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Atoll-dependent variation in depth zonation of benthic communities on remote reefs

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Atoll-dependent variation in depth zonation of benthic communities on remote reefs

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	John R. Turner, PhD
	Ronan C. Roche, PhD
Abstract:	The distribution and organisation of benthic organisms on tropical reefs are typically heterogenous yet display distinct zonation patterns across depth gradients. However, there are few datasets which inform our understanding of how depth zonation in benthic community composition varies spatially among and within different reef systems. Here, we assess the depth zonation in benthic forereef slope communities in the Central Indian Ocean, prior to the back-to-back bleaching events in 2014–2017. We compare benthic communities between shallow (5–10 m) and deep (20–25 m) sites, at two spatial scales: among and within 4 atolls. Our analyses showed the variation in both major functional groups and hard coral assemblages between depth varied among atolls, and within-atoll comparisons revealed distinct differences between shallow and deep forereef slope communities. Indicator taxa analyses characterising the hard coral community between depths revealed a higher number of coral genera characteristic of the deep forereef slopes (10) than of the shallow forereef slopes (6). Only two coral genera consistently associated with both depths across all atolls, and these were *Acropora* and *Porites* . Our results reveal spatial variation in depth zonation of benthic communities, potentially driven by biophysical processes varying across depths and atolls, and provide a baseline to understand and measure the impacts of future global climate change on benthic communities across depths.
Suggested Reviewers:	Peter J. Edmunds, PhD Professor of Biology, California State University Northridge peter.edmunds@csun.ed Prof Edmunds research focus on the ecology of tropical reef corals and studied depth zonation on shallow reefs. we would value his views regarding the vertical zonation aspect of this paper.
	James Leichter, PhD Assistant professor/research, University of California San Diego Scripps Institution of Oceanography jleichter@ucsd.edu Professor Leichter research focuses on benthic marine ecology and could provide insightful reviews on the variability in benthic community structure.
	Kaylyn McCoy, PhD Marine ecosystems research specialist, NOAA Fisheries Pacific Islands Fisheries Science Center kaylyn.mccoy@noaa.gov Dr McCoy's is a marine ecosystem research specialist whose work focus is on tropical reef systems.
	Michael Bradley, PhD Lecturer/research scientist, James Cook University michael.bradley@jcu.edu.au

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	Dr Bradley research focuses on marine ecosystem and coral reefs
Response to Reviewers:	

Registered charity number: 1141565

Professor I. Sokolova,
Editor
Marine Environmental Research
01 November 2021

Re. Resubmission of Atoll-dependent variation in depth zonation of benthic communities on remote reefs (Manuscript number: MERE-D-21-00487R1)

Dear Prof Sokolova,

Thank you for the opportunity to submit a revised version of our paper. We are very pleased that the reviewer feels that we have addressed all their previous comments accordingly, and we are very grateful for the helpful comments which the reviewer and you have provided.

Overall, the reviewer suggestions were to make few edits and rewording. We believe that the suggested changes have improved and will ease reading of the manuscript.

Following this letter are reviewer comments with our point-by-point responses. We have uploaded a new revised manuscript, and one version with track changes for readability. The revision of this manuscript has been developed and approved in consultation with all co-authors.

We hope you will find this revised version of the manuscript suitable for publication in Marine Environmental Research.

Yours sincerely,

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COMMENTS TO THE AUTHOR:

Reviewer #1 General:
The authors have adequately addressed all of my comments. However, after reading through the manuscript, I have a few minor edits/suggestions which could be easily fixed with rewording.

Response – We are really pleased that the reviewer has found that we have addressed all their comments accordingly, and we are grateful that there are now only few minor corrections to ease reading of the manuscript.

Reviewer #1 Comment 1
L15 I'm not sure what is meant by the last part of this sentence…."varies spatially depending on the scale of investigation".. among and within different reef systems?

Response – Thank you for this comment. We agree the last part of this sentence can be ambiguous, and we have now amended the sentence as suggested by the reviewer.

L12-14: "However, there are few datasets which inform our understanding of how depth zonation in benthic community composition varies spatially among and within different reef systems."

Reviewer #1 Comment 2
L19 What is the archipelago scale? All available data? This is the first mention of the study being done within an archipelago, so either introduce the term earlier in the abstract or delete to avoid introducing a new term to describe spatial scale which is not mentioned in the previous text.

Response – Thank you for highlighting this point. We used the term "archipelago scale" to refer to all surveyed atolls across the archipelago. We can see how without introducing the term beforehand can lead to confusion among readers. We have now clarified the sentence by removing it.

L18-20: "Our analyses showed the variation in both major functional groups and hard coral assemblages between depth varied among atolls, and within-atoll comparisons revealed distinct differences between shallow and deep forereef slope communities."

Reviewer #1 Comment 3
L89-92 ....and after bleaching in 1998? These reefs have bleached before and this should be acknowledged

Response – Thank you for this comment. We have now amended this sentence to include the 1998 bleaching as well as the 2014-2017 bleaching events.

L88-91: "Here we examined depth zonation in benthic community composition at two spatial scales (among and within atolls) in the Chagos Archipelago, a relatively isolated reef system in the Central

Indian Ocean, prior to pan tropical bleaching events in 2014–2017 (Eakin et al. 2019) and post 1998 bleaching (Sheppard 1999a).”

Reviewer #1 Comment 4
L95 measure the extent of 'further' climate change impacts
Response – Thank you for highlighting this point. We have now amended this sentence.

L94-95: “… to measure the extent of further climate change impacts and how these vary across depths”

Reviewer #1 Comment 5
L221 correct typo "cCoral"
Response – Thank you for highlighting this typographical mistake. It has now been corrected.

Reviewer #1 Comment 6
L265-267 this sentence is true but seems to be in the wrong place as it doesn't flow well with the previous sentence.

Response – Thank you for raising this point. We agree this sentence is misplaced. We have now moved this sentence and references to L246-252, where we elaborate on the variation of physical gradients across depth and how they structure benthic communities.

L246-252: “Physical variables that co-vary with depth, such as light (Edmunds et al. 2018), wave exposure (Williams et al. 2013; Gove et al. 2015), reef slope (Sheppard 1982), seasonal thermocline (Kahng and Kelley 2007), resource availability (Fox et al. 2018; Williams et al. 2018), internal wave activities (Leichter and Salvatore 2006; Radice et al. 2019), and disturbance history, e.g. storms (Hughes and Connell 1999) and climate-induced bleaching events (Bridge et al. 2013, 2014; Adjeroud et al. 2018), have been shown to influence reef communities.”

Reviewer #1 Comment 7
L284-295 worth noting in this paragraph that these two genera also contain large numbers of species with different morphologies and environmental tolerances, which may explain why the genera are found across the depth gradient studied here.

Response – We thank you for this comment. We have now amended this sentence and included the appropriate reference to highlight the high species diversity within *Acropora* and *Porites* genera.

L284-287: “These typically depth generalist genera contain large numbers of species (Veron et al. 2019) that have different physiological and phenotypical traits which give them the ability to persist in diverse environments across depth gradients (Toda et al. 2007; Darling et al. 2012).”

Reviewer #1 Comment 8

L296 "Increasing depth had a positive effect on turf algae and CCA cover." The main finding of the study is benthic assemblages differ among atolls, even when at similar depths. Hence it is important to note here that greater CCA and turf at deeper reefs was really only observed at a single atoll, rather than suggesting this is a pattern consistently observed among atolls. i.e. Interpretation of results should be based on the significant interaction term. Also, the mechanism put forward to explain more CCA and turf at deeper reefs is higher grazing pressure on shallow reefs, but wouldn't that cause more CCA and possibly turf at shallow not deep reefs?

Response – Thank you for raising this important point. We have now clarified this sentence to only highlight the atolls where a significant interaction was obtained. We also made amendments to the paragraph to clearly pinpoint to the concerned atolls while discussing our results.

L295: "Increasing depth had a positive effect on turf algae at PB and CCA cover at EG.

L302-304: "Within EG, high grazing intensity coupled with elevated herbivore and excavator biomass between 8–17 m, were associated with CCA dominated habitats on forereef slopes (Samoilys et al. 2018; Sheppard et al. 2013b)."

L304-306: "A lower biomass of herbivorous fishes has also been reported on the deeper forereefs of the Chagos Archipelago (Andradi-Brown et al. 2019), which could potentially explain the observed higher turf cover on the deep reefs of PB."

Reviewer #1 Comment 9

L314 as mentioned above there was an interaction between atoll and depth so this effect was only observed at some atolls and the generalization that soft coral cover and sponge increase with depth is not strongly supported by findings

Response – Thank you for highlighting this point. We have clarified this sentence to highlight the significant interactions at the concerned atolls.

L314: "Soft coral and sponge cover increased with depth, notably at EG and PB."

L314-317: "Previous findings in Indo-Pacific reef systems (Reichelt et al. 1986; Barnes and Bell 2002), including the Chagos Archipelago (Sheppard 1981; Schleyer and Benayahu 2010) show similar increase in soft coral and sponge cover with depth."

Reviewer #1 Comment 10

L352 this data will provide insights into impact of the 2014-2017 event as well as subsequent recovery

Response – We thank you for this comment, and we have amended this sentence as suggested by the reviewer.

L351-353: “These benthic community data from 2013 will provide insights into the impact of the 2014–2017 back-to-back bleaching events as well as subsequent recovery.”

Highlights

- Significant depth-by-atoll interactions drove benthic community structure.
- CCA, turf algae, sponge and soft coral cover were highest on deep reefs.
- Hard coral, dead coral and bare substrate cover were highest on shallow reefs.
- *Acropora, Stylophora* and *Pocillopora* characterised shallow reefs.
- *Acropora* and *Porites* consistently associated with both shallow and deep reef zones.

Manuscript File Click here to view linked References

Title: Atoll-dependent variation in depth zonation of benthic communities on remote reefs

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Abstract

The distribution and organisation of benthic organisms on tropical reefs are typically heterogenous yet display distinct zonation patterns across depth gradients. However, there are few datasets which inform our understanding of how depth zonation in benthic community composition varies spatially among and within different reef systems~~depending on the scale of investigation~~. Here, we assess the depth zonation in benthic forereef slope communities in the Central Indian Ocean, prior to the back-to-back bleaching events in 2014–2017. We compare benthic communities between ~~the~~ shallow (5–10 m) and deep (20–25 m) sites, at two spatial scales: among and within 4 atolls. Our analyses showed the variation in both major functional groups and hard coral assemblages between depth varied among atolls, ~~at the archipelago scale,~~ and within-atoll comparisons revealed distinct differences between shallow and deep forereef slope communities. Indicator taxa analyses characterising the hard coral community between depths revealed a higher number of coral genera characteristic of the deep forereef slopes (10) than of the shallow forereef slopes (6). Only two coral genera consistently associated with both depths across all atolls, and these were *Acropora* and *Porites*. Our results reveal spatial variation in depth zonation of benthic communities, potentially driven by biophysical processes varying across depths and atolls, and provide a baseline to understand and measure the impacts of future global climate change on benthic communities across depths.

Keywords: depth zonation, coral reefs, remote systems, benthic ecology, community composition, hard coral assemblages

1. Introduction

One of the main goals in ecology is to understand how communities occupy space. Biotic (González et al. 2017; Des Roches et al. 2018), abiotic (McGill et al. 2006; Agrawal et al. 2007), and stochastic processes (Hubbell 2005) that are responsible for the organisation of ecological communities, interact and create natural environmental gradients in biophysical resources (Leibold and McPeek 2006; Vellend 2010; Brandl et al. 2019). These naturally occurring gradients combine to limit the distribution, abundance, and diversity of communities (Holt 2003; Peischl et al. 2015). Similar natural variations occur across water depth gradients

on tropical reef systems, where biophysical conditions known to influence the physiology of reef organisms co-vary, such as light availability (Brakel 1979; Hoegh-Guldberg and Jones 1999; Cooper et al. 2007), temperature, salinity (Kleypas et al. 1999), and wave and current regimes (Lowe and Falter 2015; Radice et al. 2019). Coral reef species develop different traits to survive within variations of these parameters across depths (Kneitel and Chase 2004; McGill et al. 2006; Darling et al. 2012).As a result, distinct and predictable ecological zonation patterns in coral reef ecosystems can be observed across depths (Sheppard 1982; Done 1983; Roberts et al. 2015; Karisa et al. 2020).

Different zones on shallow coral reef systems are usually defined by the occurrence of one or more dominant organisms that occupy a certain depth in a location (Goreau 1959; Sheppard 1982; Done 1983). For instance, zonation patterns in shallow forereef slope communities are described as being predictably dominated by structurally robust species. Coral species exposed to high light regimes and large temperature fluctuations on shallow areas of the reef slope have adapted morpho-physiologically to this dynamic environment (Titlyanov and Titlyanova 2002; Iglesias-Prieto et al. 2004; Marcelino et al. 2013; Guest et al. 2016). Often prone to high exposure to wave and surge energy (Done 1983), some shallow water species are adapted to thrive in areas where frequent sediment resuspension occurs, forming robust morphologies which can resist high water flow and physical forces (Todd 2008; Duckworth et al. 2017). In contrast, deeper forereefs which are more sheltered from surface wave exposure and receive lower irradiance due to light attenuation with depth (Done 1983; Rex et al. 1995), are characterised by coral communities that frequently adopt encrusting and foliose growth forms to increase light capture efficiency (Titlyanov and Titlyanova 2002; DiPerna et al. 2018a). There is also an increase in mixotrophic and heterotrophic traits in marine organisms, such as hard corals, soft corals and sponges to offset limited light availability in deeper reef zones (Fabricius and Klumpp 1995; Fabricius and De'ath 2008; Houlbrèque and Ferrier-Pagès 2009).

Our understanding of the consistency of how coral reef benthic communities vary spatially across depths remains unclear (Edmunds and Leichter 2016; Roberts et al. 2019). This may be due to the complex interactive effects of biophysical processes that drive ecological community structure, which vary across multiple spatial and temporal scales (Hatcher et al. 1987; Magurran 2004; Leibold and McPeek 2006; Vellend 2010; Brandl et al. 2019), resulting

in highly heterogenous coral reef communities (Edmunds and Bruno 1996; Huntington and Lirman 2012; Obura 2012; Dalton and Roff 2013; McClanahan et al. 2014; Ford et al. 2020). In addition, much of our current understanding of depth zonation patterns on reefs is based on observations made decades ago (Goreau 1959; Done 1982; Sheppard 1982; Done 1983), prior to subsequent climate change impacts that have altered coral reef communities (Dubinsky and Stambler 2010; Williams et al. 2019).

Coral reefs around the world are increasingly vulnerable to more intense and frequent climate-driven disturbances (Anthony 2016; Hughes et al. 2017, 2018; Perry and Alvarez-Filip 2019). However, the extent at which coral reefs are affected by anthropogenic stressors is not uniform across space and varies across depths (Bongaerts et al. 2010; Bridge et al. 2013; Baird et al. 2018). Examining depth zonation of benthic communities in the context of systemic disturbance has provided important insights into complex dynamics such as diverging ecological trajectories and regime shifts, but these studies have been generally limited to shallow (3–10 m) depth ranges (Graham et al. 2015; Gouezo et al. 2019). This focus on shallow depth ranges has limited our understanding of how benthic community composition change across different depths within contemporary shallow tropical reefs (<30 m) (Bridge et al. 2014; Edmunds and Leichter 2016).

Here we examined depth zonation in benthic community composition at two spatial scales (among and within atolls) in the Chagos Archipelago, a relatively isolated reef system in the Central Indian Ocean, prior to pan--tropical bleaching events in 2014–2017 (Eakin et al. 2019) and post 1998 bleaching (Sheppard 1999a). Isolated reefs can be used an ecological reference point (Sandin et al. 2008; Smith et al. 2008; Williams et al. 2013; Heenan et al. 2017; Head et al. 2019) and examining benthic communities, prior to the back-to-back bleaching event in 2014–2017, establishes a baseline to measure the extent of further climate change impacts and how these vary across depths. Specifically, we compare benthic composition among and within four atolls, between two depth ranges: 5–10 m and 20–25 m on the forereef slopes. With our current knowledge of depth dependent zonation on coral reefs (Done 1982; Sheppard 1982; Done 1983), we expected to find zonation across depth in benthic community composition that was consistent amongst atolls.

2. Methods

2.1 Study sites

The Chagos Archipelago is located in the centre of the Indian Ocean, at the remote southern end of the Laccadives-Maldives-Chagos ridge, ~500 km from south of Maldives (Sheppard 1999b). The archipelago is comprised of 5 atolls, 52 islands, and constitutes 9400 km^2 of submerged shallow reefs (<40 m depth) (Dumbraveanu and Sheppard 1999; Sheppard et al. 2013a). The archipelago has been largely uninhabited since the early 1970s (Sheppard, 1999), with the exception of Diego Garcia (DG), the southern-most atoll that hosts a US naval facility, where strict environmental regulations are enforced, prohibiting all commercial fishing and extractive activities at sea (Purkis et al. 2008). In this study, a total of 26 sites; including 13 at 5–10m depth (hereafter 'shallow' reefs) and 13 at 20–25m depth (hereafter 'deep' reefs), were surveyed on forereef slopes across 4 atolls: Peros Banhos (PB), Salomon (SA) (northern atolls), Great Chagos Bank (GCB) and Egmont (EG) (southern atolls) (Figure 1, Table S1).

2.2 Benthic composition

At each site, benthic composition was quantified from 30 digital photo-quadrats taken in February and March 2013 (total across all sites, n = 780). Digital photo-quadrats were randomly extracted as still images from 10 min continuous video-swims at both 5–10 m and 20–25 m depths. The housing was equipped with two spotlights and two red laser pointers set at 10 cm apart to provide a consistent scale-measurement of the benthos and to adjust for lower-light levels at greater depth to facilitate benthic image analysis. The camera was maintained approximately 0.5 m above the substrate and at a 45° angle to capture benthic organisms under overhangs and canopies (Goatley and Bellwood 2011).

Each video was converted into an image sequence (25 frames per sec; in Pinnacle Studio, v22.2.0). To ensure that images selected for analysis did not contain the same section of the forereef, frames were randomly selected, but separated by a minimum of 80–100 frames (Matlab, R2018a.Ink). Benthic image analysis was carried out by SSP, RR, and LR using Coral Point Count with excel extensions (CPCe) (Kohler and Gill 2006) . To account for any variation in observer bias in identification of benthic composition, the frames were equally divided

among observers and analysed (10 images each per person per site). Proportional cover of benthic categories was quantified by identifying substrate and benthic organisms under fifteen randomly allocated points on each image, with one point assigned within a 3 x 5 grid cell stratification (Suchley 2014).

Substrate type and benthic organisms were categorised as: hard coral (identified to genus), soft coral (identified to family), non-scleractinian coral (*Millepora, Heliopora* and *Distichopora*), sponge, crustose coralline algae (CCA), macroalgae, turf algae, bare substrate with algal film (hereafter bare substrate), sand, rubble (< 10 cm maximum length), dead coral, bleached coral, diseased coral, 'other live' and unknown. 'Other live' included all sessile invertebrates such as bryozoans, tunicates, bivalves, giant clams, corallimorphs, anemones and zoanthids. Soft corals were identified and grouped within the four most common families occurring in the archipelago – Alcyoniidae, Xeniidae, Nepthtiidae and Nidaliidae (Schleyer and Benayahu 2010), or other soft coral. Where image quality limited identification of hard corals to genus level or morphology (approximately 0.1–0.5%), corals were classified as 'other'. The classification of benthic categories for this study was based on NOAA Coral Reef Information System (2014), Dennis et al, (2017) and the CATAMI classification system (Althaus et al. 2015).

2.3 Data analysis

To assess whether benthic composition varied across depths, and if depth zonation varied among atolls, benthic community composition was first visualised at two levels: 1) proportional cover of major functional groups (hard coral, soft coral, sponge, CCA, macroalgae, turf algae, bare substrate with algal film, sand and rubble, non-scleractinian coral, bleached coral, dead coral, diseased coral, 'other live'), and 2) proportional cover of hard coral assemblages, identified to genera. Benthic composition was visualised across: a) depth, and b) atoll, using non-metric Multidimensional Scaling (nMDS: vegan package; Oksanen et al., 2012), based on a Bray-Curtis dissimilarity matrix of square root transformed data. A scree plot was used to evaluate ordination stress and a Shepard stress plot to confirm correlation between the original dissimilarity matrix and the distances on the final nMDS plot. The nMDS was computed on 3 dimensions (k = 3) with a stress value ≤ 0.1. The envfit function (vegan

package) was used to fit vectors of major functional groups and coral genera, to their respective nMDS ordinations.

To assess differences in benthic composition across depth and atolls, we performed two-way nested permutational multivariate analyses of variance (PERMANOVA; Anderson 2017) on: 1) major functional groups, and 2) coral genera, as a function of the interaction between atolls (4 atolls; fixed factors) and depths (2 depths; fixed factors), with sites (random factors) nested in atoll (9999 permutations; adonis2 function: vegan package). Average within-group dispersion was examined using a multivariate homogeneity test (betadisper: vegan package). Where a significant interaction between depth and atoll was found, we tested for variation in 1) major functional groups, and 2) coral genera across depths at each individual atoll using one-way nested PERMANOVAs. Data were square-root transformed and analysed using Type III sum of squares to accommodate an unbalanced design, in both one-way and two-way PERMANOVA.

Indicator taxa analyses were used to determine the association between coral genera and the depth ranges at which they occur. Coral genera that significantly associated with shallow and deep reefs across each atoll, were used to infer on the biotic and abiotic state of the environment that prevail at the different depth ranges (Cáceres and Legendre 2009). Prior to analysis, the proportional cover matrix of the coral genera assemblage was converted into presence/absence data. Coral genera characteristic of shallow and deep reefs were identified using a p-value threshold of <0.05 (9999 permutations, indicators: indicspecies package; Cáceres 2020).

Generalised linear mixed-effects models (GLMMs) with a binomial distribution and logit-link function were used to model major functional groups within each atoll, treating depth as a fixed effect and sites as a random effect (glmer: lme4 package, Bates et al. 2015). GLMMs were also performed on coral genera that consistently characterised the hard coral assemblage across both depths and all atolls. When major functional groups or coral genera cover had a high number of zeros and did not fit the standard binomial distribution ($>$ 55% of the data consisted of zero values), a zero-inflated generalised linear mixed-effect models with a beta distribution was fitted (depth as a fixed factor and sites as a random factor; glmmtmb: glmmTMB package; Brooks et al. 2017). All analyses were performed using R 3.5.1 (R Development Core Team 3.5.1, 2018).

3. Results

3.1 Variation in major functional groups

Within-atoll analyses revealed significant variation in major functional groups between shallow and deep reefs across all four atolls (PERMANOVA, all: p =0.001, Table 1). There was also an interactive effect of depth and atoll (PERMANOVA, Pseudo $F_{3, 779}$ = 13.54, p = 0.001) and dispersion (Table S4) on benthic composition, indicating the variation in major functional groups between depth varied among atolls; notably at EG and PB (Table 1, Table S5a).

A decreasing hard coral, bare substrate and dead coral cover was observed with increasing depth compared to CCA, macroalgae, sand and rubble and sponge cover which increased on the deep forereef slopes at EG (Table 1b). At PB, hard coral and dead coral cover also decreased with depth compared to sand and rubble, sponge, soft coral and turf algae cover which increased on the deep forereef slopes (Table 1b). At GCB, only dead coral cover varied significantly with depth (Table 1b). At SA, macroalgae and 'other live' cover increased significantly with depth while dead coral showed a significant decrease with increasing depth (Table 1b).

3.2 Variation in hard coral assemblage

Thirty-seven coral genera were recorded across all sites, with a higher number of coral genera were recorded at deep reefs (34) than shallow reefs (23). SA contained the highest coral genera richness (29), followed by GCB (22 genera), PB (20 genera) and EG (16 genera). Within-atoll variation revealed significant differences in hard coral assemblages between depths (PERMANOVA, all: p =0.001, Table 2a). However, significant depth-by-atoll interactions (PERMANOVA, Pseudo $F_{3, 650}$ = 7.40, p = 0.001; Figure S1) and dispersion (Table S4), indicate the variation in hard coral assemblages between depth varied among atolls across the archipelago, particularly at SA and PB (Table S5b).

Indicator taxa analyses identified a total of 14 coral genera as well as the 'other' category that characterised the hard coral community across all atolls and depth combinations

(Table 3). A higher number of coral genera (10) characterised the deeper reefs than the shallow reefs (6). Coral genera significantly associated with shallow reefs in EG were *Acropora*, *Porites* and *Pocillopora*. ~~e~~Coral genera significantly associated with deep reefs - in EG were *Favia*, *Pachyseris* and *Pavona*. *Porites* was the only genus that significantly characterised the shallow reefs in GCB. The hard coral assemblage on deep reefs- in GCB was characterised by *Acropora*, *Echinopora*, *Pachyseris* and *Symphyllia*. The shallow reefs of both northern atolls, PB and SA were characterised by *Acropora*, *Pocillopora*, *Porites* and *Stylophora*. The only coral genus that significantly associated with the deep reefs in PB was *Tubastrea*. In SA, the hard coral community on deep reefs was characterised by *Acanthastrea*, *Goniastrea*, *Montipora*, *Pachyseris* and *Seriatopora* (Table 3).

Acropora and *Porites* were the only genera that were consistently associated with both depths across all atolls. Univariate analyses showed that the cover of *Acropora* decreased with increasing depth at EG and SA (Table 2b). Increasing depth also had a negative effect on the cover of *Porites* at EG and PB (Table 2b).

4. Discussion

Our results showed the variation in the benthic community structure of the Chagos Archipelago was driven by significant depth-by-atoll interactions. Although the zonation patterns of the benthic community varied across atolls, a distinct contrast was observed between shallow (5–10 m) and deep (20–25 m) communities, both in terms of the major functional groups and hard coral assemblages, within each atoll. Several earlier coral reef studies report predictable vertical zonation in benthic communities and hard coral assemblages (e.g. Goreau 1959; Done 1982, 1983; Sheppard 1982). However, the among-atoll variation in depth effect observed in this study is consistent with recent research documenting spatial heterogeneity in tropical reefs (Edmunds and Bruno 1996; Williams et al. 2013; Edmunds and Leichter 2016; Karisa et al. 2020; Ford et al. 2020). Spatial variation in depth zonation may be indicative of local biophysical gradients at each atoll that are interacting with depth to structure benthic assemblages (Whittaker 1972; Reice 1994; Vellend 2010). Physical variables that co-vary with depth, such as light (Edmunds et al. 2018), wave exposure (Williams et al. 2013; Gove et al. 2015), reef slope (Sheppard 1982), seasonal thermocline (Kahng and Kelley 2007),

resource availability (Fox et al. 2018; Williams et al. 2018), internal wave activities (Leichter and Salvatore 2006; Radice et al. 2019), and disturbance history, e.g. storms (Hughes and Connell 1999) and climate-induced bleaching events (Bridge et al. 2013, 2014; Adjeroud et al. 2018), have been shown to influence reef communities.

The distinct variation in benthic composition across depth within each atoll, is comparable to changes with depth in several other Indo-Pacific locations: Central Pacific Kingman and Palmyra atoll (Williams et al. 2013), French Polynesia (Edmunds and Leichter 2016), New Caledonia (Adjeroud et al. 2019), the Maldives (Ciarapica and Passeri 1993), and Kenya (Karisa et al. 2020). Coral genera that consistently associated with shallow reefs were *Acropora*, *Pocillopora* and *Stylophora*. These coral genera frequently exhibit arborescent and bushy morphologies in shallow areas (Sheppard 1982) and have better light-scattering properties (Titlyanov and Titlyanova 2002; Marcelino et al. 2013). They are therefore better adapted to the high light regimes that can be experienced in shallow reef environments (Hoegh-Guldberg and Jones 1999; Winters et al. 2003). These species also have effective mechanisms, such as polyp inflation, tentacular action and mucus production to shed sediment particles that are resuspended due to wave action (Erftemeijer et al. 2012; Duckworth et al. 2017) at highly exposed shallow reefs (Fulton et al. 2001). ~~Both light and wave regimes strongly affect the structure and dynamics of benthic coral reef communities (Gove et al. 2015; Edmunds et al. 2018).~~

Pachyseris, Pavona, Echinopora, Acanthastrea, Goniastrea, Montipora and *Symphyllia* were characteristic of the hard coral assemblage on deep reefs. These coral genera frequently adopt foliose, encrusting and massive growth forms on deeper forereef slopes (Sheppard 1982). As irradiance levels decrease with increasing depths, morphological adaptations including the development of larger surface areas, such as foliose and encrusting growth forms, help increase efficiency in light capture to optimise photosynthetic activities (Done 1983; DiPerna et al. 2018b). Foliose and massive species also contain higher densities of photosynthetic dinoflagellates *(Symbiodinium)* for maximising food production in low light regimes (Li et al. 2008). Many of the deeper dwelling massive and sub-massive species exhibit heterotrophic traits; with larger polyp sizes and longer tentacles to allow energy requirements to be met by zooplankton feeding (Hoogenboom et al. 2015; Tremblay et al. 2015). The occurrence of the azooxanthellate *Tubastrea* as a characteristic coral genera across the deep

overhangs of the northern atoll, PB (Andradi-Brown et al. 2019) provides evidence of the presence of highly productive waters in the area. We hypothesise that that the deeper forereef areas of the archipelago are more likely recipient of cooler, nutrient-rich upwelling waters than shallow reef areas (Sheppard 2009; Sheppard et al. 2017).

Acropora and *Porites*~~-~~ characterised both shallow and deep forereef slopes across all atolls. Previous studies in the Chagos Archipelago have also highlighted the dominance of these two coral genera at both shallow and deep forereef slopes (Sheppard et al. 2008). These typically depth generalist ~~corals have~~genera contain large numbers of species (Veron et al. 2019) that have different physiological and phenotypical traits which give them the ability to persist in diverse environments across depth gradients (Toda et al. 2007; Darling et al. 2012). Both genera have high larval dispersion rates facilitating settlement across depths (Holstein et al. 2016; Serrano et al. 2016). *Acropora* and *Porites* have been found to host diverse endosymbionts to optimise photosynthesis in decreased light (Muir et al. 2015; Ziegler et al. 2015; Tan et al. 2020). *Acropora* are often characterised as a fast growing weedy species which have overtopping abilities and can encroach neighbouring species (Riegl and Purkis 2009). *Porites* with massive morphologies can grow taller and larger, and physically outcompete other surrounding species (Potts et al. 1985).

Increasing depth had a positive effect on turf algae at PB and CCA cover at EG. Several previous studies have found that turf algae and CCA were more abundant in shallow reef environments (Williams et al. 2013; Marlow et al. 2019; Karisa et al. 2020). The high cover of turf algae and CCA we observed at deep~~-~~ forereef slopes of the Chagos Archipelago may be related to the grazing pressure across depth (Heenan and Williams 2013). Intensive herbivory promotes the removal of epiphytic turf algae (Rasher et al. 2012; Osuka et al. 2018; Roff et al. 2019) and provides space for the growth of the rapid colonising CCA (Airoldi 2000; Russell 2007). Within EG, ~~H~~high grazing intensity coupled with elevated herbivore and excavator biomass between 8–17 m, were ~~found in shallow sites~~ associated with ~~turf and~~ CCA dominated habitats on forereef slopes~~,~~ ~~especially at EG~~ (Samoilys et al. 2018; Sheppard et al. 2013b). A lower biomass of herbivorous fishes has also been reported on the deeper forereefs of the Chagos Archipelago (Andradi-Brown et al. 2019), which could potentially explain the observed higher turf cover on the deep reefs of PB.

Among all measured major functional groups, dead coral was the only group which had consistently higher cover in shallow forereef slopes across all atolls. During the 1998 massive bleaching events, all shallow ocean-facing reefs in the Chagos Archipelago were highly impacted, leaving large quantities of dead corals (Sheppard, 1999). Several subsequent bleaching events in shallow waters in the 2000s also resulted in localised mortality (Harris and Sheppard 2008; Sheppard et al. 2008), which may have inhibited recruitment and growth, explaining the higher dead coral cover at 5–10m across the archipelago.

Soft coral and sponge cover increased with depth, notably at EG and PB. ~~and this is supported by p~~Previous findings in Indo-Pacific reef systems (Reichelt et al. 1986; Barnes and Bell 2002), including the Chagos Archipelago (Sheppard 1981; Schleyer and Benayahu 2010) show similar increase in soft coral and sponge cover with depth. Sponges and soft corals species have phototrophic, heterotrophic and mixotrophic abilities (Wilkinson 1983; Fabricius and Klumpp 1995). Their high cover in deeper forereef can result from photoadaptation of autotrophic species to increased depths (Fabricius and De'ath 2008; Shoham and Benayahu 2017). Mixotrophic and heterotrophic sponges and soft corals can feed from large flows of inorganic nutrients that are delivered by cold water upwelling and/or internal waves that occur on deeper reef sites (Lesser 2006; Pupier et al. 2019). Deep steep walls are also less prone to sedimentation creating favourable habitat for octocorals (Bridge et al. 2011). Accentuated by the steep walls of deep sites of PB (Sheppard 1980; Winterbottom et al. 1989), deep rich waters may upregulate heterotrophic feeding in soft corals and sponges, explaining the observed higher cover in its deep forereef slopes (Schleyer and Benayahu 2010; Sheppard et al. 2013b).

It is important to understand the reef community composition of the Chagos Archipelago in the context of disturbances that have affected its reefs. Classic ecological theories suggest that following a disturbance, communities undergo secondary succession (Horn 1974). A major disturbance event prior to 2013 was the pan tropical bleaching event in 1998 (Wilkinson et al. 1999). Previous studies provided evidence that the benthic community of the Chagos Archipelago has transitioned through different successional stages since the 1998 bleaching event. A recovery occurred from minimal hard coral cover (~12% in 1999; Sheppard, 1999) to a coral-dominated community where no significant divergence was apparent in 2012, relative to the pre-1998 community (Sheppard et al. 2008, 2013b). Despite the overall reassembly towards a coral-dominated reef, there was significant variability in benthic

community recovery, across depths and atolls (Sheppard et al. 2008). In 2001, less degradation was observed in deep sites of the northern atolls (PB and SA) (high mortality observed at <10–15 m) while the southern atolls (GCB and EG) showed significant mortality at depths >35 m (Sheppard et al. 2002). In 2006, the hard coral assemblages in shallow sites (4–10 m) recovered faster than deep forereef slopes (20–25 m) across PB, SA and GCB, with the exception of EG where no recovery was observed at either depth (Sheppard et al. 2008). In 2012, a general decrease in hard coral cover and increase in sponge and soft coral cover could be observed with increasing depth (5–25 m) across the archipelago (Sheppard et al. 2013b). This rapid recovery in shallow sites (8–10 m) may be driven by the high growth rates in *Acropora*-dominated shallow communities within the archipelago (Perry et al. 2015).

Our results reveal the spatial variation in depth zonation of benthic communities, potentially linked to previously described biophysical gradients occurring across these depths and atolls (Sheppard 2009; Fasolo 2013; Sheppard et al. 2017). These ~~Using~~ benthic community data from 2013 will provide insights into the impact of the 2014–2017 back-to-back bleaching event as well as subsequent recovery.~~, we set a baseline that can provide insights into recovery patterns and re-assembly across depths, following the 2014-2017 back-to-back bleaching event.~~ It is becoming more important to understand the spatial variability in reef ecosystems in order to infer and predict how communities might respond to the effects of increasing disturbances (Bridge et al. 2014; Hughes et al. 2019). There is therefore a need to incorporate spatial variation in depth effect within ecological studies, as contemporary shallow reefs are changing rapidly across depths.

Author contributions

Sivajyodee S Pilly: Conceptualization, Formal analysis, Validation, Data curation, Writing- Original draft preparation, Writing – Review and Editing, Visualisation. **Laura Richardson, Ronan Roche**: Validation, Writing – Review and Editing. **John Turner, Ronan Roche**: Methodology, Investigation, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

All authors have seen and approved the final version of the manuscript being submitted. We confirm that this manuscript has not been published nor been considered elsewhere, and declare they have no conflict of interest (see submitted form).

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Title: Atoll-dependent variation in depth zonation of benthic communities on remote reefs

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Abstract

The distribution and organisation of benthic organisms on tropical reefs are typically heterogenous yet display distinct zonation patterns across depth gradients. However, there are few datasets which inform our understanding of how depth zonation in benthic community composition varies spatially among and within different reef systems. Here, we assess the depth zonation in benthic forereef slope communities in the Central Indian Ocean, prior to the back-to-back bleaching events in 2014–2017. We compare benthic communities between shallow (5–10 m) and deep (20–25 m) sites, at two spatial scales: among and within 4 atolls. Our analyses showed the variation in both major functional groups and hard coral assemblages between depth varied among atolls, and within-atoll comparisons revealed distinct differences between shallow and deep forereef slope communities. Indicator taxa analyses characterising the hard coral community between depths revealed a higher number of coral genera characteristic of the deep forereef slopes (10) than of the shallow forereef slopes (6). Only two coral genera consistently associated with both depths across all atolls, and these were *Acropora* and *Porites*. Our results reveal spatial variation in depth zonation of benthic communities, potentially driven by biophysical processes varying across depths and atolls, and provide a baseline to understand and measure the impacts of future global climate change on benthic communities across depths.

Keywords: depth zonation, coral reefs, remote systems, benthic ecology, community composition, hard coral assemblages

1. Introduction

One of the main goals in ecology is to understand how communities occupy space. Biotic (González et al. 2017; Des Roches et al. 2018), abiotic (McGill et al. 2006; Agrawal et al. 2007), and stochastic processes (Hubbell 2005) that are responsible for the organisation of ecological communities, interact and create natural environmental gradients in biophysical resources (Leibold and McPeek 2006; Vellend 2010; Brandl et al. 2019). These naturally occurring gradients combine to limit the distribution, abundance, and diversity of communities (Holt 2003; Peischl et al. 2015). Similar natural variations occur across water depth gradients on tropical reef systems, where biophysical conditions known to influence the physiology of

reef organisms co-vary, such as light availability (Brakel 1979; Hoegh-Guldberg and Jones 1999; Cooper et al. 2007), temperature, salinity (Kleypas et al. 1999), and wave and current regimes (Lowe and Falter 2015; Radice et al. 2019). Coral reef species develop different traits to survive within variations of these parameters across depths (Kneitel and Chase 2004; McGill et al. 2006; Darling et al. 2012).As a result, distinct and predictable ecological zonation patterns in coral reef ecosystems can be observed across depths (Sheppard 1982; Done 1983; Roberts et al. 2015; Karisa et al. 2020).

Different zones on shallow coral reef systems are usually defined by the occurrence of one or more dominant organisms that occupy a certain depth in a location (Goreau 1959; Sheppard 1982; Done 1983). For instance, zonation patterns in shallow forereef slope communities are described as being predictably dominated by structurally robust species. Coral species exposed to high light regimes and large temperature fluctuations on shallow areas of the reef slope have adapted morpho-physiologically to this dynamic environment (Titlyanov and Titlyanova 2002; Iglesias-Prieto et al. 2004; Marcelino et al. 2013; Guest et al. 2016). Often prone to high exposure to wave and surge energy (Done 1983), some shallow water species are adapted to thrive in areas where frequent sediment resuspension occurs, forming robust morphologies which can resist high water flow and physical forces (Todd 2008; Duckworth et al. 2017). In contrast, deeper forereefs which are more sheltered from surface wave exposure and receive lower irradiance due to light attenuation with depth (Done 1983; Rex et al. 1995), are characterised by coral communities that frequently adopt encrusting and foliose growth forms to increase light capture efficiency (Titlyanov and Titlyanova 2002; DiPerna et al. 2018a). There is also an increase in mixotrophic and heterotrophic traits in marine organisms, such as hard corals, soft corals and sponges to offset limited light availability in deeper reef zones (Fabricius and Klumpp 1995; Fabricius and De'ath 2008; Houlbrèque and Ferrier-Pagès 2009).

Our understanding of the consistency of how coral reef benthic communities vary spatially across depths remains unclear (Edmunds and Leichter 2016; Roberts et al. 2019). This may be due to the complex interactive effects of biophysical processes that drive ecological community structure, which vary across multiple spatial and temporal scales (Hatcher et al. 1987; Magurran 2004; Leibold and McPeek 2006; Vellend 2010; Brandl et al. 2019), resulting in highly heterogenous coral reef communities (Edmunds and Bruno 1996; Huntington and

Lirman 2012; Obura 2012; Dalton and Roff 2013; McClanahan et al. 2014; Ford et al. 2020). In addition, much of our current understanding of depth zonation patterns on reefs is based on observations made decades ago (Goreau 1959; Done 1982; Sheppard 1982; Done 1983), prior to subsequent climate change impacts that have altered coral reef communities (Dubinsky and Stambler 2010; Williams et al. 2019).

Coral reefs around the world are increasingly vulnerable to more intense and frequent climate-driven disturbances (Anthony 2016; Hughes et al. 2017, 2018; Perry and Alvarez-Filip 2019). However, the extent at which coral reefs are affected by anthropogenic stressors is not uniform across space and varies across depths (Bongaerts et al. 2010; Bridge et al. 2013; Baird et al. 2018). Examining depth zonation of benthic communities in the context of systemic disturbance has provided important insights into complex dynamics such as diverging ecological trajectories and regime shifts, but these studies have been generally limited to shallow (3–10 m) depth ranges (Graham et al. 2015; Gouezo et al. 2019). This focus on shallow depth ranges has limited our understanding of how benthic community composition change across different depths within contemporary shallow tropical reefs (<30 m) (Bridge et al. 2014; Edmunds and Leichter 2016).

Here we examined depth zonation in benthic community composition at two spatial scales (among and within atolls) in the Chagos Archipelago, a relatively isolated reef system in the Central Indian Ocean, prior to pan-tropical bleaching events in 2014–2017 (Eakin et al. 2019) and post 1998 bleaching (Sheppard 1999a). Isolated reefs can be used an ecological reference point (Sandin et al. 2008; Smith et al. 2008; Williams et al. 2013; Heenan et al. 2017; Head et al. 2019) and examining benthic communities, prior to the back-to-back bleaching event in 2014–2017, establishes a baseline to measure the extent of further climate change impacts and how these vary across depths. Specifically, we compare benthic composition among and within four atolls, between two depth ranges: 5–10 m and 20–25 m on the forereef slopes. With our current knowledge of depth dependent zonation on coral reefs (Done 1982; Sheppard 1982; Done 1983), we expected to find zonation across depth in benthic community composition that was consistent amongst atolls.

2. Methods

2.1 Study sites

The Chagos Archipelago is located in the centre of the Indian Ocean, at the remote southern end of the Laccadives-Maldives-Chagos ridge, ~500 km from south of Maldives (Sheppard 1999b). The archipelago is comprised of 5 atolls, 52 islands, and constitutes 9400 km^2 of submerged shallow reefs (<40 m depth) (Dumbraveanu and Sheppard 1999; Sheppard et al. 2013a). The archipelago has been largely uninhabited since the early 1970s (Sheppard, 1999), with the exception of Diego Garcia (DG), the southern-most atoll that hosts a US naval facility, where strict environmental regulations are enforced, prohibiting all commercial fishing and extractive activities at sea (Purkis et al. 2008). In this study, a total of 26 sites; including 13 at 5–10m depth (hereafter 'shallow' reefs) and 13 at 20–25m depth (hereafter 'deep' reefs), were surveyed on forereef slopes across 4 atolls: Peros Banhos (PB), Salomon (SA) (northern atolls), Great Chagos Bank (GCB) and Egmont (EG) (southern atolls) (Figure 1, Table S1).

2.2 Benthic composition

At each site, benthic composition was quantified from 30 digital photo-quadrats taken in February and March 2013 (total across all sites, n = 780). Digital photo-quadrats were randomly extracted as still images from 10 min continuous video-swims at both 5–10 m and 20–25 m depths. The housing was equipped with two spotlights and two red laser pointers set at 10 cm apart to provide a consistent scale-measurement of the benthos and to adjust for lower-light levels at greater depth to facilitate benthic image analysis. The camera was maintained approximately 0.5 m above the substrate and at a 45° angle to capture benthic organisms under overhangs and canopies (Goatley and Bellwood 2011).

Each video was converted into an image sequence (25 frames per sec; in Pinnacle Studio, v22.2.0). To ensure that images selected for analysis did not contain the same section of the forereef, frames were randomly selected, but separated by a minimum of 80–100 frames (Matlab, R2018a.Ink). Benthic image analysis was carried out by SSP, RR, and LR using Coral Point Count with excel extensions (CPCe) (Kohler and Gill 2006) . To account for any variation in observer bias in identification of benthic composition, the frames were equally divided

among observers and analysed (10 images each per person per site). Proportional cover of benthic categories was quantified by identifying substrate and benthic organisms under fifteen randomly allocated points on each image, with one point assigned within a 3 x 5 grid cell stratification (Suchley 2014).

Substrate type and benthic organisms were categorised as: hard coral (identified to genus), soft coral (identified to family), non-scleractinian coral (*Millepora, Heliopora* and *Distichopora*), sponge, crustose coralline algae (CCA), macroalgae, turf algae, bare substrate with algal film (hereafter bare substrate), sand, rubble (< 10 cm maximum length), dead coral, bleached coral, diseased coral, 'other live' and unknown. 'Other live' included all sessile invertebrates such as bryozoans, tunicates, bivalves, giant clams, corallimorphs, anemones and zoanthids. Soft corals were identified and grouped within the four most common families occurring in the archipelago – Alcyoniidae, Xeniidae, Nepthtiidae and Nidaliidae (Schleyer and Benayahu 2010), or other soft coral. Where image quality limited identification of hard corals to genus level or morphology (approximately 0.1–0.5%), corals were classified as 'other'. The classification of benthic categories for this study was based on NOAA Coral Reef Information System (2014), Dennis et al, (2017) and the CATAMI classification system (Althaus et al. 2015).

2.3 Data analysis

To assess whether benthic composition varied across depths, and if depth zonation varied among atolls, benthic community composition was first visualised at two levels: 1) proportional cover of major functional groups (hard coral, soft coral, sponge, CCA, macroalgae, turf algae, bare substrate with algal film, sand and rubble, non-scleractinian coral, bleached coral, dead coral, diseased coral, 'other live'), and 2) proportional cover of hard coral assemblages, identified to genera. Benthic composition was visualised across: a) depth, and b) atoll, using non-metric Multidimensional Scaling (nMDS: vegan package; Oksanen et al., 2012), based on a Bray-Curtis dissimilarity matrix of square root transformed data. A scree plot was used to evaluate ordination stress and a Shepard stress plot to confirm correlation between the original dissimilarity matrix and the distances on the final nMDS plot. The nMDS was computed on 3 dimensions (k = 3) with a stress value ≤ 0.1. The envfit function (vegan

package) was used to fit vectors of major functional groups and coral genera, to their respective nMDS ordinations.

To assess differences in benthic composition across depth and atolls, we performed two-way nested permutational multivariate analyses of variance (PERMANOVA; Anderson 2017) on: 1) major functional groups, and 2) coral genera, as a function of the interaction between atolls (4 atolls; fixed factors) and depths (2 depths; fixed factors), with sites (random factors) nested in atoll (9999 permutations; adonis2 function: vegan package). Average within-group dispersion was examined using a multivariate homogeneity test (betadisper: vegan package). Where a significant interaction between depth and atoll was found, we tested for variation in 1) major functional groups, and 2) coral genera across depths at each individual atoll using one-way nested PERMANOVAs. Data were square-root transformed and analysed using Type III sum of squares to accommodate an unbalanced design, in both one-way and two-way PERMANOVA.

Indicator taxa analyses were used to determine the association between coral genera and the depth ranges at which they occur. Coral genera that significantly associated with shallow and deep reefs across each atoll, were used to infer on the biotic and abiotic state of the environment that prevail at the different depth ranges (Cáceres and Legendre 2009). Prior to analysis, the proportional cover matrix of the coral genera assemblage was converted into presence/absence data. Coral genera characteristic of shallow and deep reefs were identified using a p-value threshold of <0.05 (9999 permutations, indicators: indicspecies package; Cáceres 2020).

Generalised linear mixed-effects models (GLMMs) with a binomial distribution and logit-link function were used to model major functional groups within each atoll, treating depth as a fixed effect and sites as a random effect (glmer: lme4 package, Bates et al. 2015). GLMMs were also performed on coral genera that consistently characterised the hard coral assemblage across both depths and all atolls. When major functional groups or coral genera cover had a high number of zeros and did not fit the standard binomial distribution ($>$ 55% of the data consisted of zero values), a zero-inflated generalised linear mixed-effect models with a beta distribution was fitted (depth as a fixed factor and sites as a random factor; glmmtmb: glmmTMB package; Brooks et al. 2017). All analyses were performed using R 3.5.1 (R Development Core Team 3.5.1, 2018).

3. Results

3.1 Variation in major functional groups

Within-atoll analyses revealed significant variation in major functional groups between shallow and deep reefs across all four atolls (PERMANOVA, all: p =0.001, Table 1). There was also an interactive effect of depth and atoll (PERMANOVA, Pseudo $F_{3, 779}$ = 13.54, p = 0.001) and dispersion (Table S4) on benthic composition, indicating the variation in major functional groups between depth varied among atolls; notably at EG and PB (Table 1, Table S5a).

A decreasing hard coral, bare substrate and dead coral cover was observed with increasing depth compared to CCA, macroalgae, sand and rubble and sponge cover which increased on the deep forereef slopes at EG (Table 1b). At PB, hard coral and dead coral cover also decreased with depth compared to sand and rubble, sponge, soft coral and turf algae cover which increased on the deep forereef slopes (Table 1b). At GCB, only dead coral cover varied significantly with depth (Table 1b). At SA, macroalgae and 'other live' cover increased significantly with depth while dead coral showed a significant decrease with increasing depth (Table 1b).

3.2 Variation in hard coral assemblage

Thirty-seven coral genera were recorded across all sites, with a higher number of coral genera were recorded at deep reefs (34) than shallow reefs (23). SA contained the highest coral genera richness (29), followed by GCB (22 genera), PB (20 genera) and EG (16 genera). Within-atoll variation revealed significant differences in hard coral assemblages between depths (PERMANOVA, all: p =0.001, Table 2a). However, significant depth-by-atoll interactions (PERMANOVA, Pseudo $F_{3, 650}$ = 7.40, p = 0.001; Figure S1) and dispersion (Table S4), indicate the variation in hard coral assemblages between depth varied among atolls across the archipelago, particularly at SA and PB (Table S5b).

Indicator taxa analyses identified a total of 14 coral genera as well as the 'other' category that characterised the hard coral community across all atolls and depth combinations

(Table 3). A higher number of coral genera (10) characterised the deeper reefs than the shallow reefs (6). Coral genera significantly associated with shallow reefs in EG were *Acropora*, *Porites* and *Pocillopora*. Coral genera significantly associated with deep reefs in EG were *Favia*, *Pachyseris* and *Pavona*. *Porites* was the only genus that significantly characterised the shallow reefs in GCB. The hard coral assemblage on deep reefs in GCB was characterised by *Acropora*, *Echinopora*, *Pachyseris* and *Symphyllia*. The shallow reefs of both northern atolls, PB and SA were characterised by *Acropora*, *Pocillopora*, *Porites* and *Stylophora*. The only coral genus that significantly associated with the deep reefs in PB was *Tubastrea*. In SA, the hard coral community on deep reefs was characterised by *Acanthastrea*, *Goniastrea*, *Montipora*, *Pachyseris* and *Seriatopora* (Table 3).

Acropora and *Porites* were the only genera that were consistently associated with both depths across all atolls. Univariate analyses showed that the cover of *Acropora* decreased with increasing depth at EG and SA (Table 2b). Increasing depth also had a negative effect on the cover of *Porites* at EG and PB (Table 2b).

4. Discussion

Our results showed the variation in the benthic community structure of the Chagos Archipelago was driven by significant depth-by-atoll interactions. Although the zonation patterns of the benthic community varied across atolls, a distinct contrast was observed between shallow (5–10 m) and deep (20–25 m) communities, both in terms of the major functional groups and hard coral assemblages, within each atoll. Several earlier coral reef studies report predictable vertical zonation in benthic communities and hard coral assemblages (e.g. Goreau 1959; Done 1982, 1983; Sheppard 1982). However, the among-atoll variation in depth effect observed in this study is consistent with recent research documenting spatial heterogeneity in tropical reefs (Edmunds and Bruno 1996; Williams et al. 2013; Edmunds and Leichter 2016; Karisa et al. 2020; Ford et al. 2020). Spatial variation in depth zonation may be indicative of local biophysical gradients at each atoll that are interacting with depth to structure benthic assemblages (Whittaker 1972; Reice 1994; Vellend 2010). Physical variables that co-vary with depth, such as light (Edmunds et al. 2018), wave exposure (Williams et al. 2013; Gove et al. 2015), reef slope (Sheppard 1982), seasonal thermocline (Kahng and Kelley 2007),

resource availability (Fox et al. 2018; Williams et al. 2018), internal wave activities (Leichter and Salvatore 2006; Radice et al. 2019), and disturbance history, e.g. storms (Hughes and Connell 1999) and climate-induced bleaching events (Bridge et al. 2013, 2014; Adjeroud et al. 2018), have been shown to influence reef communities.

The distinct variation in benthic composition across depth within each atoll, is comparable to changes with depth in several other Indo-Pacific locations: Central Pacific Kingman and Palmyra atoll (Williams et al. 2013), French Polynesia (Edmunds and Leichter 2016), New Caledonia (Adjeroud et al. 2019), the Maldives (Ciarapica and Passeri 1993), and Kenya (Karisa et al. 2020). Coral genera that consistently associated with shallow reefs were *Acropora*, *Pocillopora* and *Stylophora*. These coral genera frequently exhibit arborescent and bushy morphologies in shallow areas (Sheppard 1982) and have better light-scattering properties (Titlyanov and Titlyanova 2002; Marcelino et al. 2013). They are therefore better adapted to the high light regimes that can be experienced in shallow reef environments (Hoegh-Guldberg and Jones 1999; Winters et al. 2003). These species also have effective mechanisms, such as polyp inflation, tentacular action and mucus production to shed sediment particles that are resuspended due to wave action (Erftemeijer et al. 2012; Duckworth et al. 2017) at highly exposed shallow reefs (Fulton et al. 2001).

Pachyseris, Pavona, Echinopora, Acanthastrea, Goniastrea, Montipora and *Symphyllia* were characteristic of the hard coral assemblage on deep reefs. These coral genera frequently adopt foliose, encrusting and massive growth forms on deeper forereef slopes (Sheppard 1982). As irradiance levels decrease with increasing depths, morphological adaptations including the development of larger surface areas, such as foliose and encrusting growth forms, help increase efficiency in light capture to optimise photosynthetic activities (Done 1983; DiPerna et al. 2018b). Foliose and massive species also contain higher densities of photosynthetic dinoflagellates *(Symbiodinium)* for maximising food production in low light regimes (Li et al. 2008). Many of the deeper dwelling massive and sub-massive species exhibit heterotrophic traits; with larger polyp sizes and longer tentacles to allow energy requirements to be met by zooplankton feeding (Hoogenboom et al. 2015; Tremblay et al. 2015). The occurrence of the azooxanthellate *Tubastrea* as a characteristic coral genera across the deep overhangs of the northern atoll, PB (Andradi-Brown et al. 2019) provides evidence of the presence of highly productive waters in the area. We hypothesise that that the deeper forereef

areas of the archipelago are more likely recipient of cooler, nutrient-rich upwelling waters than shallow reef areas (Sheppard 2009; Sheppard et al. 2017).

Acropora and *Porites* characterised both shallow and deep forereef slopes across all atolls. Previous studies in the Chagos Archipelago have also highlighted the dominance of these two coral genera at both shallow and deep forereef slopes (Sheppard et al. 2008). These typically depth generalist genera contain large numbers of species (Veron et al. 2019) that have different physiological and phenotypical traits which give them the ability to persist in diverse environments across depth gradients (Toda et al. 2007; Darling et al. 2012). Both genera have high larval dispersion rates facilitating settlement across depths (Holstein et al. 2016; Serrano et al. 2016). *Acropora* and *Porites* have been found to host diverse endosymbionts to optimise photosynthesis in decreased light (Muir et al. 2015; Ziegler et al. 2015; Tan et al. 2020). *Acropora* are often characterised as a fast growing weedy species which have overtopping abilities and can encroach neighbouring species (Riegl and Purkis 2009). *Porites* with massive morphologies can grow taller and larger, and physically outcompete other surrounding species (Potts et al. 1985).

Increasing depth had a positive effect on turf algae at PB and CCA cover at EG. Several previous studies have found that turf algae and CCA were more abundant in shallow reef environments (Williams et al. 2013; Marlow et al. 2019; Karisa et al. 2020). The high cover of turf algae and CCA we observed at deep forereef slopes of the Chagos Archipelago may be related to the grazing pressure across depth (Heenan and Williams 2013). Intensive herbivory promotes the removal of epiphytic turf algae (Rasher et al. 2012; Osuka et al. 2018; Roff et al. 2019) and provides space for the growth of the rapid colonising CCA (Airoldi 2000; Russell 2007). Within EG, high grazing intensity coupled with elevated herbivore and excavator biomass between 8–17 m, were associated with CCA dominated habitats on forereef slopes (Samoilys et al. 2018; Sheppard et al. 2013b). A lower biomass of herbivorous fishes has also been reported on the deeper forereefs of the Chagos Archipelago (Andradi-Brown et al. 2019), which could potentially explain the observed higher turf cover on the deep reefs of PB.

Among all measured major functional groups, dead coral was the only group which had consistently higher cover in shallow forereef slopes across all atolls. During the 1998 massive bleaching events, all shallow ocean-facing reefs in the Chagos Archipelago were highly impacted, leaving large quantities of dead corals (Sheppard, 1999). Several subsequent

bleaching events in shallow waters in the 2000s also resulted in localised mortality (Harris and Sheppard 2008; Sheppard et al. 2008), which may have inhibited recruitment and growth, explaining the higher dead coral cover at 5–10m across the archipelago.

Soft coral and sponge cover increased with depth, notably at EG and PB. Previous findings in Indo-Pacific reef systems (Reichelt et al. 1986; Barnes and Bell 2002), including the Chagos Archipelago (Sheppard 1981; Schleyer and Benayahu 2010) show similar increase in soft coral and sponge cover with depth. Sponges and soft corals species have phototrophic, heterotrophic and mixotrophic abilities (Wilkinson 1983; Fabricius and Klumpp 1995). Their high cover in deeper forereef can result from photoadaptation of autotrophic species to increased depths (Fabricius and De'ath 2008; Shoham and Benayahu 2017). Mixotrophic and heterotrophic sponges and soft corals can feed from large flows of inorganic nutrients that are delivered by cold water upwelling and/or internal waves that occur on deeper reef sites (Lesser 2006; Pupier et al. 2019). Deep steep walls are also less prone to sedimentation creating favourable habitat for octocorals (Bridge et al. 2011). Accentuated by the steep walls of deep sites of PB (Sheppard 1980; Winterbottom et al. 1989), deep rich waters may upregulate heterotrophic feeding in soft corals and sponges, explaining the observed higher cover in its deep forereef slopes (Schleyer and Benayahu 2010; Sheppard et al. 2013b).

It is important to understand the reef community composition of the Chagos Archipelago in the context of disturbances that have affected its reefs. Classic ecological theories suggest that following a disturbance, communities undergo secondary succession (Horn 1974). A major disturbance event prior to 2013 was the pan tropical bleaching event in 1998 (Wilkinson et al. 1999). Previous studies provided evidence that the benthic community of the Chagos Archipelago has transitioned through different successional stages since the 1998 bleaching event. A recovery occurred from minimal hard coral cover (~12% in 1999; Sheppard, 1999) to a coral-dominated community where no significant divergence was apparent in 2012, relative to the pre-1998 community (Sheppard et al. 2008, 2013b). Despite the overall reassembly towards a coral-dominated reef, there was significant variability in benthic community recovery, across depths and atolls (Sheppard et al. 2008). In 2001, less degradation was observed in deep sites of the northern atolls (PB and SA) (high mortality observed at <10–15 m) while the southern atolls (GCB and EG) showed significant mortality at depths >35 m (Sheppard et al. 2002). In 2006, the hard coral assemblages in shallow sites (4–10 m) recovered

faster than deep forereef slopes (20–25 m) across PB, SA and GCB, with the exception of EG where no recovery was observed at either depth (Sheppard et al. 2008). In 2012, a general decrease in hard coral cover and increase in sponge and soft coral cover could be observed with increasing depth (5–25 m) across the archipelago (Sheppard et al. 2013b). This rapid recovery in shallow sites (8–10 m) may be driven by the high growth rates in *Acropora*-dominated shallow communities within the archipelago (Perry et al. 2015).

Our results reveal the spatial variation in depth zonation of benthic communities, potentially linked to previously described biophysical gradients occurring across these depths and atolls (Sheppard 2009; Fasolo 2013; Sheppard et al. 2017). These benthic community data from 2013 will provide insights into the impact of the 2014–2017 back-to-back bleaching events as well as subsequent recovery. It is becoming more important to understand the spatial variability in reef ecosystems in order to infer and predict how communities might respond to the effects of increasing disturbances (Bridge et al. 2014; Hughes et al. 2019). There is therefore a need to incorporate spatial variation in depth effect within ecological studies, as contemporary shallow reefs are changing rapidly across depths.

Author contributions

Sivajyodee S Pilly: Conceptualization, Formal analysis, Validation, Data curation, Writing- Original draft preparation, Writing – Review and Editing, Visualisation. **Laura Richardson, Ronan Roche**: Validation, Writing – Review and Editing. **John Turner, Ronan Roche**: Methodology, Investigation, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

All authors have seen and approved the final version of the manuscript being submitted. We confirm that this manuscript has not been published nor been considered elsewhere, and declare they have no conflict of interest (see submitted form).

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Figure list Click here to access/download;Figure;MER_Fig_captions.docx

List of figures:

Figure 1.EPS: Map of Chagos Archipelago showing sampled sites (red points) around surveyed atolls (in bold) – northern atolls: Peros Banhos (PB), Salomon (SA) and southern atolls Great Chagos Bank (GCB) and Egmont (EG) - see Table S1 for list of sites and coordinates.

Figure 2.EPS: Non-metric dimensional scaling (nMDS) of a) major functional groups (left) and b) coral genera assemblage (right), showing clustering by depths, based on Bray-Curtis dissimilarities of square-root transformed data in a total of 26 sites in the Chagos Archipelago. Coloured ellipses represent dispersion of depth centroids at 95% confidence limit – blue: shallow sites (5–10 m) and red: deep site (20–25 m). Symbols represent surveyed atolls – Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA). *Bottom*: Vectors represent a) major functional groups (left) and b) coral genera (right) distribution to the patterns on the ordination plot. Red labels in (a) indicate a significant contribution and black labels indicate a non-significant contribution

Figure 3.EPS: Variation in major functional groups (generalised linear mixed effects models) between depth (5–10 m (grey) and 20–25 m (black)) across atolls - Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA) in Chagos Archipelago 2013. * represent $p < 0.05$ (see Table S2)

Figure1

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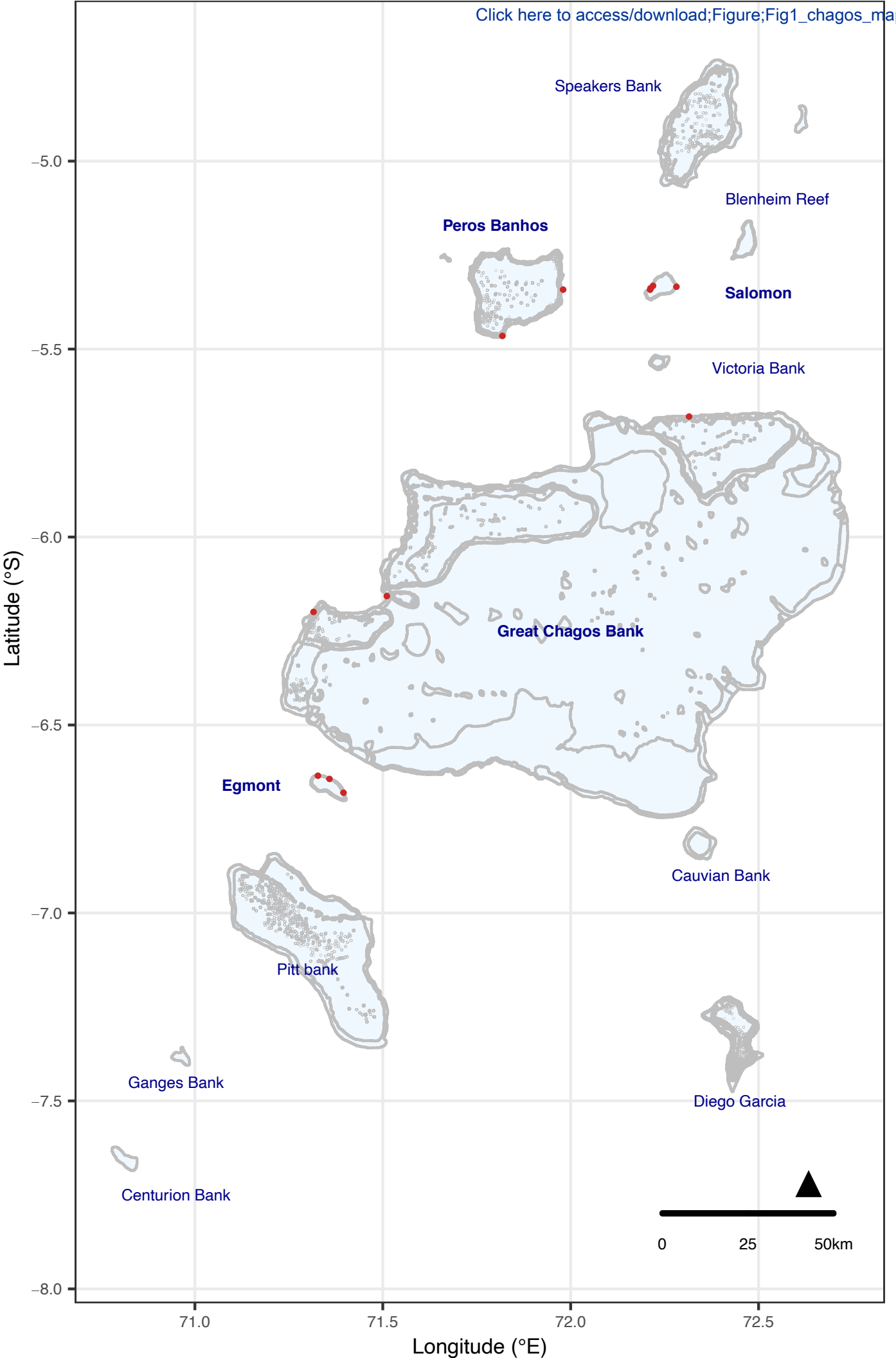

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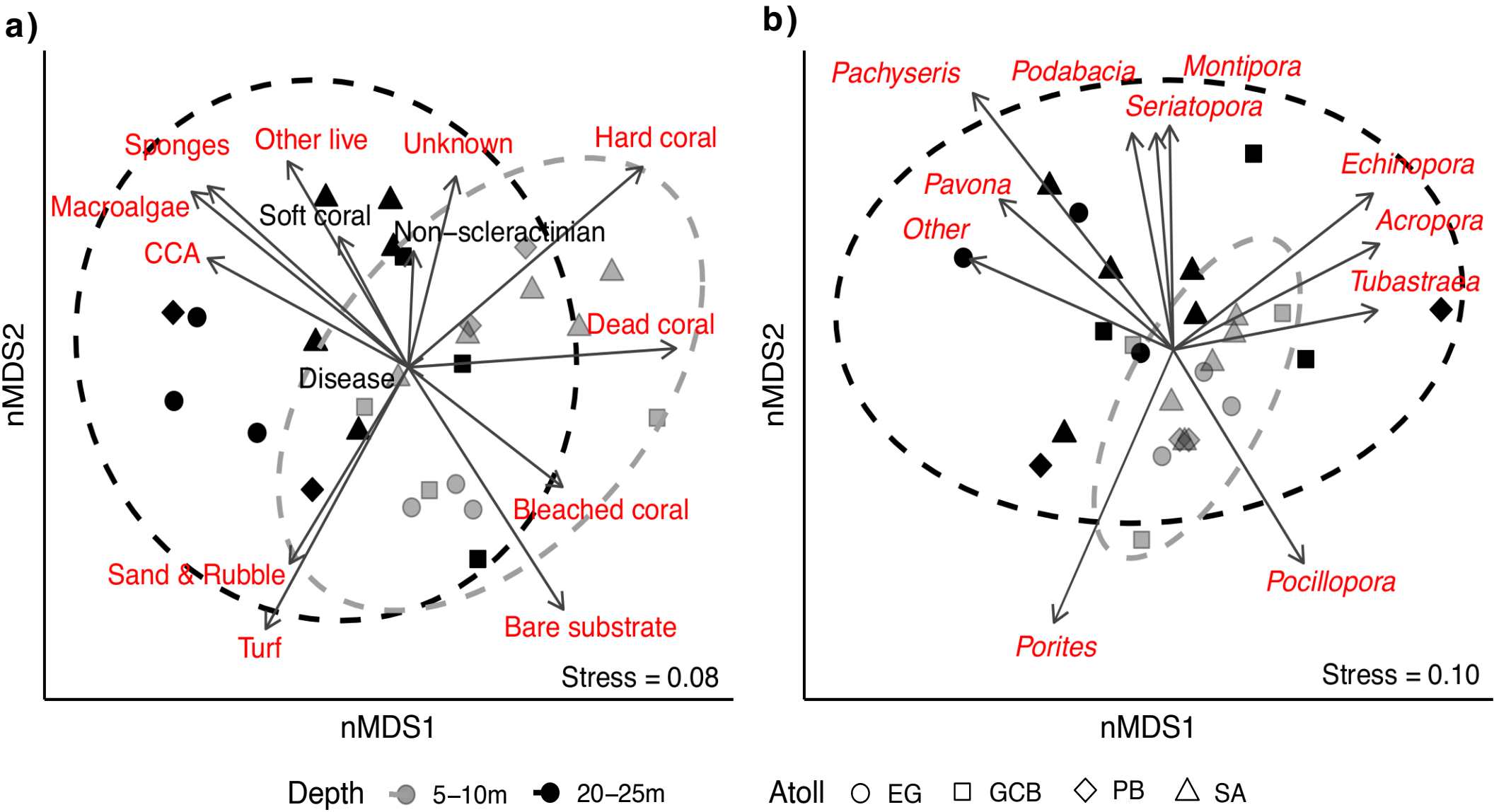

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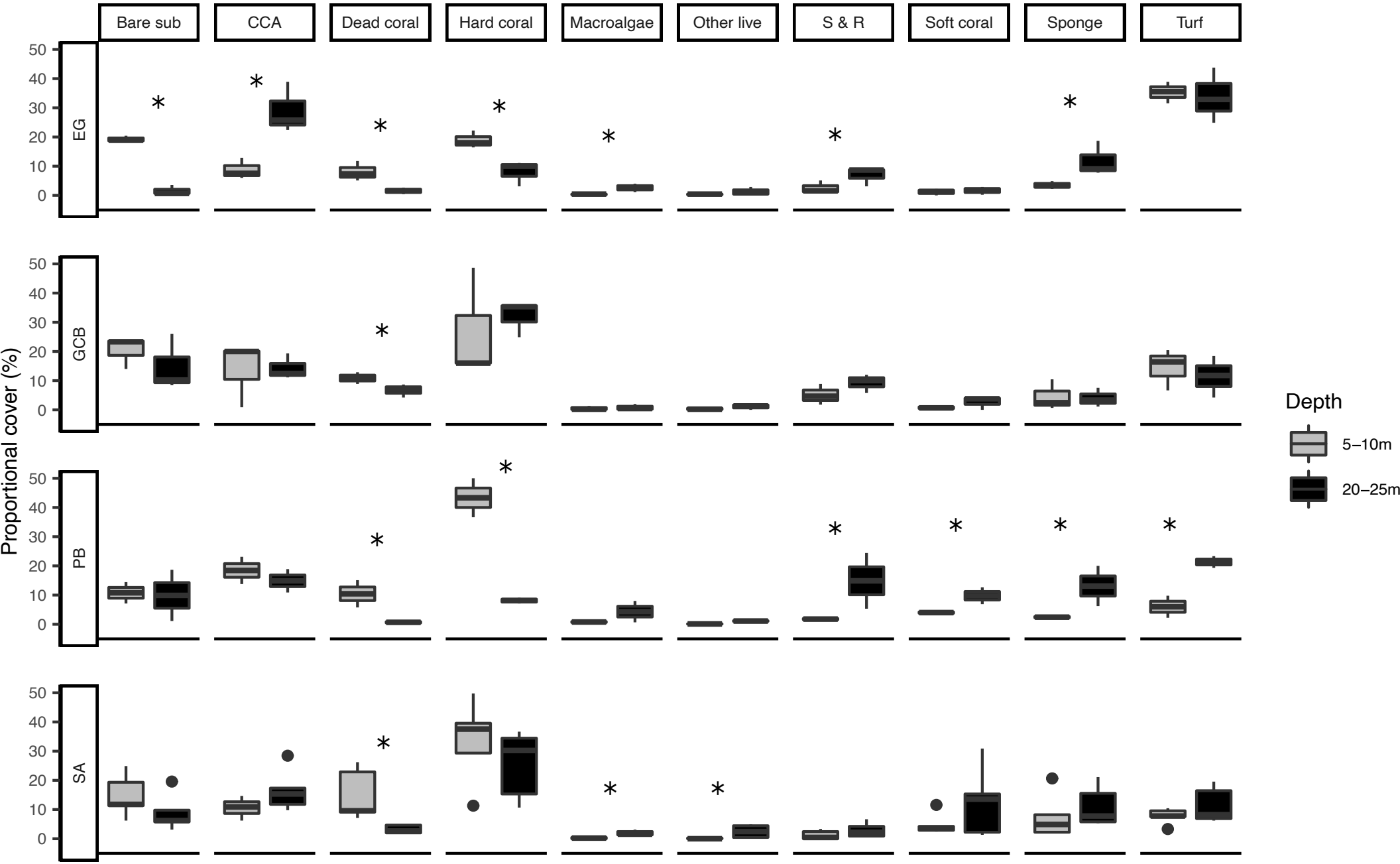

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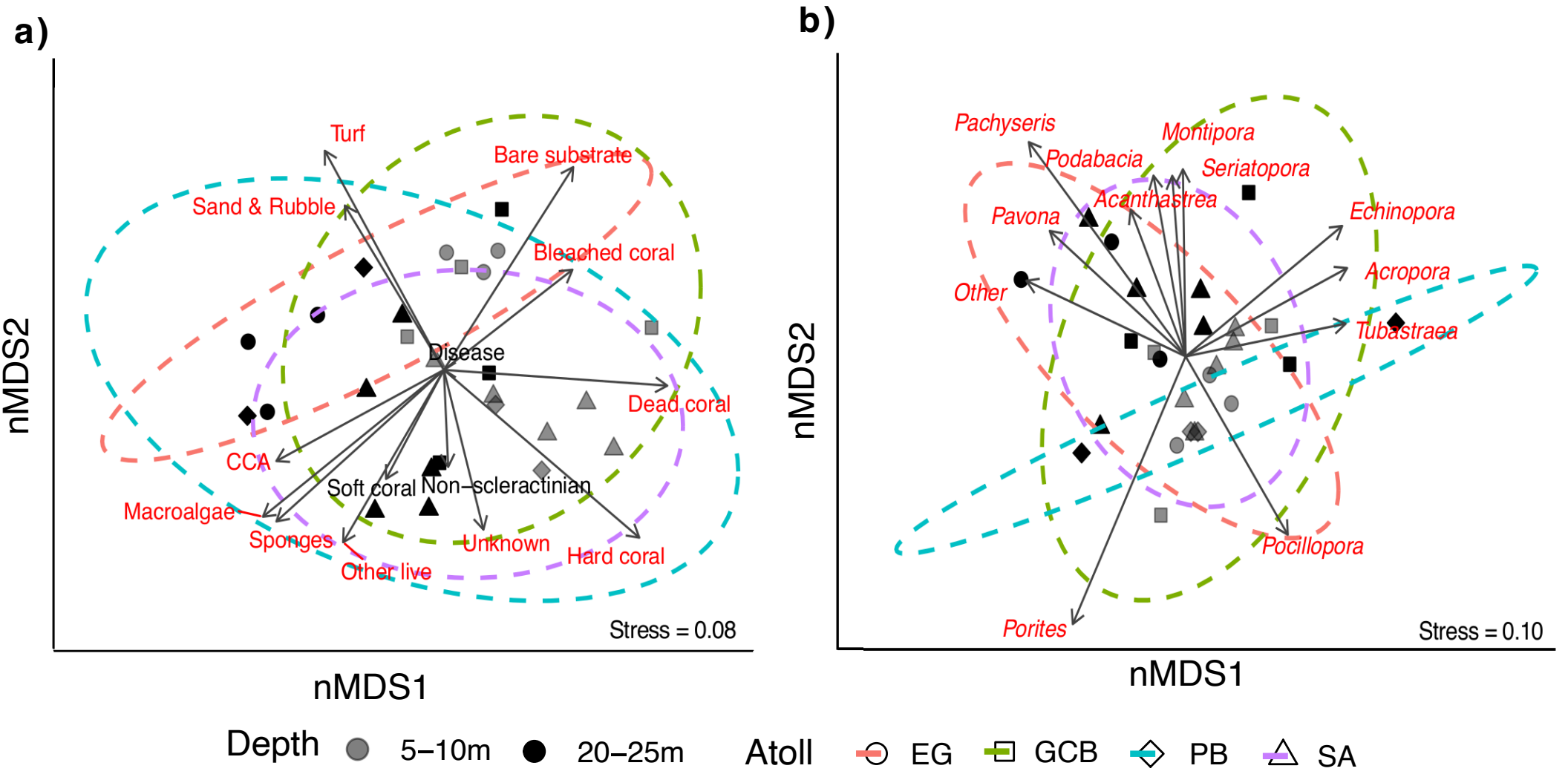

FigureS2

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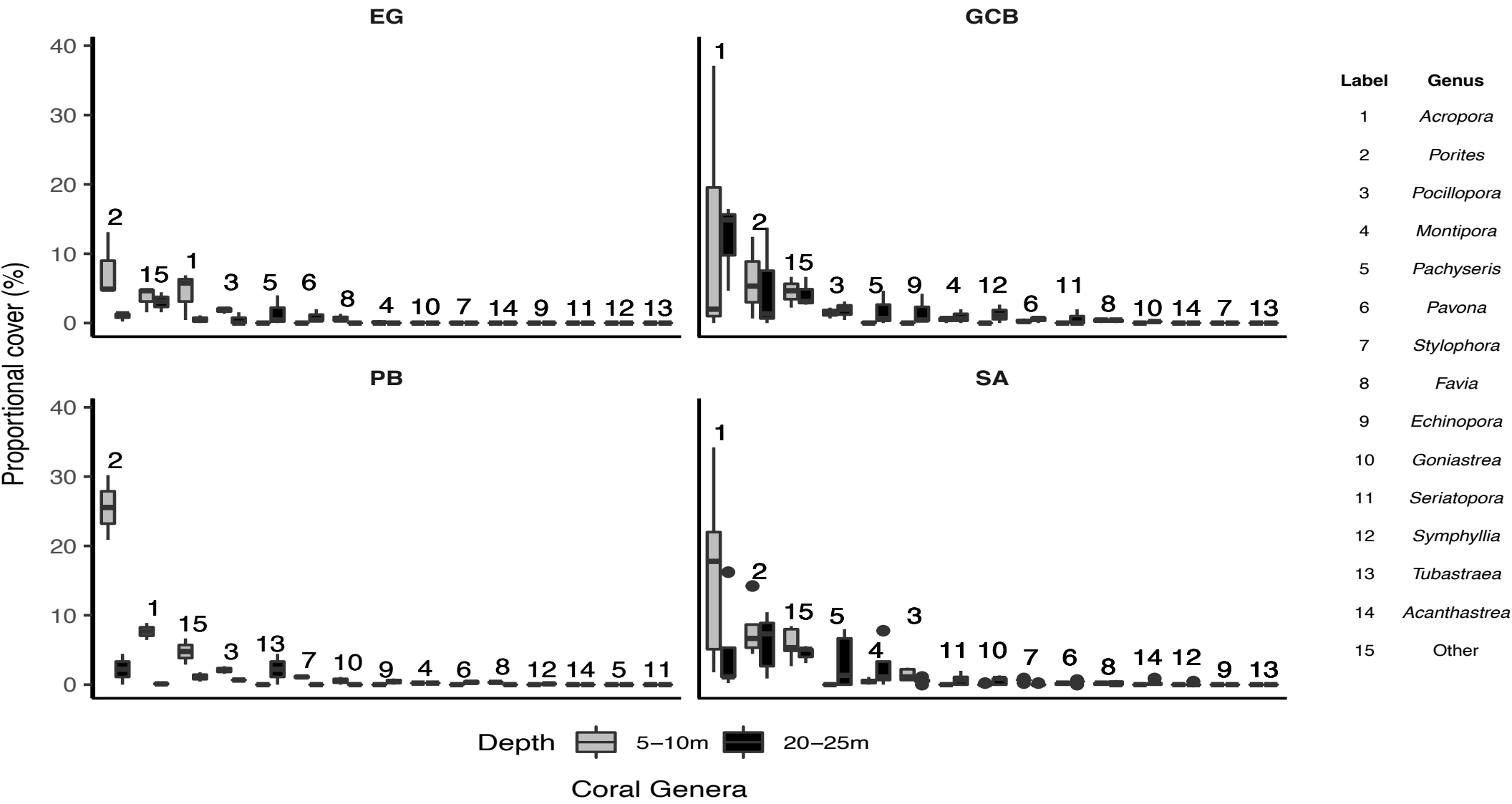

Label	Genus
1	*Acropora*
2	*Porites*
3	*Pocillopora*
4	*Montipora*
5	*Pachyseris*
6	*Pavona*
7	*Stylophora*
8	*Favia*
9	*Echinopora*
10	*Goniastrea*
11	*Seriatopora*
12	*Symphyllia*
13	*Tubastraea*
14	*Acanthastrea*
15	Other

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List of tables:

Table 1: Variation in major functional groups between depth (5–10m vs 20–25m) on a) multivariate scale (One-way permutational analysis of variance (PERMANOVA) and b) on a univariate scale (generalised linear mixed effect models (GLMM)) within atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA) in the Chagos Archipelago in 2013. BS – Bare substrate, CCA – crustose coralline algae, HC – hard coral, MA – macroalgae, DC- dead coral, OL – other live, SR – sand and rubble, SP – sponge, T – turf, BL – bleached coral, UK – unknown, NS – non-scleractinian coral. In bold are significant p values. df- degree of freedom

a)

Atoll	PERMANOVA		
	PseudoF-ratio	df	p-value
EG	46.844	1, 179	**<0.001**
GCB	5.156	1, 179	**<0.001**
PB	48.943	1, 119	**<0.001**
SA	28.208	1, 229	**<0.001**

b)

Atoll		GLMM												
		BS	CCA	HC	MA	DC	OL	SR	SC	SP	T	BL	UK	NS
EG	Coeff	0.628	-1.464	1.052	-2.189	1.742	-1.269	-1.158	-0.393	-1.294	0.078	-	0.032	-
	SE	0.210	0.287	0.322	0.607	0.397	1.009	0.521	0.865	0.340	0.215		0.461	
	p-value	**0.003***	**<0.001**	**0.001**	**<0.001**	**<0.001**	0.209	**0.026**	0.650	**<0.001**	0.717		0.946	
GCB	Coeff	0.466	-0.573	-0.356	-0.456	0.5418	-1.122	-0.733	-1.021	-0.105	0.321	0.321	0.740	-
	SE	0.384	0.867	0.461	1.204	0.189	0.978	0.418	0.991	0.819	0.499	0.499	1.153	

	p-value	0.225	0.509	0.440	0.705	**0.004**	0.251	0.079	0.303	0.898	0.520	0.193	0.521	
PB	Coeff	0.732	0.260	2.165	-1.399	2.864	-0.359	-2.096	-0.944	-1.698	-1.622	-	0.088	-
	SE	1.092	0.320	0.244	1.035	0.657	0.624	0.710	0.293	0.543	0.519		0.167	
	p-value	0.503	0.416	**<0.001**	0.176	**<0.001**	0.566*	**0.003**	**0.001**	**0.002**	**0.002**		0.589*	
SA	Coeff	0.642	-0.490	0.398	-2.119	1.628	-2.966	-1.292	-0.698	-0.624	-0.395	-	0.150	-0.791
	SE	0.392	0.252	0.418	0.516	0.357	0.948	0.840	0.650	0.509	0.303		0.335	1.983
	p-value	0.101	0.052	0.341	**<0.001**	**<0.001**	**0.002**	0.124	0.283	0.221	0.192		0.654	0.690

'-' could not compare as groups did not occur at both depths, '*' zero inflated model using GLMMTMB

Table 2: Variation in the hard coral assemblage between depth on a) multivariate scale (One-way permutational analysis of variance (PERMANOVA) and b) variation in common indicator coral genera on a univariate level (generalised linear mixed effect models (GLMM)) within atolls: Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA) in the Chagos Archipelago in 2013. In bold are significant p values. * indicate where zero-inflated generalised mixed effect models were performed. df – degree of freedom, Coeff- coefficient estimates, SE- Standard error.

a)

Atoll	PERMANOVA		
	PseudoF-ratio	df	p-value
EG	17.016	1, 116	**<0.001**
GCB	6.494	1, 160	**<0.001**
PB	25.461	1, 95	**<0.001**
SA	15.150	1, 276	**<0.001**

b)

Variable	Atoll	Effect	Coeff	SE	z-statistics	p-value
Acropora	EG	Intercept	-5.636	0.758	-7.437	<0.001
		Depth	2.145	0.972	2.208	**0.027**
Porites		Intercept	-4.725	0.397	-11.900	<0.001
		Depth	2.113	0.493	4.290	**<0.001**
*Pocillopora**		Intercept	-1.647	0.239	-6.886	<0.001
		Depth	-0.285	0.269	-1.058	0.290
Other		Intercept	-3.518	0.267	-13.183	<0.001
		Depth	0.197	0.369	0.533	0.594

Acropora	GCB	Intercept	-2.137	1.101	-1.941	0.052
		Depth	-1.607	1.608	-0.999	0.318
Porites		Intercept	-4.339	1.090	-3.981	<0.001
		Depth	1.062	1.490	0.713	0.476
Pocillopora		Intercept	-4.076	0.340	-12.006	<0.001
		Depth	-0.192	0.475	-0.405	0.686
Other		Intercept	-3.205	0.261	-12.297	<0.001
		Depth	0.090	0.365	0.248	0.804
*Acropora**	PB	Intercept	-2.245	0.776	-2.891	0.004
		Depth	0.491	0.783	0.627	0.531
Porites		Intercept	-4.719	1.041	-4.532	<0.001
		Depth	3.632	1.341	2.708	**0.007**
*Pocillopora**		Intercept	-1.344	0.259	-5.183	<0.001
		Depth	-0.707	0.294	-2.407	**0.016**
Other		Intercept	-4.563	0.430	-10.614	<0.001
		Depth	1.508	0.531	2.841	**0.004**
Acropora	SA	Intercept	-3.838	0.625	-6.146	<0.001
		Depth	1.771	0.865	2.047	**0.041**
Porites		Intercept	-2.980	0.313	-9.529	<0.001
		Depth	0.430	0.435	0.989	0.323
Pocillopora		Intercept	-5.288	0.338	-15.627	<0.001
		Depth	0.987	0.409	2.412	**0.016**
Other		Intercept	-3.056	0.151	-20.283	<0.001
		Depth	0.245	0.208	1.175	0.240

Table 3: Indicator coral genera at atolls- Egmont (EG), Great Chagos Bank (GCB), Peros Banhos (PB) and Salomon (SA) at shallow (5-10m) and deep (20-25m) sites. `A` represents the specificity of a genera as an indicator of the depth group, `B` is the fidelity of the genera as an indicator of the samples collected within the respective depth group and `sqrtIV` represents the square-root of the indicator value index. The lower and upper confidence interval (CI) were calculated using bootstrapping technique (Cáceres and Legendre 2009).

Atoll	Depth	Coral genera	A	Lower CI	Upper CI	B	Lower CI	Upper CI	sqrtIV	Lower CI	Upper CI	p-value
EG	5-10m	*Acropora*	0.842	0.643	1.000	0.178	0.089	0.267	0.387	0.239	0.475	0.001
		Favia	1.000	1.000	1.000	0.056	0.013	0.114	0.236	0.115	0.338	0.029
		Pocillopora	0.813	0.600	1.000	0.144	0.073	0.213	0.343	0.221	0.438	0.009
		Porites	0.844	0.737	0.930	0.600	0.482	0.700	0.712	0.610	0.785	0.0001
	20-25m	*Pachyseris*	1.000	1.000	1.000	0.056	0.011	0.096	0.236	0.103	0.318	0.028
		Pavona	1.000	1.000	1.000	0.089	0.037	0.149	0.298	0.191	0.391	0.004
GCB	5-10m	*Porites*	0.651	0.500	0.762	0.456	0.347	0.567	0.544	0.443	0.636	0.002
	20-25m	*Acropora*	0.594	0.479	0.710	0.456	0.347	0.564	0.520	0.419	0.615	0.034
		Echinopora	1.000	1.000	1.000	0.078	0.030	0.133	0.279	0.177	0.364	0.007
		Pachyseris	0.909	0.667	1.000	0.111	0.047	0.180	0.318	0.195	0.411	0.005
		Symphyllia	1.000	1.000	1.000	0.078	0.027	0.133	0.279	0.163	0.364	0.007
PB	5-10m	*Acropora*	0.970	0.893	1.000	0.533	0.404	0.640	0.719	0.628	0.796	0.0001
		Other	0.763	0.613	0.905	0.483	0.375	0.594	0.607	0.491	0.703	0.0001
		Pocillopora	0.846	0.600	1.000	0.183	0.089	0.274	0.394	0.242	0.513	0.008
		Porites	0.873	0.794	0.945	0.917	0.845	0.984	0.895	0.832	0.946	0.0001
		Stylophora	1.000	1.000	1.000	0.150	0.068	0.246	0.387	0.260	0.496	0.001
	20-25m	*Tubastraea*	1.000	1.000	1.000	0.217	0.120	0.328	0.465	0.346	0.573	0.0003
SA	5-10m	*Acropora*	0.696	0.600	0.766	0.580	0.497	0.660	0.635	0.552	0.703	0.0001
		Pocillopora	0.694	0.537	0.846	0.167	0.107	0.225	0.340	0.248	0.412	0.009
		Porites	0.573	0.488	0.655	0.473	0.390	0.556	0.521	0.450	0.588	0.021
		Stylophora	0.917	0.769	1.000	0.073	0.039	0.122	0.259	0.186	0.349	0.004

20-25m	*Acanthastrea*	1.000	1.000	1.000	0.033	0.006	0.070	0.183	0.083	0.270	0.032
	Goniastrea	0.917	0.714	1.000	0.073	0.033	0.115	0.259	0.163	0.330	0.004
	Montipora	0.727	0.595	0.865	0.160	0.105	0.216	0.341	0.259	0.418	0.005
	Pachyseris	1.000	1.000	1.000	0.147	0.086	0.195	0.383	0.292	0.442	0.0001
	Seriatopora	1.000	1.000	1.000	0.080	0.041	0.128	0.283	0.203	0.357	0.0002

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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