



Bleaching threatens positive carbonate budgets on Bahraini reefs

Reem K. AlMealla^{1,2} · Brisneve Edullantes^{1,3} · Leanne J. Hepburn¹

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Abstract

Bleaching events impact coral reef functionality and carbonate budget dynamics, which is reflected in reduced reef framework accretion, hindering reef ability to keep pace with sea-level rise projections. Reefs in the Arabian Gulf exist in harsh environmental conditions with seasonal temperatures ranging between 16 and 36 °C. Despite the high thermal thresholds (~35 °C) of corals in this region, extensive bleaching and high coral mortality have been reported regionally in 2017. We quantify reef carbonate budgets at a near shore and an offshore reef site in Bahrain pre-bleaching in May 2017 and post-bleaching in May 2018 to assess the impacts of the 2017 severe bleaching event on the budgetary state. Results indicate an overall decrease in hard coral cover from 14.2 ± 5.5 to $8.5 \pm 1.4\%$ and a decline in the net carbonate budget state from 3.6 ± 2.2 to 0.3 ± 0.3 kg $\text{CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ at the shallow nearshore Fasht Al Adhm reef indicating a shift from a positive budgetary state to net neutral, while the deeper offshore Reef Bul Thamah has increased positively from 3.7 ± 1.2 to 4.2 ± 0.6 kg $\text{CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$. We attribute the decline in the nearshore reef to the bleaching event which took place between July and October 2017, resulting in high coral mortality rates and subsequent reduced framework carbonate production. Predicted warming trends present a threat to the structural integrity of shallow Bahraini reefs, compromising their ability to keep pace with future sea-level rise projections.

Keywords Accretional health · Reef carbonate budgets · Climate change · Coral bleaching · Arabian Gulf · Thermal history

Introduction

Coral reefs are experiencing rapid change on a global scale as a result of climate-induced disturbances (e.g., ocean warming and acidification; Anthony et al. 2008; Hughes et al. 2017a, b) coupled with local pressures, such as overfishing and declining water quality due to nutrient runoffs and excessive sedimentation (Hughes et al. 2003; Ove Hoegh-Guldberg 2011; de Bakker et al. 2019). These changes include loss of coral cover resulting in modification of the 3-D framework of reefs which in turn compromises

their structural integrity (Perry and Morgan 2017) and loss of architectural complexity such as that described in the Caribbean by Alvarez-Filip et al. (2009). Changes in the functionality of reef associated fish have also been documented and strong negative effects of coral loss were noted on the individual abundance of coral reef fish (Pratchett et al. 2011) with many reefs showing shifts in coral and associated species community composition (Hoey et al. 2016; Ryan et al. 2019).

In Bahrain which is situated in the Arabian Gulf (AG), coral reef areas (locally known as “fashts”) occupy a total area of 850 km², which is larger than the land area of Bahrain with Fasht Al Adhm itself covering 200 km² and mostly restricted to the east and north of the main island (Burt et al. 2013). In the 1980s, 30 coral species were recorded in Bahrain with *Acropora* dominating communities in shallow (<5 m) habitats, while *Poritids* and *Faviids* dominated the deeper (<20 m) habitats (Alkhuzai et al. 2009); however, prior to this, little information is available on corals reefs in Bahrain (Sheppard 1988; Vousden 1988, 1995; Burt et al. 2013). In 1988, dense coral cover of 50–90% dominated by *Acropora* was reported on Bahraini reefs (Sheppard 1988;

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✉ Reem K. AlMealla
reem@nuwat.org

¹ School of Life Sciences, University of Essex, Colchester, UK

² Nuwat for Environmental Research and Education, Al Jasrah, Kingdom of Bahrain

³ Department of Biology and Environmental Science, College of Science, University of Philippines Cebu, Lahug, 6000 Cebu, Philippines

Vousden 1988, 1995); however, just a few years later, reports documented an estimated loss of > 90% of coral cover (Wilkinson 1998; Uwate and Shams 1999). This loss was linked to mass bleaching events in 1996 and 1998 when temperatures reached 37.7 °C and 38 °C, respectively, making Bahrain the worst affected AG country by these bleaching events (Uwate and Shams 1999; Rezai et al. 2004; Al-kuwari 2006).

Reef accretion is essential to reef survival in the face of rising sea levels (Perry et al. 2015, 2018a, b) and there are concerns around the ability of reefs to maintain their 3-D structural framework, which underpins the ecological functioning of coral reefs and the services they provide through continuous accumulation of calcium carbonate (CaCO₃) (Graham and Nash 2013; Kennedy et al. 2013; Yanovski et al. 2017; Perry et al. 2018a).

Carbonate budgets measure the balance between CaCO₃ production and erosion and allow estimation of reef accretion rates. Detecting changes in budget states can inform reef functionality change and/or stressors; it is therefore important to understand the magnitude of changes in reef carbonate budgets through time, between regions or following disturbances.

CaCO₃ is precipitated by primary (hermatypic corals; Stearn and Scoffin 1977; Hubbard 1986; Hubbard et al. 1986; Perry and Hepburn 2008) and secondary reef builders (calcareous encrusters, e.g., coralline algae, Goreau 1963; Choi and Ginsburg 1983; Hepburn et al. 2015), which, together with incorporation of carbonate sediment into the reef framework, lead to carbonate accumulation. Bioerosion is the counter process and is driven by a diverse range of taxa including parrotfish, urchins, bioeroding sponges, and other macro- and micro-endolithic taxa.

Sea surface temperatures (SST) have been documented to increase globally, with records reporting an average rise of 1.0 °C between 1951 and 2015 (i.e., 0.15 °C/decade) in the Indian Ocean (Roxy et al. 2020), while the South Pacific and Western South Atlantic are reported to have experienced a rise in SST of ~0.4 °C/decade (Risaro et al. 2022). Short-term temperature anomalies (i.e., marine heat waves) are increasing and have been shown to cause coral bleaching and mortality (Berkelmans and Oliver 1999; Baker et al. 2004; Hughes et al. 2017a, b). An increase in temperature anomaly above a coral's local tolerance level by 1–2 °C is sufficient to cause bleaching (Hoegh-Guldberg 1999; Purkis and Riegl 2005; Heron et al. 2016; Hoegh-Guldberg et al. 2017), negatively impacting carbonate budgets and reef capacity to sustain framework development and vertical growth (Januchowski-Hartley et al. 2017; Perry and Morgan 2017).

In the AG, corals are subjected to large and unique seasonal variations in temperatures (16–36 °C) (Coles and Riegl 2013; Hume et al. 2013). In the last 2 decades, reefs in this region have been exposed to severe temperature anomalies

(~2 °C above the average daily temperature in the summer) at a frequent and highly recurring rate (Riegl 2002; Sheppard and Loughland 2002; Burt et al. 2012), similar to those projected (1.5–2 °C above pre-industrial levels) to occur globally by 2100 (IPCC 2014). Due to their extreme tolerances to seasonal temperature changes, coral communities in AG have the highest bleaching threshold (i.e., 35 °C) globally (Rezai et al. 2004; Riegl et al. 2012; Kavousi et al. 2014; Shuail et al. 2016). However, despite their high threshold, they are still susceptible to bleaching and it is reported that 70% of original AG reef cover (i.e., 3800 km²) may be considered to have suffered bleaching-related mortality, and a further 27% threatened or at critical stages of degradation with declines linked to major bleaching events, e.g., 1998 (Wilkinson 2008; van Lavieren et al. 2011). In recent years, one-third of the world's coral reefs experienced huge losses due to the 2016 heat wave (Schiermeier 2018), whereas the AG reefs experienced a 1-year (2017) delay which resulted in severe mortality (Burt et al. 2019; Paparella et al. 2019). Over the past decades, efforts have been made to calculate reef carbonate budgets (Stearn and Scoffin 1977; Hutchings and Bamber 1985; Holmes et al. 2000; Hepburn 2006; Mallega and Perry 2007; Browne 2011). Bleaching-associated declines in reef carbonate budgets have been found in the central Indian ocean (Perry et al. 2014; Januchowski-Hartley et al. 2017; Perry and Morgan 2017; Lange and Perry 2019); however, no previous attempt has been made to assess reef carbonate budgets in the AG. Therefore, this paper will examine a nearshore and an offshore reef in Bahrain both pre- and post-the 2017-bleaching event with the aim to characterize the benthic composition of carbonate producers and eroders, quantify reef carbonate budgets, and report on the impacts on budgetary states caused by the 2017 warming event.

Materials and methods

Site description

Bahrain is an archipelago of 33 low-lying islands (Fig. 1) and its coral reefs were among the most extensive in the southern basin of the Arabian Gulf (Riegl 2003; Purkis and Riegl 2005; Kavousi et al. 2014). However, in the last 4 decades, these reefs have undergone significant decline in coral cover due to large-scale coastal development in pursuit of socio-economic growth. This has added 13% to the Kingdom's total land area between 1961 (690 km²) and 2021 (780 km²) (World Bank 2021).

To understand the thermal profile experienced on Bahraini reefs, we analyzed the time series weekly SST mean for the period 1982–2017 and the degree heating weeks (DHW) and thermal stress anomaly (TSA), giving an

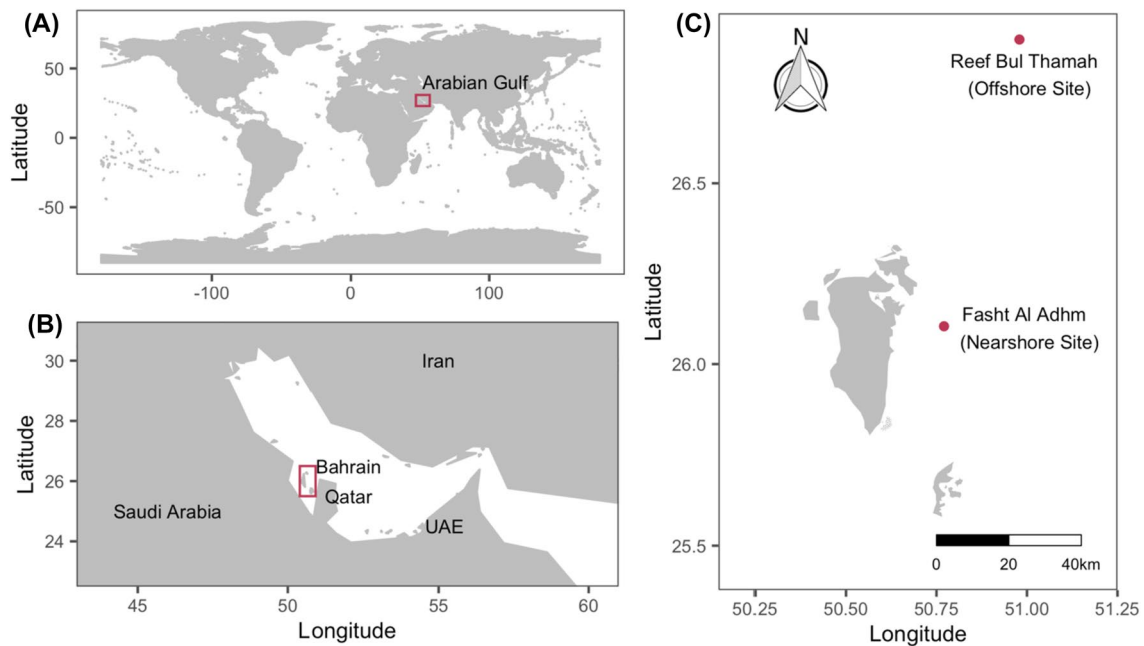


Fig. 1 Location of study sites: **A** location of Arabian Gulf (AG); **B** location of Bahrain within AG; **C** location of selected study sites within Bahrain-Fasht Al Adhm (Nearshore) and Reef Bul Thamah

(Offshore). Shapefiles were created using google earth, while all maps were created using R

indication of the delineation between coral bleaching and mortality levels. Data were derived from CoRTAD version 6 database (Fig. 2; refer to supplementary material for method of acquisition and processing in addition to definition and calculation methods of SST thermal history metrics).

In subsequent years following the 1998 bleaching episode, recovery of Bahraini reefs was observed to be limited, (Lough 2000; Uwate et al. 2000) with reports observing the reefs to be dominated by rock (66.9%) and sand (30.6%) with low coral cover (0.6%) in Fasht Al Adhm and no observations of the formerly dominant *Acropora* (Uwate et al. 2000).

For the purpose of this study, two reefs in Bahrain were investigated in April/May 2017 (pre-bleaching) and 2018 (post-bleaching; Fig. 1c) comparing a nearshore site at Fasht Al Adhm (Site Nearshore, 5–7 m depth, turbid conditions) and an offshore site at Reef Bul Thamah (Site Offshore, 10–12 m, clear conditions). Table 1 provides details of the environmental characteristics of each site. Surveying depths differ due to natural topography of the sites; Site Nearshore is a gently sloping shallow reef, with a maximum depth of 7 m and minimal relief due to the site being relatively homogenous and lacking more typical reef structural complexity. Site Offshore is also relatively homogenous, with a gentle slope starting at 10 m and continuing to 12 m where Pleistocene bedrock continues to a depth of 18 m, after which the substrate becomes patchier with sand and bedrock formations as it slopes off into the

deep (> 50 m). Due to limitations related to access to sites, time, and funding constrains, only two sites could be studied over the 2 years.

Results derived from the CoRTAD dataset illustrated that over the 35 years (1982–2017), the minimum SST experienced by Site Nearshore and Site Offshore were 15.5 °C and 16.5 °C, respectively, while the maximum SST was 37.0 °C at Site Nearshore and 36.2 °C at Site Offshore. The annual mean temperature at Site Nearshore was 26.0 ± 0.1 °C and Site Offshore was 26.2 ± 0.1 °C. Trends in the accumulated thermal stress [expressed as degree heating weeks (DHW)] shows that prior to the 1998 bleaching event, all DHWs were constantly lower than 4 °C-weeks. However, since 1998, DHWs were recorded to reach ≥ 8 °C-weeks with an exception observed in 1998 and 2017 where DHW reached ≥ 15 °C-weeks (Fig. 2). In addition, the bleaching threshold at Site Nearshore was calculated to be 34.5 °C and 34.1 °C at Site Offshore. It is important to note that these values were calculated based on the thermal stress metrics obtained from satellite data instead of in situ measurements. Given this, the 2017-bleaching event experienced on the reefs in Bahrain is expected to have taken place between July and October 2017 where temperatures exceeded 34 °C for ≥ 15 °C-weeks (Fig. 2). The surveys for this study were undertaken in April/May 2017 (pre-bleaching) and 2018 (post-bleaching).

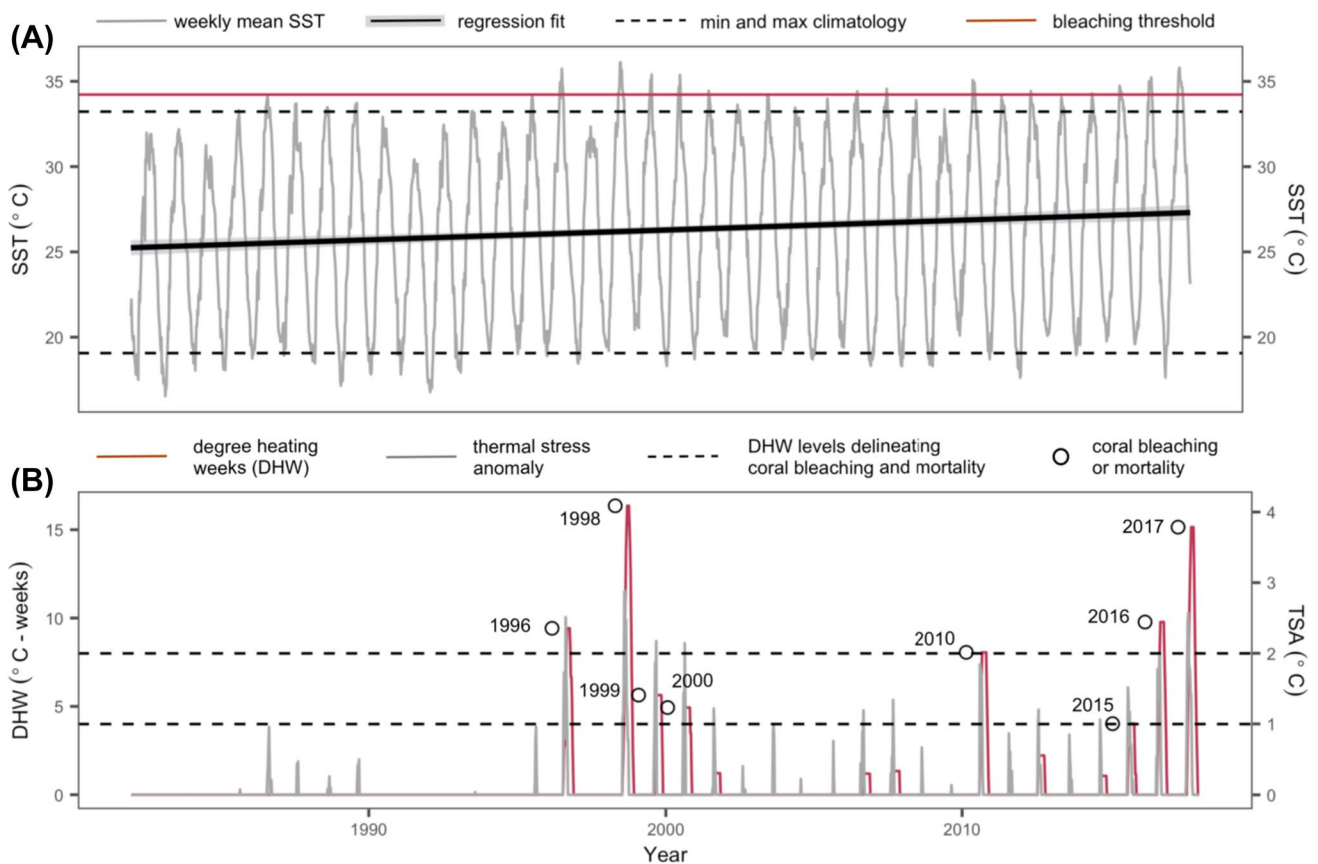


Fig. 2 **A** Time series weekly SST mean for the period (1982–2017; $n=1878$) illustrating the change in SST across the two study sites in Bahrain. The blue and red dotted lines indicate the minimum and maximum climatology (defined here as the long-term mean of SST conditions). Positive or negative values of SST exceed long-term mean SST (climatology) of a particular area, which indicates whether SST is warmer or cooler than usual (Heron et al. 2016), respectively, while the red solid line indicates the bleaching threshold. The blue solid line indicates the linear fit with standard error of the regression in dark gray shading. **B** Degree heating weeks (DHW; in red solid lines) defined as of accumulated daily hotspots over 12 consecutive weeks when the thermal stress anomaly (TSA; in black solid lines)

is ≥ 1 °C. The gray dotted lines indicate the DHW values of 4 and 8 °C-weeks, which corresponds to delineation between coral bleaching and mortality levels. Years that correspond to coral bleaching and mortality were highlighted in blue and red fonts, respectively. Data were derived from the CoRTAD version 6 database (Coral Reef Temperature Anomaly Database (CoRTAD) which is a dataset of SST and related thermal stress metrics, developed by NOAA specifically for coral reef ecosystem applications. The CoRTAD Version 6 database used in this study contains global ~4 km resolution SST data on a weekly time scale for the period 1982–2017. <ftp://ftp.nodc.noaa.gov/pub/data.nodc/cortad/README.html>)

Quantifying carbonate budget states

Gross carbonate production and erosion rates were calculated to determine net carbonate production ($\text{kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ hereafter expressed as G , while \pm represents the SE of all values stated) using the international standardised census-based *ReefBudget* methodology (Indo-Pacific version) (Perry et al. 2018a, b) hereafter referred to as *ReefBudget* methodology. The natural reef topography in Bahrain is gently sloping (< 2 m), and thus, all transects were conducted on the bottom flat of the reef at a depth of ~5–7 m at Site Nearshore and ~10 m at Site Offshore.

At each site, data were collected along 6×10 m replicate transects laid parallel to each other with a spacing of 5 m between each transect both in 2017 and 2018. Data were

collected from each transect to assess benthic substrate composition, surface rugosity, eroder populations, specifically echinoid, scaridae, and macro- and microbioeroders as per the *ReefBudget* methodology outlined in Perry et al. (2018a, b) (Table 2). Benthic substrate composition was recorded using the LIT method where each benthic component present directly under the transect line was recorded along with its linear length, while rugosity was calculated from the total surface distance for each linear 1 m of reef using a flexi-tape.

Quantifying carbonate production

Primary carbonate producers To calculate carbonate production rates, primary producers (Scleractinian coral colonies) when encountered beneath the transect line were:

Table 1 Site description and characterization of study sites in Bahrain, Arabian Gulf

Site	Site code	Depth (m)	Temp (°C)	Salinity (ppt)	Sedimentation rates (mg cm ⁻² day ⁻¹) ^a	Light attenuation (K_d PAR) ^b	Distance	Impacts
Fasht Al Adhm	Nearshore	5–7	20–36	42–44	0.23 ± 0.04	0.02 ± 0.04	~11 km east of the main island	Heavily impacted due to anthropogenic activities mainly reclamation and dredging
Reef Bul Thamah	Offshore	10–12			0.19 ± 0.04	0.04 ± 0.07	~80 km northeast of the main island	Although located within a Marine Protected National Park (MPA), the site is subjected to illegal and destructive fishing practices

^aDue to time restrictions, sediment traps ($n=6$) were deployed for a period of 3 days at each site in May 2018, although robust data on sedimentation rates is unavailable for these sites, local knowledge was used to gain insights as to the nature of the sites

^bData were logged using a hobologger (Model: UA-002-64) at a 1-min interval at two depths (Offshore=5 m and 10 m; Nearshore=3 m and 7 m) over 5 days. Units were converted from Lux to $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (as per Long et al. 2012) for light attenuation coefficients (K_d (PAR), m^{-1})

Table 2 Details of carbonate budget components and number of replicates at each study site conducted in 2017 and 2018 in Bahrain, Arabian Gulf

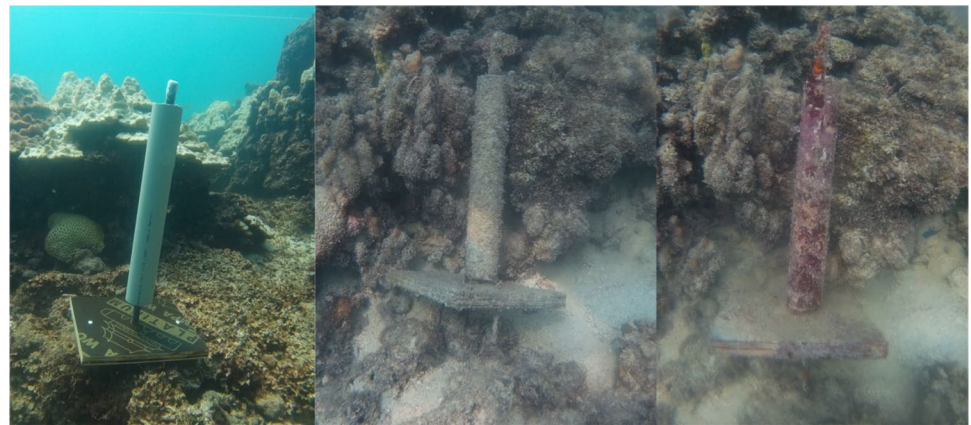
Carbonate budget component	Variable	Number of transects	Length of transect (m)
Carbonate production rate	Benthic composition assessment	6	10
	Rugosity	6	10
	Carbonate producers	6	10
Carbonate erosion rate	Echinoids (Urchins)	6	10
	Scaridae (Parrotfish)	3 (in 2017) and 6 (in 2018)	30
	Macroborers	6	10
	Microborers	6	10

(a) identified to genus level, e.g., *Porites* spp., (b) measured for colony size [calculated based on linear coverage (length × width) using a flexi-tape and categorized based on morphology]. Although the *Reefbudget* methodology advises that 3D coral colony measurements should be used for more accurate colony measurements, 2D colony measurements were taken for this study due to field limitations both terms of time and human resources. To date, there are no published growth rates or skeletal densities for corals in the Arabian Gulf, with the exception of two species (*Platygyra daedalea* and *Cyphastrea microphthalma*) (Howells et al. 2018). Therefore, coral growth rates and skeletal density data used in this study were those provided in the open source “Indo-Pacific data entry spreadsheets” of the *ReefBudget* methodology which are derived from published literature. The data were then inserted in the spreadsheets that have been set up with standardized *Reefbudget* equations that automatically calculate the carbonate production

rates for each transect. Datasheets can be downloaded for use through: <https://geography.exeter.ac.uk/reefbudget/>

Secondary carbonate producers Secondary carbonate production rates were quantified based on the weight per unit area derived using six PVC pipes which were deployed in September 2017 for a period of 1 year at each study site measuring 35 cm × 16 cm (length × circumference of the pipe; Fig. 3). Following the 1-year period, pipes were photographed underwater, placed in a plastic bag secured with cable ties over the upper part of the pipe for removal. All pipes were successfully retrieved using the *ReefBudget* methodology from Site Nearshore ($n=6$); however, only one out of six pipes was found and retrieved at Site Offshore. Evidence of illegal destructive fishing practices, including trawling was witnessed at the site which could have resulted in the displacement and loss of the other pipes. Once in the lab, pipes were examined and photographed in detail fol-

Fig. 3 CaCO₃ production by secondary carbonate producers over a 1-year period on PVC pipes deployed at Nearshore (Fasht Al Adhm). NB: exposed=high light, cryptic=low light



September 2017

September 2018 (Exposed Side)

September 2018 (Cryptic Side)

lowing which they were placed in 10% sodium hypochlorite (bleach) for 36 h. Once removed from the bleach, the pipes were left to dry after which, they were weighed three times. The pipes were then soaked in 10% HCl for another 36 h. Once all the calcium carbonate was dissolved, the pipes were taken out and weighed for a second time (in replicates of three). This allowed for a weight per unit area to be derived. To calculate secondary carbonate production, the weight per unit area previously derived through the 1-year experiment was inserted in the *Reefbudget* calculation spreadsheets in the growth rates column thereby automatically including it in the overall production budget calculation. The *Reefbudget* methodology uses locally derived data on the rate of total secondary carbonate production in addition to the data on available substrate for secondary producers (e.g., CCA) recorded by the benthic transects (Perry et al. 2018a, b).

Quantifying carbonate erosion

For calculating carbonate erosion rates, species, density, and size class measurements were recorded for grazers, such as echinoids (urchins) and Scaridae (parrotfish) along the belt transect area.

- *Echinoids*: The area surveyed along each of the six transects was 1 m on either side of the 10 m transect line covering a total of 20 m² per transect (10 m length × 2 m width). The number of individuals along each transect was counted, identified to species level and recorded in the following size class which is the width of the echinoid without the spines: 0–20 mm, 21–40 mm, 41–60 mm, 61–80 mm, and 81–100 mm. Data were then inputted into the *Reefbudget* calculation spreadsheets which automatically calculates the carbonate erosion rate of echinoids based on species level.
- *Scaridae*: The area surveyed along each of the transects (3 replicates in 2017 and 6 replicates in 2018) was 4 m

in width of the 30 m transect line covering a total of 120 m² per transect (30 m length × 4 m width). The number of individuals encountered along each transect were counted, identified to species level and recorded in the following size class based on total length: 5–10 cm, 11–20 cm, 21–30 cm 31–40 cm, and > 40 cm along with their life phase (i.e., juvenile or adult). Biomass of parrotfish was calculated using published species-specific length–weight relationships as provided by the *Reefbudget* calculation spreadsheets where the data were inputted for carbonate erosion rate contributed by parrotfish.

- *Macroborers*: The *Reefbudget* (Indo-Pacific version) defines macroborers as those that produce boreholes with diameters of > 1 mm. These include endolithic sponges, bivalves, decapods, polychaete and sipunculid worms, and cirripeds, of these, sponges dominate the macroborer community, comprising 75–90% by proportion of substrate infestation (Perry et al. 2018). In general, the macroborer community is less characterized than that of the Caribbean in both the Indian and Pacific Oceans, many bioeroders especially clionaid sponges are cryptic in general making their identification difficult on the field. In addition, macroerosion measurements tend to rely on deploying of experimental substrates (e.g., coral blocks) and/or using X-rays or CT scans to estimate internal rates of bioerosion using cored or slabbed corals (Perry et al. 2018a, b). Therefore, the *Reefbudget* methodology uses published rates of the total macrobioerosion with data on available substrate for bioerosion (including dead carbonate substrate and live coral colonies) derived from the benthic transects (Perry et al. 2018a, b). Thus, macrobioerosion rates are automatically calculated in the *Reefbudget* calculation spreadsheets using the benthic substrate data.
- *Microborers*: Endolithic microborers such as cyanobacteria, chlorophytes, and fungi are able to exist inside car-

bonate substrates. Similar to macrobioerosion, the assessment of microbioerosion rates tend to rely on deploying of experimental substrates (Chazottes et al. 1995; Tribollet and Golubic 2005). The *Reefbudget* methodology acknowledges data scarcity on microbioerosion processes and despite the challenges in measuring microbioerosion on the field, it recognizes that microborers can have the potential to contribute to bioerosion on reefs in a non-negligible amount. Thus, since published rates on microbioerosion are within similar ranges to those of macroborers, the rates are automatically calculated in the *Reefbudget* calculation spreadsheets using the benthic substrate data.

Data analysis

Data processing, analysis, and visualization were conducted in the software “R” and “RStudio” version 3.5.1 (R Core Team 2018) utilizing the following R packages: ggplot (Hothorn et al. 2008), tidyverse (Wickham et al. 2019), stats package (R Core Team 2021), and multcomp package (Hothorn et al. 2008). Mean \pm standard error (SE) is stated throughout along with the median (md) values for primary producers, gross carbonate production, and gross carbonate erosion. Using the glm function in stats package, generalized linear models (GLMs) were used to test the effects of bleaching events on the percentage cover of carbonate producers (i.e., hard coral cover and CCA), rugosity, density of eroders (i.e., Scaridae and echinoids), gross carbonate production, gross carbonate erosion, and net carbonate production at both sites (Supplementary Tables 1 and 2). Likelihood ratio tests (LRT) were conducted to analyze the deviance between null and alternative models to determine the effect of the interaction between bleaching events and sites on the observations using the anova function in the stats package (Supplementary Table 3). The interaction term was included in the model if LRT was found to be significant. Post hoc comparison tests were implemented using the glht function in the multcomp package (Hothorn et al. 2008) with all significant test results reported in the text and additional results presented in Supplementary Table 4.

Results

Site characterization

Carbonate producers

Dominant hard corals recorded at both sites included *Platygyra* spp., *Favia* spp., and *Porites* spp., all of which were either massive, sub-massive, or encrusting with no branching corals observed at any of the study sites either year

(with the exception of one colony of *Pocillopora* sp. seen in 2017 at Site Nearshore). Hard coral cover declined from $13.6 \pm 7.0\%$, pre-bleaching to $1.4 \pm 0.6\%$, post-bleaching at Site Nearshore, while Site Offshore maintained its coral cover (pre-bleaching = $14.8 \pm 4.1\%$, $n = 6$; post-bleaching = $15.5 \pm 2.2\%$); however, no significant difference was observed between sites in 2017 (Site Nearshore: GLM, $z = -2.1$, $p > 0.05$; Site Offshore: GLM, $z = 0.1$, $p > 0.05$) (Figs. 4, 5 and 6a). No branching coral colonies were observed at either study site in 2018 and no change in the coral community was observed as the dominant coral groups remain to be either massive, sub-massive, or encrusting.

CCA cover was dominant at Site Nearshore pre-bleaching (mean = $42.2 \pm 12.9\%$, md = 38.9); however, this declined significantly to $13.2 \pm 3.5\%$, md = 14.5 (GLM, $z = -2.7$, $p < 0.05$) post-bleaching (Figs. 5 and 6b). CCA was also observed to decline at Site Offshore post-bleaching (pre-bleaching = $10.1 \pm 7.0\%$, md = 4.2; post-bleaching = $1.73 \pm 0.4\%$, md = 1.8) but was statistically non-significant (Fig. 6b—Supplementary Material, Table 4). No change in reef rugosity was noted in Site Offshore (pre-bleaching = 1.8 ± 0.14 ; post-bleaching = 1.7 ± 0.04), while a decline in rugosity was noted in Site Nearshore (pre-bleaching = 1.7 ± 0.17 ; post-bleaching = 1.4 ± 0.05). The largest dominating benthic group at Site Offshore was algae, including turf algae (pre-bleaching = $25.5 \pm 7.6\%$, post-bleaching = $34.4 \pm 6.6\%$) and macroalgae (mainly *Halimeda* sp. and *Padina* sp.; pre-bleaching = $19.6 \pm 3.5\%$; post-bleaching = $23.4 \pm 2.1\%$) (Fig. 5). At Site Nearshore, macroalgae (mainly *Halimeda* sp.; pre-bleaching = $2.7 \pm 1.5\%$, post-bleaching = $3.6 \pm 1.7\%$) was seen to be low in comparison to Site Offshore in both years. However, turf algae was higher at Site Nearshore with an increase of 50% post-bleaching (pre-bleaching = $31.5 \pm 14.2\%$, post-bleaching = $63.1 \pm 6.0\%$) (Fig. 5). The remaining benthic substrate for both Site Nearshore and Site Offshore was composed of sand, rubble, sponge, soft coral, and other (e.g., other calcareous encrusters and ascidians) (Fig. 5).

Carbonate eroders

At Site Nearshore, echinoid densities were higher pre-bleaching (25.0 ± 6.4 individuals per 20 m^2) than post-bleaching (8.0 ± 2.5 individuals per 20 m^2) with a significant reduction of 68% (GLM, $z = 3.6$, $p < 0.01$) (Fig. 6c), but echinoids were observed to be larger post-bleaching, i.e., pre-bleaching: size class = 41–60 mm and 61–80 mm; post-bleaching: size class = 61–80 mm and 81–100 mm. *Echinometra mathei* (short-spined urchin) was the only species of echinoid recorded along the transects at Site Nearshore throughout the study period and no parrotfish were observed either pre- or post-bleaching (Fig. 6d). At Site Offshore, no echinoids were observed; however, parrotfish of the species



Fig. 4 Example photographs of reefscape pre- and post-bleaching at **A** Fasht Al Adhm (Site Nearshore) and **B** Reef Bul Thamah (Site Offshore), Bahrain. NB: Photos were taken in September, 2017 while the

bleaching period is estimated to have taken place from July to October 2017 based on satellite data derived from the CORTAD version 6 database

Fig. 5 Mean percentage cover (%) of the reef benthic community structure pre (2017) and post (2018) bleaching at Site Nearshore and Site Offshore ($n=6$), Bahrain

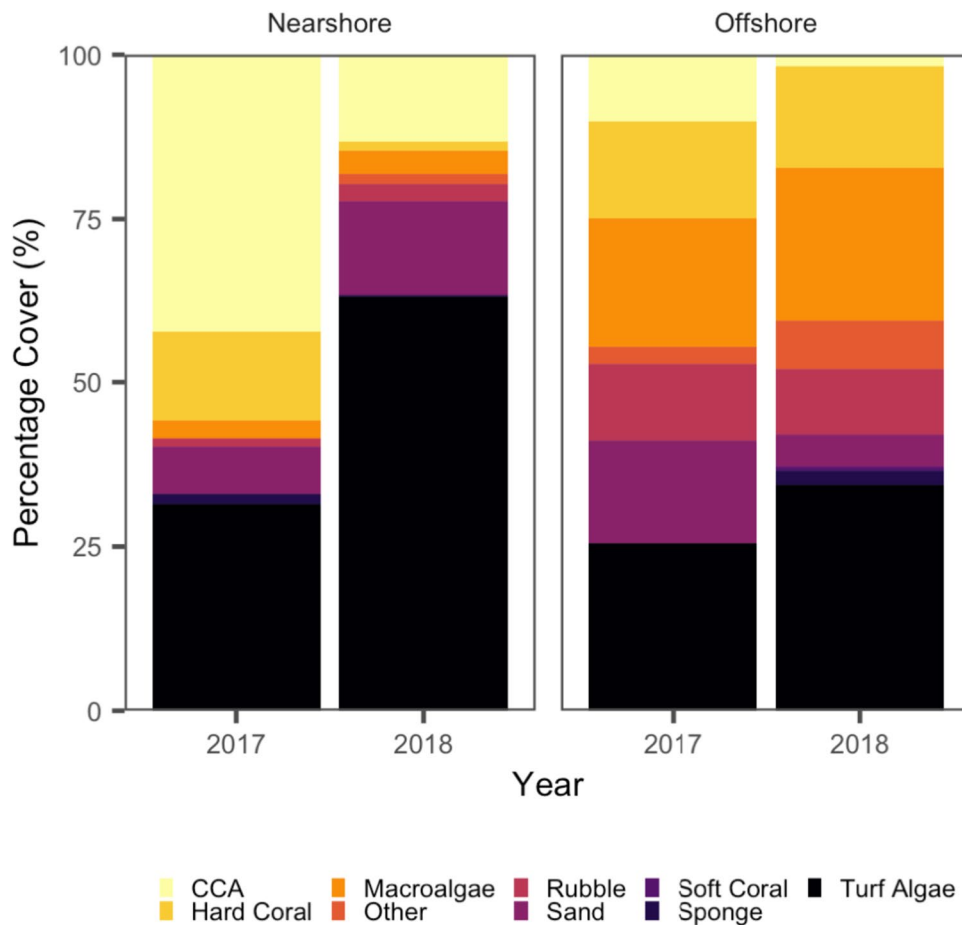
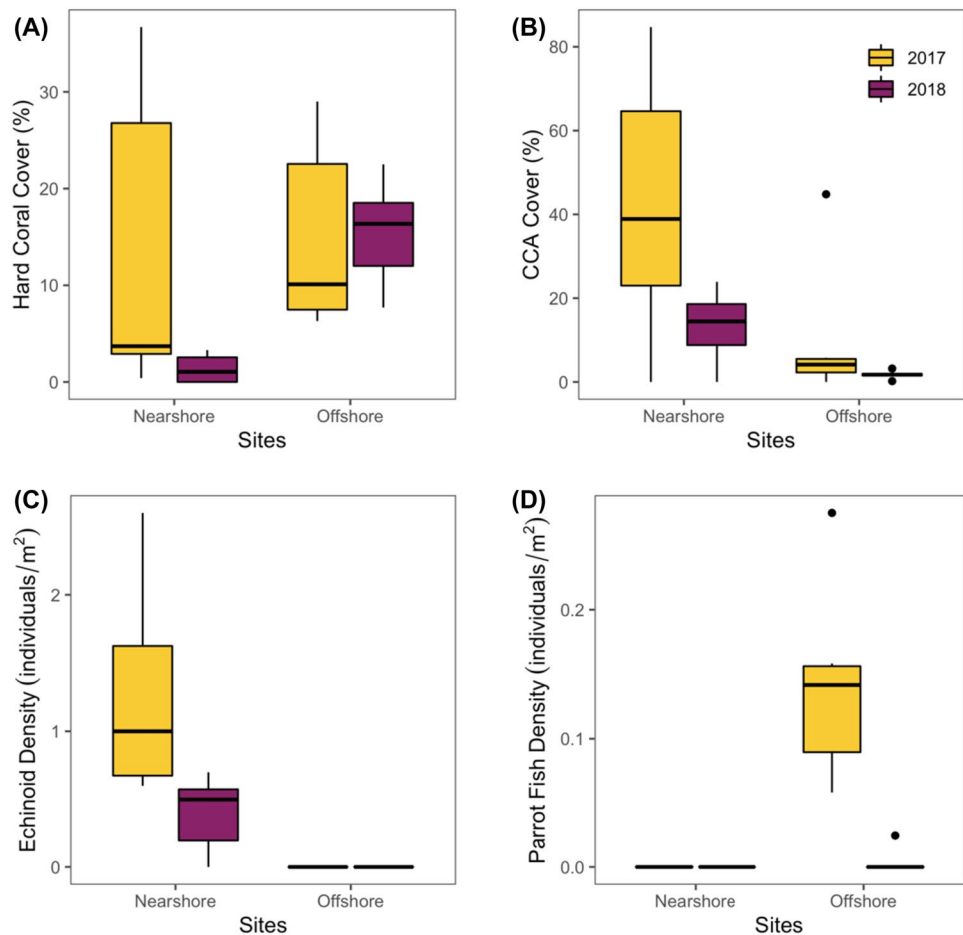


Fig. 6 Percentage cover of carbonate producers in 2017 and 2018: **A** Hard corals ($n=6$) and **B** CCA = crustose coralline algae ($n=6$); density (count per unit m^2) of carbonate eroders: **C** Echinoids ($n=6$; area = $20 m^2$ per transect; Nearshore) and **D** Scaridae ($n=3$; area = $120 m^2$ per transect) at Site Nearshore and Site Offshore, Bahrain



Chlorurus sordidus, *Scarus ghobban*, and *Scarus persicus* were recorded pre-bleaching (17.0 ± 3.8 individuals per $120 m^2$), which were mainly scrapers in their initial phase of life; contrastingly, very few individuals were observed post-bleaching (1.0 ± 0.5 individuals per $120 m^2$) (Fig. 6d).

Carbonate budgetary state|pre- and post-bleaching (2017–2018)

Gross carbonate production rates decreased at Site Nearshore from 4.1 ± 2.3 G pre-bleaching to 0.5 ± 0.2 G post-bleaching, whereas Site Offshore maintained its gross carbonate production (pre-bleaching = 4.0 ± 1.1 G; post-bleaching = 4.2 ± 0.6 G) (Fig. 7a). No significant differences in gross carbonate production rates were detected in both Site Nearshore (GLM, $z = -1.9$, $p > 0.01$) and Site Offshore (GLM, $z = 0.1$, $p > 0.01$). In addition, the calcification rate for secondary producers derived from the 1-year experiment was $0.027 g cm^2 year^{-1}$ at Site Nearshore. In terms of gross carbonate erosion, Site Nearshore had a higher rate of gross erosion with 0.5 ± 0.1 G pre-bleaching which was seen to significantly decrease to 0.2 ± 0.1 G post-bleaching (GLM, $z = -3.4$, $p < 0.01$)

(Fig. 7 (b)). The majority of erosion at Site Nearshore is dominated by echinoids with negligible contribution by macroborers, while at Site Offshore, erosion was dominated by parrotfish which was observed to be minimal especially post-bleaching (Supplementary Table 5). Site Offshore did experience a decline in gross carbonate erosion from the pre-bleaching value of 0.3 ± 0.1 G to post-bleaching value of 0.01 ± 0.01 G (GLM, $z = -3.0$, $p < 0.01$) (Fig. 7 (b)).

Overall, a decrease in the net carbonate production rates was recorded on Site Nearshore, while Site Offshore reported an increase. Specifically, Site Nearshore showed a decline in net carbonate production rate following the 2017-bleaching (pre = 3.6 ± 2.2 ; post = 0.3 ± 0.3 G) indicating a shift from a positive budget state to a nearly a net neutral budget state (Fig. 7c). Contrastingly, Site Offshore documented an increase in its net carbonate production from 3.7 ± 1.2 to 4.2 ± 0.6 G, therefore maintaining its positive budgetary state. Both sites did not experience significant differences in net carbonate production rates (Site Nearshore: GLM, $z = -1.8$, $p > 0.01$); Site Offshore: GLM, $z = 0.3$, $p > 0.01$).

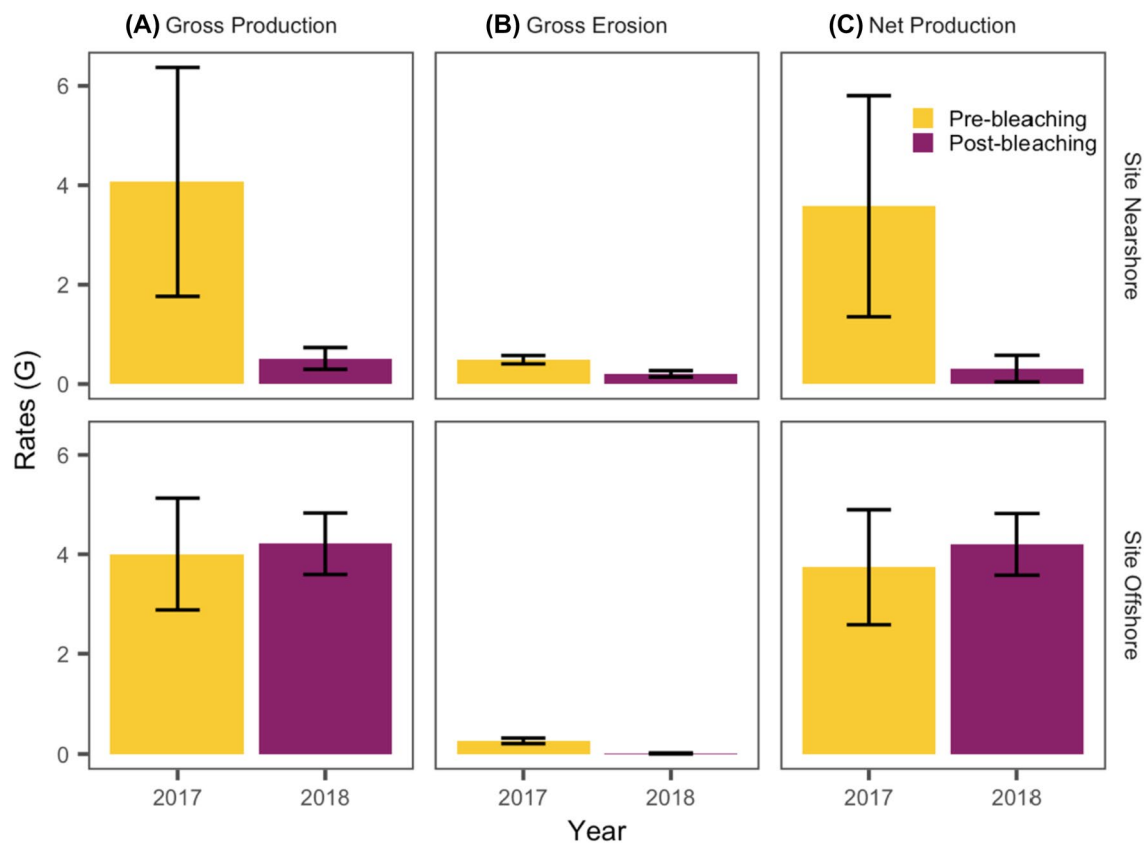


Fig. 7 Reef carbonate budget rates ($\text{kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ expressed as G) across study sites Nearshore and Offshore pre- and post-2017 bleaching illustrating: **A** gross carbonate production; **B** gross carbonate erosion; **C** net carbonate production, Bahrain

Discussion

This study quantified carbonate budgets for two reefs in Bahrain. Here, we report on the impacts observed on the budgetary state of these reefs as a result of the 2017 warming event, which is the most intense bleaching event experienced by these reefs since 1998.

Carbonate production

Hard coral (primary reef producers) cover declined at Site Nearshore between 2017 and 2018. In 2012, it was reported that the live coral coverage at this site averaged 9.8% (Burt et al. 2013). Our results from 2017 indicated that this reef had recovered somewhat between 2010 and 2017, with coral cover at $13.6 \pm 6.9\%$ despite facing two bleaching events in that duration. Our observations are in line with what has been reported in the latest Global Coral Reef Monitoring Network (GCRMN) report (2020) which states that live coral in AG has experienced a decline from 30.1 to 18.0% between 1997 and 2002, followed by a period of recovery (2002–2015) when coral cover recovered to 30.2%, almost comparable to the pre-bleaching period. Although there

are not much published data which is exclusive or directly focused on the impacts of the bleaching events between 2010 and 2017, consequences of bleaching on reefs in the North of the AG have been reported by Kavousi et al. (2021) where coral mortality between 81 and 100% was experienced due to consecutive bleaching (2014–2017), while the south of the AG experienced a loss of 73% of coral cover in one year (2017–2018) (Burt et al. 2019). Currently, there are no published data on the bleaching rates on Bahraini reefs. Unfortunately, following the 2017-bleaching event, coral cover decreased to $1.4 \pm 0.6\%$ at the nearshore site. One of the factors that could have contributed toward this decline could be the shallow depth of the reef ($< 7 \text{ m}$) which could subject the reef to warmer waters and higher erosion rates than those occurring at deeper reefs, since bioerosion is dependent on numerous environmental factors including depth and light availability (Chazottes et al. 1995; Mallela 2007). In nearshore reefs that are subjected to higher wave action, turbid conditions are expected especially if the shoreline is low and flat. Wave action influences the sedimentary processes on these reefs, and thus, turbidity induced by the suspended sediment reduces the light level corals are exposed to. This could lead coral communities to be dominated by massive

and sub-massive coral groups, thereby transiting the reef from a high accretion reef due to its vertical 3-D framework growth to one that is of low accretion like the reefs in Bahrain. It has been previously mentioned that carbonate erosion and dissolution rates on reefs that exist with low light levels (including mesophotic reefs) exceed carbonate production (Hoegh-Guldberg et al. 2017). In addition, nearshore reefs are shallower and hence are associated with warmer waters. Increased temperatures combined with more acidic conditions have been documented to trigger responses from bioeroding organisms such as microbioeroders which were seen to enhance skeletal dissolution due to increased biomass (Reyes-Nivia et al. 2013) and bioeroding sponge (such as *Cliona orientalis*) were previously reported to have increased both in biomass and bioerosion (Fang et al. 2013; Hoegh-Guldberg et al. 2017). This coupled with bleaching episodes that reduce calcification rates could subject nearshore reefs to higher erosion reefs. Furthermore, land-based runoff could lead to overproliferation of turf algae and macroalgae, increasing the abundance of echinoids (Kriegisch et al. 2020). Nevertheless, the recovery witnessed prior to the 2017-bleaching event creates a positive outlook for the post-2017-bleaching period as temporal data indicate the reef's ability for recovery despite encountering multiple bleaching events in previous years (e.g., 2010; Fig. 2). Nevertheless, it is evident that fundamental changes have occurred to the ecology of this shallow reef. Prior to the 2017 warming event, over 50% of the reef was dominated by primary and secondary producers; however, by 2018, these groups covered only 30% of the reef substrate. On the contrary, Site Offshore (> 10 m) demonstrated a 2% increase in hard coral cover reaching $14.8 \pm 4.1\%$ in 2018, maintaining its coral cover, which was reported to be 16.3% in 2012 (Burt et al. 2013). It is important to note that in addition to thermal anomalies, reefs in Bahrain are known to be impacted by various anthropogenic activities such as reclamation and dredging which has contributed significantly toward diminishing coral cover at Site Nearshore (Naser 2012; Burt et al. 2013).

It is of particular note that no branching or tabular coral taxa (e.g. *Acropora* spp.) were observed throughout the study period at either site as this has major ecological implications on both habitat diversity and complexity, as well as overall trends in reef accretion and budgetary dynamics. Branching corals such as *Acropora* spp. are responsible for the majority of calcification and structural complexity due to their morphology and rapid growth (e.g., Lizard Island, GBR = ~ 7.31 cm year⁻¹; Anderson et al. 2017). Acroporids are, therefore, an important functional genus in terms of structural complexity, which contributes toward habitat provisioning for reef associated species (Alvarez-Filip et al. 2013; Anderson et al. 2017; Roff 2020), as well as contributing to reef accretion and enhancing the ability for reefs to

track sea-level rise (SLR). The disappearance of fast growing, branching corals such as *Acropora* spp. from Bahraini reefs since 1998, is exacerbating reef framework decline and has resulted in shifts from these competitive corals (i.e., fast growing and branching) to opportunistic and stress-tolerant corals (i.e., low growing, thermally tolerant, e.g., *Porites* spp. and *Siderastrea* spp.) thereby compromising reef structural integrity. These shifts have also been documented in the Indian Ocean (Perry and Morgan 2017) and Caribbean (Baumann et al. 2016).

In general, the morphological and physiological attributes of reef associated species are closely linked to the coral assemblages and their life-history strategies which is key to the functionality of coral reefs (Darling et al. 2012; Alvarez-Filip et al. 2011). Changes in the functionality of reef associated fish have been documented with links associating coral cover decline to fish diversity decline, thereby impacting various functional groups, e.g., obligate corallivores associated with tabulate *Acropora* spp. (Pratchett et al. 2011). This was evident on these Bahraini reefs as many functional groups were observed to either be absent, e.g., obligate corallivores (*Chaetodon* sp.) or represented by only a handful of species. Moreover, many reefs reported shifts in coral and associated species community composition, e.g., shifts toward sponge-dominated reefs in Indonesia (Bell et al. 2013) and shifts toward massive stress-tolerant reefs in the Maldives, e.g., *Porites* spp., *Goniopora* spp., and *Platygyra* spp. (Ryan et al. 2019). This is evident on Bahraini reefs with the community composition shifting from primary carbonate producers associated with massive stress-tolerant corals to algal cover dominated communities. Reefs dominated by massive stress-tolerant corals could impact fish recruitment, diversity, and abundance due to limited resources and lack of structural complexity. This in turn tends toward a decrease in species richness, which could accelerate the collapse of the reef ecosystem. It is an accepted view that ecosystems with high species richness have a higher resilience to environmental change due to increased diversity of functional traits that facilitate successful recruitment of both coral and fish, thereby enabling reef resilience and recovery (Emslie et al. 2014; Hughes et al. 2012; Pratchett et al. 2011; Yachi and Loreau 1999). In addition, the shifts from competitive corals to opportunistic and stress-tolerant corals impact the ability of reefs to function as natural barriers through decreasing their efficiency to absorb wave energy and compromises coastal protection (Hoegh-Guldberg et al. 2007).

Interestingly, CCA percentage cover was extremely high at Site Nearshore pre-bleaching (mean = $42.2 \pm 12.9\%$), perhaps due to the presence of high rubble cover caused by previous dredging activities in the area (Vousden 1988). In addition to being an important carbonate producer, CCA plays a key role in binding the reef through colonizing reef substrate and contributing to cementation and stability

(Rasser and Riegl 2002; Langer 2008; Perry and Hepburn 2008; Fujita et al. 2009). This promotes accretion, enhances larval recruitment and maintains wave-resistant reef fronts (Rasser and Riegl 2002; Mallela and Perry 2007). During the field surveys in April/May 2017, extensive rubble binding was witnessed following what was suspected to be a dredging event (c. 10 years), and this could have contributed to the rise in coral cover between the period 2010 and 2017. Following the bleaching event, the reef has experienced a change from CCA domination to turf algae which increased by 50% post-bleaching. This finding aligns with other studies in various locations, such as Hawaii (Foo et al. 2022) and New Caledonia (Tanvet et al. 2022), all of which is attributed to SST warming (Cornwall et al. 2019). Therefore, the high presence of CCA is evidence that this reef was in recovery but has been affected by this warming event which is impacting the recovery process (Teichert et al. 2020; Roth et al. 2018). Most importantly, it has been demonstrated that CCA can match or exceed the contribution of corals to reef carbonate production; however, they are often inaccurately recorded in benthic surveys and sometimes missed in the reef carbonate budget analysis (Cornwall et al. 2023). Finally, the calcification rate (i.e., $0.027 \text{ g cm}^{-2} \text{ year}^{-1}$) for secondary producers derived from the 1-year experiment was observed to be similar to those recorded in the Indo-Pacific (Perry et al. 2018a, b).

Bioerosion

Erosion rates in Bahrain both pre- and post-bleaching ($0.4\text{--}0.1$ and $0.1\text{--}0.1$ G, respectively) are generally lower than other regions, e.g., Caribbean = $1.0\text{--}3.7$ G (Perry et al. 2014); South China Sea = $0.1\text{--}0.7$ G (Dumont et al. 2013), and the Red Sea = $1.9\text{--}2.9$ G (Roik et al. 2017). This could be due to lower eroder (fish and urchin) diversity and abundance and could be attributed to lower sedimentation offshore, and other environmental factors (Tribollet and Golubic 2005 at Great Barrier reef; Morris et al. 2022 at Florida Keys).

Similarly, parrotfish were observed only at Site Offshore pre-bleaching, in low numbers, while none were found at Site Nearshore. This could be attributed to extensive overfishing activities at both sites (Morgan 2006) as despite Site Offshore being a marine national park, there is no law enforcement or patrol in the area. In addition, lower erosion rates by parrotfish in the AG could be linked to lower fish biomass (e.g., D'Agostino et al. 2021 and Feary et al. 2010). Erosion rates in Bahrain caused by macroborers (dominated by bioeroding sponges) are negligible and fall well below other regions such as Brazil ($0.2\text{--}3.0$ G) (Reis and Leão 2000), Bonaire (Caribbean) ($0.01\text{--}0.1$ G) (Perry et al. 2012), and Gulf of Aqaba (Red Sea) (0.34 G) (Zundelich et al. 2007). However, we suggest further examining

the contribution of macroborers and microborers to reef erosion, as bioerosion was previously reported to be high in the AG with bioeroders removing $9.2 \pm 1.6\%$ of the skeletal surface area of *Porites daedalea* and $26.4 \pm 1.6\%$ in *Cyphastrea microphthalma* with variation in colony morphology being attributed to the differences between species (Al-Mansoori et al. 2019). Bioerosion in the AG appears to be related to environmental stress and past bleaching exposure (Al-Mansoori et al. 2019).

Carbonate budgets

Thermal anomalies are known to reduce calcification rates in coral (De'ath et al. 2009) and, therefore, carbonate production and reef accretion rates. This is observed in a 20 year dataset from the Seychelles, which showed a 62.5% difference in reef carbonate budget rates post-bleaching (-1.5 G (erosive state)) compared to pre-bleaching (~ 4 G (positive state); Januchowski-Hartley et al. 2017). Our results show a similar trend on the shallow nearshore reefs of Bahrain, highlighting a decrease by 88% (pre = 3.6 ± 2.2 ; post = 0.3 ± 0.3 G), while the deeper offshore reefs reported an increase in budgetary state (3.7 ± 1.2 to 4.2 ± 0.6 G) which could be attributed to the decrease of erosion rate post-bleaching at Site Offshore. The near collapse of the reef budget at Site Nearshore is directly linked to the widespread mortality of corals resulting from the thermal anomaly episode in 2017 (Fig. 2). It is worth noting that massive stress-tolerant corals have been reported to be able to maintain positive carbonate production on reefs, e.g., reefs in the Maldives (Ryan et al. 2019) despite their comparative lack of vertical growth, which was evident at Site Nearshore prior to September 2017; however, following the 2017-bleaching event, we report a shift to nearly a negative state in the reef carbonate budget for this nearshore site. It is important to note that in this study, there may have been an over-estimation of coral growth rates, since rates used for the *ReefBudget* calculation were not site specific due to unavailable published literature on coral growth rates in the AG, with the exception of growth rates of two species (*Platygyra daedalea* and *Cyphastrea microphthalma*; Howells et al. 2018). Similarly, CCA and other secondary producers growth rates could be overestimated as utilizing different experimental substrates could yield different results (Mallela et al. 2017). In addition, it is important to note that the *ReefBudget* method does not take into account the physical loss and chemical dissolution rates, and hence, this could also be an additional cause for overestimation of the reef budget rates. In general, Bahraini reef budget rates (including pre- and post-bleaching) (range = $0.3\text{--}4.2$ G) were seen to be in the lower scale, most similar to those in the Caribbean (e.g., Jamaica = 1.1 G (Land 1979) and Barbados = 4.5 G (Scoffin et al. 1980)) and the Indian Ocean (e.g., Maldives = 2.5 ± 2.5 G (Ryan

et al. 2019) and Seychelles 4 G (pre-bleaching) and – 1.5 G (post-bleaching) (Januchowski-Hartley et al. 2017)) in comparison to reefs in the Indo-Pacific, where, for example, net carbonate production were reported to be as high as 22.6 G in some areas of the Great Barrier Reef (Brown et al. 2021). Both sites retained low gross erosion rates accompanying the low gross production rates.

In conclusion, to our knowledge, no study has been conducted to quantify carbonate budgets of reefs in Bahrain or AG making this the first attempt. Reefs in AG are unique, particularly in relation to the capability of corals to sustain themselves in such extreme environmental conditions with seasonal temperature fluctuations. However, SST warming events, which are projected to increase in frequency and intensity with climate change, may jeopardize the resilience of these reefs and impacting their ecological functionality. Based on these trends, we predict suppressed budgetary states in AG. This, along with associated IPCC projected sea-level rise, will limit the capacity of Bahraini reefs to perform their natural breakwater function and therefore threaten island stability.

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Author contributions Study conception and design by LJH and RKA. RKA collected all field data. RKA and BE analyzed the data. RKA and LJH wrote the initial draft of the manuscript. All authors have contributed critically to the drafts and gave the final approval for publication.

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Data availability The datasets generated and analyzed for this study can be found in the University of Essex Repository (<https://dx.doi.org/10.5526/ERDR-00000192>).

Declarations

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

Informed consent This study did not involve any species that were used, captured, and/or experimented on in captivity. All applicable international and national guidelines were followed when handling the species that were encountered along the transect lines of the surveys.

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