li/Mg ratio of corals (Fowell et al., 2016; Fowell, 2017; Tanaka et al., 2015). For identical SSTs, culture experiments on Sideastrea siderea show an increase of 0.325 mmol/mol in Li/Mg per decreasing pH_{sw} unit (Fowell, 2017). However, comparatively high Li/Mg values found in the Masirah corals are present year-round, while exceptionally low pH_{sw} is limited to the three monthly 480 southwest monsoonal upwelling season (Omer, 2010; Takahashi et al., 2014). This suggests that skeletal Li/Mg is not directly sensitive to the external pH_{sw}, but rather to the carbonate chemistry of the calcification fluid, which through modification is independent of external variations in pH_{sw} (McCulloch et al., 2017). Conditions within the calcifying fluid must permanently alter skeletal Li/Mg of Porites at Masirah Island towards higher values compared to published SST-Li/Mg calibrations reported 485 in the literature, which might imply year-round stable but low pH_{cf}.

low seawater pH can cause high Li/Mg ratios by lowering the skeletal Mg content (Tanaka et al., 2015). A generally enhanced Mg/Ca_{sw} variability found within regions affected by coastal upwelling is also assumed to cause biases in coral Li/Mg from undisturbed environments (Lebrato et al., 2020).



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Figure <u>68</u>: Instrumental SSTs (<u>green line</u>) compared to multi coral monthly mean SSTs inferred from Li/Mg ratios of the Masirah corals using the calibration of this study (red line) and calibrations reported from the literature. Published Li/Mg_—SST calibrations cause variable degrees of underestimation of coral growth temperatures at Masirah Island. <u>Seasonal abbreviations</u>; <u>Seasons are</u> <u>shown as-NEM</u> (northeast monsoon), SIM (spring intermonsoon), SWM (southwest monsoon), <u>und</u> AIM (autumn intermonsoon).

4.32 Annual records of coralSkeletal calcification

4.3.1 Monthly records of coral calcification

- 500 Monthly variability in calcification rate is largely driven by extension rate across all samples (Fig.5ure), similar to that reported for *Porites* from the Indo-Pacific region (Lough and Barnes, 2000). However, the typical positive correlation between monthly extension rate and SST does not exist in our data (Fig.6b). All three specimens reveal noticeably small extension growth during April and May despite of high SIM temperatures. Interestingly, coral spawning at Omani reef sites is reported to take place between March and May (Howells et al., 2014). Correspondingly, a reduction of extension rate during SIM could be linked to
- 505 high-energy expenditures required for reproduction (Cabral-Tena et al., 2013). All specimens show lower SWM calcification rate compared to that observed for NEM, which is attributed to smaller extension rate during the upwelling (Table 3). Declining extension rate during upwelling season is in agreement with growth studies on *Pocillopora damicornis* from the Gulf of Panama (Glynn, 1977). For corals from Masirah Island, at least part of the seasonal difference in extension rate between SWM and NEM might be related to slightly lower SSTs during the southwest monsoonal
- 510 upwelling (Table 1). Given an increase in extension rate of 0.33 cm yr⁻¹ per 1°C as suggested for Indo-Pacific *Porites*, differences in extension rate between SWM and NEM could be fully explained by temperature for coral 5.21, but only to some extent for coral 5.10 and 5.13 (Lough and Barnes, 2000). Intensive eutrophication might have additional impact on growth of

<u>Masirah corals</u>, with detrimental effects on extension rate during the upwelling season (Tomascik, 1990). Assuming direct detrimental effects of the essential nutrients on coral growth, the inhibiting effect of NO_3^- would have to outweigh the

- 515 promoting effect of PO_4^{3-} on SWM extension rate of the Masirah corals (Koop et al., 2001; Dunn et al., 2012; Bucher and Harrison, 2001). However, the northern Arabian Sea is characterized by a high PO_4^{3-} to NO_3^{-} ratio, making this direct effect of nutrients on the extension rate unlikely (Kleypas, 1999). As a general consequence of the excessively high nutrient concentrations, primary productivity in the Arabian Sea increases rapidly during the upwelling season, leading to high levels of turbidity associated with low light transparency of the water column (Anderson et al., 1992; Bauer et al., 1991; Quinn and
- 520 Johnson, 1996). Reduced photosynthetic efficiency of the micro-algae symbionts seems to be a potential factor for diminished extension rate in response to reduced energy reserves during upwelling (Al Shehhi et al., 2014; Logan and Tomascik, 1991; Muscatin et al., 1981; Sun et al., 2008; Tomascik, 1990). Energy through heterotrophic feeding does not seem to be sufficient for Masirah corals to fully compensate for reduced levels of photosynthates (Tomascik and Sander, 1985). Interestingly, highest monthly extension rate occur immediately before and after the upwelling season during June and October, respectively
- 525 (Fig.5). A decrease in the extension rate during the SWM sets on immediately at the beginning of the upwelling, only to recover rapidly again afterwards. We therefore conclude that the coral's energy reserves available for skeletal upward growth response instantaneous to monthly environmental changes (i.e., turbidity), without delays or extended times for recovery. In contrast to *Porites* from the Indo-Pacific region showing only a moderate dependence of skeletal density on SST, Li/Mg-
- SSTs at Masirah Island are strongly correlated with the monthly variation in skeletal density in coral 5.10 and 5.13 (Lough and Barnes, 2000). This is however not observed for coral 5.21, as a weakly developed HDB during SWM worsens a causal relationship with SST (Fig.6c). This comparatively low density during southwest monsoonal upwelling coincides with relatively high SWM extension rate in coral 5.21 compared to all other samples (Table 3; Fig.6b). Excellent negative correlation between southwest monsoonal data of monthly density and extension rate across the three corals (n = 9, $r^2 = 0.88$, p = 0.0002) indicates density during upwelling to be substantially controlled by extension rate (Fig.7). A simple model in
- 535 which the active calcification surface to which CaCO₃ is accreted is relatively large at high extension rate, resulting in thin skeletal elements and low bulk density (and vice versa for HDBs) might explain inter-specimen variability in skeletal density patterns of the Masirah corals during SWM (DeCarlo and Cohen, 2017). No evidence supports an immediate detrimental impact of upwelling, i.e., a temporally low Ω_{sw} , on sub-annual patterns in skeletal density. Given density being controlled by the carbonate chemistry of the calcification fluid, we propose Ω_{cf} is kept relatively constant by modification independent of
- 540 <u>external variations in Ω_{sw} during upwelling and non-upwelling seasons (DeCarlo et al., 2018; McCulloch et al., 2017; Mollica et al., 2018).</u>

4.3.2 Annual records of coral calcification

- 545 Mean annual calcification rate at Masirah Island is indistinguishable from those of *Porites* from Indo-Pacific and Atlantic reef sites, which are unaffected by upwelling (Fig.9a). Although a poor replication of *Porites* calcification data from the upwelling areas of Panama and the South China Sea (n = 1, respectively) does not enable a proper comparison, statistically robust data reported from two sites located within the Galapagos upwelling zone (n = 7-8 cores per site) reveal an identical result (Manzello et al., 2014; Mollica et al., 2018). However, patterns of calcification in *Porites* from Masirah Island and Galapagos differ from
- 550 those found in regions without upwelling by showing enhanced extension rate at concurrently lower skeletal density, similar to the pattern termed "stretching modulation of skeletal growth" by Carricart-Ganivet (2004) (Fig.9b, 9c). High mean annual *Porites* extension rate at Galapagos is discussed by the authors in terms of the stimulating effect of nutrients on upward growth (Manzello et al., 2014). Nutrient-stimulated growth is also suggested for enhanced annual extension growth of *Pocillopora damicornis* and *Pavona clavus* from the Panama upwelling zone compared to data from regions unaffected by upwelling
- 555 (Glynn, 1977; Wellington and Glynn, 1983). In fact, enhanced annual extension rate of *Pavona clavus* from Panama is the result of high extension growth during the non-upwelling season, a pattern also applicable to the herein presented *Porites* from Masirah Island (Wellington and Glynn, 1983) (Table 3). Hence, a stimulating effect of nutrients on extension rate during the non-upwelling seasons is possible, in particular because in the northern Arabian Sea moderate nutrient concentrations with high PO₄³⁻ to NO₃⁻ ratio exist year-round (Dunn et al., 2012; Kleypas et al., 1999; Koop et al., 2001).
- 560 Low skeletal density of coral specimens from Masirah Island is consistent with low skeletal density reported in the literature for *Porites* from the upwelling regions of the eastern Pacific and the China Sea (Mollica et al., 2018; Manzello et al., 2014) (Fig.9c). Boron isotope analyses on some of these samples have revealed the low skeletal density to be driven by a relatively low Ω_{cf} compared to corals from regions unaffected by upwelling (Mollica et al., 2018). Low Ω_{cf} in these specimens is maintained year-round, independent of external variations in Ω_{sw} (i.e., seasonal upwelling) (N. Mollica, personal
- 565 communication, 2021). With regard to relatively low skeletal density of the Masirah corals, which persists year-round and does not show an immediate response to SWM upwelling, we consider transferring the same mechanism of a constant low Ω_{ef} . This argument is also supported by the Li/Mg ratios of the Masirah corals, which are offset to higher values than those expected from the literature (Fig.8). As this offset is present throughout the year, it cannot be attributed to temporarily low pH_{sw} associated to seasonal upwelling, but rather reflects year-round constant conditions within the calcifying fluid (Fowell, 2017;
- 570 McCulloch et al., 2017). This finding implies that there is no intensified upregulation of internal Ω_{cf} relative to Ω_{sw} during the non-upwelling seasons (McCulloch et al., 2017; DeCarlo et al., 2018; D'Olivo and McCulloch, 2017). As an explanation, we propose that internal upregulation processes of corals affected by seasonal upwelling are not capable to adapt completely to ocean chemistry change on a quarterly scale. As a consequence, a relatively low Ω_{cf} is maintained year-round so as to avoid high gradients to the external Ω_{sw} during southwest monsoonal upwelling.



Figure 9: Annual means inof *Porites* calcification rate (a), extension rate (b) and skeletal bulk density (c) versus sea surface temperature (SST) from various Indo-Pacific and Western Atlantic reef sites. Red circles indicate sites affected by seasonal upwelling.

- Annual bulk density and linear extension rate documented for Masirah *Porites* during this study reveal strong discrepancies to the reference data set of corals from Hawaii and the GBR (Lough and Barnes, 2000) (Fig. 7a b). Multi-coral annual mean skeletal density of the Masirah corals is 28 % lower, and mean annual linear extension rate is 20 % higher compared to the reference corals growing at equal temperatures at the GBR and Hawaii (Table 2). Unusually high extension rates were also reported from Omani reef sites at the Kuria Muria Islands (+44 %; Southern Arabian Sea, Oman; Montone, 2010) and Bandar Khayran (+56 %; Gulf of Oman, Oman; Watanabe et al., 2017) (Fig. 1). Conversely, two corals from Marbat (southern Arabian Sea, Oman; Tudhope et al., 1996) show extension rates of massive *Porites* corals were also reported from the eastern equatorial Pacific upwelling zone. For instance, mean linear extension rate +60 % relative to western Pacific reef sites were reported from Galapagos Archipelago (Manzello et al., 2014), but -42 % from Saboga Island (Gulf of Panama) (Mollica et al., 2018)
 (Fig. 7b). Thus, skeletal extension rates of corals from sites affected by upwelling are not a simple function of SST, neither
- within four spatially distinct coral regions from Oman nor at far distant reef sites of the eastern equatorial Pacific. In contrast, bulk density of reef corals from sites affected by seasonal upwelling is consistently lower than those reported for the reference data set (Galapagos: 38 % (Manzello et al., 2014); Saboga: 27 % (Mollica et al., 2018)) (Fig. 7a, Table 2).



[W15]

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Figure 7: Annual means in skeletal bulk density, linear extension rate and calcification rate versus sea surface temperature (SST) of corals from sites affected by intense seasonal upwelling (coloured) and reference corals from Hawaii and the GBR (grey). Error bars refer to variations in multi coral annual means (vertical) and in proxy derived SSTs. Linear regression and 95 % prediction interval (grey shaded) refer to the Indo-Pacific reference data (Lough & Barnes, 2000).

A strong enhancement of coral linear extension rate, associated with a simultaneous loss in skeletal density was observed in response to nutrient fertilization (Dunn et al., 2012; Koop et al., 2001; Bucher and Harrison, 2001; Dodge and Brass, 1984, D'Olivo et al., 2013; Risk and Sammarco, 1991; Manzello et al., 2015). Nonetheless, published records reveal no correlation 605 between annual extension rate and nutrients, neither NO_3^- nor PO_4^{3-} at coral sites are affected by seasonal upwelling ($r^2 (NO_3^-)$) = 0.26, p = 0.30; $r^2(PO_4^2) = 0.05$, p = 0.68) (Table 1). In contrast, however, extension rate is strongly correlated with the PO_4³- $/NO_3$ -ratio (P/N) (r² = 0.91, p = 0.003) rather than with annual SST (r² = 0.57, p = 0.085) when seasonal upwelling occurs (Fig. 8a,b). When extension rates are expressed as the deviation from the values predicted by the reference corals (Eq. 2), the residuals still were well related to P/N (r^2_{-} = 0.71, p = 0.036) (Fig. 8c). However, the quality of correlation is strongly 610 determined by the data of the Porites from Saboga (Mollica et al., 2018). This is because the extremely low extension rate at relatively high SST downgrade the positive relationship apparent from the data of the remaining corals from upwelling sites (Fig. 8a). An imbalanced P/N with disproportionally high NO₃-within the Gulf of Panama (Table 1) likely inhibits linear growth, outweighing the stimulating effect of high SSTs on extension rate (Koop et al., 2001). Diminished extension rate within the Gulf of Panama compared to sites unaffected by upwelling is also reported for Pocillopora damicornis (Glynn, 615 1977; Manzello, 2010). Pavona clavus, however, shows enhanced growth rates within the Gulf of Panama compared to sites unaffected by upwelling, while growth rates of *Pavona gigantea* are indistinguishable (Manzello, 2010; Wellington and Glynn, 1983). Variable coral growth rates at one and the same site might either demonstrate (1) genus/species related differences of growth sensitivities to ambient P/N, (2) local heterogeneities in nutrient distribution over intra reef scales or (3) variable conditions for linear growth, e.g. light penetration (Omata et al., 2008).



Figure 8: Mean annual extension rates of *Porites* from upwelling regions as a function of (a) SST, (b) P/N. Deviations between measured extension rates and those predicted by the reference corals (Lough and Barnes, 2000) as function P/N (c). The grey shaded area represents the 95 % confidence interval of the regressions (solid black line).

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Published data of bulk density from sites affected by strong seasonal upwelling are extremely sparse (n = 2). Including this study, a total number of three site averaged data values on bulk density brought up no unambiguous correlations with either SST, NO₃₋₇, PO₄₋₃- or P/N. Mollica et al. (2018) showed, however, that low skeletal density of the coral from the Panama upwelling zone (Saboga) is caused by a diminished aragonite saturation state of the calcifying fluid (Ω_{ef}) compared to corals from sites unaffected by upwelling. Hence, an equal underlying mechanism can also be assumed to account for low skeletal density of corals from Masirah Island and Galapagos.

Assuming annual extension rates being in accordance to those of the reference corals, diminished skeletal density of the Masirah and Galapagos corals would result in net calcification rates of 24.8 % (ΔCalc = 0.37 g cm⁻² yr⁻¹) and 42.1 % (ΔCalc = 0.27 g cm⁻² yr⁻¹), respectively. However, enhanced extension rates at Masirah and Galapagos attenuate this effect, resulting
 635 in calcification rates only 10.86 % and 7.32 %, respectively, lower than that of the reference corals (Table 2). This compensating effect of high extension rates on calcification rates is not present in the *Porites* from Saboga. Rather, low extension rates amplify the negative effect of low density on calcification rate. This demonstrates the stimulating (inhibiting)

effect of a high (low) P/N on extension rate also significantly determines the calcification rate.

645 Table 2: Comparison of site-specific measured annual mean calcification parameters (skeletal density, extension rate, calcification rate) of corals affected by strong seasonal upwelling to values predicted for annual SSTs by the western Pacific reference data set (Hawaii and GBR) (Lough and Barnes, 2000). Empty cells indicate the lack of measured data. Galapagos calcification data involves the sites Devil's Crown and Urvina Bay (Manzello et al., 2014).

			ł	Measured value	5	Predicted values				∆ (measured — predicted)						
	n	SST [°С]	Bulk den. [g cm ⁻³]	Ext. rate [cm yr ⁻¹]	Calc. rate [g cm ⁻² yr ⁻¹]	Bulk den. [g cm ⁻³]	Ext. rate [cm yr ⁻¹]	Calc. rate [g cm ⁻² yr ⁻¹]	<u>∆ Bul</u> _[g cm ⁻³]	k den. [%]	<u>∆ Ext</u> _[cm yr ⁻¹]	t. rate [%]	∆ Cal -[g cm ⁻² yr	c. rate '] <u>[%]</u>		
Masirah Island (this study)	3	25.85 ± 0.91	0.97 ± 0.05	1.38 ± 0.15	1.32 ± 0.21	1.35	1.15	1.48	-0.38	-28.08	0.228	19.86	-0.16	-10.86		
Marbat (Tudhope et al., 1996)	2	26.30	-	1.25	-	-	1.29	-	-	-	-0.04	-2.82	-	-		
Kuria Muria (Montone, 2010)	4	26.38	-	1.90	-	-	1.31	-	-	-	0.59	44.74	-	-		
Bandar Khayran (Watanabe et al., 2017)	4	27.70	-	2.70	-	-	1.72	-	-	-	0.97	56.42	-	-		
Galapagos (Manzello et al., 2014)	2	23.33 ± 0.00	1.03 ± 0.06	0.58 ± 0.12	0.59 ± 0.09	1.65	0.36	0.64	-0.63	- <u>38.18</u>	0.22	59.68	-0.05	- 7.32		
Saboga (Mollica et al., 2018)	4	26.50	0.93	0.78	0.73	1,28	1.35	1.70	-0.35	-27.34	-0.57	-4 2.22	-0.98	-57.35		

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4.3 Monthly records of coral calcification

Multi coral mean monthly calcification data of the three corals from Masirah Island demonstrate that the deficit of skeletal density found within the annually resolved data exists also over the entire year and co-varies consistently with mean monthly SST ($r^2 = 0.95$, p < 0.0001) while no link is apparent with a certain season, i.e. the upwelling (Fig. 9a). Nonetheless, the largest 655 difference in mean monthly skeletal density to values predicted by the reference data occur during the monsoon seasons (Apswed $= 0.51 \pm 0.05$ g cm³; $\Delta \rho_{\text{NEM}} = 0.44 \pm 0.07$ g cm³), the lowest differences during the inter monsoon seasons ($\Delta \rho_{\text{SEM}} = 0.26$ $\pm 0.03 \text{ g cm}^3$; $\Delta \rho_{AIM} = 0.33 \pm 0.06 \text{ g cm}^3$). Excessively high nutrient concentrations and low Ω_{au} hardly explain year round low skeletal density, because the nutrient pulse and simultaneously diminished Ω_{sw} are temporally limited to the SWM (Fig. 2). Year round low skeletal density is therefore rather related to permanently low aragonite saturation at the site of calcification 660 (Ω_{ef}) (Mollica et al., 2018). A similar pattern of relatively constant, but low Ω_{ef} over the entire year, independent from external variations in $\Omega_{\rm w}$ -caused by upwelling, was reported also for the Saboga coral (N. Mollica, personal communication, 2021). This finding would imply that there is no intensified upregulation of internal Ω_{ac} relative to Ω_{ac} during the non-upwelling seasons and a rather low level of internal $\Omega_{\rm er}$ is maintained over the entire year (McCulloch et al., 2017; DeCarlo et al., 2018; D'Olivo and McCulloch, 2017). Since the non-upwelling season in the Arabian Sea lasts for approximately nine months, coral 665 growth occurs at $\Omega_{\rm m}$ of 3.5 4 for most of the time (Omer. 2010), which is above values assumed to impede skeletal calcification (Kleypas et al., 1999). Similar $\Omega_{\rm sw}$ are reported also from several undisturbed Pacific coral reefs which are unaffected by upwelling, though internal $\Omega_{a^{+}}$ of these corals is approximately 25 % higher compared to those being affected by upwelling (Mollica et al., 2018). As an explanation, we propose that internal upregulation processes of corals from Masirah Island are not capable to adapt completely to the ocean chemistry change on a quarterly scale, therefore maintaining a low gradient between Ω_{sw} and Ω_{ef} in order to survive the more harsh condition during SWM.

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Figure 9: Multi coral monthly means in skeletal density, extension rate and calcification rate of the Masirah corals (green) and values predicted based on SSTs (black) by the Indo-Pacific reference data (Lough and Barnes, 2000). The grey shaded area represents variations (1σ) between multi-year monthly means of the three Masirah corals.

Multi coral mean monthly extension rate is only weakly positively correlated with SST ($r^2 = 0.26$, p = 0.094), which is caused by noticeably small extension rates during April and May despite of high SIM temperatures (Fig. 9b). SIM constitutes the only season, when extension rates fall below values predicted by the western Pacific reference coral dataset (AExt_{SIM} = 0.33 ± 0.33 680 0.41 cm yr⁻¹). Interestingly, coral spawning at Omani reef sites is reported to take place between March and May (Howells et al., 2014). Correspondingly, a reduction of extension rate during SIM could be linked to high energy expenditures required for reproduction (Cabral-Tena et al., 2013). Irrespective of low extension rates during April and May, the monthly variation of extension rate during the remaining annual period is strong positively related to SSTs ($r^2 = 0.67$, p = 0.0038). Best accordance between measured extension rates and values predicted by western Pacific corals occur during AIM ($\Delta Ext_{AIM} = 0.24 \pm 0.20$ 685 cm yr⁻¹). In contrast, skeletal extension during the monsoon season is remarkably higher than predicted for ambient SSTs $(\Delta Ext_{SWM}: 0.46 \pm 0.16 \text{ cm yr}^{-1}: \Delta Ext_{NEM}: 0.62 \pm 0.20 \text{ cm yr}^{-1})$. While the nutrient pulse associated with upwelling would only affect SWM extension rates (Fig. 2), constantly high levels of nutrients and/or a constantly high P/N during the entire year are potentially to buffer the negative effect of low temperatures on extension rates during NEM and SWM (Dunn et al., 2012; Koop et al., 2001; Smith, 2001). Here, we infer a mechanism in which nutrients promote biochemical processes keeping 690 efficiency of symbiont photosynthesis upright despite of low temperatures, thus allowing for the maintenance of a relatively thick tissue layer. The tissue layer thickness is supposed to control monthly upward growth of the coral (DeCarlo and Cohen, 2017; Godinot et al., 2011). It has been shown from coral growths at the upper temperature threshold that the availability of

nutrients, in particular a high P/N increases the resilience to bleaching by maintaining photosynthesis upright (Ezzat et al.,

2016; Riegl et al., 2019; Rosset et al., 2017; Wiedemann et al., 2013). Hence, the decline of the tissue layer thickness is less

- 695 expressed leading to smaller decreases in monthly extension rate (Marangoni et al. 2021; DeCarlo and Cohen, 2017). We assume an equal mechanism to account for sustaining relatively high extension rates of the Masirah corals at the lower temperature limits, in particular because P/N in northern Arabian Sea is high (Kleypas et al., 1999). A comparable mechanism of nutrient stimulated tissue growth and a concomitant increase in linear growth was also proposed for *Pavona clavus* from the Gulf of Panama (Wellington and Glynn, 1983).
- Multi coral mean monthly calcification rate inferred from data of this study is essentially controlled by the effects of extension rate (r² = 0.88, p < 0.0001) rather than skeletal density (r² = 0.016, p = 0.70). Calcification rate during SIM shows the highest deficits compared to western Pacific reference corals (ΔCalc_{SIM} = 0.92 ± 0.42 g cm⁻² yr⁻¹) because both, extension rate and skeletal density are low at the same time. Best accordance to values predicted from the reference data set is documented for the AIM (ΔCalc_{AIM} = 0.14 ± 0.19 g cm⁻² yr⁻¹). During both monsoon seasons, calcification is higher than of corals from the reference data set, because elevated extension rates overcompensate for diminished skeletal density (ΔCalc_{NEM} = 0.31 ± 0.26 g cm⁻² yr⁻¹).

4.4 Prospective view on coral calcification under low Ω_{sw} and eutrophic conditions

The results of this study show, that seawater nutrients have potential to attenuate the negative effect of ocean acidification on reef coral calcification. This is because nutrient stimulated linear extension rates can compensate the negative effect of low

- 710 Ω_{sw}-driven decrease in skeletal bulk density. However, while a low Ω_{sw}-environment has an unconditionally detrimental effect on reef coral bulk density, the positive effect of eutrophication on linear extension rate highly depends on optimal nutrient conditions i.e. the concentrations and balance between the essential nutrients e.g. P/N. As shown by the coral from Saboga, low P/N has a negative effect on extension rate, which amplifies the negative effect of low skeletal density on net calcification. In contrast, high P/N in the northern Arabian Sea upwelling zone stimulates linear extension rates, which compensate the loss
- 715 in skeletal bulk density and thus enable to maintain relatively high calcification rates. On an intra annual basis, we found periods during which increased extension of the Masirah corals (Arabian Sea) fully compensate and even overcompensate for the diminished skeletal bulk density.

In addition to upwelling regions being heralded as refuges for tropical coral species in times of rising SST (Riegl & Piller, 2002; Chollett et al., 2010), patterns of reef coral calcification from these regions provide further implications to the future

720 evolution of coral reefs under low pH and eutrophic conditions. The here presented data suggest optimal nutrient environments (e.g. a high P/N) to have high potential to compensate the negative effect of ocean acidification on reef coral calcification. In this case, a skeletal thickening strategy, which is present in typical modern tropical coral reefs, will change into an extension strategy (Carricart Ganivet, 2004). A relatively high net calcification maintained in this process is beneficial to the positive balance of carbonate accumulation on tropical coral reefs, thereby preserving the fundamental prerequisite for the reef habitat 725 and the health of the associated ecosystem. The identification of valuable refuges with particular significance for the conservation of tropical coral reefs should therefore consider not only SST but also nutrient conditions.

5 Conclusion

This study investigates the effect of seasonal upwelling on sub-annual and annual patterns of calcification in reef corals *(Porites)* from the northern Arabian Sea (Masirah Island, Oman). On a sub-annual basis, calcification rate is lower during the

- 730 <u>upwelling season compared to periods of near identical SST in the non-upwelling season. This is attributed to a rapid decline</u> in extension rate with the onset of the upwelling season. We attribute this decline to a reduction of photosynthetic performance of the micro-algae symbionts by enhanced turbidity of ambient seawater through elevated primary production. Patterns of skeletal density exhibit no instant response to the external decline in Ω_{sw} during upwelling, which indicates stable levels of Ω_{ef} to be maintained throughout the year. Nonetheless, mean annual skeletal density is significantly lower than in *Porites* from
- 735 typical reef environments of the Indo-Pacific and Atlantic Ocean. As opposedIn contrast, mean annual extension rate is high, likely due to the simulating effect of moderate seawater nutrient concentrations during the non-upwelling seasons. As high extension rate compensates for the deficit in skeletal density at Masirah Island, annual calcification rate is indistinguishable from *Porites* growing in regions unaffected by upwelling.
- As a conclusion of this study, wThese results suggeste anticipate that temporarily reduced Ω_{sw} (seasonal upwelling) to haves no instantaneous impact on sub-annual variability in skeletal density but causes a permanent adaptation towards year-round unexpected low skeletal density. Unless the low skeletal density is compensated through high extension rate, this will yield detrimental effects on the net carbonate accumulation in coral reefs. Furthermore, this study highlights variable effects of nutrients on extension rate, with negative effects at excessively high nutrient levels (i.e., upwelling season) and stimulatory effects at moderate nutrient levels (i.e., non-upwelling season).
- 745 This study documents patterns of skeletal calcification in corals (*Porites*) from the Arabian Sea upwelling zone (Masirah Island, Oman). Compared to corals from typical reef sites unaffected by upwelling used as a reference dataset (Hawaii and Great Barrier Reef), mean annual skeletal density is reduced by 28 %, which is in good agreement with values reported from corals of eastern Pacific upwelling zones. The intra annual variability of skeletal density is negatively related to SST, but skeletal density remains consistently too low throughout the entire year relative to the reference data set, likely because of a
- comparatively low aragonite saturation state at the site of calcification (Ω_{ef}). Ω_{ef} is assumed to be kept low by the coral, but relatively constant and independent of changes in external Ω_{sw}-between the upwelling and non-upwelling seasons.
 Mean annual extension rate is 20 % higher than for the reference data set. In particular, extension rates are greatly enhanced during the cool monsoon seasons, presumably due to a permanently high P/N contributing to the maintenance of a thick tissue layer that promotes rapid upward growth of the skeleton. The stimulating effect of nutrients was not observed during the two
 warm inter monsoon seasons, despite a year round high P/N in the Arabian Sea. However, while extension rate is compatible
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with the western Pacific reference data during autumn inter monsoon, it is noticeably diminished during spring inter monsoon, likely corresponding with spawning cycles.

Enhanced annual extension rate result in the negative effect of low density on the calcification rate being attenuated from 25 % to 11 %. As intra annual calcification is also strongly controlled by extension, calcification rates during the inter monsoon seasons are lower and during the monsoons higher than those of the reference corals.

As a conclusion of this study, we recommend more consideration to be spend to local nutrient conditions when identifying suitable refuges for tropical coral reefs. Optimal nutrient environments (e.g. a high P/N) have significantly higher potential to compensate the negative effect of ocean acidification on reef coral calcification. Adequate rates of carbonate accumulation are the fundamental prerequisite to the preservation of reef habitats and enable the persistence of this unique ecosystem.

765 Authors contribution

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P._-M. Spreter designed this research in close collaboration with T. C. Brachert and M. Reuter. Field work was carried out by P._M. Spreter, T._C. Brachert, M. Reuter and substantially supported by O. Taylor. Laboratory analyses were performed by P. M. Spreter and R. Mertz-Kraus. All authors had a contribution in writing and improving the manuscript.

Competing interests

770 The authors declare that they have no conflict of interest.

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