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# Coral carbonate production across depth: homogenisation after bleaching?

Sivajyodee Sannassy Pilly<sup>1</sup> · Ronan C. Roche<sup>1</sup> · Ines D. Lange<sup>2</sup> · Chris T. Perry<sup>2</sup> · Andrew O. M. Mogg<sup>3</sup> · Kathryn Dawson<sup>3</sup> · John R. Turner<sup>1</sup>

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**Abstract** Recurrent climate-driven warming events, which can induce severe coral bleaching and mortality on tropical reefs, are predicted to cause homogenisation of coral communities and loss of ecosystem functions in shallow reef systems (< 30 m). However, data documenting the variation in coral carbonate production across depth are limited. Here we explore differences in coral cover, community composition, coral colony size structure and carbonate production rates between two depths (10 m and 17.5 m) across four atolls in the remote Chagos Archipelago. We show higher coral carbonate production rates at 10 m ( $4.82 \pm 0.27$  G, where  $G = \text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ) compared to sites at 17.5 m ( $3.1 \pm 0.18$  G). The main carbonate producers at 10 m consisted of fast-growing branching and tabular corals (mainly Acroporids) and massive corals (mainly *Porites*), with high abundances of medium- and large-sized colonies. In contrast, coral carbonate production at 17.5 m was driven by slow-growing encrusting and foliose morphotypes and small colony sizes. Utilising a dataset following 6–7 years of recovery after the 2015–2017 bleaching event, our results show that depth-homogenisation of coral communities was temporary and

carbonate production rates at 10 m depth recovered quicker at 3 of 4 studied atolls. The exception is Great Chagos Bank where slower recovery of branching and tabular corals at 10 m has led to a longer-lasting depth-homogenisation of carbonate production rates. The latter example cautions that more frequent bleaching events may drive increasing homogenisation of carbonate production rates across depth gradients, with implications for vital reef geo-ecological functions.

**Keywords** Coral carbonate production rates · Depth zonation · Colony size · Coral morphotypes · Coral reefs · Remote reef system

## Introduction

Reef carbonate budgets are a measure of the net balance between calcium carbonate production and erosion on coral reefs (Chave et al. 1972). A positive net balance is necessary for the structural development and maintenance of a functional coral reef framework (Perry et al. 2008). Scleractinian corals dominate carbonate production and serve as foundation species by providing the three-dimensional structure, with additional carbonate deposited by crustose coralline algae (CCA) and sedimentary import (Chave et al. 1972; Perry et al. 2012). Erosion on reefs occurs as a result of physical disturbances (cyclones and storms), chemical dissolution, bioerosion by grazing parrotfish and sea urchins, and bioerosion by endolithic macro- and microborers such as sponges, worms and bivalves (Scoffin 1993; Glynn and Manzello 2015). By summing calcium carbonate production and bioerosion, the biological aspects of reef carbonate budgets can serve as a quantitative metric to assess vital reef geo-ecological functions (Mace et al. 2014; Brandl et al.

Ines D. Lange and Ronan C. Roche have contributed equally to this work.

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✉ Sivajyodee Sannassy Pilly  
s.pilly@bangor.ac.uk

<sup>1</sup> School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey LL59 5AB, UK

<sup>2</sup> Faculty of Environment, Science and Economy, University of Exeter, Exeter, UK

<sup>3</sup> Tritonia Scientific, Oban, UK

2019). These functions include the provision of habitat for fish and other reef-associated organisms (Graham and Nash 2013; Ferrari et al. 2018), coastal protection through wave energy dissipation (Ferrario et al. 2014; Beck et al. 2018) and sediment generation to maintain beaches and shorelines (Kench and Cowell 2000; Laing et al. 2020); which in turn affect ecosystem goods and services that coral reefs provide (Kennedy et al. 2013; Woodhead et al. 2019).

Regulated by various biophysical factors, carbonate budgets can vary greatly within and across reefs (Takeshita et al. 2018; Brown et al. 2021; Edmunds and Perry 2023; Kahng et al. 2023). Abiotic variables such as light, temperature, pH, alkalinity, nutrient regime, and aragonite saturation state drive variation in calcification and dissolution rates across reefs (Albright et al. 2016; Januchowski-Hartley et al. 2017; Ross et al. 2019). Larger scale oceanographic forcings such as wave exposure, currents and upwelling import and export nutrients and sediments (Falter et al. 2013; Eyre et al. 2014), alter seawater chemistry through water circulation, thereby influencing reef community composition and reef-building capacity (Lange et al. 2021; Rodriguez-Ruano et al. 2023). Whilst reefs with few hard corals tend to display low-positive or net-negative budget states as bioerosion from parrotfish, urchins and sponges exceeds carbonate production (Perry et al. 2014; Edmunds and Perry 2023), coral-dominated reefs typically show highly positive net carbonate budgets (van Woessik and Cacciapaglia 2018; Lange and Perry 2019; Brown et al. 2021; Cornwall et al. 2023). Additionally, variation in coral population structure, including coral diversity, colony size and morphology drives differences in carbonate budgets across reefs (Carlot et al. 2021; Lange et al. 2022).

Given the natural depth-zonation patterns of coral reef communities (Edmunds and Leichter 2016; Roberts et al. 2019; Sannassy Pilly et al. 2022), that occur as a result of biophysical changes across depth gradients (Levin 1992; Couce et al. 2012; Williams et al. 2018), it is assumed that reef carbonate budgets will also vary markedly with depth (Perry and Alvarez-Filip 2019). While an increasing number of studies are now assessing temporal and spatial changes in reef carbonate budgets, the variability across depth gradients is largely unknown (97% of carbonate budget data are from reefs  $\leq 10$  m depth, Lange et al. 2020). As light, temperature, aragonite saturation state and wave exposure attenuate with increasing depth, coral community assemblages shift (Roik et al. 2018). Slow-growing encrusting and foliose growth forms gain an advantage (Kahng et al. 2019) as these morphologies can optimise light capture in deeper reef zones (Titlyanov and Titlyanova 2002; DiPerna et al. 2018), but have low calcification rates (Kahng et al. 2023). In contrast, exposed shallow areas are typically dominated by structurally complex branching and massive species with high calcification rates (Marcelino et al. 2013; Guest et al. 2016). These changes

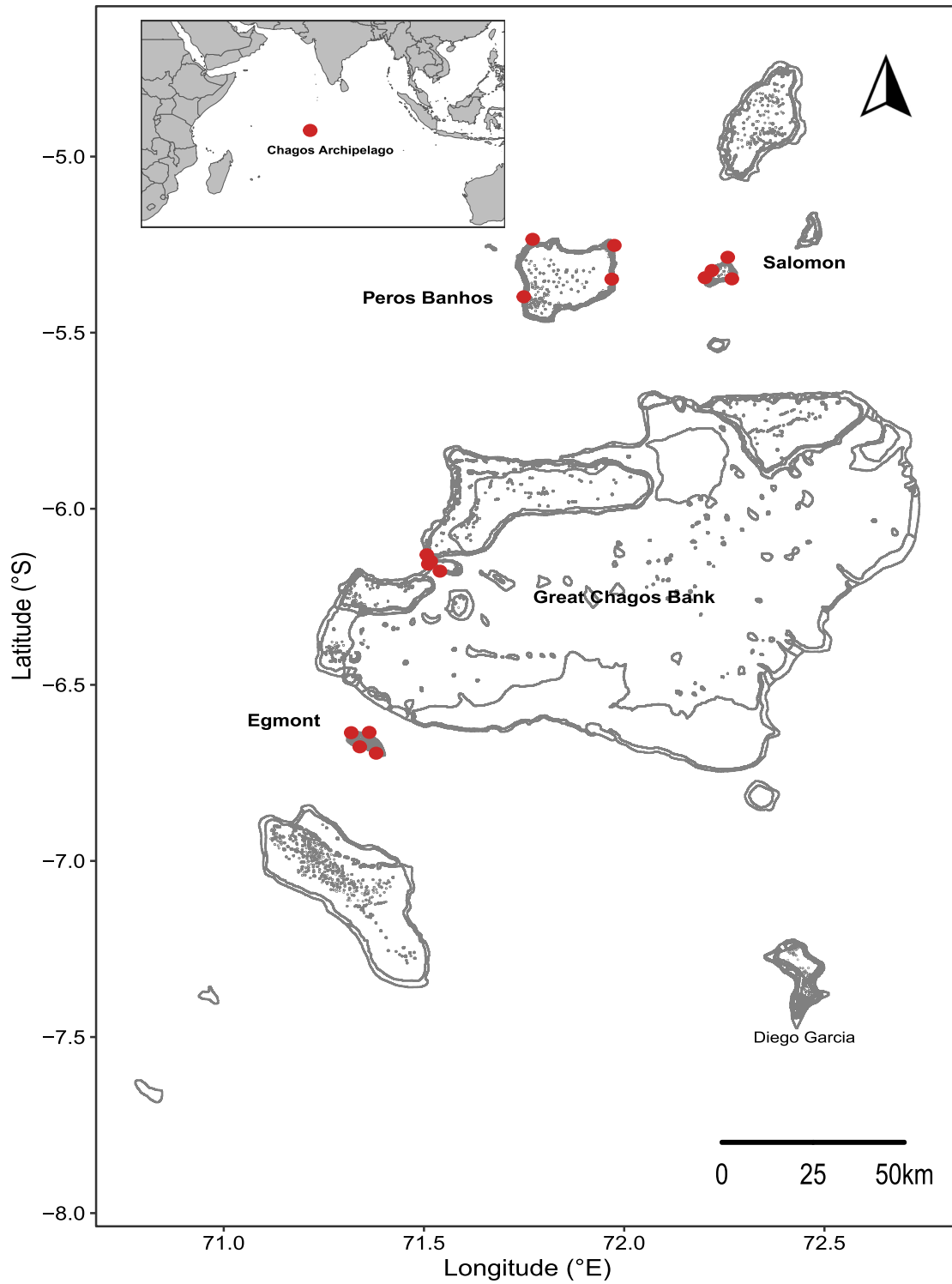
in coral community composition with increasing depth are expected to alter community carbonate production.

Whilst it is evident that ocean-warming events can significantly alter reef carbonate production and erosion processes on shallow reefs (Lange et al. 2022; Edmunds and Perry 2023), the magnitude of these changes at intermediate depths ( $\geq 10$  m  $\leq 30$  m) are poorly described. Given increasing evidence of bleaching and mortality across both shallow ( $< 30$  m) and mesophotic reefs ( $> 30$  m) (Smith et al. 2016; Sheppard et al. 2017; Muir et al. 2017; Morais and Santos 2018; Schramek et al. 2018; Frade et al. 2018; Baird et al. 2018; Crosbie et al. 2019; Venegas et al. 2019; Diaz et al. 2023b), it is reasonable to assume that subsequent alterations in coral reef communities will impact carbonate budgets across depth. However, a lack of data currently limits our understanding of whether bleaching events lead to depth-homogenisation of primary framework production. Here, we address this knowledge gap by examining differences in coral carbonate production rates across two depths (10 m and 17.5 m) on forereefs of four atolls in the remote Chagos Archipelago, 6–7 years after the 2015–2017 bleaching event. We evaluate the influence of coral cover, coral morphotypes, and colony size classes on carbonate production rates and discuss variable depth effects across atolls.

## Method

### Study Sites

Coral carbonate production rates were estimated on the forereef slopes of the Chagos Archipelago. Uninhabited since the early 1970s (except the US military base in the southern atoll, Diego Garcia), this remote reef system constitutes five atolls, located in the central Indian Ocean, about 500 km south of the Maldives (Sheppard 1999). A total of 16 sites ( $n = 4$  sites/atoll) were surveyed from December 2021 to January 2022, spanning four atolls: Peros Banhos, Salomon, Great Chagos Bank and Egmont (Fig. 1, Table S1). At each site, data were collected at two depths: 10 m and 17.5 m, using 30 photo quadrats ( $0.5 \times 0.5$  m area) laid along three 10 m long transects ( $n = 10$  photo-quadrats/transect) at each depth. All sites showed an overall decline in hard coral cover following successive marine heatwaves from 2015–2017 across depths from 5–25 m (Sannassy Pilly et al. 2024). The greatest loss in coral cover was observed between 5 and 10 m and declined with increasing depth (Sannassy Pilly et al. 2024). In 2021, coral communities in the shallows ( $< 10$  m) showed an overall shift from branching and tabular



**Fig. 1** Map of sampled sites (red points) around surveyed atolls (in bold) in the Chagos Archipelago—northern atolls; Peros Banhos, Salomon and southern atolls; Great Chagos Bank and Egmont—see Table S1 for list of sites and coordinates

morphologies to dominance by *Porites* spp. and encrusting taxa across all sites (Lange et al. 2022).

### Benthic community composition

Benthic community composition at each site was assessed using the web-based annotation tool CoralNet (Beijbom et al. 2015). Using a stratified random design, 15 points were overlaid on each photo quadrat to identify benthic groups directly below, including: hard coral, soft coral, crustose coralline algae (CCA), turf algae, fleshy macroalgae, *Halimeda* spp., sponge, sand, rubble, reef pavement, dead coral, bleached coral and `Other` (comprising zoanthids, bryozoans, ascidians, corallimorphs, anemones, clams, and bivalves). Where benthic group identification was limited due to shadowing or blurriness, the `Unknown` classification was chosen. The `hard coral` group was further classified as 7 morphotype classes and 2 dominant coral genera: tabular *Acropora*, branching *Acropora*, massive *Porites*, branching, massive, columnar, encrusting, foliose, and free-living. The classification of benthic groups was based on the NOAA Coral Reef Information System (NOAA 2014) and the 2022 edition of the Indo–Pacific Coral Finder (Kelley 2022).

### Coral carbonate production

Coral carbonate production rates were estimated using the Indo-Pacific *ReefBudget* methodology (Perry et al. 2018; Lange et al. 2022) after converting coral colony lengths measured from planar quadrat images to colony contour lengths using the Coral Colony Rugosity Index (CCRI) (Husband et al. 2022). First, each photo-quadrat was calibrated in the image analysis software JMicrovision (v1.3.4) by drawing a 10 cm line along a scale placed in each photo-quadrat. After calibration, using the 1D measuring function, the planar length of every live coral colony along 3 horizontal lines (50 cm each) was measured in each photo-quadrat. This provided 1.5 m of survey line per photo-quadrat and a total of 15 m of survey line per transect (1.5 m × 10 photo-quadrats/transect). Each coral colony was identified to genus (a total of 37 genera were identified) and morphological level (7 different morphotypes) (e.g., *Acropora* tabular, *Porites* massive, etc.). Where a line fell on a coral colony that could not be identified to genus level due to partial visibility, corals were assigned a morphotype classification only (e.g., branching coral, massive coral). The planar length of each coral colony was then converted to its topographic contour length using appropriate taxa-specific rugosity values ( $R_{\text{coral}}$ ) from the CCRI method (sensu Husband et al. 2022):

$$\text{Coral colony contour length} = \text{Colony planar length} \times \text{Taxa-specific } R_{\text{coral}} \text{ value}$$

To calculate total coral carbonate production rates, or Coral G (where  $G = \text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ), the contour length of each coral colony along with the genera-morphotype information was input into the Indo-Pacific *ReefBudget* coral carbonate spreadsheet (Perry et al. 2018; available at <https://geography.exeter.ac.uk/reefbudget/>). The spreadsheet was modified to include local coral growth rates and skeletal densities to provide more accurate carbonate production estimates for the Chagos Archipelago (sensu Lange et al. 2022). Coral growth rates were measured for 64 individual coral colonies from 22 dominant genera-morphotypes (Lange and Perry 2020), and skeletal densities assessed for 136 individual coral colonies from 35 genera-morphotypes (Lange et al. 2022). In the absence of coral growth rates at depths > 10 m, calcification rates from 8–10 m sites were used as a proxy to estimate total carbonate production rates at both 10 m and 17.5 m.

### Coral colony size structure

Coral colony sizes were extracted from the dataset to assess the variability in colony size structure across depths and atolls. As described above, coral colony size was measured as planar length but converted to contour length using the Coral Colony Rugosity Index (CCRI) (Husband et al. 2022). Identified genera were grouped into: tabular *Acropora*, branching *Acropora* (mainly caespitico-corymbose, digitate and few arborescent), massive *Porites*, branching (all taxa excluding *Acropora*), and massive (all other massive, sub-massive and columnar taxa), encrusting (all taxa), foliose (all taxa) and `other` (plating, frondose and free-living), following Lange et al. (2022). A total of 4858 colony sizes were recorded across all morphotypes, depths, atolls, and sites.

## Statistical analyses

### Community composition

To assess whether benthic communities varied across depths and atolls, composition was visualised at two taxonomic levels: 1) proportional cover of benthic groups (hard coral, soft coral, sponge, turf algae, fleshy macroalgae, CCA, *Halimeda* spp., sand, rubble, reef pavement, dead coral, and `Other`) and 2) proportional cover of the hard coral assemblage (identified to genus level), using non-metric multidimensional scaling (nMDS: vegan package, Oksanen 2015) based on Bray–Curtis dissimilarity matrices on square-root transformed data. The nMDS was computed on 3 dimensions

( $k=3$ ) with ordination stress values  $<0.2$ , which was evaluated with a scree plot. Envfit analyses were performed to identify: 1) benthic groups, and 2) coral taxa that significantly contributed to average dissimilarity among sites and across depth (envfit: vegan package). The strength of the association of benthic groups and coral taxa to the ordination was determined by permutation-based  $p$ -values using 9999 permutations.

To examine differences in benthic community composition across depths and atolls, two-way nested permutational multivariate analyses of variance (PERMANOVA; Anderson 2017) were performed on: 1) benthic groups, and 2) hard coral assemblage as a function of the interaction between depth (2 levels, fixed factor) and atolls (4 levels, fixed factor), with site (random factor) nested in atoll (using 9999 permutations; adonis2: vegan package). Where a significant interaction between depth and atoll was found, further within-atoll analyses were carried out to identify the depth-dependent effects at each atoll, using one-way nested PERMANOVAs. Where benthic groups and hard coral assemblage varied significantly among atolls, pairwise tests were used to compare differences among atolls (using 9999 permutations, permanova\_pairwise: ecole package, Smith 2021). Multivariate homogeneity tests (betadisper: vegan package) indicated similar dispersion means for benthic groups and hard coral assemblages among atolls. Marginally lower dispersion means were observed in hard coral assemblages at 10 m compared to sites at 17.5 m, indicating differences in hard coral assemblages between depths might not be solely due to variation in hard coral composition, but also due to differences in dispersion (Table S3).

### Coral cover and carbonate production

To assess the difference in proportional coral cover and total coral carbonate production across depths and atolls, we ran linear hierarchical models within a Bayesian framework (brm: brms package, Bürkner 2018). Using a gaussian distribution, a) total coral cover and b) coral carbonate production (response variables) were modelled as a function of an interaction between depth and atoll (population-level effects). Site (group-level effect) was nested in atoll to control for the natural variation in proportional coral cover and coral carbonate production between sites. Models were fitted with 2000 iterations across 4 chains, using the Markov Chain Monte Carlo (MCMC) algorithm and weakly informative priors on the regression parameters in the model (Table S2). All posterior samples were extracted from 4000 draws to simulate the response variables. Posterior distributions were assessed using Gelman–Rubin convergence  $R$ -hat values of  $<1.05$  and a minimum effective sample size (ESS) of  $>1000$  for all parameters (Gelman et al. 2013). Posterior predictive checks were used to assess model fits (bayesplot

package, Gabry and Mahr 2017 and tidybayes package Kay 2022). The influence of each predictor (depth and atoll) on response variables was assessed using average marginal effects (emmeans: emmeans package, Lenth 2022). Uncertainty related to the models' posterior estimates (median) was interpreted with 65% and 95% credible intervals. Strong and weak evidence of an effect was interpreted when 95% and 65% of the intervals did not intercept zero, respectively (Robinson et al. 2019; González-Barrios et al. 2021).

The effect of depth on the proportional contribution of different coral morphotypes to total carbonate production was examined using a set of generalised linear mixed-effects models (GLMMs). GLMMs, fitted with a beta distribution and logit-link function, and zero-inflation extensions when proportional data were over-dispersed and zero-inflated (glmmTMB: glmmTMB package, Brooks et al. 2017), were used to model the difference in proportional contribution of six coral morphotypes (tabular *Acropora*, branching *Acropora*, massive *Porites*, branching, massive, encrusting/foliose) across depths (fixed factor: 2 levels) and atolls (fixed factor: 4 levels). Site (random effect) was nested in atoll to constrain natural variation across transects at site level. Assumptions of normality and homoskedasticity were visually assessed using residual plots (plotQQunif, plotResiduals: DHARMA package, Hartig 2022). Rarely occurring morphotypes such as free-living, plating, and frondose were not included in these analyses.

### Coral colony size structure

Size-frequency distributions and size-class abundance across depths and atolls were plotted to visualise the difference in colony size structure for: 1) all colonies and 2) each morphotype. Following statistical analyses in Dietzel et al (2020) and Lange et al (2022), general linear mixed effect models (lmer: lmerTest package, Kuznetsova et al. 2017) were run to assess the difference in mean size and standard deviation (SD) of all colonies and skewness of size-frequency distribution across depth and atolls. Homogeneity of variance and normality checks were performed using Shapiro–Wilk and Levene tests and visualised using residual plots. Size-class abundance were obtained for log-transformed colony size data, which were binned into small (first quintile), medium (second-fourth quintile) and large (fifth quintile) colonies. Using bootstrap resampling ( $n=1000$ ), uncertainties in the difference in size-class between depths were assessed for: 1) all colonies, and 2) each morphotype. The relative percentage difference in size-class abundance was then calculated as follows:

$$\frac{\text{No of colonies at 17.5m} - \text{No of colonies at 10 m}}{\text{No of colonies at 10 m}} \times 100$$

All statistical analyses were carried out in R 4.1.1 (R Development Core Team 2021). Data were visually assessed using tidyverse package (Wickham et al. 2019).

## Results

### Benthic community composition

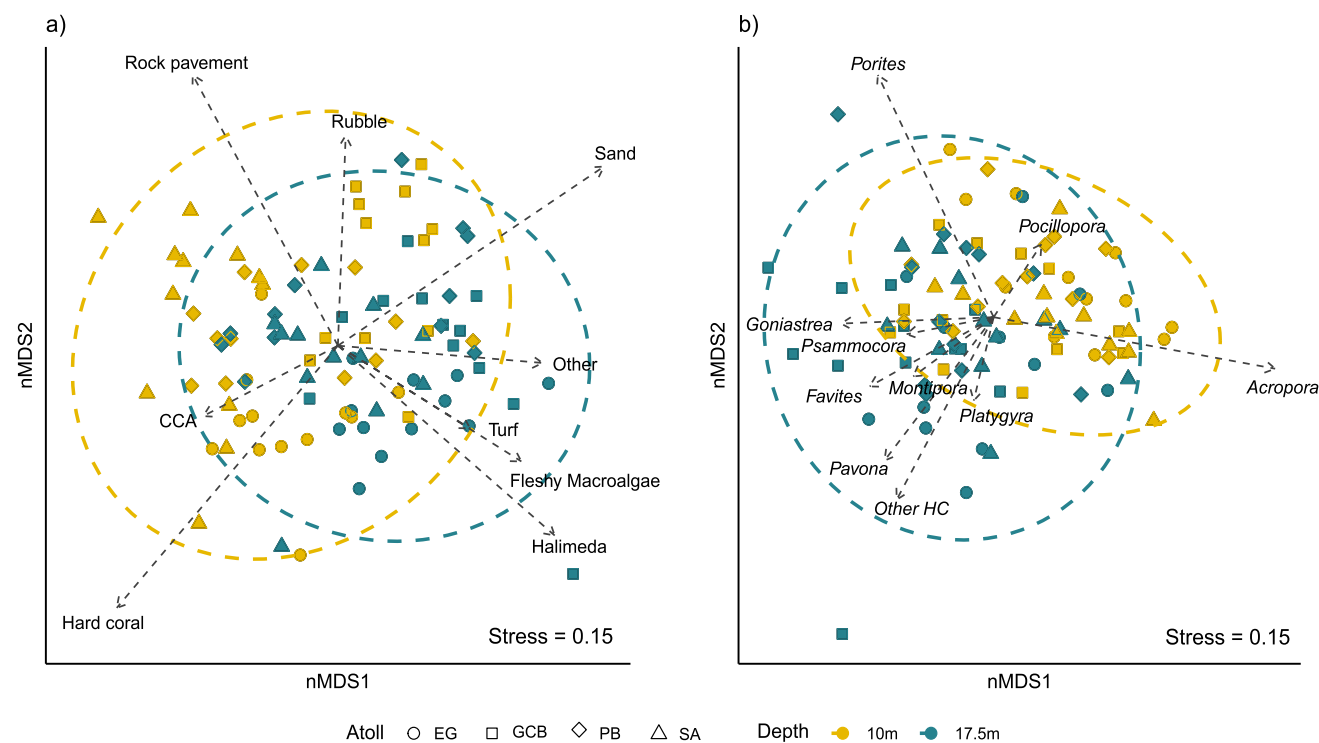
Benthic community composition was different across depths, with higher cover of hard coral and CCA at 10 m and higher cover of macroalgae and turf algae at 17.5 m (Fig. 2). PERMANOVAs indicated significant depth-by-atoll interactions (Table S3), indicating that the difference in benthic communities with depth varied among atolls. However, within-atoll analyses revealed significant variation in benthic community composition between depths in each of the four atolls, which in the case of Great Chagos Bank could partially be influenced by variation among sites (Figure S1, Table S3).

Hard coral assemblages showed significant differences across depths and atolls, with higher cover of *Acropora* and other branching corals at 10 m and at Salomon and Egmont (Fig. 2, Table S3). Pairwise comparisons indicated that the

overall hard coral assemblage at Egmont was significantly different from those in the Great Chagos Bank, Peros Banhos and Salomon, and the hard coral community at Great Chagos Bank was significantly different to that at Salomon (Table S4).

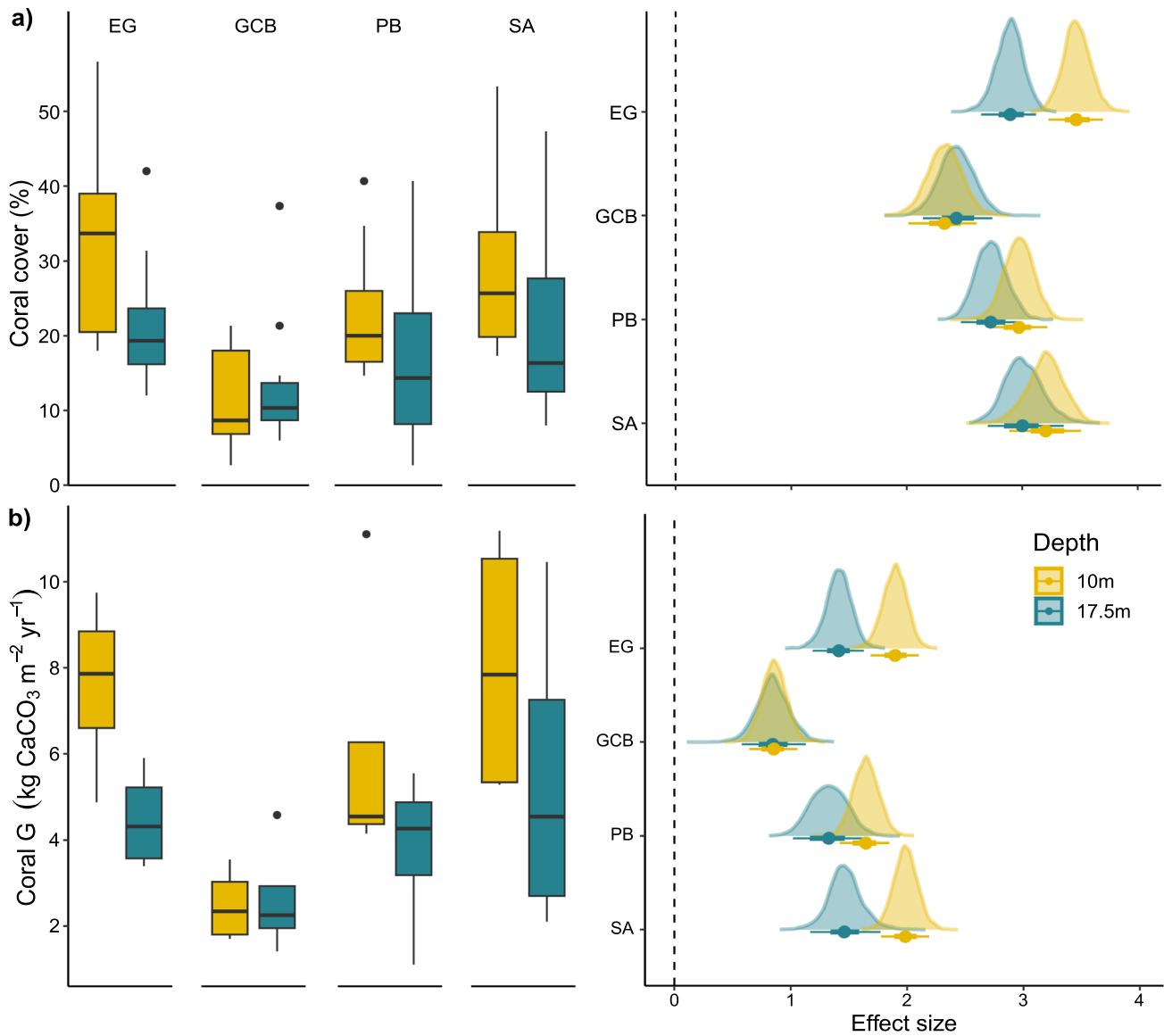
### Coral cover and carbonate production

Total hard coral cover ranged from  $10.9 \pm 0.7\%$  to  $33.4 \pm 2.1\%$  (mean  $\pm$  standard error of the mean [SEM]) across both depths and was consistently higher at 10 m ( $22.9 \pm 1.5\%$ ) than at 17.5 m ( $17.3 \pm 0.8\%$ ) (Fig. 3, Table 1). There was significant variation in total hard coral cover among atolls, with both Egmont and Salomon showing higher hard coral cover compared to Peros Banhos and Great Chagos Bank at both depths (Fig. 3, Table 1). Similar trends were observed in coral carbonate production rates across depths. Mean coral carbonate production was higher at 10 m ( $5.6 \pm 0.4$  G) than at 17.5 m ( $4.0 \pm 0.2$  G) for all atolls, except at Great Chagos Bank where carbonate production rates were low and no difference was observed between depths, as indicated by the overlap in posterior distributions (Fig. 3, Table 1).



**Fig. 2** Non-metric multi-dimensional scaling (nMDS) plots of (a) benthic groups and (b) hard coral assemblage from 16 sites in the Chagos Archipelago, showing clustering of communities between depth: 10 m and 17.5 m, based on Bray–Curtis dissimilarities of square-root transformed data. Ellipses represent dispersion of communities at 10 m (yellow) and 17.5 m (blue) from community cen-

roids at 95% confidence interval—symbols indicate surveyed atolls—Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). Overlaid (a) benthic groups and (b) coral taxa represent taxonomic groups that significantly contributed to the patterns on the ordination configuration



**Fig. 3** Comparison of (a) coral cover and (b) total coral carbonate production between 10 m and 17.5 m reefs and predicted posterior distributions of standardised effects of depth at atolls: Egmont (EG),

Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). Points in posterior distributions indicate median estimates and bars represent 65% and 95% credible intervals

**Contribution of coral morphotypes to total coral carbonate production**

There was significant variation in the relative contribution of different coral morphotypes to coral carbonate production between depths (Figure S2, Table 2, Table S5). Reefs at 10 m had higher contributions from both branching *Acropora* (10 m: 29.8 ± 3.4%; 17.5 m: 20.1 ± 3.0%; Table S6) and tabular *Acropora* (10 m: 10.8 ± 2.5%; 17.5 m: 3.5 ± 1.1%; Table S5). Encrusting and foliose (10 m: 20.0 ± 2.0%; 17.5 m: 33.7 ± 2.4%, Table S5) and massive corals (10 m: 2.6 ± 0.6%; 17.5 m: 7.8 ± 1.2%, Table S5) contributed more

at 17.5 m depth. There was no significant difference in carbonate production from massive *Porites* (10 m: 19.9 ± 2.6%; 17.5 m: 19.4 ± 1.9%; Table S5) and other branching corals (10 m: 12.8 ± 2.1%; 17.5 m: 10.0 ± 2.2%; Table S5) between depths.

All coral morphotypes, except massive *Porites* showed significant atoll-dependent variation in their relative contribution to total carbonate production (Table S5). Pairwise comparisons indicated that Egmont had higher relative carbonate production from branching *Acropora* than Great Chagos Bank (Tukey,  $t(85) = 2.69, p = 0.04$ ), but had significantly lower relative contributions from other



**Table 1** Coral cover and total coral carbonate production (Coral G) (from multilevel Bayesian models, mean  $\pm$  SE) at 10 m and 17.5 m reefs at atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA)

Atoll	Depth	Coral cover	Coral G
		Mean $\pm$ SE	Mean $\pm$ SE
EG	10 m	32.9 $\pm$ 3.6	6.0 $\pm$ 0.7
	17.5 m	21.4 $\pm$ 2.5	2.9 $\pm$ 0.5
GCB	10 m	11.4 $\pm$ 1.9	1.7 $\pm$ 0.3
	17.5 m	13.4 $\pm$ 2.5	2.0 $\pm$ 0.4
PB	10 m	22.9 $\pm$ 2.5	3.6 $\pm$ 0.5
	17.5 m	16.8 $\pm$ 3.3	2.1 $\pm$ 0.5
SA	10 m	29.1 $\pm$ 3.6	5.4 $\pm$ 0.6
	17.5 m	20.4 $\pm$ 3.3	3.0 $\pm$ 0.5

branching corals compared to Great Chagos Bank (Tukey,  $t(85) = -3.81$ ,  $p = 0.002$ ) and Peros Banhos (Tukey,  $t(85) = -3.00$ ,  $p = 0.02$ ). Salomon showed higher relative carbonate production from tabular *Acropora* than Peros Banhos (Tukey,  $t(85) = -3.69$ ,  $p = 0.002$ ) but had lower relative contributions from massive corals compared to Great Chagos Bank (Tukey,  $t(85) = 3.50$ ,  $p = 0.004$ ).

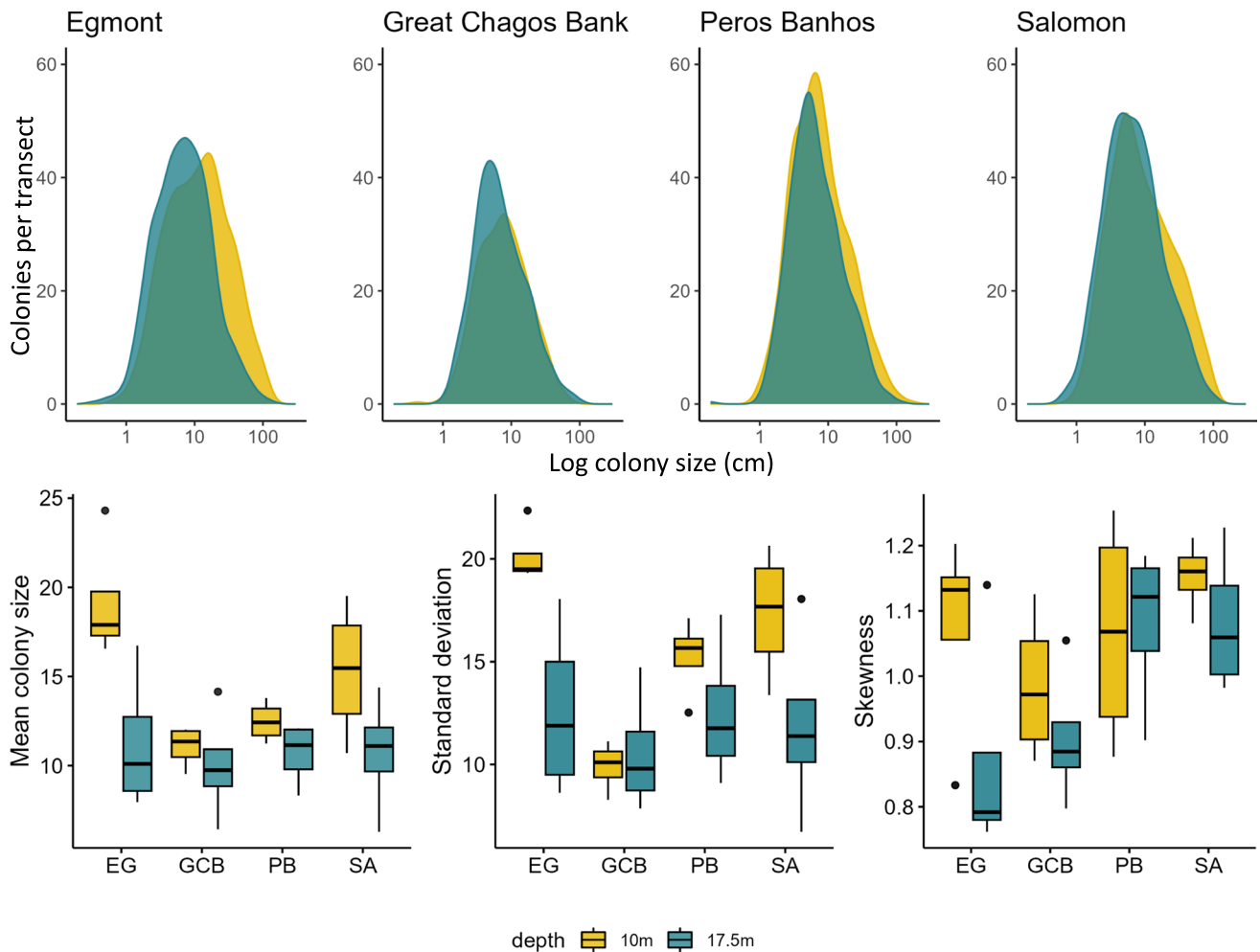
## Coral colony size structure

Significant variation in coral population size structures was recorded between depths and among atolls. A total of 2485 and 2373 coral colonies were recorded at 10 m and 17.5 m, respectively, with a higher mean coral colony size at 10 m (14.7  $\pm$  0.4 cm) compared to 17.5 m sites (10.6  $\pm$  0.3 cm) (Fig. 4, Table S6, Table S7). The standard deviation (SD) of colony size also declined with increasing depth (except at Great Chagos Bank and Peros Banhos, Fig. 4, Table S6, Table S7), indicating a less varied colony size structure on 17.5 m reefs compared to those at 10 m. These differences in coral population structure between depths were most pronounced at Egmont (Table S7, Table S8, Tukey, mean colony size:  $t(12) = 7.79$ ,  $p < 0.001$ ; SD:  $t(12) = 4.17$ ,  $p = 0.001$ ) and Salomon (Table S7, Table S8, Tukey, mean colony size:  $t(12) = 4.49$ ,  $p < 0.001$ ; SD:  $t(12) = 3.01$ ,  $p = 0.011$ ). Overall coral colony size distributions were positively skewed and showed higher positive values at 10 m independent of atoll (Fig. 4, Table S6, Table S7), suggesting that the shallower reefs of all atolls had a higher abundance of medium- and large-sized colonies.

Comparisons of taxa-specific size class distributions showed more detailed differences among both depths and

**Table 2** Percentage cover (%) and proportional contribution of morphotypes to total coral carbonate production (prop Coral G%) between 10 m and 17.5 m reefs at atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). Enc/Fol: Encrusting/Foliose, Branch Acro: Branching *Acropora*, Massive Por: Massive *Porites*, Tab Acro: Tabular *Acropora*

Atoll	MCG	Cover (%)		Prop Coral G (%)	
		10 m	17.5 m	10 m	17.5 m
EG	Branching	2.77 $\pm$ 0.79	2.52 $\pm$ 1.35	3.40 $\pm$ 1.03	2.44 $\pm$ 1.34
	Enc/Fol	11.33 $\pm$ 1.78	36.60 $\pm$ 6.12	12.51 $\pm$ 2.34	35.37 $\pm$ 5.62
	Massive	1.45 $\pm$ 0.29	10.98 $\pm$ 2.95	1.22 $\pm$ 0.31	10.33 $\pm$ 2.80
	Branch Acro	45.57 $\pm$ 7.46	25.66 $\pm$ 6.50	46.24 $\pm$ 7.65	30.37 $\pm$ 7.47
	Massive Por	31.71 $\pm$ 7.79	20.26 $\pm$ 5.15	27.09 $\pm$ 7.36	15.69 $\pm$ 4.27
	Tab Acro	5.21 $\pm$ 2.52	1.07 $\pm$ 0.79	7.65 $\pm$ 3.46	1.86 $\pm$ 1.32
GCB	Branching	9.44 $\pm$ 2.52	13.90 $\pm$ 7.18	11.66 $\pm$ 2.99	15.43 $\pm$ 7.24
	Enc/Fol	31.70 $\pm$ 4.73	39.84 $\pm$ 5.08	31.23 $\pm$ 4.47	38.83 $\pm$ 5.25
	Massive	3.74 $\pm$ 1.50	10.01 $\pm$ 2.13	4.62 $\pm$ 1.86	9.46 $\pm$ 2.66
	Branch Acro	23.53 $\pm$ 5.73	6.20 $\pm$ 2.22	24.08 $\pm$ 6.16	7.92 $\pm$ 3.18
	Massive Por	26.21 $\pm$ 4.16	26.01 $\pm$ 4.05	21.40 $\pm$ 3.92	22.13 $\pm$ 3.87
	Tab Acro	1.68 $\pm$ 1.13	0.00 $\pm$ 0.00	2.36 $\pm$ 1.59	0.00 $\pm$ 0.00
PB	Branching	17.79 $\pm$ 5.53	10.08 $\pm$ 3.16	18.70 $\pm$ 5.61	11.49 $\pm$ 3.80
	Enc/Fol	18.38 $\pm$ 3.51	29.27 $\pm$ 4.62	18.14 $\pm$ 3.77	29.78 $\pm$ 4.34
	Massive	3.11 $\pm$ 1.08	11.46 $\pm$ 3.38	2.11 $\pm$ 0.72	8.63 $\pm$ 2.61
	Branch Acro	24.07 $\pm$ 6.30	15.49 $\pm$ 5.08	27.46 $\pm$ 6.61	20.17 $\pm$ 6.14
	Massive Por	26.42 $\pm$ 4.97	26.45 $\pm$ 3.64	20.56 $\pm$ 4.28	21.79 $\pm$ 3.71
	Tab Acro	2.55 $\pm$ 1.28	0.88 $\pm$ 0.61	5.09 $\pm$ 1.97	1.60 $\pm$ 0.96
SA	Branching	16.49 $\pm$ 4.09	9.91 $\pm$ 2.55	17.40 $\pm$ 4.55	10.63 $\pm$ 2.92
	Enc/Fol	19.37 $\pm$ 3.61	32.66 $\pm$ 3.85	17.94 $\pm$ 3.59	30.87 $\pm$ 4.01
	Massive	2.05 $\pm$ 0.48	3.79 $\pm$ 0.70	2.24 $\pm$ 0.81	2.97 $\pm$ 0.57
	Branch Acro	20.93 $\pm$ 4.01	17.66 $\pm$ 4.87	21.53 $\pm$ 4.18	22.03 $\pm$ 5.41
	Massive Por	15.11 $\pm$ 4.81	23.28 $\pm$ 4.25	10.66 $\pm$ 3.55	17.95 $\pm$ 3.52
	Tab Acro	23.84 $\pm$ 6.49	6.53 $\pm$ 2.37	28.13 $\pm$ 7.07	10.56 $\pm$ 3.40



**Fig. 4** Comparison of coral colony size-frequency distributions between 10 m and 17.5 m reefs at atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA) (*top*); and varia-

tion in mean colony size, standard deviation in colony size and skewness of size distributions of all coral colonies between depth among atolls (*bottom*)

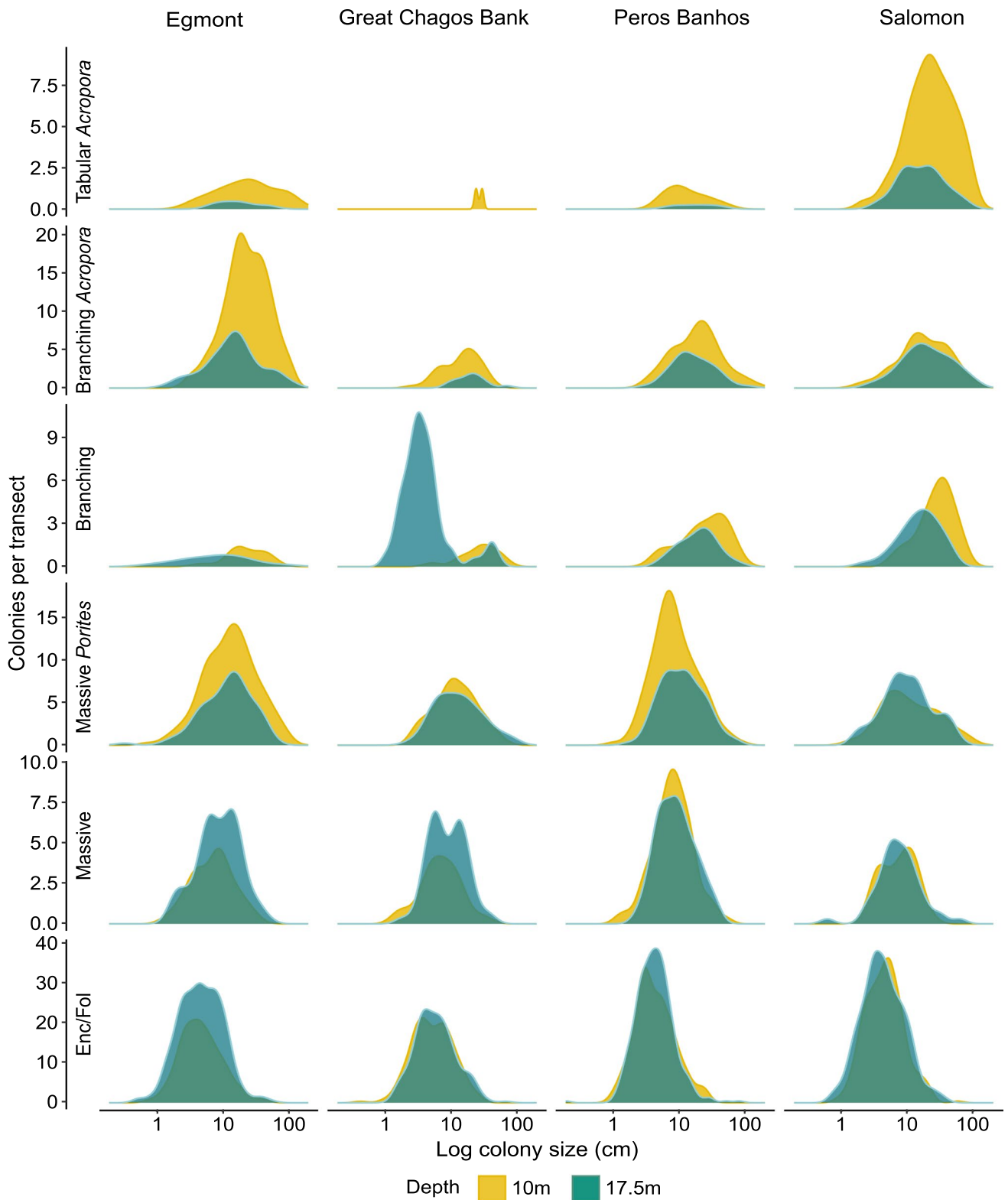
atolls (Fig. 5, Table S8, Table S9). Coral communities at 10 m showed higher abundance of tabular *Acropora*, branching *Acropora* and massive *Porites* of all size classes, as well as higher abundances of large branching corals. While Great Chagos Bank had relatively few *Acropora* colonies, abundances of medium-sized branching corals showed a pronounced peak at the deeper site. Abundances of encrusting/foliose corals of all size classes were higher at 17.5 m, especially at Egmont. Abundances of massive corals (excluding massive *Porites*) were also higher at 17.5 m, especially at Egmont and Great Chagos Bank.

## Discussion

This study identified significant differences in benthic community composition, coral cover, and carbonate production rates between depths, and across atolls. Whilst the atoll-scale

variation is consistent with existing evidence of spatial variation in coral carbonate productivity among different sites, reef habitats and across wider seascapes at depths  $\leq 10$  m (van Woesik and Cacciapaglia 2018; Lange et al. 2020), our results additionally highlight the vertical zonation of coral carbonate production rates within shallow reef systems. Comparable to two early studies that surveyed carbonate production across large depth gradients (10–60 m: Land 1979; 10–30 m: Heiss 1995), our results indicate higher community level carbonate production rates on reefs at 10 m compared to reefs at 17.5 m. This pattern is also consistent with previous studies which showed decreasing net carbonate production rates with depth within the very shallow reef zone (0–10 m) (Brown et al. 2021; Davis et al. 2021; Divan Patel et al. 2023).

Depth differences in total carbonate production rates in this study are mainly driven by differences in coral community composition, reflecting the change from fast-growing,



**Fig. 5** Size-frequency distributions of different coral morphotypes between 10 m and 17.5 m reefs at atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). Enc/Fol: encrusting and foliose coral colonies

branching corals at shallow depths to foliose and encrusting corals at deeper depths (Sheppard 1982; Sannassy Pilly et al. 2022). Similarly, higher coral carbonate production rates on 10 m reefs reflect higher abundances of medium and large-sized colonies compared to deeper sites that are mainly populated with small colonies (Bak and Nieuwland 1995; Kramer et al. 2020; Lange et al. 2022). A third driver of carbonate production differences across depths can be physiological changes in individual coral species. As coral species adapt to changes in environmental conditions, they are able to adjust individual tissue thickness, linear extension rates, calcification rates, skeletal density and colony size (Bosscher 1993). Two major factors that affect individual calcification rates across depths are light and temperature (Baker and Weber 1975; Venti et al. 2014; Diaz et al. 2023a; Kahng et al. 2023), both of which naturally decrease with increasing depth (Sheppard et al. 2017; Kahng et al. 2019; Diaz et al. 2023a). However, these depth-related differences in individual calcification rates are not reflected in the present study, as the only available growth rates that could be integrated into carbonate production estimates are from < 10 m depth. Depth differences in total carbonate production are thus conservative estimates and are likely even higher than presented here.

Differences in carbonate production rates among atolls suggest site-specific variation in abiotic environmental controls which affect community composition (Silbiger et al. 2017; Ross et al. 2022) or differences in recovery trajectories (Lange et al. 2022). Carbonate production rates at 10 m were highest at Egmont and Salomon atoll (> 7.5G), causing large depth differences at these atolls, while carbonate production rates at Great Chagos Bank were very low (2.5–2.6 G) across both depths. This may be driven by variation in large scale hydrodynamic forcings such as internal wave and upwelling activities (Sheppard 2009; Roche et al. 2022), or reef slope (Sheppard 1982) and wave exposure regimes (Falter et al. 2013; Caballero-Aragón et al. 2023), which can structure coral communities and therefore influence carbonate production rates among sites. Especially favourable biophysical settings may occur around Egmont and Salomon, increasing coral cover and carbonate production compared to the other atolls and facilitating faster recovery of reefs after the 2015–2017 bleaching event (Lange et al. 2022).

To fully understand the depth- and atoll-related variation in coral carbonate production across the Chagos Archipelago, it is important to consider past disturbance events that have affected its reefs (Brown et al. 2021; Lange et al. 2022). The third global warming event in 2015–2017 caused ~ 9–38% reduction in coral cover (relative to pre-bleaching levels in 2014) across 5–25 m depths (Sannassy Pilly et al. 2024). Significantly higher coral cover loss occurred at 5–10 m (Sannassy Pilly et al. 2024), with a 77% reduction in coral carbonate production

on shallow reefs (8–10 m) (Lange and Perry 2019). Similar patterns of declining carbonate budget states due to widespread coral bleaching were reported at shallow depths (2–10 m) in the Indian Ocean within the Maldives (Perry and Morgan 2017) and the Seychelles (Januchowski-Hartley et al. 2017), as well as the wider Pacific (Cabral-Tena et al. 2018; Courtney et al. 2022) and Caribbean (Manzello et al. 2018). However, thermal stress impacts on coral community-level carbonate production below 10 m depth are poorly understood. Growing evidence of coral bleaching and mortality across large depth gradients within both shallow (< 30 m) (Sheppard et al. 2017; Muir et al. 2017; Baird et al. 2018; Crosbie et al. 2019) and mesophotic (> 30 m) reefs (Morais and Santos 2018; Frade et al. 2018; Venegas et al. 2019; Diaz et al. 2023b) highlight the importance of examining changes in carbonate production rates across depths on shallow reef systems (Perry and Alvarez-Filip 2019; Lange et al. 2020).

Recent findings from multiple depth zones across the forereefs of the Chagos Archipelago show distinct depth-related changes in coral cover and population structure following thermal stress events: 1) a greater decline in coral cover at shallower depth (21.1% decline at 5–10 m) compared to deeper reefs (14.8% decline at 15–20 m) (Sannassy Pilly et al. 2024), 2) a steep decline in competitive species such as tabular and branching *Acropora* and *Pocillopora* and a higher persistence of stress tolerant taxa with encrusting and foliose morphologies (Lange and Perry 2019), and 3) faster recovery of Acroporids and encrusting genera at shallower reefs compared to deeper sites (Sheppard et al. 2008, 2013, 2017, 2020). In line with carbonate budget surveys in 2021 (Lange et al. 2022) and previous recovery trends across depth (Sheppard et al. 2008, 2013, 2017, 2020; Sannassy Pilly et al. 2024), higher coral carbonate production rates observed on shallow reefs in this study may be driven by faster recovery of fast-growing taxa at shallow depths compared to slow-growing taxa on deeper reefs.

Surviving coral populations are key to recovery trajectories of coral reef assemblages and their contribution to net carbonate budgets (Dietzel et al. 2020; Lange et al. 2022). A disproportionate loss of susceptible branching taxa and large mature coral colonies on shallow reefs can result in low coral recruitment densities and increased homogenisation of coral communities across depths (Bruckner and Hill 2009; Gilmour et al. 2022; Ford et al. 2023). However, our results indicate the presence of all size classes (small, medium, and large colonies) at 10 m and 17.5 m, suggesting a positive recovery trajectory of reefs and coral carbonate production rates following the 2015–2017 bleaching event in the Chagos Archipelago. Nevertheless, the variation in coral carbonate production rates among atolls highlights different recovery speeds among sites (Lange et al. 2022). This is evident at Great Chagos Bank, which suffered the greatest

loss in coral cover at 5–10 m (amongst all atolls) due to both initial and repeated thermal stress during the 2014–2017 bleaching event (Sannassy Pilly et al. 2024) and now shows very low coral carbonate production across both 10 m and 17.5 m reefs.

Our understanding of recovery trajectories could be improved further by assessing net carbonate budgets including variation in bioerosion rates across depths. Previous work within the Chagos Archipelago found similar macro and endolithic bioerosion rates between 5 and 10 m, but some evidence for higher micro-bioerosion rates at 10 m (Lloyd Newman et al. 2023). The variation in bioerosion rates and therefore net carbonate budgets across reefs deeper > 10 m within both the Chagos Archipelago and globally remains poorly constrained (Weinstein et al. 2019). As coral reefs face increasing anthropogenic pressures, they become more prone to bioerosion, resulting in loss of reef framework and structural complexity (Perry et al. 2014; Januchowski-Hartley et al. 2017). Future studies should aim to include bioerosion processes across depths to determine the ability of deeper reefs to maintain net positive carbonate budget status.

Our results capture coral carbonate production rates at a time point approaching when reefs typically recover and reassemble towards pre-disturbance coral-dominated communities (7–12 years) in the absence of further disturbance events (Johns et al. 2014; Gouezo et al. 2019). Whilst the on-going recovery of coral carbonate production rates on shallow reefs at three out of four atolls supports the assumption that the lack of direct anthropogenic impacts across the uninhabited atolls of the Chagos Archipelago promotes fast recovery of reefs, the low carbonate production rates at Great Chagos Bank highlights concerns about less predictable shifts in coral communities. It is likely that increasingly small recovery windows due to the projected increase in frequency of severe bleaching events may, in the long term, suppress carbonate production rates and compromise reefs' ability to support reef framework accretion across depths (De'Ath et al. 2012; Perry and Alvarez-Filip 2019; Cheung et al. 2021). By assessing depth- and atoll-specific differences in coral carbonate production rates in a remote reef system 6–7 years after a bleaching event, this study provides a better understanding of the long-term impacts of bleaching on primary framework production on coral reefs.

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#### Declarations

**Conflict of interest** We confirm that this manuscript has not been published nor been considered elsewhere, and declare they have no conflict of interest.

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