Coral reef carbonate budgets and ecological drivers in the central Red Sea - a naturally high temperature and high total alkalinity environment

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Abstract. The structural framework provided by corals is crucial for reef ecosystem function and services, but high seawater temperatures can be detrimental to the calcification capacity of reef-building organisms. The Red Sea is very warm, but total alkalinity (TA) is naturally high and beneficial for reef accretion. To date, we know little about how such beneficial and detrimental abiotic factors affect each other and the balance between calcification and erosion on Red Sea coral reefs, that is overall reef growth, in this unique ocean basin. To provide estimates of present-day reef growth dynamics in the central Red Sea, we measured two metrics of reef growth, i.e., *in situ* net-accretion/-erosion rates (G_{net}) determined by deployment of limestone blocks and ecosystem scale carbonate budgets (G_{budget}) along a cross-shelf gradient (25 km, encompassing near-, mid-, and offshore). Along this gradient, we assessed multiple abiotic (i.e., temperature, salinity, diurnal pH fluctuation, inorganic nutrients, and TA) and biotic (i.e., calcifier and epilithic bioeroder communities) variables. Both reef growth metrics revealed similar patterns from nearshore to offshore: net-erosive, neutral, and net-accretion states. The average cross-shelf G_{budget} was 0.66 kg $CaCO_3$ m^{-2} y^{-1}, with the highest budget of 2.44 kg $CaCO_3$ m^{-2} y^{-1} measured in the offshore reef. These data are comparable to the contemporary $G_{budgets}$ from the western Atlantic and Indian Ocean, but lie well below "optimal reef production" (5 - 10 kg $CaCO_3$ m^{-2} y^{-1}) and below maxima recently recorded in remote high coral cover reef sites. Yet, the erosive forces observed in the Red Sea nearshore reef contributed less as observed elsewhere. A higher TA accompanied reef growth across the shelf gradient, whereas stronger diurnal pH fluctuations were associated with negative budgets. Noteworthy for this oligotrophic region was the positive effect of phosphate, which is a central micronutrient for reef building corals. While parrotfish contributed substantially to bioerosion, our dataset also highlights coralline algae as important local reef-builders. Altogether, our study establishes a baseline for reef growth in the central Red Sea that should be useful in assessing trajectories of reef growth capacity under current and future ocean scenarios.

1 Introduction

Coral reef growth is mostly limited to warm, aragonite-saturated, and oligotrophic tropical oceans and is pivotal for reef ecosystem functioning (Buddemeier, 1997; Kleypas et al., 1999). The coral reef framework not only maintains a remarkable biodiversity, but also provides highly valuable ecosystem services that include food supply and coastal protection, among others (Moberg and Folke, 1999; Reaka-Kudla, 1997). Biogenic calcification, erosion, and dissolution contribute to the formation of the reef framework constructed of calcium carbonate ($CaCO_3$, mainly aragonite). The balance of carbonate loss and accretion is influenced by biotic and abiotic factors. On a reef scale, the main antagonists are calcifying benthic communities on the one hand, such as scleractinian corals and coralline algal crusts, and grazing and endolithic bioeroders on the other hand, such as parrotfish, sea urchins, microbioeroding chlorophytes, boring sponges, and other macroborers (Glynn, 1997; Hutchings, 1986; Perry et al., 2008; Tribollet and Golubic, 2011). The export or loss of carbonate as sediments is considered an essential part, in particular in the wider geomorphic perspective of reef carbonate production states (Cyronak et al., 2013; Perry et al., 2008, 2017). Temperature and carbonate chemistry parameters (e.g., pH, total alkalinity: TA, and aragonite saturation state: Ω_a, pCO_2) have been identified as important players in regulating these carbonate accretion and erosion processes (Albright et al., 2018; Schönberg et al., 2017). Furthermore, different light regimes across depths, water flow, and wave exposure can alter the rates of reef-formation processes (Dullo et al., 1995; Glynn and Manzello, 2015; Kleypas et al., 2001).

Reef growth is maintained when reef calcification produces more $CaCO_3$ than is being removed, and depends largely on the ability of benthic calcifiers to precipitate calcium carbonate from seawater (e.g., Langdon et al., 2000; Tambutté et al., 2011). TA and Ω_a, positively correlate with calcification rates (Marubini et al., 2008; Schneider and Erez, 2006), and while calcification rates of corals and coralline algae increase with higher temperature, they have upper thermal limits (Jokiel and Coles, 1990; Marshall and Clode, 2004; Vásquez-Elizondo and Enríquez, 2016). Today's Oceans are warming and high temperatures begin to exceed the thermal optima of calcifying organisms and thereby slowing down or interrupting calcification (e.g., Carricart-Ganivet et al., 2012; Death et al., 2009). At the same time, ocean acidification decreases the Oceans' pH and Ω_a (Orr et al., 2005). Arguably, calcification under these conditions becomes energetically costlier (Cai et al., 2016; Cohen and Holcomb, 2009; Strahl et al., 2015; Waldbusser et al., 2016). In addition, ocean acidification stimulates destructive processes, for instance the proliferation of bioeroding endolithic organisms (e.g., Enochs, 2015; Fang et al., 2013; Tribollet et al., 2009). Apart from that, locally impaired reef growth due to an increased intensity or frequency of extreme climate events (Eakin, 2001; Schuhmacher et al., 2005), human impacts including pollution and eutrophication (Chazottes et al., 2002; Edinger et al., 2000), and other ecological events such as population outbreaks of grazing sea urchins or crown-of-thorn starfish that feed on coral can induce reef framework degradation (Bak, 1994; Pisapia et al., 2016; Uthicke et al., 2015).

A number of studies have employed experimental limestone blocks cut from coral skeletons to study reef growth processes (Chazottes et al., 1995; Kiene and Hutchings, 1994; Silbiger et al., 2014; Tribollet and Golubic, 2005). Deployment of such blocks in a reef captures the endolithic and epilithic accretion and erosion agents and forces,

81   simultaneously allowing for the measurement of net-accretion and net-erosion rates. In particular, these studies have
82   provided insight into the colonization progression and activity of endolithic micro- and macroorganisms. To
83   comparatively assess the persistence of reef framework at the ecosystem scale, a census-based reef carbonate budget
84   (*ReefBudget*) approach that integrates reef site-specific ecological data into the calculation of the erosion-accretion
85   balance was introduced recently (Kennedy et al., 2013; Perry et al., 2012, 2015). Using the *ReefBudget* approach, a
86   recent study determined that 37 % of all current reefs that were investigated are in a net-erosive state (Perry et al.,
87   2013). For the Caribbean, it revealed a 50 % decrease of reef growth compared to historical mid- to late-Holocene
88   reef growth (Perry et al., 2013). Indeed, the use of carbonate budgets provided valuable insight into the reef growth
89   trajectories in the Seychelles, where surveys conducted since the 1990s provide important ecological baseline data
90   that were employed in reef growth calculations (Januchowski-Hartley et al., 2017). Most recently, carbonate budget
91   data were used to explore the relation of vertical reef growth potential and trends in sea level rise suggesting that reef
92   submergence poses a threat as long as climate-driven and human-made perturbations persist (Perry et al., 2018). Other
93   studies highlight the susceptibility of marginal coral reefs to ocean warming and acidification (Couce et al., 2012).
94   Such marginal reefs are found in the Eastern Pacific or in the Middle East in the Persian/Arabian Gulf, where reefs
95   exist at their environmental limits, e.g., at low pH or high temperatures, respectively (Bates et al., 2010; Manzello,
96   2010; Riegl, 2003; Sheppard and Loughland, 2002).

97

98   Although the Red Sea features high sea surface temperatures that exceed thermal thresholds of tropical corals
99   elsewhere (Kleypas et al., 1999; Osman et al., 2018), it supports a remarkable coral reef framework along its entire
100   coastline (Riegl et al., 2012). Yet, coral skeleton core samples indicate that calcification rates have been declining
101   over the past decades, which has been widely attributed to ocean warming (Cantin et al., 2010). In this regard Red
102   Sea coral reefs are on a similar trajectory as other coral reefs under global ocean warming (Bak et al., 2009; Cooper
103   et al., 2008). In the central and southern Red Sea, present-day data show reduced calcification rates of corals and
104   calcifying crusts when temperatures peak during summer (Roik et al., 2015; Sawall et al., 2015). While increasing
105   temperatures are seemingly stressful and energetically demanding for reef calcifiers, high TA values, as found in the
106   Red Sea (~ 2400 µmol kg^{-1}, Metzl et al. 1989), are indicative of a putatively beneficial environment for calcification
107   (Albright et al., 2016; Langdon et al., 2000; Tambutté et al., 2011). At present, little is known about the reef-scale
108   carbonate budgets of Red Sea coral reefs (Jones et al., 2015). Apart from one early assessment of reef growth capacity
109   for a high-latitude reef in the Gulf of Aqaba (GoA, northern Red Sea) that considered both calcification and
110   bioerosion/dissolution rates (Dullo et al., 1996), studies only report calcification rates (e.g., Cantin et al., 2010; Heiss,
111   1995; Roik et al., 2015; Sawall and Al-Sofyani, 2015) or focus on bioerosion generally caused by one group of
112   bioeroders (Alwany et al., 2009; Kleemann, 2001; Mokady et al., 1996). Therefore, we set out to determine reef growth
113   in central Red Sea coral reefs and evaluate the biotic and abiotic drivers. We show and compare two reef growth
114   metrics: G_{net} and G_{budget}. We present net-accretion/-erosion rates (G_{net}) measured *in situ* using limestone blocks
115   deployed in the reefs, which simultaneously capture the rates of epilithic accretion and epilithic and endolithic
116   bioerosion. We also apply a census-based approach adapted from the *ReefBudget* protocol (Perry et al., 2012) to
117   estimate reef growth on an ecosystem scale, as the net carbonate production state or carbonate budget (G_{budget}). Our

118   study provides a broad and first insight into reef growth dynamics and a comparative baseline to further assess the

119   effects of environmental change on reef growth in the central Red Sea.

120

2 Material and Methods

2.1 Study sites and environmental monitoring

Study sites are located in the Saudi Arabian central Red Sea along an environmental cross-shelf gradient, described in detail in Roik et al. (2015) and Roik et al. (2016). Data for this study were collected at three sites: an offshore forereef at ~25 km distance from the coastline (22° 20.456 N, 38° 51.127 E, "Shi'b Nazar"), midshore forereef at ~10 km distance (22° 15.100 N, 38° 57.386 E, "Al Fahal"), and a nearshore forereef (22° 13.974 N, 39° 01.760 E, "Inner Fsar") at ~3 km distance to shore. All sampling stations were located between 7.5 and 9 m depth. In the following, reef sites are referred to as "offshore", "midshore", and "nearshore", respectively. Abiotic variables were measured during "winter" and "summer" 2014. CTD data was collected continuously during "winter" (9th February - 7th April 2014) and "summer" (19th June - 23th October 2014). At each station, seawater samples were collected on SCUBA for 5 - 6 consecutive weeks during each of the seasons to determine inorganic nutrients, i.e., nitrate and nitrite (NO_3^- & NO_2^-), ammonia (NH_4^+), phosphate (PO_4^{3-}), and total alkalinity (TA) (Table S1).

2.2 Net-accretion/-erosion rates of limestone blocks

Net-accretion/-erosion rates (G_{net}) were assessed using a "limestone block assay". Blocks cut from "coral stone" limestone were purchased from a local building material supplier in Jeddah, KSA. Each block was fixed with one stainless steel bolt to aluminum racks permanently deployed at the monitoring station of each reef site (a total of 36 blocks, n = 4, Fig. S1). The blocks were oriented in parallel to the reef slope with one side facing up while the other side was facing down towards the reef. Block dimensions were 100 x 100 x 21 mm with an average density of $\rho = 2.3$ kg L^{-1}. Blocks were dry-weighed before and after deployment on the reefs (Mettler Toledo XS2002S, readability = 10 mg). Before weighing, the blocks were autoclaved and dried in a climate chamber (BINDER, Tuttlingen, Germany) at 40 °C for a week. Four replicate blocks were deployed at the reef sites for three different exposure periods each (Fig. 1 a) to measure natural processes of calcification and erosion. Exposure periods were 6 months (September 2012 - March 2013), 12 months (June 2013 - June 2014), and 30 months each (January 2013-June 2015). We measured a total of 12 blocks and all blocks were measured only once. Upon recovery, the blocks were treated with 10 % bleach for 24 - 36 h and rinsed with deionized water to remove organic material and any residual salts. G_{net} were expressed as normalized differences of pre-deployment and post-deployment weights [kg $CaCO_3$ m^{-2} y^{-1}] (Table 1).

2.3 Biotic parameters

To assess coral reef benthic calcifier and epilithic bioeroder communities (as input data for the reef carbonate budgets), we conducted *in situ* surveys on SCUBA along the cross-shelf gradient at each of our study sites.

2.3.1 Benthic community composition

Community composition and coverage of coral reef calcifying groups were assessed in six replicate transects per site using the belt-transect rugosity method (Perry et al., 2012) as detailed in Roik et al. (2015). From these surveys we extracted data on benthic calcifiers (% cover total hard coral, % hard coral morphs (branching, encrusting, massive, and platy/foliose), % major reef-building coral families (Acroporidae, Pocilloporidae, and Poritidae), % cover calcareous crusts, % recently dead coral, and % rock surface area for carbonate budget calculations (Table S2). In addition, benthic rugosity was assessed in the same transects following the *Chain and Tape Method* (n = 6, Perry et al., 2012).

2.3.2 Epilithic bioeroder/grazer populations along the cross-shelf gradient

For each reef site, we surveyed abundances and size classes of the two main groups of coral reef framework epilithic bioerorders, parrotfishes (Scaridae) (Bellwood, 1995; Bruggemann et al., 1996) and sea urchins (Echinoidea) (Bak, 1994). Surveys were conducted on SCUBA using stationary plots (adapted from Bannerot and Bohnsack, 1986, Text S1) and line transects (n = 6 per site), respectively. Briefly, abundances of parrotfishes and sea urchins were assessed for different size classes. Abundances for all prevalent parrotfish species were assessed in six size classes, based on estimated fork length (FL; FL size classes: 1 = 5 - 14 cm, 2 = 15 - 24 cm, 3 = 25 - 34 cm, 4 = 35 - 44 cm, 5 = 45 - 70, and 6 > 70 cm). We focused on the most abundant bioeroding parrotfish species in the Red Sea (Table S4), which encompassed two herbivorous functional groups: excavators and scrapers (Green and Bellwood 2009). Most abundant across study sites were the excavators *Chlorurus gibbus*, *Scarus ghobban*, and *Cetoscarus bicolor*, and the scrapers *Scarus frenatus*, *Chlorurus sordidus*, *Scarus niger* and *Scarus ferrugenius*, following Alwany et al., 2009. Additionally, we counted *Hipposcarus harid*, which occurred frequently at the study sites, along with members of the genus *Scarus* that could not be identified to species level and were therefore pooled in the category 'Other *Scarus*'. Both *H. harid* and *Scarus* spp. were broadly categorized as scrapers (Green and Bellwood, 2009). The sea urchin census targeted five size classes of the four most common bioerosive genera *Diadema*, *Echinometra*, *Echinostrephus*, and *Eucidaris*, based on urchin diameter (size classes 1 = 0 - 20 mm, 2 = 21 - 40 mm, 3 = 41 - 60 mm, 4 = 61 - 80 mm, 5 = 81 - 100 mm, Table S7). For details on the field surveys and data treatment for biomass conversion, refer to the supplementary materials (Text S1 and references therein).

2.4 Reef carbonate budgets

Ecosystem scale reef carbonate budgets, G_{budget} [kg $CaCO_3$ m^{-1} y^{-1}], were determined following the census-based *ReefBudget* approach by Perry et al. (2012) (Table 1). G_{budget} incorporates local census data, site-specific net-accretion/-erosion data (G_{net} over 30 months) and calcification data (buoyant weight measurements) collected for this and a previous study (Roik et al., 2015). Importantly, the approach incorporates epilithic bioerosion, which is based on abundance rather than bite or erosion rates; therefore, parrotfish and sea urchin census data collected in this study were employed in the *ReefBudget* calculations using bite and erosion rates from the literature (Alwany et al., 2009;

188 Perry et al., 2012). In summary, site-specific benthic calcification rates ($G_{benthos}$, kg $CaCO_3$ m^{-1} y^{-1}), net-accretion/-

189 erosion rates of reef "rock" surface area ($G_{netbenthos}$, kg $CaCO_3$ m^{-1} y^{-1}), and epilithic erosion rates by sea urchins (E_{echino},

190 kg $CaCO_3$ m^{-1} y^{-1}) and parrotfishes (E_{parrot}, kg $CaCO_3$ m^{-1} y^{-1}), were determined for the G_{budget} calculations (Fig. 1 (b)

191 and Fig. 3 (a)). A detailed account of Red Sea specific calculations and modifications of the *ReefBudget* approach

192 employed in this study are outlined in the supplementary materials (Text S1, Equation box S1-3, and Tables S2-S8).

193

2.5 Abiotic parameters

2.5.1 Continuous data: temperature, salinity, and diurnal pH variation

196 Factory-calibrated conductivity-temperature-depth loggers (CTDs, SBE 16plusV2 SEACAT, RS-232, Sea-Bird

197 Electronics, Bellevue, WA, USA) were deployed at the monitoring stations on tripods at ~0.5 m above the reef to

198 collect time series data of temperature, salinity, and pH_{NBS} at hourly intervals. The pH probes (SBE 18/27, Sea-bird

199 Electronics) were factory calibrated before the winter deployment (9th February - 7th April 2014). Calibrations were

200 verified using NBS scale standard buffers (pH 7 and 10, Fixanal, Fluka Analytics, Sigma Aldrich, Germany) before

201 the winter and the summer deployment (19th June - 23th October 2014).

202

2.5.2. Seawater samples: Inorganic nutrients and total alkalinity

204 Seawater samples were collected on SCUBA at each of the stations using 4 L collection containers (Table S1).

205 Simultaneously, 60 mL seawater samples were taken through a 0.45 µm syringe filter for TA measurements. Seawater

206 samples for inorganic nutrient analyses and TA measurements were transported on ice in the dark and were processed

207 on the same day. Samples were filtered over GF/F filters (0.7 µm, Whatman, UK) and filtrates were frozen at -20 °C

208 until analysis. The inorganic nutrient content (NO_3^-&NO_2^-, NH_4^+, and PO_4^{3-}) was determined using standard

209 colorimetric tests and a Quick-Chem 8000 AutoAnalyzer (Zellweger Analysis, Inc.). TA samples were analyzed

210 within 2 - 4 h after collection using an automated acidimetric titration system (Titrando 888, Metrohm AG,

211 Switzerland). Gran-type titrations were performed with a 0.01 M HCl (prepared from 0.1 HCl Standard, Fluka

212 Analytics) at an average accuracy of $\pm$ 9 µmol kg^{-1} (standard deviation of triplicate measurements).

2.6 Statistical analyses

2.6.1 Net-accretion/-erosion rates and carbonate budgets

215 G_{net} data (Table 2) were tested for effects of the factors "reef" (fixed factor: nearshore, midshore, and offshore) and

216 "deployment time" (random factor: 6, 12, and 30 months). A univariate 2-factorial PERMANOVA was performed on

217 $log_n(x)$ transformed data (i.e., $log_n(x+1-min(x_{1-n}))$ as data contained negative and near-zero values). A Euclidian

218 distance matrix and 9999 permutations of residuals under a reduced model and type III partial sum of squares were

219 employed. Pair-wise tests followed where applicable (PRIMER-E V6, Table S9).

220 G_{budget} data (Table 3) were tested for statistical differences between the reef sites (fixed factor: nearshore, midshore,

221 and offshore) using a 1-factorial ANOVA. In parallel, $G_{benthos}$ was tested using a 1-factorial ANOVA with log_{10}

222 transformed data, while non-parametric Kruskal-Wallis tests were employed for non-transformed $G_{netbenthos}$, E_{echino},

223 and E_{parrot} data. Tukey's HSD post-hoc tests or Dunn's multiple comparisons followed where applicable (Table S10).

224 Assumptions about parametric distribution of data were evaluated using the Shapiro-Wilk normality test. Statistical

225 tests were performed as implemented in R (R Core Team, 2013).

226

2.6.2 Abiotic parameters

228 All abiotic data were summarized as means and standard deviations per reef and season and over each season (Table

229 4) and boxplots were generated (Fig. 4). Diurnal pH variation was extracted from the continuous data as the pH_{NBS}

230 standard deviation per day. Outliers were detected and removed from the TA data. All outliers (data points beyond

231 the upper boxplot 1.5 IQR) clustered to one sampling day (23 June 2014), which we considered an artifact of the

232 chemical analysis and the outliers from this day were removed. All continuous abiotic variables and inorganic nutrients

233 (PO_4^{3-} after square-root transformation) fulfilled parametric assumptions and were evaluated using univariate 2-

234 factorial ANOVAs testing the factors "reef" (nearshore, midshore, and offshore) and "season" (winter and summer).

235 TA data was square-root transformed, which improved symmetry of data (Anderson et al., 2008), and tested under the

236 same 2-factorial design, as outlined above, using a PERMANOVA (Euclidian resemblance matrix and 9999

237 permutations of residuals under a reduced model and type II partial sums of squares). Within each significant factor,

238 Tukey's HSD post-hoc tests or PERMANOVA integrated pair-wise tests followed (Table S11 and S12). Assumptions

239 were evaluated by histograms and the Shapiro-Wilk normality test. Statistical tests and outlier detection were

240 performed in R or PRIMER-E V6.

241

2.6.3 Abiotic-biotic correlations

243 To evaluate the relationship of abiotic and biotic predictors of G_{net} and G_{budget}, Spearman rank correlation coefficients

244 were obtained for the predictor variables (at a confidence level of 95%) using *cor.test* in R (R Core Team, 2013;

245 Wickham and Chang, 2015). *P*-values were adjusted using *p.adjust* in R employing the Benjamini-Hochberg method.

246 Correlations were performed using G_{net} data obtained in the 30-months measurements from the reef sites (nearshore,

247 midshore, and offshore) (Table 5 and Table S13). Predictor variables were the site-specific means of CTD measured

248 variables (temperature, salinity, and diurnal pH variation), means of inorganic nutrients (NO_3^-&NO_2^-, NH_4^+, and PO_4^{3-}

249), and TA (Table 4). Biotic predictors were variables that likely impacted the limestone blocks, i.e. parrotfish

250 abundances, sea urchin abundances, calcareous crusts cover, and algal and sponge cover. Since we did not observe

251 any coral recruits of substantial size on the blocks, we did not include % coral cover and related variables in the

252 correlations.

253 G_{budget} correlations included all the above-mentioned abiotic variables and 13 biotic transect variables (i.e., parrot fish

254 abundances, sea urchin abundances, % branching coral, % encrusting coral, % massive coral, % platy/foliose coral,

255 % of Acroporidae, % Pocilloporidae, % Poritidae, % total hard coral cover, calcareous crusts cover, algal and sponge

256   cover, and rugosity). Prior to analysis, some of the predictors (i.e., % platy/foliose corals and % Poritidae) were

257     $\log_{10}(x+1)$ transformed to improve the symmetry in their distributions (Table 5 and Table S14).

258

3 Results

3.1 Net-accretion/-erosion rates of limestone blocks

Net-accretion/-erosion rates G_{net} were measured in assays over periods of 6, 12, and 30 months in the reef sites along the cross-shelf gradient. These measurements represent the result of calcification and bioerosion processes impacting the deployed limestone blocks. Visible traces of boring endolithic fauna were only found on the surface of blocks recovered after 12 and 30 months as presented in Fig. 2 (c)-(f). A brief visual inspection of the block surfaces after retrieval showed colonization by coralline algae, bryozoans, boring sponges, small size boring worms and clams, as well as parrotfish bite-marks. No coral recruits were noticed by the unaided eye. Further analyses of the established presence of calcifying and bioeroding communities were not within the scope of this study. G_{net} based on the 30-months deployment of blocks ranged between -0.96 and 0.37 kg $CaCO_3$ m^{-2} y^{-1} (Table 2). G_{net} for 12 and 30-months blocks were negative on the nearshore reef (between -0.96 and -0.6 kg $CaCO_3$ m^{-2} y^{-1}, i.e., net erosion is apparent), slightly positive on the midshore reef (0.01 - 0.06 kg $CaCO_3$ m^{-2} y^{-1}, i.e., almost neutral carbonate production state), and positive on the offshore reef (up to 0.37 kg $CaCO_3$ m^{-2} y^{-1}, i.e., net accretion of reef framework). Deployment times had a significant effect on the variability of G_{net} (Pseudo-F = 5.9, $p_{PERMANOVA}$ < 0.01, Table S9). As expected, accretion/erosion was overall higher when measured over the longer deployment period (Fig. 2 (g)) in comparison to the shorter deployment times, reflecting the continuous and exponential nature of bioerosion due to the colonization progress of fouling organisms over time. The significant interaction of reef site and deployment time (Pseudo-F = 7.3, $p_{PERMANOVA}$ < 0.001) shows that only blocks deployed over 12 and 30 months revealed significant site variability, specifically the differences between nearshore vs. offshore and midshore vs. offshore sites became evident ($p_{pair-wise}$ < 0.05, Table S9). The within-group variability was highest for the nearshore reef, where standard deviations were up to 7-times higher compared to the midshore and the offshore reefs.

3.2 Biotic parameters

3.2.1 Benthic community composition

A detailed account of benthic community structure of the study sites is provided in Roik et al. (2015). In brief, a low percentage of live substrate (20 %) and calcifier community cover (hard corals = 11 % and calcifying crusts = 1 %) were characteristic for the nearshore site, while rock (23 %) and rubble (4 %) were more abundant compared to the other sites. The midshore and offshore reefs provided live benthos cover of around 70 % and a large proportion of calcifiers (48 and 59 %). The proportion of coral and calcifying crusts, which were dominated by coralline algae, were 38 % and 10 % in the midshore reef compared to 35 % and 23 % in the offshore reef, respectively. Major reef-building coral families were Acroporidae, Pocilloporidae, and Poritidae forming 32 - 56 % of the total hard coral cover. A soft coral community (of around 25 %) occupied large areas in the midshore reef. This community was minor in the nearshore and offshore reefs with 4 % and 8.5 %, respectively. Specific benthic accretion rates $G_{benthos}$ [kg $CaCO_3$ m^{-2} y^{-1}], which were used as input data for the G_{budget} calculation, were determined using these benthic data in addition to site and calcifier specific calcification rates (Tables S2 and S3).

294

3.2.2 Epilithic bioeroder/grazer populations along the cross-shelf gradient

296 A total of 718 parrotfishes and 110 sea urchins were observed and included in subsequent *ReefBudget* analyses.
297 Parrotfish mean abundances and biomass estimates ranged between 0.08 ± 0.01 and 0.17 ± 0.60 individuals m^{-2}, and
298 24.69 ± 6.04 and 82.18 ± 46.67 g m^{-2}, respectively (Table S4). The largest parrotfish (category 5 parrotfish, i.e., > 45
299 - 70 cm fork length) were observed at the midshore site. With the exception of the midshore reef, category 1 (5 - 14
300 cm) parrotfish were commonly observed at all sites. Large parrotfish (category 6 with > 70 cm fork length) were not
301 observed during the surveys. For sea urchins, mean abundances of 0.002 ± 0.004 - 0.014 ± 0.006 individuals m^{-2} per
302 site were observed and mean biomasses 0.05 ± 0.04 - 1.43 ± 0.98 g m^{-2} estimated per site, respectively (Table S7).
303 The midshore site exhibited the largest range of sea urchin size classes (from categories 1 or 2 to the largest size class
304 5), while at the other two exposed sites, only the two smallest size classes of sea urchins were recorded.

305

3.3 Reef carbonate budgets

307 The carbonate budget, G_{budget}, averaged over all sites was 0.66 ± 2.01 kg CaCO$_3$ m^{-2} y^{-1} encompassing values ranging
308 from a negative nearshore budget (-1.48 ± 1.75 kg CaCO$_3$ m^{-2} y^{-1}) to a positive offshore budget (2.44 ± 1.03 kg CaCO$_3$
309 m^{-2} y^{-1}) (Figure 3 and Table 3). G_{budget} significantly differed between reef sites ($F = 16.7$, $p_{ANOVA} < 0.001$, Table S10),
310 where nearshore vs. offshore site and midshore vs. offshore site showed significant differences ($p_{Tukey\ HSD} < 0.01$).
311 Further, biotic variables that contribute to the final G_{budget} were diverse: $G_{benthos}$ significantly varied between midshore
312 vs. nearshore site and offshore vs. nearshore site ($p_{Tukey\ HSD} < 0.01$), $G_{netbenthos}$ varied between all site combinations
313 ($p_{Tukey\ HSD} < 0.001$), E_{echino} significantly differed between midshore and nearshore, and E_{parrot} variability was similar at
314 all sites. The within-group variation for the nearshore reef was 5-times higher compared to the midshore reef and the
315 offshore reef. Overall, the proportional loss of accreted carbonate to bioerosion was 15 % in the offshore reef, 42 %
316 in the midshore reef, and the loss even exceeded the accretion by four-fold in the nearshore reef, i.e., ~ 440 %
317 proportional loss when considering accreted carbonate to bioerosion.

318

3.4 Abiotic parameters

3.4.1 Temperature, salinity, and diurnal pH variation

321 We used abiotic monitoring data to characterize environmental conditions at each reef site throughout the year (Table
322 1, Table S11 and S12). Temperature and salinity comprised ~4400 data points per reef site in the nearshore and
323 offshore reef, and ~2700 in the midshore reef; diurnal pH standard deviations comprised 185 data points for the
324 midshore and offshore site, and 87 for the nearshore site. The seasonal mean temperature varied between 26.1 ± 0.5
325 °C in winter and 30.9 ± 0.7 °C in summer across all reefs. The cross-shelf difference was largest in summer (~0.6 °C),
326 and significant during both seasons ($F = 1042.6$, $p_{ANOVA} < 0.001$). From all sites, the nearshore site experienced the

327 lowest mean temperature (26.1 °C) in winter and the highest (31.3 °C) in summer. In comparison, the midshore and

328 offshore reefs were slightly cooler with means around 30.6 °C during summer. Overall salinity was high ranging

329 between 39.18 – 39.44 over the year. In summer nearshore salinity was significantly increased by 0.36 compared to

330 winter and by 0.18 compared to the other reefs ($F = 945.3$, $p_{ANOVA} < 0.001$). Salinity in the midshore and offshore reef

331 was not significantly different between the two sites. Mean diurnal standard deviations of pH ranged between 0.04 –

332 0.07 of pH units in the midshore and offshore reefs. The nearshore reef experienced the largest diurnal variations as

333 indicated by mean diurnal standard deviations of 0.29 pH units during winter and 0.6 pH units during summer. The

334 diurnal pH fluctuation differed significantly between all reef sites ($F = 1241$ $p_{ANOVA} < 0.001$).

335

3.4.2 Seawater samples: Inorganic nutrients and total alkalinity

337 Concentrations of all measured inorganic nutrients were below 1 μmol kg^{-1} (Table 1). NO_3^-&NO_2^- was on average

338 between 0.63 ± 0.26 and 0.28 ± 0.22 μmol kg^{-1}, NH_4^+ between 0.51 ± 0.17 and 0.35 ± 0.19 μmol kg^{-1}, and PO_4^{3-} as low

339 as 0.02 ± 0.01 and 0.09 ± 0.02 μmol kg^{-1} (the highest and lowest site-season averages are reported here). By trend,

340 mean NO_3^-&NO_2^- and NH_4^+ levels were higher in winter compared to summer with a difference of 0.29 and 0.16 μmol

341 kg^{-1}, respectively (Fig. 4, Table S11 and S12). In contrast, PO_4^{3-} was significantly higher in winter than in summer

342 with means differing on average by 0.04 μmol kg^{-1} ($F = 16$, $p_{ANOVA} < 0.001$, Table S11). Mean differences across the

343 shelf were 0.1 μmol kg^{-1} in NO_3^-&NO_2^- during winter, 0.1 μmol kg^{-1} in NH_4^+ during summer, and 0.02 μmol kg^{-1} in

344 PO_4^{3-} throughout both seasons. TA ranged between 2391 ± 15 and 2494 ± 16 μmol kg^{-1}. TA was significantly different

345 between seasons and reef sites (Pseudo-F_{season} = 297.6, Pseudo-$F_{reefsite}$ = 22.5, $p_{PERMANOVA} < 0.001$, Table S11 and

346 S12). During both seasons, TA was decreasing from the offshore to the nearshore reef. During winter, TA was slightly

347 higher with 2487 ± 20 μmol kg^{-1} compared to 2417 ± 27 μmol kg^{-1} during summer. The increase from nearshore to

348 offshore was on average between 20 and 50 μmol kg^{-1} (Fig. 4).

3.5 Abiotic-biotic correlations

350 To explore the relationship between environmental variables and reef growth, we performed correlation analyses. For

351 G_{net}, strong, positive, and significant correlates were calcareous crust cover, NO_3^-&NO_2^-, PO_4^{3-}, and TA. Negative

352 correlates were salinity, diurnal pH variation, and parrotfish abundance (strong correlates: $\rho > |0.75|$, p < 0.001). For

353 G_{budget}, abiotic correlates were NO_3^-&NO_2^-, PO_4^{3-}, and TA, the same correlates as for G_{net}. Looking at significant biotic

354 correlates of G_{budget}, we only found positive relationships, including calcareous crusts, hard corals, and rugosity.

355 Conversely, parrotfish and sea urchin abundances had a negative effect on G_{budget}, but the correlation was weak and

356 not significant ($\rho \sim -0.5$). The non-calcifying benthos, which represents the coverage by algae, soft corals, and sponges,

357 was not correlated with the dynamics of G_{budget} and was correlated only weakly and not significantly with G_{net} ($\rho \sim$

358 0.5) (Table 5, Tables S13 and S14).

359

360 **4 Discussion**

361 Central Red Sea reefs are characterized by unique environmental conditions of high temperature, salinity, TA, and
362 oligotrophy (Fahmy, 2003; Kleypas et al., 1999; Steiner et al., 2014). On a global scale they support remarkable reef
363 growth, supporting well established fringing reefs along most of the coastline. To date, processes affecting reef growth
364 in various regions of the Red Sea have mostly been investigated individually. For instance, some studies focused on
365 bioerosion by one specific group of bioeroders only (Alwany et al., 2009; Kleemann, 2001; Mokady et al., 1996),
366 while other studies assessed calcification of reef-building corals (e.g., Cantin et al., 2010; Heiss, 1995; Roik et al.,
367 2015; Sawall et al., 2015). To provide a more comprehensive picture, the present study integrated assessment of the
368 antagonistic processes of calcification and bioerosion. We achieved this in a two-step approach assessing two central
369 metrics of reef growth along a cross-shelf gradient. First, we assessed net-accretion/-erosion rates (G_{net}) from three
370 reef sites along the cross-shelf gradient *in situ* using a limestone block assay. Second, we constructed ecosystem-scale
371 estimates of reef carbonate budgets for Red Sea reef sites (G_{budget}) adapting the census-based *ReefBudget* approach by
372 Perry et al. (2012). In the following, we highlight the complex dynamics and interactions of reef growth processes and
373 discuss the importance of carbonate budgets as a powerful tool to explore the trajectories of reef growth in a global
374 and historical context.

375

376 **4.1 Net-accretion/-erosion rates (G_{net}) in the central Red Sea**

377 **4.1.1 Cross-shelf dynamics in a global context**

378 The limestone block assay revealed three reef production states in the central Red Sea: 1) net erosion (nearshore), 2)
379 near-neutrality (midshore), and 3) net accretion (offshore). This is in contrast to the pattern observed on the Great
380 barrier reef (GBR), where total bioerosion rates were higher in offshore reefs than inshore reefs as assessed from
381 limestone blocks (Tribollet et al., 2002; Tribollet and Golubic, 2005). Generally, most block assay studies conducted
382 in various reef habitats and regions found net-erosive rates. For instance, studies from reefs in the Thai Andaman Sea
383 and Indonesian Java Sea note that the accretion by calcifying crusts, such as coralline algae, were negligible compared
384 to the high degree of bioerosion measured in the limestone blocks (Edinger et al., 2000; Schmidt and Richter, 2013).
385 In contrast, our limestone block assays captured a substantial net accretion rate, in particular for the offshore reef site
386 in the central Red Sea (0.37 kg $CaCO_3$ m^{-2} y^{-1} net accretion), indicating that accretion was substantial, while erosion
387 was negligible. The midshore reef was characterized by a near-neutral or minor net accretion (0.06 kg $CaCO_3$ m^{-2} y^{-1})
388 on the order of net accretion rates recorded in French Polynesia in reef sites of uninhabited, oceanic atolls (0.08 and
389 0.62 kg $CaCO_3$ m^{-2} y^{-1}; Pari et al., 1998). Notably, our study recorded a net-erosive state only in the Red Sea nearshore
390 site (-0.96 kg $CaCO_3$ m^{-2} y^{-1}, 30 months deployment). This is a moderate rate compared to the larger net erosion
391 observed in the GBR, French Polynesia, and Thailand (-4 or -8 kg $CaCO_3$ m^{-2} y^{-1}) (Osorno et al., 2005; Pari et al.,
392 1998; Schmidt and Richter, 2013; Tribollet and Golubic, 2005).

393

394

4.1.2 Limestone block deployment duration and biotic drivers

Our data show that G_{net} values were overall higher with longer deployment times, reflecting the succession and early establishment of calcifying crust and bioeroding communities on the limestone blocks. Due to our sampling design (weight-based block assay), accretion and erosion processes however are simultaneously captured and cannot be disentangled. Overall, the block assay data are indicative of a calcifier-beneficial offshore environment and a nearshore reef habitat that is supporting endolithic bioeroders.

Following other work, carbonate loss in the 12-month blocks from the nearshore site was supposedly due to a young microbioeroder community, which is typically most active during this early phase. For instance, during the early stages of colonization by endolithic microorganisms, the chlorophyte *Ostreobium* sp. predominantly contributes to microbioerosion, while the erosion rate steadily increases with deployment time (Grange et al., 2015; Tribollet and Golubic, 2011). Microbioerosion rates have been reported to be -0.93 kg $CaCO_3$ m^{-2} y^{-1} after 12 months of block exposure, which represents the average rate at the early colonization stage when the steadily increasing microbioerosion rate has leveled off (Grange et al., 2015). This rate is slightly higher compared to our measurements of net erosion in the nearshore site after the same deployment time (i.e. -0.61 kg $CaCO_3$ m^{-2} y^{-1}), and the difference may reflect measurements encompassing both, bioerosion and accretion.

Studies have shown that site differences in total bioerosion are typically becoming visible after 1 year of deployment and are significantly enhanced after 3 years (Tribollet and Golubic, 2005). In line with this, the deployment time of 12 months in our study was sufficient to reveal differences between the nearshore and offshore reef sites. Further, calcifying crusts, specifically coralline algae, observed on all blocks from the offshore reef contributed to the respective net accretion. This is corroborated by the positive correlation of their abundances with G_{net} across all reef sites. Given that we could not identify coral recruits on any limestone block, we assume that contribution of corals to the measured accretion was minor. However, we acknowledge that we might have missed some that could be detected by more sophisticated methods (e.g. such as microscopic examination).

Significant differences in accretion/erosion between all three sites of the cross-shelf gradient became apparent after 30 months deployment, and macroborer traces were observed in blocks for the first time (Fig. 2). Over the course of 2 - 3 years, macrobioeroders such as polychaetes, sipunculids, bivalves, and boring sponges can establish communities in limestone blocks (Hutchings, 1986). Between the first two years, macrobioeroder contribution to the total bioerosion can quadruple (0.02 - 0.09 kg $CaCO_3$ m^{-2} y^{-1}), before levelling off around 3 - 4 years post-deployment (Chazottes et al., 1995).

In our study, the increase of G_{net} between the 12- and 30-month deployment (~0.30 kg $CaCO_3$ m^{-2} y^{-1} on average in the nearshore and offshore site) indicates that calcifying and eroding communities were still in a state of succession. As such, we cannot unequivocally rule out that the blocks deployed for 30 months still represented an immature community, and hence, underestimated maximal calcification and erosion rates.

Correlation analyses indicate a significant contribution of parrotfish to the net erosion rates in the nearshore reef. This observation is in line with previous work demonstrating a significant contribution of parrotfish activity to bioerosion (Alwany et al., 2009; Bellwood, 1995; Bellwood et al., 2003). By comparison, sea urchin size and abundance do not appear to be significant for bioerosion on the central Red Sea reefs. On other reefs, sea urchin bioerosion can be

432   substantial, equaling or even exceeding reef carbonate production (Bak, 1994). The low contribution of sea urchins to

433   bioerosion on central Red Sea reefs may be a result of potentially low abundances of highly erosive sea urchins

434   (McClanahan and Shafir, 1990). This is in line with the observed parrotfish bite-marks and a lack of sea urchins on

435   and in the direct vicinity of the recovered blocks. Taken together, our data confirms that endolithic micro- and

436   macrobioerosion, as well as parrotfish feeding, likely provides a substantial contribution to calcium carbonate loss.

437

4.2 Carbonate budgets (G_{budget}) in the central Red Sea

4.2.1 Cross-shelf dynamics, regional and global context

440   On an ecosystem scale, the G_{budget} data suggest that the offshore reef site in the central Red Sea loses about 15 %

441   accreted carbonates to bioerosion per year. On the mid- and nearshore reef this loss increases to to 42 % and to over

442   100 %, respectively. By comparison, on the scale of a single coral colony, the boring clam *Lithophaga lessepsiana*

443   alone can erode up to 40 % of the carbonate deposited by the coral *Stylophora pistillata* (Lazar and Loya, 1991). In

444   our study sites, the spatial dynamics of the two metrics G_{net} and the census-based G_{budget}, were consistent and suggest

445   net erosion in nearshore reef sites and net accretion in offshore reef sites in the central Red Sea. Reef growth at the

446   central Red Sea cross-shelf gradient averaged 0.66 ± 2.01 kg $CaCO_3$ m^{-2} y^{-1}, which was driven by the substantial

447   budget of the offshore reef, reflecting the location and habitat dependence for reef growth potential. That the offshore

448   reef budget is essential to maintain the entire shelf budget has also has been observed on a reef platform in the

449   Maldives. In the respective study, reef accretion was minor and highly heterogeneous at most sites and only few reef

450   sites at the platform margin promoted substantial net accretion and thereby greatly contributed to the positive average

451   budget of the entire platform (Perry et al., 2017).

452   The here presented central Red Sea G_{budget} data are within the range of contemporary reef carbonate budgets from the

453   Atlantic (2.55 ± 3.83 kg $CaCO_3$ m^{-2} y^{-1}) and Indian Ocean (1.41 ± 3.02 kg $CaCO_3$ m^{-2} y^{-1}) (Perry et al., 2018). Notably,

454   these data are below the suggested "optimal reef budget" of 5 - 10 kg $CaCO_3$ m^{-2} y^{-1} observed in "healthy", high coral

455   cover fore-reefs (see data in Perry et al., 2018 and comparisons therein; Vecsei, 2001, 2004). The decline in coral

456   cover is likely central to the reduced carbonate budgets in contemporary reefs. For instance, the reefs investigated in

457   the present study do not exceed a coral cover of 40 % (as observed in the offshore study site). In comparison, the

458   dataset compiled by Vecsei 2001 encompasses hard coral cover of up to 80% for the Indo-Pacific and up to 95 % for

459   Pacific Islands. Further, the reduced contemporary carbonate budgets coincide with the observed decrease in

460   calcification rates of Red Sea corals at large (Cantin et al., 2010; Steiner et al., 2018). As such, the effect of climate

461   change and the corresponding increase in seawater temperature may have severe consequences via overall decrease

462   in coral reef cover as well as via reduced calcification of the resident corals. Hence, although the present G_{budget} data

463   still suggest effective barrier reef formation in the central Red Sea (substantial accretion on the offshore reef),

464   carbonate accretion rates and therefore reef formation in the central Red Sea may be hampered in the long run by the

465   ongoing warming.

466

467   **4.2.2 Biotic drivers**

468   *Regional differences*

469   Cross-shelf patterns of G_{budget} drivers from the central Red Sea are distinct from other reef systems. The central Red

470   Sea system is characterized by a nearshore site with a negative G_{budget}, impacted by high parrotfish abundances and

471   erosion rates, low coral cover, and putatively considerable endolithic bioerosion rates (see discussion of G_{net} data).

472   Conversely, the offshore reef is characterized by high calcification rates, driven by high coral and coralline algae

473   abundances. In the GBR an opposing trend with high net accretion in the nearshore reefs (Browne et al., 2013)

474   coincided with high coral cover, low bioerosion rates, and lowest rates of parrotfish bioerosion (Hoey and Bellwood,

475   2007; Tribollet et al., 2002). On Caribbean reefs, parrotfish erosion rates were higher on leeward reefs (which may be

476   similar to protected nearshore habitats), but in contrast to the central Red Sea, these sites were typically characterized

477   by overall high coral cover driving a positive G_{budget} (Perry et al., 2012, 2014). This inter-regional comparison strongly

478   suggests that reef accretion/erosion dynamics encountered in any given reef system cannot be readily extrapolated to

479   other reef systems. Hence, *in situ* assessments of individual reef systems are required to unravel local dynamics and

480   responses to environmental change, and are therefore imperative for the development of effective management

481   measures.

482

483   *The role of coral and coralline crusts*

484   Benthic calcifiers, in particular reef-building corals, are major contributors to carbonate production and are considered

485   the most influential drivers of $G_{budgets}$ globally (Franco et al., 2016). Corals in particular can contribute as much as 90

486   % to the gross carbonate production across different reef zones, which also includes low coral cover lagoonal and

487   rubble habitats (Perry et al., 2017). Hence, loss of coral cover rapidly gives way to increased bioerosion and thereby

488   critically contributes to reef framework degradation (Perry and Morgan, 2017). Indeed, on Caribbean reefs, G_{budget}

489   data were reported to shift into erosional states once live hard coral cover was below 10 % (Perry et al., 2013). A live

490   coral cover threshold remains to be determined for the central Red Sea and will require evaluation of a larger dataset.

491   Yet, we find that the nearshore reef featuring a negative G_{budget} is characterized by a coral cover of 11 %, while the

492   midshore and offshore reefs, characterized by near-neutral vs. positive carbonate budgets, both feature similar average

493   coral covers (at 35 and 40 %, respectively). In this respect, our data show that a 2-fold higher abundance of coralline

494   algae and other encrusting calcifiers in the offshore reef (compared to the midshore reef) significantly added to a

495   higher G_{budget}. The positive contribution of coralline algae for central Red Sea reef accretion is corroborated by their

496   strong and significant correlation to G_{budget}. Coralline algae in particular are considered an important contributor to

497   reef growth, as they stabilize the reef framework through "cementation" (Perry et al., 2008) and by habitat priming

498   for successful coral recruitment (Heyward and Negri, 1999).

499

500   *Epilithic grazers*

501   Epilithic grazers such as parrotfish and sea urchin are considered important drivers of bioerosion on many reefs (Hoey

502   and Bellwood, 2007; Mokady et al., 1996; Pari et al., 1998; Reaka-Kudla et al., 1996). Sea urchins were identified as

503   significant bioeroders in some reefs of Réunion Island, French Polynesia, and in the GoA, northern Red Sea (Chazottes

504 et al., 1995, 2002; Mokady et al., 1996). For the northern Red Sea, sea urchins were abundant, and their removal of

505 reef carbonates was estimated to range around 13 - 22 % of total reef slope calcification (Mokady et al., 1996). In

506 contrast, sea urchins were rare in our study sites contributing to only 2 - 3 % of the total bioerosion resulting in low

507 contributions to G_{budget}. Only on the net-erosive nearshore reef were sea urchins more abundant causing 12 % of total

508 bioerosion.

509 Compared to sea urchins, parrotfish played a more important role for $G_{budgets}$ throughout the entire reef system,

510 contributing 70 - 96 % of the total bioerosion. In the correlation analyses, both grazers, i.e., sea urchins and parrotfish,

511 negatively correlated with G_{budget}, however these correlations were not very strong ($\rho \sim -0.5$) and non-significant. The

512 weak correlation may be influenced by a considerable variability in the reef census dataset, specifically regarding

513 parrotfish abundances. Observer bias (parrotfish keep minimum distance from surveyors during dives and may

514 therefore not enter survey plots; pers. obs.), natural (e.g., species distribution, habitat preferences, reef rugosity, and

515 mobility or large roving excavating species, such as *Bolbometopon muricatum*), and/or anthropogenically-driven

516 factors (e.g., differential fishing pressure) may also contribute to the observed data heterogeneity (McClanahan, 1994;

517 McClanahan et al., 1994). Indeed, the Saudi Arabian central Red Sea has been subject to decade-long fishing pressure,

518 which has significantly altered reef fish community structures and reduced overall fish biomass compared to less

519 impacted Red Sea regions (Kattan et al., 2017). Unregulated fishing could at least in part explain the differences of

520 fish abundance dynamics between the present study and reefs on the GBR and the Caribbean. The heterogeneity of

521 grazer populations further propagates into $G_{budgets}$ estimates, resulting in a considerable within-site variability that

522 reduces power of statistical tests and correlations.

523 **4.3 Abiotic factors and reef growth dynamics**

524 Reef habitats in the central Red Sea are characterized by abiotic factors that differ from the majority of tropical reef

525 environments (Couce et al., 2012; Kleypas et al., 1999). Our sites were exposed to high summer temperatures (30 -

526 33 °C) and a high salinity throughout the year (39 - 40). Inorganic nutrients were mostly far below 1 $\mu mol\ kg^{-1}$,

527 whereas TA was comparably high, 2400 – 2500 $\mu mol\ kg^{-1}$, values typical for much of the Red Sea basin (Acker et al.,

528 2008; Steiner et al., 2014). As such, the Red Sea is considered a natural model system or "laboratory", which can

529 advance our understanding of ecosystem functioning under extreme or marginal conditions of which some are

530 projected under ocean change scenarios (Camp et al., 2018). The study of such natural systems is a challenge and the

531 documentation of governing factors both abiotic and biotic will contribute to a better understanding of the dynamics

532 and interactions, which can significantly improve ecosystem scale predictions (Boyd and Hutchins, 2012; Boyd and

533 Brown, 2015; Camp et al., 2018). In the present study, reef framework decline (i.e., net erosion) was associated with

534 the reef habitat of slightly increased salinity and stronger diel pH fluctuations, which are characteristic for shallow

535 water, limited flow systems and semi-enclosed reefs (Camp et al., 2017; Shamberger et al., 2017), such as the here

536 investigated nearshore study site (Roik et al., 2016). On the other hand, positive reef growth was associated with reef

537 habitats characterized by higher TA levels, but also with slightly increased inorganic nutrient species, namely NO_3^-

538 &NO_2^- and PO_4^{3-}.

539

The nearshore site

541   The nearshore reef is located on the shelf, surrounded by shallow waters of extended residency time and has a lower

542   water exchange rate compared to the other two reef sites (Roik et al., 2016). Evaporation and limited flow, particularly

543   during summer, may increase salinity, which was overall higher at this reef site. However, the difference to the other

544   sites was minuscule and unlikely to have affected calcifying (Röthig et al., 2016) and bioeroding biota. The variability

545   of diurnal pH on the other hand presumably has stronger impacts on the performance of calcifiers and bioeroders.

546   Previously, pH variability across a reef flat and slope were demonstrated to correlate with net accretion dynamics by

547   showing higher net accretion prevailing in sites of less variable pH conditions (Price et al., 2012; Silbiger et al., 2014),

548   which reflects the pattern observe here.

549   The fluctuation in pH may (in part) represent a biotic feedback signature in reef habitats, which entails changes in sea

550   water chemistry caused by dominant biotic processes, i.e., calcification, carbonate dissolution, and

551   respiration/photosynthesis (Bates et al., 2010; Silverman et al., 2007a; Zundelevich et al., 2007). Commonly, such pH

552   fluctuations are influenced by changes in carbonate system variables, e.g. DIC and TA (Shaw et al., 2012; Silbiger et

553   al., 2014), which can modify the antagonistic processes of calcification and bioerosion/dissolution (e.g., Andersson,

554   2015; Langdon et al., 2000; Tribollet et al., 2009). In particular, in our nearshore study site, where benthic macro

555   community abundance was low, biological activity in the sandy bottom (e.g., permeable carbonate sands) might be a

556   crucial factor contributing to the biotic feedback (Andersson, 2015; Cyronak et al., 2013; Eyre et al., 2018).

557

558   *Total alkalinity and nutrients*

559   The increase in TA is often associated with increased carbonate ion concentration and Ω_a, which facilitate the

560   precipitation of carbonates supporting the performance of reef-builders (Albright et al., 2016, 2018; Langdon et al.,

561   2000; Schneider and Erez, 2006; Silbiger et al., 2014). We identified a positive correlation of TA with reef growth in

562   our dataset. The difference in TA across our study sites was small, but in the range of natural cross-shelf differences

563   reported from other reefs (e.g. reefs in Bermuda, 20 - 40 µmol kg^{-1}, Bates et al., 2010), and as high as 50 µmol kg^{-1},

564   the TA enrichment that enhanced community net calcification in a reef-enclosed lagoon (Albright et al., 2016). On

565   the other hand, high calcification rates can deplete TA, whereas dissolution of carbonates can enrich TA measurably,

566   specifically in (semi) enclosed systems (Bates et al., 2010), which we do not observe along the cross shelf gradient. It

567   remains to be further investigated how TA dynamics across the shelf relate to reef growth processes.

568   Although increased nutrients are commonly linked to reef degradation initiated through phase shifts, increased

569   bioerosion rates, and/or the decline of calcifiers (Fabricius, 2011; Grand and Fabricius, 2010; Holmes, 2000), our

570   dataset suggests that a highly oligotrophic system such as the central Red Sea reefs may benefit from slight increases

571   of certain nutrient species. Specifically, natural minor increases of N and P might have a positive effect on ecosystem

572   productivity and functioning including carbonate budgets. A moderate natural source of nutrients, e.g., from sea bird

573   populations, can indeed have a positive effect on ecosystem functioning, in contrast to anthropogenic run-off (Graham

574   et al., 2018). Interestingly, our study also identified PO_4^{3-} concentration as an abiotic correlate of reef growth. In the

575   Red Sea, high N:P ratios indicate that P is a limiting micronutrient, e.g. for phytoplankton (Fahmy, 2003). PO_4^{3-} is not

576   only essential for pelagic primary producers, but also for reef calcifiers and their photosymbionts, such as the stony

577   corals and their micro-algal Symbiodiniaceae endosymbionts (Ferrier-Pagès et al., 2016; LaJeunesse et al., 2018).

578   Experimental studies have demonstrated that PO_4^{3-} provision can maintain the coral-algae symbiosis in reef-building

579   corals under heat stress (Ezzat et al., 2016). Conversely, P limitation can increase the stress susceptibility of this

580   symbiosis (Pogoreutz et al., 2017; Rädecker et al., 2015; Wiedenmann et al., 2013). In light of our results, it will be

581   of interest to link spatio-temporal variation of inorganic nutrient ratios with patterns of reef resilience in the central

582   Red Sea to understand their effects on long-term trends of reef growth.

583

584   **4.4 Reef growth trajectories in the Red Sea**

585   Carbonate budgets provide an insight into ecosystem functioning and can be used as a powerful tool to track reef

586   trajectories through time. This includes the exploration of past and current reef trends, which may be critical for

587   prediction of future reef development (Januchowski-Hartley et al., 2017). Indeed, the absence of comparative baseline

588   data limits a historical perspective on the central Red Sea G_{budget} presented here. Previously reported Red Sea data

589   include pelagic and reefal carbonate accretion rates from 1998, estimated using basin-scale historical measurements

590   of TA (Steiner et al., 2014). Another dataset employed the census-based budget approach for a highly seasonal high-

591   latitude fringing reef in the GoA from 1994 - 1996 (Dullo et al., 1996), which is methodologically similar to the

592   *ReefBudget* approach. Both reef growth estimates provide similar rates: The TA-based reef accretion estimate from

593   1998 was 0.9 kg $CaCO_3$ m^{-2} y^{-1} and the GoA fringing reef budget from 1994 - 1996 ranged between 0.7 and 0.9 kg

594     $CaCO_3$ m^{-2} y^{-1}. Additionally, the gross calcification rate of the offshore benthic communities ($G_{benthos}$) compares well

595   with the maxima measured in the GoA reefs in 1994 (i.e., 2.7 kg $CaCO_3$ m^{-2} y^{-1}) (Heiss, 1995). The $G_{budgets}$ assessed

596   in the present study are in accordance with these data, indicating stable reef growth rates in the Red Sea basin in the

597   recent 20 years, despite the ongoing warming trend and observed impairment in coral calcification in a coral species

598   (Cantin et al., 2010; Raitsos et al., 2011). Yet, data are limited and comparisons between the central Red Sea and the

599   GoA should be interpreted with great caution. Due to the strong latitudinal gradient of temperature and salinity along

600   with differences in seasonality between the central Red Sea and the GoA, reef growth dynamics from the two regions

601   may fundamentally differ. Hence, far larger (and ideally cross-latitude) datasets will be needed to determine more

602   accurately whether a declining calcification capacity of Red Sea corals has already become a basin-scale phenomenon

603   and whether there are species-specific differences. In this study we have demonstrated that offshore reefs in the central

604   Red Sea still maintain a positive carbonate budget, yet can be considered 'underperforming' below "optimal reefal

605   production" (Vecsei, 2004). In the context of reef growth trajectories, the data presented in this study should serve as

606   a valuable contemporary baseline for comparative future studies in the central Red Sea. Importantly, these data were

607   collected before the Third Global Bleaching Event, which impacted the region during summers 2015 and 2016

608   (Monroe et al., 2018). The present effort therefore will be of great value when assessing potential (long-term) changes

609   of Red Sea $G_{budgets}$ following this substantial disturbance.

5 Conclusions

The Red Sea is a geographic region where coral reefs exist in a naturally high temperature and high salinity environment. Baseline data for reef growth from this region are scarce and particularly valuable as they provide insight into reef functioning under environmental conditions that deviate from the global average for coral reefs. As such, they can provide a potential outlook to future ocean scenarios. Overall, we found net erosion in a near shore reef site, about neutral growth in a midshore reef site, and net accretion in an offshore reef site. A comparison of central Red Sea reef growth dynamics to other major reef systems revealed important differences and argue for *in situ* studies in underexplored major reef regions. For instance, our study highlights the importance of coralline algae as a reef-building agent and shows that the erosive forces in the Red Sea are not as pronounced (yet) as observed elsewhere. Reef growth on Red Sea offshore reefs is comparable to the majority of reef growth estimates from other geographic regions, which today perform well below what has been considered a 'healthy reef' carbonate budget. A first comparison with data from recent years suggests that reef growth rates in the central Red Sea have not decreased substantially over the last two decades, despite potential negative effects of the ongoing warming trend. The absence of comparative long-term data from the region hampers long-term predictions. We therefore advocate additional research to better inform past and future trajectories of reef growth dynamics under consideration of the challenging and unique environmental settings of the Red Sea.

Data availability.

All data are provided in the manuscript and supplement. In addition, physicochemical datasets, reef census, and limestone block assay raw data are available from the Dryad Digital Repository doi:10.5061/dryad.19kd421.

The Supplementary material related to this article is available online *(will be included by Copernicus)*

Author contribution

Resources: CRV

Project administration: CRV

Conceptualization: AR

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647   Formal analysis: AR CP VS

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651   Writing - original draft: AR

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654
655   **Competing interests**

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

657

658 **References**

659 Acker, J., Leptoukh, G., Shen, S., Zhu, T. and Kempler, S.: Remotely-sensed chlorophyll a observations of the
660 northern Red Sea indicate seasonal variability and influence of coastal reefs, J. Mar. Syst., 69(3), 191–204,
661 doi:10.1016/j.jmarsys.2005.12.006, 2008.

662 Albright, R., Caldeira, L., Hosfelt, J., Kwiatkowski, L., Maclaren, J. K., Mason, B. M., Nebuchina, Y., Ninokawa, A.,
663 Pongratz, J., Ricke, K. L., Rivlin, T., Schneider, K., Sesboüé, M., Shamberger, K., Silverman, J., Wolfe, K., Zhu, K.
664 and Caldeira, K.: Reversal of ocean acidification enhances net coral reef calcification, Nature, advance online
665 publication, doi:10.1038/nature17155, 2016.

666 Albright, R., Takeshita, Y., Koweek, D. A., Ninokawa, A., Wolfe, K., Rivlin, T., Nebuchina, Y., Young, J. and
667 Caldeira, K.: Carbon dioxide addition to coral reef waters suppresses net community calcification, Nature, 555(7697),
668 516–519, doi:10.1038/nature25968, 2018.

669 Alwany, M. A., Thaler, E. and Stachowitsch, M.: Parrotfish bioerosion on Egyptian Red Sea reefs, J. Exp. Mar. Biol.
670 Ecol., 371(2), 170–176, doi:10.1016/j.jembe.2009.01.019, 2009.

671 Anderson, M. J., Gorley, R. N. and Clarke, K. R.: PERMANOVA+ for PRIMER: Guide to software and statistical
672 methods, 2008.

673 Andersson, A. J.: A Fundamental Paradigm for Coral Reef Carbonate Sediment Dissolution, Coral Reef Res., 2, 52,
674 doi:10.3389/fmars.2015.00052, 2015.

675 Bak, R. P. M.: Sea urchin bioerosion on coral reefs: place in the carbonate budget and relevant variables, Coral Reefs,
676 13(2), 99–103, doi:10.1007/BF00300768, 1994.

677 Bak, R. P. M., Nieuwland, G. and Meesters, E. H.: Coral Growth Rates Revisited after 31 Years: What is Causing
678 Lower Extension Rates in *Acropora Palmata*?, Bull. Mar. Sci., 84(3), 287–294, 2009.

679 Bannerot, S. P. and Bohnsack, J. A.: A stationary visual census technique for quantitatively assessing community
680 structure of coral reef fishes, NOAA. [online] Available from: http://core.kmi.open.ac.uk/download/pdf/11018492.pdf
681 (Accessed 1 September 2014), 1986.

682 Bates, N. R., Amat, A. and Andersson, A. J.: Feedbacks and responses of coral calcification on the Bermuda reef
683 system to seasonal changes in biological processes and ocean acidification, Biogeosciences, 7(8), 2509–2530,
684 doi:10.5194/bg-7-2509-2010, 2010.

685 Bellwood, D. R.: Direct estimate of bioerosion by two parrotfish species, *Chlorurus gibbus* and *C. sordidus*, on the
686 Great Barrier Reef, Australia, Mar. Biol., 121(3), 419–429, doi:10.1007/BF00349451, 1995.

687 Bellwood, D. R., Hoey, A. S. and Choat, J. H.: Limited functional redundancy in high diversity systems: resilience
688 and ecosystem function on coral reefs, Ecol. Lett., 6(4), 281–285, 2003.

689 Boyd, P. and Hutchins, D.: Understanding the responses of ocean biota to a complex matrix of cumulative
690 anthropogenic change, Mar. Ecol. Prog. Ser., 470, 125–135, doi:10.3354/meps10121, 2012.

691 Boyd, P. W. and Brown, C. J.: Modes of interactions between environmental drivers and marine biota, Front. Mar.
692 Sci., 2, doi:10.3389/fmars.2015.00009, 2015.

693 Browne, N. K., Smithers, S. G. and Perry, C. T.: Carbonate and terrigenous sediment budgets for two inshore turbid
694 reefs on the central Great Barrier Reef, Mar. Geol., 346, 101–123, doi:10.1016/j.margeo.2013.08.011, 2013.

695   Bruggemann, J., van Kessel, A., van Rooij, J. and Breeman, A.: Bioerosion and sediment ingestion by the Caribbean
696   parrotfish *Scarus vetula* and *Sparisoma viride*: implications of fish size, feeding mode and habitat use, Mar. Ecol.
697   Prog. Ser., 134, 59–71, doi:10.3354/meps134059, 1996.

698   Buddemeier, R. W.: Symbiosis: Making light work of adaptation, Nature, 388(6639), 229–230, doi:10.1038/40755,
699   1997.

700   Cai, W.-J., Ma, Y., Hopkinson, B. M., Grottoli, A. G., Warner, M. E., Ding, Q., Hu, X., Yuan, X., Schoepf, V., Xu,
701   H., Han, C., Melman, T. F., Hoadley, K. D., Pettay, D. T., Matsui, Y., Baumann, J. H., Levas, S., Ying, Y. and Wang,
702   Y.: Microelectrode characterization of coral daytime interior pH and carbonate chemistry, Nat. Commun., 7, 11144,
703   doi:10.1038/ncomms11144, 2016.

704   Camp, E. F., Nitschke, M. R., Rodolfo-Metalpa, R., Houlbreque, F., Gardner, S. G., Smith, D. J., Zampighi, M. and
705   Suggett, D. J.: Reef-building corals thrive within hot-acidified and deoxygenated waters, Sci. Rep., 7(1), 2434,
706   doi:10.1038/s41598-017-02383-y, 2017.

707   Camp, E. F., Schoepf, V., Mumby, P. J., Hardtke, L. A., Rodolfo-Metalpa, R., Smith, D. J. and Suggett, D. J.: The
708   Future of Coral Reefs Subject to Rapid Climate Change: Lessons from Natural Extreme Environments, Front. Mar.
709   Sci., 5, doi:10.3389/fmars.2018.00004, 2018.

710   Cantin, N. E., Cohen, A. L., Karnauskas, K. B., Tarrant, A. M. and McCorkle, D. C.: Ocean Warming Slows Coral
711   Growth in the Central Red Sea, Science, 329(5989), 322–325, doi:10.1126/science.1190182, 2010.

712   Carricart-Ganivet, J. P., Cabanillas-Terán, N., Cruz-Ortega, I. and Blanchon, P.: Sensitivity of Calcification to
713   Thermal Stress Varies among Genera of Massive Reef-Building Corals, PLoS ONE, 7(3), e32859,
714   doi:10.1371/journal.pone.0032859, 2012.

715   Chazottes, V., Campion-Alsumard, T. L. and Peyrot-Clausade, M.: Bioerosion rates on coral reefs: interactions
716   between macroborers, microborers and grazers (Moorea, French Polynesia), Palaeogeogr. Palaeoclimatol. Palaeoecol.,
717   113(2–4), 189–198, doi:10.1016/0031-0182(95)00043-L, 1995.

718   Chazottes, V., Le Campion-Alsumard, T., Peyrot-Clausade, M. and Cuet, P.: The effects of eutrophication-related
719   alterations to coral reef communities on agents and rates of bioerosion (Reunion Island, Indian Ocean), Coral Reefs,
720   21(4), 375–390, 2002.

721   Cohen, A. L. and Holcomb, M.: Why corals care about ocean acidification: uncovering the mechanism, Oceanography,
722   (22), 118–127, 2009.

723   Cooper, T. F., Death, G., Fabricius, K. E. and Lough, J. M.: Declining coral calcification in massive *Porites* in two
724   nearshore regions of the northern Great Barrier Reef, Glob. Change Biol., 14(3), 529–538, doi:10.1111/j.1365-
725   2486.2007.01520.x, 2008.

726   Couce, E., Ridgwell, A. and Hendy, E. J.: Environmental controls on the global distribution of shallow-water coral
727   reefs, J. Biogeogr., 39(8), 1508–1523, doi:10.1111/j.1365-2699.2012.02706.x, 2012.

728   Cyronak, T., Santos, I. R., McMahon, A. and Eyre, B. D.: Carbon cycling hysteresis in permeable carbonate sands
729   over a diel cycle: Implications for ocean acidification, Limnol. Oceanogr., 58(1), 131–143,
730   doi:10.4319/lo.2013.58.1.0131, 2013.

731   Death, G., Lough, J. M. and Fabricius, K. E.: Declining Coral Calcification on the Great Barrier Reef, Science,
732   323(5910), 116–119, doi:10.1126/science.1165283, 2009.

733   Dullo, P. D. W.-C., Gektidis, D. M., Golubic, P. D. S., Heiss, D. G. A., Kampmann, D. B. H., Kiene, D. W., Kroll, D.
734   Ö. D. K., Kuhrau, D. B. M. L., Radtke, D. G., Reijmer, D. J. G., Reinicke, D. G. B., Schlichter, P. D. D., Schuhmacher,

P. D. H. and Vogel, K.: Factors controlling holocene reef growth: An interdisciplinary approach, Facies, 32(1), 145–188, doi:10.1007/BF02536867, 1995.

Dullo, W.-C., Reijmer, J., Schuhmacher, H., Eisenhauer, A., Hassan, M. and Heiss, G.: Holocene reef growth and recent carbonate production in the Red Sea, [online] Available from: https://www.researchgate.net/publication/230751439_Holocene_reef_growth_and_recent_carbonate_production_in_the_Red_Sea, 1996.

Eakin, C. M.: A tale of two Enso Events: carbonate budgets and the influence of two warming disturbances and intervening variability, Uva Island, Panama, Bull. Mar. Sci., 69(1), 171–186, 2001.

Edinger, E. N., Limmon, G. V., Jompa, J., Widjatmoko, W., Heikoop, J. M. and Risk, M. J.: Normal coral growth rates on dying reefs: Are coral growth rates good indicators of reef health?, Mar. Pollut. Bull., 40(5), 404–425, 2000.

Enochs, I. C.: Ocean acidification enhances the bioerosion of a common coral reef sponge: implications for the persistence of the Florida Reef Tract, Bull. Mar. Sci., 91, 271–290, doi:10.5343/bms.2014.1045, 2015.

Eyre, B. D., Cyronak, T., Drupp, P., Carlo, E. H. D., Sachs, J. P. and Andersson, A. J.: Coral reefs will transition to net dissolving before end of century, Science, 359(6378), 908–911, doi:10.1126/science.aao1118, 2018.

Ezzat, L., Maguer, J.-F., Grover, R. and Ferrier-Pagès, C.: Limited phosphorus availability is the Achilles heel of tropical reef corals in a warming ocean, Sci. Rep., 6, 31768, doi:10.1038/srep31768, 2016.

Fabricius, K. E.: Factors Determining the Resilience of Coral Reefs to Eutrophication: A Review and Conceptual Model, in Coral Reefs: An Ecosystem in Transition, edited by Z. Dubinsky and N. Stambler, pp. 493–505, Springer Netherlands, Dordrecht. [online] Available from: http://www.springerlink.com/index/10.1007/978-94-007-0114-4_28 (Accessed 8 May 2012), 2011.

Fahmy, M.: Water quality in the Red Sea coastal waters (Egypt): Analysis of spatial and temporal variability, Chem. Ecol., 19(1), 67–77, doi:10.1080/0275754031000087074, 2003.

Fang, J. K. H., Mello-Athayde, M. A., Schönberg, C. H. L., Kline, D. I., Hoegh-Guldberg, O. and Dove, S.: Sponge biomass and bioerosion rates increase under ocean warming and acidification, Glob. Change Biol., 19(12), 3581–3591, doi:10.1111/gcb.12334, 2013.

Ferrier-Pagès, C., Godinot, C., D'Angelo, C., Wiedenmann, J. and Grover, R.: Phosphorus metabolism of reef organisms with algal symbionts, Ecol. Monogr., 86(3), 262–277, doi:10.1002/ecm.1217, 2016.

Franco, C., Hepburn, L. A., Smith, D. J., Nimrod, S. and Tucker, A.: A Bayesian Belief Network to assess rate of changes in coral reef ecosystems, Environ. Model. Softw., 80, 132–142, doi:10.1016/j.envsoft.2016.02.029, 2016.

Glynn, P. W.: Bioerosion and coral-reef growth: a dynamic balance, in Life and Death of Coral Reefs, edited by C. Birkeland, pp. 68–94, Chapman and Hall, Ney York, USA., 1997.

Glynn, P. W. and Manzello, D. P.: Bioerosion and Coral Reef Growth: A Dynamic Balance, in Coral Reefs in the Anthropocene, edited by C. Birkeland, pp. 67–97, Springer Netherlands., 2015.

Graham, N. A. J., Wilson, S. K., Carr, P., Hoey, A. S., Jennings, S. and MacNeil, M. A.: Seabirds enhance coral reef productivity and functioning in the absence of invasive rats, Nature, 559(7713), 250–253, doi:10.1038/s41586-018-0202-3, 2018.

Grand, H. M. L. and Fabricius, K. E.: Relationship of internal macrobioeroder densities in living massive *Porites* to turbidity and chlorophyll on the Australian Great Barrier Reef, Coral Reefs, 30(1), 97–107, doi:10.1007/s00338-010-0670-x, 2010.

774   Grange, J. S., Rybarczyk, H. and Tribollet, A.: The three steps of the carbonate biogenic dissolution process by
775   microborers in coral reefs (New Caledonia), Environ. Sci. Pollut. Res., doi:10.1007/s11356-014-4069-z, 2015.

776   Green, A. L. and Bellwood, D. R.: Monitoring functional groups of herbivorous reef fishes as indicators of coral reef
777   resilience: a practical guide for coral reef managers in the Asia Pacific region, International Union for Conservation
778   of   Nature,   IUCN,   Gland,   Switzerland.   [online]   Available   from:
779   ftp://ftp.library.noaa.gov/noaa_documents.lib/CoRIS/IUCN_herbivorous_reef-fishes_2009.pdf   (Accessed   30
780   September 2017), 2009.

781   Heiss, G. A.: Carbonate production by scleractinian corals at Aqaba, Gulf of Aqaba, Red Sea, Facies, 33(1), 19–34,
782   doi:10.1007/BF02537443, 1995.

783   Heyward, A. J. and Negri, A. P.: Natural inducers for coral larval metamorphosis, Coral Reefs, 18(3), 273–279, 1999.

784   Hoey, A. S. and Bellwood, D. R.: Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef, Coral
785   Reefs, 27(1), 37–47, doi:10.1007/s00338-007-0287-x, 2007.

786   Holmes, K. E.: Effects of eutrophication on bioeroding sponge communities with the description of new West Indian
787   sponges, *Cliona* spp. (Porifera: Hadromerida: Clionidae), Invertebr. Biol., 119(2), 125–138, doi:10.1111/j.1744-
788   7410.2000.tb00001.x, 2000.

789   Hutchings, P. A.: Biological destruction of coral reefs, Coral Reefs, 4(4), 239–252, doi:10.1007/BF00298083, 1986.

790   Januchowski-Hartley, F. A., Graham, N. A. J., Wilson, S. K., Jennings, S. and Perry, C. T.: Drivers and predictions
791   of coral reef carbonate budget trajectories, Proc R Soc B, 284(1847), 20162533, doi:10.1098/rspb.2016.2533, 2017.

792   Jokiel, P. L. and Coles, S. L.: Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature, Coral
793   Reefs, 8(4), 155–162, doi:10.1007/BF00265006, 1990.

794   Jones, N. S., Ridgwell, A. and Hendy, E. J.: Evaluation of coral reef carbonate production models at a global scale,
795   Biogeosciences, 12(5), 1339–1356, doi:10.5194/bg-12-1339-2015, 2015.

796   Kattan, A., Coker, D. J. and Berumen, M. L.: Reef fish communities in the central Red Sea show evidence of
797   asymmetrical fishing pressure, Mar. Biodivers., 1–12, doi:10.1007/s12526-017-0665-8, 2017.

798   Kennedy, E. V., Perry, C. T., Halloran, P. R., Iglesias-Prieto, R., Schönberg, C. H. L., Wisshak, M., Form, A. U.,
799   Carricart-Ganivet, J. P., Fine, M., Eakin, C. M. and Mumby, P. J.: Avoiding Coral Reef Functional Collapse Requires
800   Local and Global Action, Curr. Biol., 23(10), 912–918, doi:10.1016/j.cub.2013.04.020, 2013.

801   Kiene, W. E. and Hutchings, P. A.: Bioerosion experiments at Lizard Island, Great Barrier Reef, Coral Reefs, 13(2),
802   91–98, 1994.

803   Kleemann, K.: The Pectinid Bivalve *Pedum spondyloideum* (Gmelin 1791): Amount of Surface and Volume Occupied
804   in Host Corals From the Red Sea, Mar. Ecol., 22(1–2), 111–133, doi:10.1046/j.1439-0485.2001.01749.x, 2001.

805   Kleypas, J., Buddemeier, R. and Gattuso, J.-P.: The future of coral reefs in an age of global change, Int. J. Earth Sci.,
806   90(2), 426–437, doi:10.1007/s005310000125, 2001.

807   Kleypas, J. A., McManus, J. W. and Menez, L. A. B.: Environmental Limits to Coral Reef Development: Where Do
808   We Draw the Line?, Am. Zool., 39, 146–159, 1999.

809   LaJeunesse, T. C., Parkinson, J. E., Gabrielson, P. W., Jeong, H. J., Reimer, J. D., Voolstra, C. R. and Santos, S. R.:
810   Systematic Revision of Symbiodiniaceae Highlights the Antiquity and Diversity of Coral Endosymbionts, Curr. Biol.,
811   28(16), 2570-2580.e6, doi:10.1016/j.cub.2018.07.008, 2018.

812 Langdon, C., Takahashi, T., Sweeney, C., Chipman, D., Goddard, J., Marubini, F., Aceves, H., Barnett, H. and
813 Atkinson, M. J.: Effect of calcium carbonate saturation state on the calcification rate of an experimental coral reef,
814 Glob. Biogeochem. Cycles, 14(2), 639–654, doi:10.1029/1999GB001195, 2000.

815 Lazar, B. and Loya, Y.: Bioerosion of coral reefs - A chemical approach, Limnol. Oceanogr., 36, 377–383, 1991.

816 Manzello, D. P.: Ocean acidification hotspots: Spatiotemporal dynamics of the seawater CO_2 system of eastern Pacific
817 coral reefs, Limnol. Oceanogr., 55(1), 239–248, doi:10.4319/lo.2010.55.1.0239, 2010.

818 Marshall, A. T. and Clode, P.: Calcification rate and the effect of temperature in a zooxanthellate and an
819 azooxanthellate scleractinian reef coral, Coral Reefs, 23(2), 218–224, doi:10.1007/s00338-004-0369-y, 2004.

820 Marubini, F., Ferrier-Pagès, C., Furla, P. and Allemand, D.: Coral calcification responds to seawater acidification: a
821 working hypothesis towards a physiological mechanism, Coral Reefs, 27(3), 491–499, doi:10.1007/s00338-008-0375-
822 6, 2008.

823 McClanahan, T. R.: Kenyan coral reef lagoon fish: effects of fishing, substrate complexity, and sea urchins, Coral
824 Reefs, 13(4), 231–241, doi:10.1007/BF00303637, 1994.

825 McClanahan, T. R. and Shafir, S. H.: Causes and consequences of sea urchin abundance and diversity in Kenyan coral
826 reef lagoons, Oecologia, 83(3), 362–370, doi:10.1007/BF00317561, 1990.

827 McClanahan, T. R., Nugues, M. and Mwachireya, S.: Fish and sea urchin herbivory and competition in Kenyan coral
828 reef lagoons: the role of reef management, J. Exp. Mar. Biol. Ecol., 184(2), 237–254, doi:10.1016/0022-
829 0981(94)90007-8, 1994.

830 Metzl, N., Moore, B., Papaud, A. and Poisson, A.: Transport and carbon exchanges in Red Sea Inverse Methodology,
831 Glob. Biogeochem. Cycles, 3(1), 1–26, doi:10.1029/GB003i001p00001, 1989.

832 Moberg, F. and Folke, C.: Ecological goods and services of coral reef ecosystems, Ecol. Econ., 29, 215–233, 1999.

833 Mokady, O., Lazar, B. and Loya, Y.: Echinoid bioerosion as a major structuring force of Red Sea coral reefs, Biol.
834 Bull., 190(3), 367–372, 1996.

835 Monroe, A. A., Ziegler, M., Roik, A., Röthig, T., Hardenstine, R. S., Emms, M. A., Jensen, T., Voolstra, C. R. and
836 Berumen, M. L.: *In situ* observations of coral bleaching in the central Saudi Arabian Red Sea during the 2015/2016
837 global coral bleaching event, PLoS ONE, 13(4), e0195814, doi:10.1371/journal.pone.0195814, 2018.

838 Orr, J. C., Fabry, V. J., Aumont, O., Bopp, L., Doney, S. C., Feely, R. A., Gnanadesikan, A., Gruber, N., Ishida, A.,
839 Joos, F., Key, R. M., Lindsay, K., Maier-Reimer, E., Matear, R., Monfray, P., Mouchet, A., Najjar, R. G., Plattner,
840 G.-K., Rodgers, K. B., Sabine, C. L., Sarmiento, J. L., Schlitzer, R., Slater, R. D., Totterdell, I. J., Weirig, M.-F.,
841 Yamanaka, Y. and Yool, A.: Anthropogenic ocean acidification over the twenty-first century and its impact on
842 calcifying organisms, Nature, 437(7059), 681–686, doi:10.1038/nature04095, 2005.

843 Osman, E. O., Smith, D. J., Ziegler, M., Kürten, B., Conrad, C., El-Haddad, K. M., Voolstra, C. R. and Suggett, D. J.:
844 Thermal refugia against coral bleaching throughout the northern Red Sea, Glob. Change Biol., 24(2), e474–e484,
845 doi:10.1111/gcb.13895, 2018.

846 Osorno, A., Peyrot-Clausade, M. and Hutchings, P. A.: Patterns and rates of erosion in dead *Porites* across the Great
847 Barrier Reef (Australia) after 2 years and 4 years of exposure, Coral Reefs, 24(2), 292–303, doi:10.1007/s00338-005-
848 0478-2, 2005.

849 Pari, N., Peyrot-Clausade, M., Le Champion-Alsumard, T., Hutchings, P., Chazottes, V., Gobulic, S., Le Champion,
850 J. and Fontaine, M. F.: Bioerosion of experimental substrates on high islands and on atoll lagoons (French Polynesia)
851 after two years of exposure, Mar. Ecol. Prog. Ser., 166, 119–130, 1998.

852 Perry, C., Edinger, E., Kench, P., Murphy, G., Smithers, S., Steneck, R. and Mumby, P.: Estimating rates of
853 biologically driven coral reef framework production and erosion: a new census-based carbonate budget methodology
854 and applications to the reefs of Bonaire, Coral Reefs, 31(3), 853–868, doi:10.1007/s00338-012-0901-4, 2012.

855 Perry, C. T. and Morgan, K. M.: Bleaching drives collapse in reef carbonate budgets and reef growth potential on
856 southern Maldives reefs, Sci. Rep., 7, 40581, doi:10.1038/srep40581, 2017.

857 Perry, C. T., Spencer, T. and Kench, P. S.: Carbonate budgets and reef production states: a geomorphic perspective
858 on the ecological phase-shift concept, Coral Reefs, 27(4), 853–866, doi:10.1007/s00338-008-0418-z, 2008.

859 Perry, C. T., Murphy, G. N., Kench, P. S., Smithers, S. G., Edinger, E. N., Steneck, R. S. and Mumby, P. J.: Caribbean-
860 wide decline in carbonate production threatens coral reef growth, Nat. Commun., 4, 1402, doi:10.1038/ncomms2409,
861 2013.

862 Perry, C. T., Murphy, G. N., Kench, P. S., Edinger, E. N., Smithers, S. G., Steneck, R. S. and Mumby, P. J.: Changing
863 dynamics of Caribbean reef carbonate budgets: emergence of reef bioeroders as critical controls on present and future
864 reef growth potential, Proc. R. Soc. B Biol. Sci., 281(1796), 20142018–20142018, doi:10.1098/rspb.2014.2018, 2014.

865 Perry, C. T., Murphy, G. N., Graham, N. A. J., Wilson, S. K., Januchowski-Hartley, F. A. and East, H. K.: Remote
866 coral reefs can sustain high growth potential and may match future sea-level trends, Sci. Rep., 5, 18289,
867 doi:10.1038/srep18289, 2015.

868 Perry, C. T., Morgan, K. M. and Yarlett, R. T.: Reef Habitat Type and Spatial Extent as Interacting Controls on
869 Platform-Scale Carbonate Budgets, Front. Mar. Sci., 4, doi:10.3389/fmars.2017.00185, 2017.

870 Perry, C. T., Alvarez-Filip, L., Graham, N. A. J., Mumby, P. J., Wilson, S. K., Kench, P. S., Manzello, D. P., Morgan,
871 K. M., Slangen, A. B. A., Thomson, D. P., Januchowski-Hartley, F., Smithers, S. G., Steneck, R. S., Carlton, R.,
872 Edinger, E. N., Enochs, I. C., Estrada-Saldívar, N., Haywood, M. D. E., Kolodziej, G., Murphy, G. N., Pérez-
873 Cervantes, E., Suchley, A., Valentino, L., Boenish, R., Wilson, M. and Macdonald, C.: Loss of coral reef growth
874 capacity to track future increases in sea level, Nature, 1, doi:10.1038/s41586-018-0194-z, 2018.

875 Pisapia, C., Burn, D., Yoosuf, R., Najeeb, A., Anderson, K. D. and Pratchett, M. S.: Coral recovery in the central
876 Maldives archipelago since the last major mass-bleaching, in 1998, Sci. Rep., 6, 34720, doi:10.1038/srep34720, 2016.

877 Pogoreutz, C., Rädecker, N., Cárdenas, A., Gärdes, A., Voolstra, C. R. and Wild, C.: Sugar enrichment provides
878 evidence for a role of nitrogen fixation in coral bleaching, Glob. Change Biol., 8, 23:3838–3848,
879 doi:10.1111/gcb.13695, 2017.

880 Price, N. N., Martz, T. R., Brainard, R. E. and Smith, J. E.: Diel Variability in Seawater pH Relates to Calcification
881 and Benthic Community Structure on Coral Reefs, PLoS ONE, 7(8), e43843, doi:10.1371/journal.pone.0043843,
882 2012.

883 R Core Team: R: A language and environment for statistical computing, R   Foundation for Statistical Computing,
884 Vienna, Austria. [online] Available from: http://www.R-project.org/, 2013.

885 Rädecker, N., Pogoreutz, C., Voolstra, C. R., Wiedenmann, J. and Wild, C.: Nitrogen cycling in corals: the key to
886 understanding holobiont functioning?, Trends Microbiol., doi:10.1016/j.tim.2015.03.008, 2015.

887 Raitsos, D. E., Hoteit, I., Prihartato, P. K., Chronis, T., Triantafyllou, G. and Abualnaja, Y.: Abrupt warming of the
888 Red Sea, Geophys. Res. Lett., 38(14), L14601, doi:10.1029/2011GL047984, 2011.

889 Reaka-Kudla, M., Feingold, J. and Glynn, W.: Experimental studies of rapid bioerosion of coral reefs in the Galapagos
890 Islands, Coral Reefs, 15(2), 101–107, 1996.

891   Reaka-Kudla, M. L.: The Global Biodiversity of Coral Reefs: A Comparison with Rainforests, in Biodiversity II:
892   Understanding and Protecting Our Biological Resources, edited by M. L. Reaka-Kudla, D. E. Wilson, and E. O.
893   Wilson, pp. 83–106, The Joseph Henry Press, USA., 1997.

894   Riegl, B.: Climate change and coral reefs: different effects in two high-latitude areas (Arabian Gulf, South Africa),
895   Coral Reefs, 22(4), 433–446, doi:10.1007/s00338-003-0335-0, 2003.

896   Riegl, B. M., Bruckner, A. W., Rowlands, G. P., Purkis, S. J. and Renaud, P.: Red Sea Coral Reef Trajectories over 2
897   Decades Suggest Increasing Community Homogenization and Decline in Coral Size, PLoS ONE, 7(5), e38396,
898   doi:10.1371/journal.pone.0038396, 2012.

899   Roik, A., Roder, C., Röthig, T. and Voolstra, C. R.: Spatial and seasonal reef calcification in corals and calcareous
900   crusts in the central Red Sea, Coral Reefs, 1–13, doi:10.1007/s00338-015-1383-y, 2015.

901   Roik, A., Röthig, T., Roder, C., Ziegler, M., Kremb, S. G. and Voolstra, C. R.: Year-Long Monitoring of Physico-
902   Chemical and Biological Variables Provide a Comparative Baseline of Coral Reef Functioning in the Central Red Sea,
903   PLOS ONE, 11(11), e0163939, doi:10.1371/journal. pone.0163939, 2016.

904   Röthig, T., Ochsenkühn, M. A., Roik, A., van der Merwe, R. and Voolstra, C. R.: Long-term salinity tolerance is
905   accompanied by major restructuring of the coral bacterial microbiome, Mol. Ecol., 25(6), 1308–1323,
906   doi:10.1111/mec.13567, 2016.

907   Sawall, Y. and Al-Sofyani, A.: Biology of Red Sea Corals: Metabolism, Reproduction, Acclimatization, and
908   Adaptation, in The Red Sea, edited by N. M. A. Rasul and I. C. F. Stewart, pp. 487–509, Springer Berlin Heidelberg.
909   [online] Available from: http://link.springer.com/chapter/10.1007/978-3-662-45201-1_28 (Accessed 7 April 2015),
910   2015.

911   Sawall, Y., Al-Sofyani, A., Hohn, S., Banguera-Hinestroza, E., Voolstra, C. R. and Wahl, M.: Extensive phenotypic
912   plasticity of a Red Sea coral over a strong latitudinal temperature gradient suggests limited acclimatization potential
913   to warming, Sci. Rep., 5, 8940, doi:10.1038/srep08940, 2015.

914   Schmidt, G. M. and Richter, C.: Coral Growth and Bioerosion of *Porites lutea* in Response to Large Amplitude
915   Internal Waves, PLoS ONE, 8(12), e73236, doi:10.1371/journal.pone.0073236, 2013.

916   Schneider, K. and Erez, J.: The effect of carbonate chemistry on calcification and photosynthesis in the hermatypic
917   coral *Acropora eurystoma*, Limnol. Oceanogr., 51(3), 1284–1293, 2006.

918   Schönberg, C. H. L., Fang, J. K. H., Carreiro-Silva, M., Tribollet, A. and Wisshak, M.: Bioerosion: the other ocean
919   acidification problem, ICES J. Mar. Sci., 74(4), 895–925, doi:10.1093/icesjms/fsw254, 2017.

920   Schuhmacher, H., Loch, K., Loch, W. and See, W. R.: The aftermath of coral bleaching on a Maldivian reef—a
921   quantitative study, Facies, 51(1–4), 80–92, doi:10.1007/s10347-005-0020-6, 2005.

922   Shamberger, K. E. F., Lentz, S. J. and Cohen, A. L.: Low and variable ecosystem calcification in a coral reef lagoon
923   under natural acidification, Limnol. Oceanogr., doi:10.1002/lno.10662, 2017.

924   Shaw, E. C., McNeil, B. I. and Tilbrook, B.: Impacts of ocean acidification in naturally variable coral reef flat
925   ecosystems, J. Geophys. Res. Oceans, 117(C03038), doi:10.1029/2011JC007655, 2012.

926   Sheppard, C. and Loughland, R.: Coral mortality and recovery in response to increasing temperature in the southern
927   Arabian Gulf, Aquat. Ecosyst. Health Manag., 5(4), 395–402, doi:10.1080/14634980290002020, 2002.

928   Silbiger, N. J., Guadayol, O., Thomas, F. I. M. and Donahue, M. J.: Reefs shift from net accretion to net erosion along
929   a natural environmental gradient, Mar. Ecol. Prog. Ser., 515, 33–44, doi:10.3354/meps10999, 2014.

930 Silverman, J., Lazar, B. and Erez, J.: Community metabolism of a coral reef exposed to naturally varying dissolved
931 inorganic nutrient loads, Biogeochemistry, 84(1), 67–82, doi:10.1007/s10533-007-9075-5, 2007.

932 Steiner, Z., Erez, J., Shemesh, A., Yam, R., Katz, A. and Lazar, B.: Basin-scale estimates of pelagic and coral reef
933 calcification in the Red Sea and Western Indian Ocean, Proc. Natl. Acad. Sci., 1414323111,
934 doi:10.1073/pnas.1414323111, 2014.

935 Steiner, Z., Turchyn, A. V., Harpaz, E. and Silverman, J.: Water chemistry reveals a significant decline in coral
936 calcification rates in the southern Red Sea, Nat. Commun., 9(1), 3615, doi:10.1038/s41467-018-06030-6, 2018.

937 Strahl, J., Stolz, I., Uthicke, S., Vogel, N., Noonan, S. H. C. and Fabricius, K. E.: Physiological and ecological
938 performance differs in four coral taxa at a volcanic carbon dioxide seep, Comp. Biochem. Physiol. A. Mol. Integr.
939 Physiol., 184, 179–186, doi:10.1016/j.cbpa.2015.02.018, 2015.

940 Tambutté, S., Holcomb, M., Ferrier-Pagès, C., Reynaud, S., Tambutté, É., Zoccola, D. and Allemand, D.: Coral
941 biomineralization: From the gene to the environment, J. Exp. Mar. Biol. Ecol., 408(1–2), 58–78,
942 doi:10.1016/j.jembe.2011.07.026, 2011.

943 Tribollet, A. and Golubic, S.: Cross-shelf differences in the pattern and pace of bioerosion of experimental carbonate
944 substrates exposed for 3 years on the northern Great Barrier Reef, Australia, Coral Reefs, 24(3), 422–434,
945 doi:10.1007/s00338-005-0003-7, 2005.

946 Tribollet, A. and Golubic, S.: Reef Bioerosion: Agents and Processes, in Coral Reefs: An Ecosystem in Transition,
947 edited by Z. Dubinsky and N. Stambler, pp. 435–449, Springer Netherlands, Dordrecht. [online] Available from:
948 http://www.springerlink.com/index/10.1007/978-94-007-0114-4_25 (Accessed 7 August 2012), 2011.

949 Tribollet, A., Decherf, G., Hutchings, P. and Peyrot-Clausade, M.: Large-scale spatial variability in bioerosion of
950 experimental coral substrates on the Great Barrier Reef (Australia): importance of microborers, Coral Reefs, 21(4),
951 424–432, doi:10.1007/s00338-002-0267-0, 2002.

952 Tribollet, A., Godinot, C., Atkinson, M. and Langdon, C.: Effects of elevated pCO_2 on dissolution of coral carbonates
953 by microbial euendoliths, Glob. Biogeochem. Cycles, 23(3), doi:10.1029/2008GB003286, 2009.

954 Uthicke, S., Doyle, J., Duggan, S., Yasuda, N. and McKinnon, A. D.: Outbreak of coral-eating Crown-of-Thorns
955 creates continuous cloud of larvae over 320 km of the Great Barrier Reef, Sci. Rep., 5, doi:10.1038/srep16885, 2015.

956 Vásquez-Elizondo, R. M. and Enríquez, S.: Coralline algal physiology is more adversely affected by elevated
957 temperature than reduced pH, Sci. Rep., 6, 19030, doi:10.1038/srep19030, 2016.

958 Vecsei, A.: Fore-reef carbonate production: development of a regional census-based method and first estimates,
959 Palaeogeogr. Palaeoclimatol. Palaeoecol., 175(1–4), 185–200, doi:10.1016/S0031-0182(01)00371-6, 2001.

960 Vecsei, A.: A new estimate of global reefal carbonate production including the fore-reefs, Glob. Planet. Change, 43(1–
961 2), 1–18, doi:10.1016/j.gloplacha.2003.12.002, 2004.

962 Waldbusser, G. G., Hales, B. and Haley, B. A.: Calcium carbonate saturation state: on myths and this or that stories,
963 ICES J. Mar. Sci. J. Cons., 73(3), 563–568, doi:10.1093/icesjms/fsv174, 2016.

964 Wickham, H. and Chang, W.: ggplot2: An Implementation of the Grammar of Graphics. [online] Available from:
965 http://cran.r-project.org/web/packages/ggplot2/index.html (Accessed 25 June 2015), 2015.

966 Wiedenmann, J., D'Angelo, C., Smith, E. G., Hunt, A. N., Legiret, F.-E., Postle, A. D. and Achterberg, E. P.: Nutrient
967 enrichment can increase the susceptibility of reef corals to bleaching, Nat. Clim. Change, 3(2), 160–164,
968 doi:10.1038/nclimate1661, 2013.

969   Zundelevich, A., Lazar, B. and Ilan, M.: Chemical versus mechanical bioerosion of coral reefs by boring sponges -
970   lessons from *Pione cf. vastifica*, J. Exp. Biol., 210(1), 91–96, doi:10.1242/jeb.02627, 2007.

971

972   **Figures**

973

974   **Figure 1. Design of studies and reef sites in the central Red Sea.** Maps (a) and (b) indicate geographic location and
975   the study sites along a cross-shelf gradient. Schemes in (c) – (e) summarize the study designs for the assessment of
976   the two reef growth metrics, G_{net} and G_{budget}, and the characterization of the abiotic environments in the central Red
977   Sea. Maps have been adapted from Roik et al. (2015).

978

979   **Figure 2. Net-accretion/-erosion rates (G_{net}) in the central Red Sea.** G_{net} were measured *in situ* using limestone
980   blocks (100 x 100 mm) that were deployed along the cross-shelf gradient, three sets of blocks were deployed for 6,
981   12, or 30 months, respectively. Photos (a), (b), and (c), show freshly collected limestone blocks that were recovered
982   after 30 months deployment. The photos (d), (e), and (f) show the same blocks after bleaching and drying. Boring
983   holes of endolithic sponges are clearly visible in blocks from the nearshore and midshore reef sites. Blocks from the
984   midshore and offshore reefs are covered with crusts of biogenic carbonate mostly accreted by coralline algae
985   assemblages (scales in the photos show cm). G_{net} data obtained from the limestone block assay are plotted in (g). All
986   data are presented as mean ± standard deviation.

987

988   **Figure 3. Census-based carbonate budgets in the central Red Sea.** A schematic overview of the census-based
989   carbonate budget approach that was adapted from the *ReefBudget* methodology byPerry et al., (2012) is displayed in
990   (a). Details on input data and equations, employed in the calculations, are available as Supplementary Materials (Text
991   S1 and respective Supplemental Tables). In (b) reef carbonate budgets are plotted in dark grey (G_{budget}) and related
992   biotic variables in white. The biotic variables, i.e., site-specific calcification rates of benthic communities ($G_{benthos}$),
993   net-accretion/-erosion rates of reef "rock" surface area ($G_{netbenthos}$), and the epilithic erosion rates of echinoids and
994   parrotfishes (E_{echino}, E_{parrot}) contribute to the total reef carbonate budget (G_{budget}) at each reef site. All data are presented
995   as mean ± standard deviation. Images from www.ian.umces.edu*; photos by A.Roik.*

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997
998   **Figure 4. Abiotic conditions in the reef sites.** Temperature, salinity, and diurnal pH_{NBS} variation (= diurnal standard
999   deviations) were measured continuously over the respective seasons by CTDs (conductivity-temperature-depth
1000   loggers including an auxiliary pH probe). Furthermore, inorganic nutrients and total alkalinity (TA) were measured in
1001   discrete samples across reef sites and seasons. Boxplots illustrate the differences of seawater parameters between the
1002   reefs within each season (box: 1st and 3rd quartiles, whiskers: 1.5-fold inter-quartile range, points: raw data scatter).
1003

1004 **Tables**

1005 **Table 1. Glossary of reef growth metrics.**

Metric	Description	Input data for calculation of the metric
G_{net}	Site-specific net-accretion/-erosion rates (internal and epilithic) measured *in situ* using limestone blocks	-
*G_{budget}	Ecosystem-scale census-based carbonate budget of a reef site	$G_{benthos}$, $G_{netbenthos}$, $G_{netbenthos}$, E_{echino}, E_{parrot}
$G_{benthos}$	Census-based calcification rate of benthic calcifier community (corals and coralline algae) per reef site	Site-specific benthic calcification rates (collated from this study and from Roik et al. 2015)
$G_{netbenthos}$	Census-based net-accretion/-erosion rates of reef "rock" surface area per reef site	Site-specific net-accretion/-erosion rates measured in this study using limestone blocks (G_{net})
E_{echino}	Census-based echinoid (sea urchin) erosion rates per reef site	Genus and size specific erosion rates for sea urchins from literature
E_{parrot}	Census-based parrotfish erosion rate per reef site	Genus and size specific erosion rates for parrotfishes from literature

1006   *The method of G_{budget} calculation is described in the supplements (please refer to Text S1).
1007
1008

1009 **Table 2. Net-accretion/-erosion rates G_{net} [kg CaCO$_3$ m^{-2} y^{-1}] in coral reefs along a cross-shelf gradient in the central Red**
1010 **Sea.** G_{net} was calculated using weight gain/loss of limestone blocks that were deployed in the reefs. For each deployment duration,
1011 6, 12, and 30 months, a set of 4 replicate blocks was used. Each block was measured once. Provided are means per reef site and
1012 standard deviations (in brackets).

G_{net}	Deployment time [months]		
Reef site	6	12	30
Offshore	0.14(0.11)	0.08(0.09)	0.37(0.08)
Midshore	0.11(0.16)	0.01(0.07)	0.06(0.12)
Nearshore	0.11(0.07)	-0.61(0.49)	-0.96(0.75)

1013

1014

Table 3. Reef carbonate budgets and contributing biotic variables [kg CaCO$_3$ m^{-2} y^{-1}] along a cross-shelf gradient in the central Red Sea. Calcification rates of benthic calcifiers (G$_{benthos}$), net-accretion/-erosion rates of the reef "rock" surface area (G$_{netbenthos}$), and the erosion rates of echinoids and parrotfishes (E$_{echino}$, E$_{parrot}$) contribute to the total carbonate budget (G$_{budget}$) at a reef site. Shown are means per site are shown and standard deviations (in brackets).

Reef	G$_{budget}$	G$_{benthos}$	G$_{netbenthos}$	E$_{echino}$	E$_{parrot}$
Offshore	2.44(1.03)	2.81(0.65)	0.09(0.02)	-0.02(0)	-0.44(0.7)
Midshore	1.02(0.35)	1.76(0.24)	0.01(0)	-0.02(0.04)	-0.73(0.31)
Nearshore	-1.48(1.75)	0.43(0.15)	-0.31(0.13)	-0.23(0.19)	-1.36(1.89)

1020 **Table 4. Abiotic parameters relevant for reef growth at the study sites along a cross-shelf gradient in the central Red Sea.**
1021 Temperature (Temp), salinity (Sal), and diurnal pH variation (diurnal SDs of pH_{NBS} measurements) were continuously measured
1022 using *in situ* probes (CTDs). Weekly collected seawater samples were used for the determination of inorganic nutrient
1023 concentrations, i.e. nitrate and nitrite (NO_3^- & NO_2^-), ammonia (NH_4^+), phosphate (PO_4^{3-}), and total alkalinity (TA). Provided are
1024 means and standard deviations (in brackets).

Site / Season	Temp	Sal	Diurnal pH variation	NO_3^- & NO_2^-	NH_4^+	PO_4^{3-}	TA
	[°C]			[µmol kg⁻¹]	[µmol kg⁻¹]	[µmol kg⁻¹]	[µmol kg⁻¹]
Avg. winter	26.07(0.54)	39.18(0.18)	0.11(0.12)	0.32(0.19)	0.38(0.29)	0.08(0.02)	2487(20)
Avg. summer	30.85(0.69)	39.44(0.18)	0.05(0.05)	0.61(0.25)	0.54(0.34)	0.04(0.05)	2417(27)
Offshore / winter	25.97(0.36)	39.18(0.16)	0.04(0.02)	0.4(0.23)	0.38(0.41)	0.09(0.02)	2492(21)
Offshore / summer	30.68(0.63)	39.38(0.17)	0.04(0.04)	0.59(0.24)	0.51(0.17)	0.04(0.03)	2439(15)
Midshore / winter	26.1(0.49)	39.17(0.2)	0.07(0.04)	0.28(0.22)	0.35(0.19)	0.07(0.02)	2494(16)
Midshore / summer	30.56(0.61)	39.39(0.14)	0.05(0.05)	0.63(0.26)	0.7(0.53)	0.06(0.08)	2422(26)
Nearshore / winter	26.13(0.69)	39.2(0.17)	0.23(0.14)	0.29(0.12)	0.4(0.29)	0.07(0.01)	2476(19)
Nearshore / summer	31.32(0.59)	39.56(0.15)	0.09(0.06)	0.6(0.28)	0.42(0.16)	0.02(0.01)	2391(15)

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Table 5. Coefficients from Spearman rank order correlations for abiotic and biotic predictor variables vs. G_{net} and G_{budget}.
The means of abiotic and biotic variables per reef site were correlated with G_{net} (= net-accretion/-erosion rates of limestone blocks) and G_{budget} (= census-based carbonate budgets). Strong and significant correlations (ρ values > |0.75|) are marked in **bold**. *P*-values were adjusted by the Benjamini-Hochberg method. CCA = crustose coralline algae; CC = calcifying crusts

	G_{net}		G_{budget}	
Abiotic variables	ρ	*p*(adj.)	ρ	*p*(adj.)
Temperature	-0.47	*n.s.*	-0.52	*n.s*
Salinity	**-0.82**	*< 0.01*	**-0.82**	*0.001*
Diurnal pH variation	**-0.95**	*< 0.001*	**-0.89**	*< 0.001*
NO_3^-&NO_2^-	**0.95**	*< 0.001*	**0.89**	*< 0.001*
NH_4^+	0.47	*n.s.*	0.52	*n.s.*
PO_4^{3-}	**0.82**	*< 0.01*	**0.82**	*0.001*
TA	**0.95**	*< 0.001*	**0.89**	*< 0.001*
Biotic variables	ρ	*p*(adj.)	ρ	*p*(adj.)
% cover CCA/CC	**0.95**	*< 0.001*	**0.78**	*< 0.01*
% cover Algae/Soft coral/Sponge	0.47	*n.s.*	0.26	*n.s.*
Parrot fish abundance	**-0.95**	*< 0.001*	-0.49	*n.s.*
Echinoid abundance	0.47	n.s.	-0.54	*n.s.*
% cover branching hard corals			-0.25	*n.s.*
% cover encrusting hard corals			0.26	*n.s.*
% cover massive hard corals			0.34	*n.s.*
% cover foliose hard corals			0.50	*n.s.*
% cover Acroporidae			0.27	*n.s.*
% cover Pocilloporidae			0.51	*n.s.*
% cover Poritidae			0.45	*n.s.*
% cover hard coral			0.63	*n.s.*
Rugosity			**0.75**	*< 0.01*

1031