

Wave exposure shapes reef community composition and recovery trajectories at a remote coral atoll

Lange, Ines D.; Benkwitt, Cassandra E.; McDevitt-Irwin, Jamie M.; Tietjen, Kristina L.; Taylor, Brett; Chinkin, Mark; Gunn, Rachel L.; Palmisciano, Melissa ; Steyaert, Margaux; Wilson, Bry; East, Holly K.; Turner, John; Graham, Nicholas A.J.; Perry, Chris T.

Coral Reefs

DOI:
[10.1007/s00338-021-02184-w](https://doi.org/10.1007/s00338-021-02184-w)

Published: 01/12/2021

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):

Lange, I. D., Benkwitt, C. E., McDevitt-Irwin, J. M., Tietjen, K. L., Taylor, B., Chinkin, M., Gunn, R. L., Palmisciano, M., Steyaert, M., Wilson, B., East, H. K., Turner, J., Graham, N. A. J., & Perry, C. T. (2021). Wave exposure shapes reef community composition and recovery trajectories at a remote coral atoll. *Coral Reefs*, 40(6), 1819-1829. <https://doi.org/10.1007/s00338-021-02184-w>

Hawliau Cyffredinol / General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

1 **Wave exposure shapes reef community composition and recovery**
2 **trajectories at a remote coral atoll**

3

4 Ines D Lange^{1,*}, Cassandra E Benkwitt^{2,**}, Jamie M McDevitt-Irwin^{3,**}, Kristina L Tietjen^{4,**}, Brett
5 Taylor⁵, Mark Chinkin⁵, Rachel L Gunn², Melissa Palmisciano³, Margaux Steyaert^{6,7}, Bry Wilson⁶,
6 Holly K East⁸, John Turner⁹, Nicholas A J Graham², Chris T Perry¹

7

8 ¹ Geography, College of Life and Environmental Sciences, University of Exeter, Exeter EX4 4RJ, UK

9 ² Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK

10 ³ Hopkins Marine Station, Stanford University, Pacific Grove 93950, USA

11 ⁴ Department of Biology, University of Victoria, Victoria BC V8W 2Y2, Canada

12 ⁵ Australian Institute of Marine Science, Indian Ocean Marine Research Centre, Crawley, WA 6009,
13 Australia

14 ⁶ Department of Zoology, University of Oxford, Oxford OX1 3SZ, UK

15 ⁷ Institute of Zoology, Zoological Society of London, London NW1 4RY, UK

16 ⁸ Department of Geography and Environmental Sciences, Northumbria University, Newcastle upon
17 Tyne NE1 8ST, UK

18 ⁹ School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey LL59 5AB, Wales, UK

19

20 *Corresponding author: i.lange@exeter.ac.uk

21 **these authors contributed equally to this work

22

23 **keywords:** community composition; biophysical coupling; wave exposure; wave forcing; exposed;
24 sheltered; recovery trajectory; remote coral reef

25

26 **Abstract**

27 In a time of unprecedented ecological change, understanding natural biophysical relationships
28 between reef resilience and physical drivers is of increasing importance. This study evaluates how
29 wave forcing structures coral reef benthic community composition and recovery trajectories after the
30 major 2015/2016 bleaching event in the remote Chagos Archipelago, Indian Ocean. Benthic cover and
31 substrate rugosity were quantified from digital imagery at 23 fore reef sites around a small coral atoll
32 (Salomon) in 2020 and compared to data from a similar survey in 2006 and opportunistic surveys in
33 intermediate years. Cluster analysis and principal component analysis show strong separation of
34 community composition between exposed (modelled wave exposure $>1000 \text{ J m}^{-3}$) and sheltered sites
35 ($<1000 \text{ J m}^{-3}$) in 2020. Differences are driven by relatively high cover of *Porites* sp., other massive
36 corals, encrusting corals, soft corals, rubble and dead table corals at sheltered sites versus high cover
37 of pavement and sponges at exposed sites. Total coral cover and rugosity were also higher at sheltered
38 sites. Adding data from previous years shows benthic community shifts from distinct exposure-driven
39 assemblages and high live coral cover in 2006 towards dominance of bare pavement, dead *Acropora*
40 tables and rubble after the 2015/2016 bleaching event. The subsequent, and still ongoing, recovery
41 trajectories at sheltered and exposed sites are surprisingly parallel and lead communities towards their
42 respective pre-bleaching communities. These results demonstrate that in the absence of human
43 stressors, community patterns on fore reefs are strongly controlled by wave exposure, even during and
44 after widespread coral loss from bleaching events.

45

46 **Introduction**

47 Coral reef structure, function and resilience are influenced by a combination of physical and
48 anthropogenic drivers. As reefs worldwide are degrading and shifting to alternative regimes (Pandolfi
49 et al. 2003; Norström et al. 2009), and climate-driven bleaching events are increasing in frequency
50 and severity (Hoegh-Guldberg 1999; Hughes et al. 2018), the understanding of these drivers in
51 shaping reef communities and supporting recovery after disturbances is of vital importance (Hughes et
52 al. 2010; Pandolfi et al. 2011; Page et al. 2019). Physical drivers of reef communities include wave

53 forcing, temperature, nutrients, primary production and turbidity (Robinson et al. 2018; Wedding et
54 al. 2018; Ceccarelli et al. 2020), often in turn shaped by spatial gradients in waves, currents and local
55 bathymetry.

56 Spatial gradients in wave energy strongly influence benthic and fish community patterns at the scale
57 of individual islands and coral atolls (Williams et al. 2013; Jouffray et al. 2019; Karkarey et al. 2020).
58 For instance, high wave forcing can reduce overall coral cover and favour wave-tolerant
59 morphologies, such as encrusting corals (Dollar 1982; Storlazzi et al. 2005; Franklin et al. 2013) or
60 may even shift the entire benthic community to a dominance by low-lying algal species, such as turf
61 algae and crustose coralline algae (CCA) (Williams et al. 2013; Gove et al. 2015). Coral vulnerability
62 to high wave energy is mainly determined by colony morphotype and size, with large corymbose or
63 table corals experiencing high mortality through hydrodynamic dislodgement (Madin and Connolly
64 2006; Madin et al. 2014). After a disturbance, hydrodynamic forces can furthermore affect the rate at
65 which new coral habitat is formed and old coral habitat degrades (Madin et al. 2016), potentially
66 influencing recovery trajectories. Anthropogenic drivers such as fishing and coastal development lead
67 to sedimentation, nutrient enrichment and overfishing of herbivores (McManus et al. 2000; Fabricius
68 2005) which can initiate shifts to different reef regimes (Hughes 1994; McCook 1999; Jouffray et al.
69 2019) and decouple natural relationships between reef assemblages and physical drivers (Williams et
70 al. 2015; Ford et al. 2020).

71 To disentangle effects of anthropogenic and physical drivers, remote reefs are invaluable places to
72 study impacts of natural environmental gradients in the absence of direct human disturbance (Gilmour
73 et al. 2013; Hays et al. 2020). However, remote areas are often associated with access limitations,
74 leading to sparse temporal and spatial data resolution. In order to evaluate the status and recovery
75 potential of reef communities on a meaningful scale, strategic monitoring over large areas and with
76 high spatial resolution is necessary. This study evaluates how wave exposure structures coral reef
77 benthic community composition and recovery trajectories after a major bleaching event in the remote
78 Chagos Archipelago, Indian Ocean. In 2020, 23 fore reef sites around the entire Salomon atoll were
79 surveyed to address the following question: 1) Does benthic community structure around the atoll
80 vary predictably based on wave exposure? Average community compositions at sheltered and

81 exposed sites were then compared to cover data in 2006 and intervening years to explore the
82 subsequent question: 2) Are pre-bleaching status and recovery trajectories after the 2015/2016
83 disturbance event impacted by wave exposure? The results increase our understanding of wave
84 exposure as a driver of reef ecology in remote atolls and its effects on recovery trajectories after major
85 disturbance events.

86

87 **Methods**

88 **Study site and wave exposure**

89 The Chagos Archipelago in the central Indian Ocean consists of five atolls with islands and numerous
90 submerged banks. All atolls, except for Diego Garcia, have been uninhabited since the 1970s and
91 have therefore experienced minimal direct or local impacts from fishing, sewage or shoreline
92 modifications for the last 50 years (Sheppard et al. 2017). In 2010, the Archipelago and surrounding
93 sea was declared one of the largest no-take marine protected areas, benefitting benthic and pelagic
94 ecosystems alike (Hays et al. 2020). However, despite minimal local impacts, two major global
95 heating events in 1997/1998 and 2015/2016 reduced coral cover values from >40 to <10% across the
96 Archipelago and affected reefs down to 25 m water depth (Sheppard et al. 2017; Head et al. 2019).
97 Coral reefs recovered to pre-bleaching levels 7-10 years after the 1997/1998 event, while recovery
98 after 2015/2016 is currently ongoing (Sheppard et al. 2017). Due to the remoteness of the Archipelago
99 and related access limitations, research effort has strongly focused on repeat monitoring of the same
100 sites to build a time-series of observations, while most areas remain understudied. Salomon atoll is
101 located in the northeast of the Chagos Archipelago, covering approximately 38 km² (Fig. 1a). A reef
102 crest and 10 small islands enclose a shallow lagoon (<30 m depth), harbouring sheltered backreef and
103 coral knoll habitats. The fore reef terrace surrounds the whole atoll and gently slopes from 3 to ~10 m
104 depth before dropping off steeply, with a passage to the lagoon on the northern side (Fig. 1c).

105

106 The seasonally-shifting wind regime in the central Indian Ocean, with the predominant wind direction
107 being from the south-east (Fig. 1d), results in marked spatial variations in wave energy around the

108 atoll. Wave exposure at each site was modelled as a function of wind speed, wind direction, and fetch
109 length (i.e. the distance over open ocean that wind can travel in a specific direction unobstructed by
110 land or reefs) using a model developed for a previous study (detailed information in supplementary
111 material of Perry et al. 2015). Based on the model outputs (Fig. 1b) and a natural break in the rank
112 order of data, sites were classified into ‘exposed’ ($>1000 \text{ J m}^{-3}$), encompassing northeast and
113 southeast facing shores, or ‘sheltered’ ($<1000 \text{ J m}^{-3}$), encompassing southwest and northwest facing
114 shores. We suspect that sites at the NE margin might have slightly lower wave exposure than
115 calculated by the model, as the prominent current runs along-shelf and has to cross larger distances
116 over the length of the reef terrace, but available bathymetry data prevents the model factoring for this.
117

118 **Benthic community composition 2020**

119 To determine whether benthic community structure around the atoll varies predictably based on wave
120 exposure, a detailed survey of Salomon’s fore reefs was conducted on 22 March 2020 by
121 circumnavigating the atoll in a clockwise direction. The 23 sites (Fig. 1b) were chosen prior to the
122 survey by placing GPS waypoints on a map at 1 km distance from each other. At each site, the depth
123 of the reef terrace was checked with a handheld Echotest 2 depth sounder and the survey location
124 adjusted to 6-8 m water depth. Two observers took planar photographs of the reef substrate from the
125 surface and from ~3 m distance to the benthos by swimming and duck diving on a parallel transect to
126 the reef crest in opposite directions, with a spacing of $>3 \text{ m}$ between photographs to ensure
127 independence of replicates. Both observers used Canon Powershot G7X in underwater housings,
128 automatic underwater mode and raw image quality. A third observer took short videos of the substrate
129 at an oblique angle to evaluate the rugosity at each site, which was rated on a scale of 1-5 (5 = highest
130 complexity) by three independent observers and averaged.

131

132 The photographs taken from approximately 3 m above the reef surface ($n=10/\text{site}$, 230 total) were
133 uploaded to CoralNet (www.coralnet.ucsd.edu), a web-based tool for coral reef analysis supporting
134 semi-automated annotation of images (Beijbom et al. 2015). Fifty random points were projected on
135 each photograph (excluding the outer 10% of the image to avoid any blurry areas caused by camera

136 distortion) and the substrate directly below was identified to scleractinian coral genus and morphotype
137 level (Acropora_table, Acropora_branching, Pocillopora_branching, Stylophora_branching,
138 Other_branching, Porites_massive, Other_massive, All_encrusting), or to other categories of benthic
139 substrate (Soft coral, Sponge, Sand, Rubble, Dead_Acropora_table, Pavement, Halimeda,
140 Other_Macroalgae). Note that Pavement includes cover of crustose coralline algae (CCA) and fine
141 turf algae, which were not easily distinguishable in the photographs. The percent cover data for each
142 picture were downloaded and some categories were combined due to very small values (Pocillopora +
143 Stylophora + Other_branching = Other_branching; Halimeda + Other_Macroalgae = Macroalgae).
144 Cover values were averaged over replicates at each site to yield site-level data (accessible at [doi](#) –
145 [data table attached, will be deposited in repository upon acceptance]).

146

147 To evaluate differences in community composition we used the beta diversity metric Bray-Curtis on
148 log transformed cover data. Hierarchical agglomerative clustering (CLUSTER analysis) and a
149 similarity profile test (SIMPROF) were performed to group sites with similar community composition
150 at 0.1% and 5% significance levels ('simprof' function in *clustsig* package) (Clarke et al. 2008).

151 Principal Component Analysis (PCA) was then used to visualize differences in community
152 composition ('PCA' in *FactoMineR* and 'fviz_pca_biplot' in *factoextra*) (Husson et al. 2010). To
153 display which coral and major benthic categories drove the community differences, correlation
154 vectors were tested for significance ('envfit' in *vegan* with 999 permutations) and overlaid on the
155 PCA plot. Sites were grouped according to wave exposure ($p < 0.001$), displayed by concentration
156 ellipses at ellipse.level=0.95. Additionally, impacts of wave exposure on total coral cover, cover of
157 individual benthic categories and rugosity were tested using Welch's t-tests ('t.test' in *base*) to
158 account for unequal variances between groups (Derrick et al. 2016). All statistical analyses were
159 performed using R 4.0.3 (R Core Team 2020).

160

161 **Pre-bleaching status and recovery trajectories**

162 To determine whether pre-bleaching status and recovery trajectories after the 2015/2016 disturbance
163 event were impacted by wave exposure, we compared the 2020 data to several previous surveys. A

164 similar complete assessment of Salomon's fore reefs was conducted in 2006, taking benthic
165 photographs from the surface at 22 sites (n=1/site) around the atoll at similar locations (Online
166 Resource 1) and depth (6-8 m). These pictures were analysed in CoralNet as described above and
167 benthic cover (accessible at [doi](#)) was averaged over sheltered (n=12) and exposed sites (n=10)
168 according to location on the fore reef terrace. Welch's t-tests were used to compare total coral cover
169 and cover of individual categories in 2006 and 2020 ('t.test' in *base*) for both sheltered and exposed
170 sites.

171 Additionally, cover data for several years between 2006 and 2020 were extracted from published and
172 unpublished datasets to assist analysis of trajectories of coral recovery at both sheltered and exposed
173 sites. These data were collected from a smaller subset of sites (Online Resource 1) and using different
174 methods, but are able to give a broad and general indication of benthic trajectories, as the different
175 benthic survey methods used have been shown to be comparable (Jokiel et al. 2015). Data for 2010
176 were collected using Point-Intercept transects (n=4/site, 50 m transects, 100 points/transect) at six
177 sites (3 sheltered, 3 exposed) in 8 m depth (Graham et al. 2013). Data for 2016 (2 exposed sites), 2018
178 (3 sheltered sites) and 2019 (3 sheltered, 3 exposed sites) describe the status of reef communities after
179 the bleaching event and were extracted from video transects in 8-10 m depth (n=3/site, 30 m transect,
180 60 still images/transect, 10 points/image) for 2016 (Head et al. 2019), 3D line-intercept transects in 8
181 m depth (n=4/site, 10 m transect, continuous cover along reef contour) for 2018 (Lange and Perry
182 2019) and 2019 (Lange, unpublished data) and Point-Intercept transects as described above for 2019
183 (Benkwitt and Graham, unpublished data).

184

185 Cover data were averaged over all available replicates of sheltered or exposed sites each year
186 (accessible at [doi](#)) before coral community trajectories were visualized using non-metric
187 multidimensional scaling (nMDS) ('metaMDS' function in *vegan* package) (Oksanen et al. 2020).
188 The metaMDS function applied square root transformation and Wisconsin double standardization of
189 cover data before calculating Bray-Curtis dissimilarity. Correlation vectors were overlaid on the
190 nMDS plot, with significant groups indicated on the plot ('envfit' function with 999 permutations).

191

192 **Results & Discussion**

193 Our study demonstrates that wave exposure is a significant driver of coral reef benthic community
194 composition and recovery trajectories at a remote and uninhabited atoll in the Indian Ocean. In 2020,
195 sheltered reefs along the western shore had significantly higher coral cover and rugosity, while
196 exposed reefs along the eastern shore were characterised by flat, bare pavement and boring sponges.
197 Temporal patterns indicate distinct exposure-driven assemblages with high live coral cover in 2006,
198 extensive coral mortality after the 2015/2016 bleaching event, and ongoing parallel recovery
199 trajectories towards their respective pre-bleaching communities at both sheltered and exposed sites.

200

201 **Benthic community composition and influence of wave exposure**

202 We found a strong influence of wave exposure on site-level benthic community composition
203 (CLUSTER/SIMPROF and PCA: sheltered versus exposed sites formed distinct groups at $p=0.001$,
204 Fig. 2b). Differences were driven by relatively high cover of *Porites*, other massive corals, encrusting
205 corals, soft corals, rubble and dead table corals at sheltered sites (each variable contributing $>7.5\%$ to
206 PC1) versus high cover of pavement ($>7.5\%$) and sponges ($>5\%$) at exposed sites. Within this broad
207 separation, there were additional sub-groups of statistically distinct benthic communities
208 (CLUSTER/SIMPROF at $p=0.05$, Fig. 2a). Sites along the NE shore formed a small subgroup within
209 the exposed sites, characterized by relatively high cover of branching *Acropora* and other branching
210 corals (both contributing $>7.5\%$ to PC2). Reasons may be a reduction in wave exposure compared to
211 the SE shore, as south-easterly along-shelf currents cross larger distances on the reef terrace, or a
212 weaker exposure to other local-scale physical forcings such as internal tides or patterns of lagoon
213 outflow which could not be accounted for (Williams et al. 2013). Three sites in the sheltered group
214 were characterized by relatively high cover of *Porites* and soft corals, but less rubble or dead
215 *Acropora* tables than at most other wave protected sites, and were therefore likely clustered with the
216 exposed sites in the SIMPROF analysis (Fig. 2a). The other two sites that were isolated in the cluster
217 analysis are located at the southwest corner of the atoll and were characterised by either very high
218 *Acropora* cover or high dead *Acropora* table cover compared to other sheltered sites.

219
220 In 2020, sheltered sites had significantly higher coral cover than exposed sites ($t(19.27)=2.55$,
221 $p=0.019$). But while average coral cover along the SE side of the atoll was 8.6% (range: 5.2-17.6%),
222 sites at the NE shore, which were also classified as exposed by the wave exposure model, showed
223 much higher coral cover (mean: 20.3%, range: 13.2-26.2%), similar to averages along the protected
224 NW (mean: 21.6%, range: 14.0-38.6%) and SW shores (mean: 20.1%, range: 19.8-20.4%). Again, this
225 may be explained by lower wave exposure at the NE compared to SE shore. At remote Pacific reefs,
226 horizontal gradients in wave energy explained benthic community patterns and variation in hard coral
227 cover at Kingman Reef, but not at Palmyra (Williams et al. 2013). However, a more detailed
228 nearshore hydrodynamic model around Palmyra captured additional physical forcings and
229 consequently found wave forcing and geomorphology to be major drivers of benthic regimes,
230 especially if hard corals were modelled at the morphology level (Gove et al. 2015).

231
232 Substrate rugosity around Salomon atoll was also significantly affected by wave exposure
233 ($t(18.14)=3.65$, $p=0.002$). Markedly low rugosity values were recorded along the exposed SE side of
234 the atoll (range: 1-2), which presently consists of a flat surface of probably pre-Holocene reef rock
235 where all new coral growth gets episodically stripped off during high wave energy events (Grigg
236 1998). Notable exceptions were the two most eastern stations (2.5 and 3) which were characterized by
237 pronounced spur and groove formations, indicating highest exposure to the main direction of wind-
238 driven swell (Storlazzi et al. 2003; Duce et al. 2016). Rugosity at the remaining sites along the NE,
239 SW and NW side of the atoll ranged from 2-3.5.

240 Comparing the cover of individual benthic categories, sheltered sites showed higher cover of
241 *Porites*_massive, *Other*_massive, *Other*_encrusting, Soft corals, Rubble and *Dead*_Acropora_table,
242 while exposed sites were characterized by higher cover of Pavement, Sponge, Sand and Macroalgae
243 (all $p<0.05$). Cover of *Acropora*_branching, *Acropora*_table and *Other*_branching was not
244 significantly different between exposure groups. Previous studies reported that high wave forcing
245 favours wave-tolerant morphologies, such as encrusting and massive corals (Storlazzi et al. 2005;
246 Madin et al. 2006; Gove et al. 2015), which in our study were more abundant at sheltered sites while

247 *Acropora* cover was not different between exposures. It is important to remember, however, that
248 Salomon's reefs in 2020 represent assemblages at four years post-disturbance and will inherently
249 differ from mature communities (especially in cover of *Acropora* spp.). The dominance of pavement
250 with low-lying algal species (turf algae and CCA) at high exposure sites on the other hand is
251 consistent with reports from other remote areas (Williams et al. 2013; Gove et al. 2015). Fleshy
252 macroalgal cover in this study was generally very low (<2% at all sites), but significantly higher at
253 exposed than at sheltered sites. This disagrees with observed macroalgae dominance in regions of low
254 wave forcing where vulnerability to physical dislodgement is lowest (Gove et al. 2015), but supports
255 studies finding lower richness, biomass and bite rates of herbivores at highly exposed sites (Karkarey
256 et al. 2020). Dead table corals and rubble were much less prevalent at exposed sites, because they
257 tend to be rapidly removed by high energy monsoonal waves at wind exposed reefs (Yadav et al.
258 2016).

259

260 To summarise, in 2020 the reef structure along the exposed eastern margin of Salomon atoll consisted
261 of a flat surface, in some parts heavily infested by *Cliona* spp. sponges, with relatively small
262 branching and table coral colonies growing on top of it. In contrast, the reef structure along the
263 sheltered western side of the atoll consisted of massive *Porites* colonies, recently dead coral rock
264 which still retained a high structural complexity, and large dead *Acropora* tables, themselves often
265 colonised with juvenile branching coral. This suggests synergistic effects between daily wave
266 exposure and periodic high energy wave events from storms in structuring coral communities, similar
267 to patterns observed around the Hawaiian Islands (Dollar 1982; Grigg 1983; Franklin et al. 2013).
268 Despite the relatively clear impact of wave exposure on community composition, a more detailed
269 nearshore hydrodynamic model and the inclusion of additional physical drivers such as temperature
270 and nutrient concentrations would presumably capture additional physical forcings and may serve as
271 an enhanced tool for exploring biophysical coupling in more detail (Williams et al. 2013; Gove et al.
272 2015).

273

274 **Pre-bleaching status and recovery trajectories**

275 A key question arising from the above observations relates to the extent to which reef communities
276 around Salomon atoll differed before the 2015/2016 bleaching event. Our analysis of photographs
277 from 2006 also showed very distinct spatial community patterns, with higher cover of total live coral
278 ($t(19.05)=2.49, p=0.022$) and table *Acropora* ($t(15.34)=3.37, p=0.004$) at sheltered sites, and higher
279 cover of branching *Acropora* ($t(10.01)=2.94, p=0.014$), soft corals ($t(12.05)=2.41, p=0.033$) and
280 sponges ($t(9.29)=2.92, p=0.017$) at exposed sites (Fig. 3).

281

282 It must be noted that reefs in 2006 do not necessarily represent pristine communities, as they reflect
283 conditions eight years after the 1997/1998 bleaching event, when recovery was still ongoing. Coral
284 cover across the Chagos Archipelago actually reached a peak in 2012/2013, after which the
285 dominating large table *Acropora* suffered partial mortality from white band disease (Sheppard et al.
286 2017). However, the comparison of reef communities in 2006 (8 years post-bleaching) and 2020 (4
287 years post-bleaching) highlights significant differences. At sheltered sites, total live coral cover
288 decreased from $48.3\pm 6.3\%$ (mean \pm SE) in 2006 to $6.8\pm 0.8\%$ after the 2015/16 bleaching event (Lange
289 and Perry 2019), but had recovered to $20.5\pm 2.4\%$ by 2020 (42% of 2006 levels; $t(14.08)=4.12,$
290 $p=0.001$). Remaining differences are mainly due to very low cover of tabular *Acropora* ($30.8\pm 6.6\%$ in
291 2006 and $4.1\pm 1.7\%$ in 2020) (Fig. 3). At exposed sites, total coral cover dropped from $29\pm 4.5\%$ in
292 2006 to $9.9\pm 3.5\%$ in 2016 (Head et al. 2019) and recovered slightly to $12.5\pm 2.1\%$ in 2020 (43% of
293 2006 levels; $t(12.74)=3.34, p=0.006$). As *Acropora* cover was comparatively low even pre-bleaching
294 (branching: $8.8\pm 2.2\%$, table: $6.4\pm 3.0\%$), the difference is mainly due to loss of massive *Porites* cover
295 ($8.6\pm 2.8\%$ in 2006 to $0.8\pm 0.4\%$ in 2020) (Fig. 3). Dead *Acropora* tables were much less prevalent in
296 2006 ($0.8\pm 0.7\%$) than in 2020 ($10.0\pm 2.0\%$) at sheltered sites, and generally absent at exposed sites,
297 where degradation of dead reef structure may be faster due to continuously high prevalence of boring
298 sponges and physical substrate stripping. However, differences in rubble and sand cover between
299 2006 and 2020 were small at all sites (Fig. 3), indicating that the breakdown of reef substrate after the
300 bleaching event is still ongoing (sheltered sites) or that rubble was rapidly transported off-reef
301 (exposed sites).

302

303 Adding data from intermediate years, the profound influence of wave exposure on community
304 patterns around Salomon atoll becomes even more apparent. After a benthic community shift from
305 live coral categories in 2006 and 2010 towards high cover of pavement, dead *Acropora* tables and
306 rubble following the 2015/2016 bleaching event, trajectories of coral cover and community
307 composition show recovery trends towards pre-bleaching levels at all sites. Interestingly, the
308 trajectories of reef communities at sheltered and exposed sites are proceeding in a surprisingly parallel
309 way, with reefs in both exposure regimes retaining their distinct communities throughout (Fig. 4).

310

311 Figure 4 raises the question of whether exposed reefs are heading towards a new sponge dominated
312 system, but the observed cover of boring sponges in 2006 and 2020 was similar ($14.6 \pm 4.6\%$ in 2006
313 and $10.4 \pm 2.1\%$ in 2020) and therefore not a result of the recent disturbance. This indicates either a
314 permanently high infestation of the reef framework at exposed sites or an increase in sponge cover
315 after the 1997/1998 bleaching event. The ongoing recovery process towards pre-2015 communities
316 may take longer at wave exposed sites, as the recovery of lost cover of massive corals is slower than
317 that of fast growing *Acropora*. However, coral colonies at exposed sites are generally smaller and
318 coral cover does not reach the same levels as at sheltered sites due to a constant turnover associated
319 with mortality from breakage, scour and abrasion (Grigg 1998; Madin et al. 2006). This indicates that
320 pre-bleaching coral cover levels may actually be reached faster than at sheltered sites. Also, the
321 mechanical stability of settlement structures is critical in determining post-settlement coral survival
322 (Yadav et al. 2016), so the high prevalence of dead *Acropora* tables may slow recovery at sheltered
323 sites as juveniles preferentially settle on this unstable substrate (Arthur et al. 2006; Sheppard et al.
324 2017).

325

326 **Future community trajectories**

327 The current status of Salomon's reefs in combination with data from previous years indicates that both
328 sheltered and exposed sites are on a trajectory of recovery to their distinct pre-bleaching communities.
329 Specifically, there is no indication of coral species dominance changes compared to pre-bleaching
330 compositions as reported for some reefs in the central Indian Ocean after the 1997/1998 bleaching

331 event (Arthur et al. 2006; Morri et al. 2015). Consistently low macroalgal cover further suggests that
332 reefs are unlikely to shift to algal-dominated states as observed for several reefs in the more
333 anthropogenically impacted Seychelles after 1998 (Graham et al. 2015). However, most fore reefs in
334 the Central Indian Ocean have low cover of fleshy macroalgae, probably due to high abundance of
335 herbivorous fishes (Arthur et al. 2005; Arthur et al. 2006; Graham et al. 2015; Morri et al. 2015).
336 Similar to other remote reefs in the Indo-Pacific, substrata made available by the death of corals is
337 instead colonised by fine turfing and coralline algae (Gilmour et al. 2013), which are not likely to
338 prevent coral settlement. This is of especially high importance for remote reefs, as without an external
339 supply of recruits, it is assumed that reefs will be slow to recover from severe disturbance (Roberts
340 1997; Graham et al. 2006; McClanahan et al. 2012) and recruit numbers in the Chagos Archipelago in
341 2017 were indeed very low (Sheppard et al. 2017). However, we observed high numbers of juvenile
342 *Acropora* colonies around Salomon atoll at both sheltered and exposed sites in 2020, indicating
343 surplus grazing capacity within the system that assisted coral recruitment and survival of locally
344 produced larvae (Mumby and Steneck 2008). This gives reason to hope that reproductive output,
345 recruitment, coral cover and community structure will recover to pre-disturbance levels within a
346 decade as observed for remote Indian Ocean reefs after the 1997/1998 bleaching event (Gilmour et al.
347 2013; Sheppard et al. 2017). Ultimately, the recovery of reefs in this region will depend on the
348 recurrence intervals and magnitudes of heat stress events in the near future (Van Hooidonk et al.
349 2016).

350

351 Due to its remote environment and absence of direct human impact, Salomon atoll provided a unique
352 opportunity to study the effects of wave exposure on reef benthic community patterns and recovery
353 potential. The distinct communities at sheltered and exposed sites both before and after a major
354 disturbance event confirm the capacity for hard coral assemblages to maintain competitive dominance
355 at an intra-atoll scale in response to wave forcing. Importantly, our results highlight that communities
356 remained distinct during widespread coral loss in 2015/2016 and the following recovery trajectories,
357 and that communities at all sites are on their way to pre-bleaching levels. This emphasises the

358 importance of managing local pressures on reefs to promote natural biophysical coupling and
359 resilience to climate change in the future.

360

361

362 **Author Contributions:** CTP conceived the idea with IDL, CEB, JM-I, KLT, BT, MC, RLG, MP, MS
363 and BW contributing to discussions; IDL, KLT, BT and CTP conducted the fieldwork in 2020 and
364 HKE, NAJG, JT, CEB and IDL provided additional data; data analysis and manuscript writing was
365 led by IDL with contributions to data analysis by CEB, JM-I and KLT and contributions to
366 manuscript writing by CTP and NAJG. All authors have read and agreed to the final version of the
367 manuscript.

368

369 **Acknowledgements:** This research was funded by the Bertarelli Foundation as part of the Bertarelli
370 Programme in Marine Science and was conducted under permit number 0003SE20. We thank Rachel
371 Jones, Heather Koldewey and Emma Levy as well as the captain and crew of the support vessel for
372 logistical help and for bringing us home during a global pandemic.

373

374 **Data:** Site information and benthic cover data from picture analysis and referenced data sets can be
375 downloaded from University of Exeter Repository at [doi](#) [*deposited upon acceptance*]

376

377 **Conflict of Interest:** On behalf of all authors, the corresponding author states that there is no conflict
378 of interest.

379 **References**

380 Arthur R, Done TJ, Marsh H (2005) Benthic recovery four years after an El Niño-induced coral mass mortality in the
381 Lakshadweep atolls. *Current Science* 89:694-699
382 Arthur R, Done TJ, Marsh H, Harriott V (2006) Local processes strongly influence post-bleaching benthic recovery in the
383 Lakshadweep Islands. *Coral Reefs* 25:427-440
384 Beijbom O, Edmunds PJ, Roelfsema C, Smith J, Kline DI, Neal BP, Dunlap MJ, Moriarty V, Fan T-Y, Tan C-J (2015)
385 Towards automated annotation of benthic survey images: Variability of human experts and operational modes of
386 automation. *PloS One* 10:e0130312
387 Ceccarelli DM, Evans RD, Logan M, Mantel P, Puotinen M, Petus C, Russ GR, Williamson DH (2020) Long-term dynamics
388 and drivers of coral and macroalgal cover on inshore reefs of the Great Barrier Reef Marine Park. *Ecological*
389 *Applications* 30:e02008
390 Clarke KR, Somerfield PJ, Gorley RN (2008) Testing of null hypotheses in exploratory community analyses: similarity
391 profiles and biota-environment linkage. *Journal of Experimental Marine Biology and Ecology* 366:56-69
392 Derrick B, Toher D, White P (2016) Why Welch's test is Type I error robust. *The Quantitative Methods in Psychology* 12
393 Dollar S (1982) Wave stress and coral community structure in Hawaii. *Coral Reefs* 1:71-81
394 Duce S, Vila-Concejo A, Hamylton S, Webster JM, Bruce E, Beaman RJ (2016) A morphometric assessment and
395 classification of coral reef spur and groove morphology. *Geomorphology* 265:68-83
396 Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine*
397 *Pollution Bulletin* 50:125-146
398 Ford AK, Jouffray J-B, Norström AV, Moore BR, Nugues MM, Williams GJ, Bejarano S, Magron F, Wild C, Ferse SC
399 (2020) Local human impacts disrupt relationships between benthic reef assemblages and environmental predictors.
400 *Frontiers in Marine Science* 7:571115
401 Franklin EC, Jokiel PL, Donahue MJ (2013) Predictive modeling of coral distribution and abundance in the Hawaiian
402 Islands. *Marine Ecology Progress Series* 481:121-132
403 Gilmour JP, Smith LD, Heyward AJ, Baird AH, Pratchett MS (2013) Recovery of an isolated coral reef system following
404 severe disturbance. *Science* 340:69-71
405 Gove JM, Williams GJ, McManus MA, Clark SJ, Eshes JS, Wedding LM (2015) Coral reef benthic regimes exhibit non-
406 linear threshold responses to natural physical drivers. *Marine Ecology Progress Series* 522:33-48
407 Graham NAJ, Pratchett MS, McClanahan TR, Wilson SK (2013) The status of coral reef fish assemblages in the Chagos
408 Archipelago, with implications for protected area management and climate change. In: Sheppard, CRC(ed) *Coral*
409 *reefs of the United Kingdom overseas territories*. Springer, pp.253-270
410 Graham NAJ, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus
411 rebound potential in coral reefs. *Nature* 518:94-97
412 Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Bijoux JP, Robinson J (2006) Dynamic fragility of oceanic coral reef
413 ecosystems. *Proceedings of the National Academy of Sciences* 103:8425-8429
414 Grigg R (1998) Holocene coral reef accretion in Hawaii: a function of wave exposure and sea level history. *Coral Reefs*
415 17:263-272
416 Grigg RW (1983) Community structure, succession and development of coral reefs in Hawaii. *Marine Ecological Progress*
417 *Series* 11:1-14
418 Hays GC, Koldewey HJ, Andrzejczek S, Attrill MJ, Barley S, Bayley DT, Benkwitt CE, Block B, Schallert RJ, Carlisle AB
419 (2020) A review of a decade of lessons from one of the world's largest MPAs: conservation gains and key
420 challenges. *Marine Biology* 167:159
421 Head CE, Bayley DT, Rowlands G, Roche RC, Tickler DM, Rogers AD, Koldewey H, Turner JR, Andradi-Brown DA
422 (2019) Coral bleaching impacts from back-to-back 2015–2016 thermal anomalies in the remote central Indian
423 Ocean. *Coral Reefs* 38:605-618
424 Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater*
425 *Research* 50:839-866
426 Hughes TP (1994) Catastrophes, Phase Shifts, and Large-Scale Degradation of a Caribbean Coral Reef. *Science* 265:1547-
427 1551
428 Hughes TP, Graham NA, Jackson JB, Mumby PJ, Steneck RS (2010) Rising to the challenge of sustaining coral reef
429 resilience. *Trends in Ecology & Evolution* 25:633-642
430 Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC,
431 Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison H, Hobbs JPA, Hoey AS, Hoogenboom M, Lowe RJ,
432 McCulloch MT, Pandolfi JM, Pratchett M, Schoepf V, Torda G, Wilson SK (2018) Spatial and temporal patterns
433 of mass bleaching of corals in the Anthropocene. *Science* 359:80-83
434 Husson F, Lê S, Pagès J (2010) Exploratory multivariate analysis by example using R. Chapman and Hall
435 Jokiel PL, Rodgers KS, Brown EK, Kenyon JC, Aeby G, Smith WR, Farrell F (2015) Comparison of methods used to
436 estimate coral cover in the Hawaiian Islands. *PeerJ* 3:e954
437 Jouffray J-B, Wedding LM, Norström AV, Donovan MK, Williams GJ, Crowder LB, Erickson AL, Friedlander AM,
438 Graham NA, Gove JM (2019) Parsing human and biophysical drivers of coral reef regimes. *Proceedings of the*
439 *Royal Society B* 286:20182544
440 Karkarey R, Rathod P, Arthur R, Yadav S, Theo A, Alcoverro T (2020) Wave exposure reduces herbivory in post-disturbed
441 reefs by filtering species composition, abundance and behaviour of key fish herbivores. *Scientific Reports* 10:9854
442 Lange ID, Perry CT (2019) Bleaching impacts on carbonate production in the Chagos Archipelago: influence of functional
443 coral groups on carbonate budget trajectories *Coral Reefs* 38:619-624
444 Madin JS, Connolly SR (2006) Ecological consequences of major hydrodynamic disturbances on coral reefs. *Nature*
445 444:477-480

446 Madin JS, Black KP, Connolly SR (2006) Scaling water motion on coral reefs: from regional to organismal scales. *Coral*
447 *Reefs* 25:635-644

448 Madin JS, Baird AH, Dornelas M, Connolly SR (2014) Mechanical vulnerability explains size-dependent mortality of reef
449 corals. *Ecology Letters* 17:1008-1015

450 Madin JS, Anderson KD, Andreasen MH, Bridge TCL, Cairns SD, Connolly SR, Darling ES, Diaz M, Falster DS, Franklin
451 EC, Gates RD, Harmer AMT, Hoogenboom MO, Huang DW, Keith SA, Kosnik MA, Kuo CY, Lough JM,
452 Lovelock CE, Luiz O, Martinelli J, Mizerek T, Pandolfi JM, Pochon X, Pratchett MS, Putnam HM, Roberts TE,
453 Stat M, Wallace CC, Widman E, Baird AH (2016) The Coral Trait Database, a curated database of trait
454 information for coral species from the global oceans. *Scientific Data* 3:160017

455 McClanahan TR, Donner SD, Maynard JA, MacNeil MA, Graham NA, Maina J, Baker AC, Beger M, Campbell SJ, Darling
456 ES (2012) Prioritizing key resilience indicators to support coral reef management in a changing climate. *PLoS One*
457 7:e42884

458 McCook LJ (1999) Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for
459 the Great Barrier Reef. *Coral Reefs* 18:357-367

460 McManus JW, Menez LA, Kesner-Reyes KN, Vergara SG, Ablan M (2000) Coral reef fishing and coral-algal phase shifts:
461 implications for global reef status. *ICES Journal of Marine Science* 57:572-578

462 Morri C, Montefalcone M, Lasagna R, Gatti G, Rovere A, Parravicini V, Baldelli G, Colantoni P, Bianchi CN (2015)
463 Through bleaching and tsunamis: Coral reef recovery in the Maldives. *Marine Pollution Bulletin* 98:188-200

464 Mumby PJ, Steneck RS (2008) Coral reef management and conservation in light of rapidly evolving ecological paradigms.
465 *Trends in Ecology & Evolution* 23:555-563

466 Norström AV, Nyström M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: beyond coral-macroalgal phase
467 shifts. *Marine Ecology Progress Series* 376:295-306

468 Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlenn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P,
469 Stevens MHH, Szoecs E, Wagner H (2020) *vegan: Community Ecology Package*. R package version 2.5-7

470 Page CE, Leggat W, Heron SF, Choukroun SM, Lloyd J, Ainsworth TD (2019) Seeking Resistance in Coral Reef
471 Ecosystems: The Interplay of Biophysical Factors and Bleaching Resistance under a Changing Climate: The
472 Interplay of a Reef's Biophysical Factors Can Mitigate the Coral Bleaching Response. *BioEssays* 41:1800226

473 Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL (2011) Projecting Coral Reef Futures Under Global Warming and Ocean
474 Acidification. *Science* 333:418-422

475 Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenahan L, Newman MJ,
476 Paredes G (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955-958

477 Perry CT, Murphy GN, Graham NA, Wilson SK, Januchowski-Hartley FA, East HK (2015) Remote coral reefs can sustain
478 high growth potential and may match future sea-level trends. *Scientific Reports* 5:18289

479 R Core Team (2020) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing,
480 Vienna, Austria

481 Roberts CM (1997) Connectivity and management of Caribbean coral reefs. *Science* 278:1454-1457

482 Robinson JP, Williams ID, Yeager LA, McPherson JM, Clark J, Oliver TA, Baum JK (2018) Environmental conditions and
483 herbivore biomass determine coral reef benthic community composition: Implications for quantitative baselines.
484 *Coral Reefs* 37:1157-1168

485 Sheppard CRC, Sheppard A, Mogg A, Bayley D, Dempsey AC, Roche R, Turner J, Purkins S (2017) Coral bleaching and
486 mortality in the Chagos Archipelago. *Atoll Research Bulletin* 613:1-26

487 Storlazzi C, Logan J, Field M (2003) Quantitative morphology of a fringing reef tract from high-resolution laser bathymetry:
488 Southern Molokai, Hawaii. *Geological Society of America Bulletin* 115:1344-1355

489 Storlazzi C, Brown E, Field M, Rodgers K, Jokiel P (2005) A model for wave control on coral breakage and species
490 distribution in the Hawaiian Islands. *Coral Reefs* 24:43-55

491 van Hooedonk R, Maynard J, Tamelander J, Gove J, Ahmadi G, Raymundo L, Williams G, Heron SF, Planes S (2016)
492 Local-scale projections of coral reef futures and implications of the Paris Agreement. *Scientific Reports* 6:39666

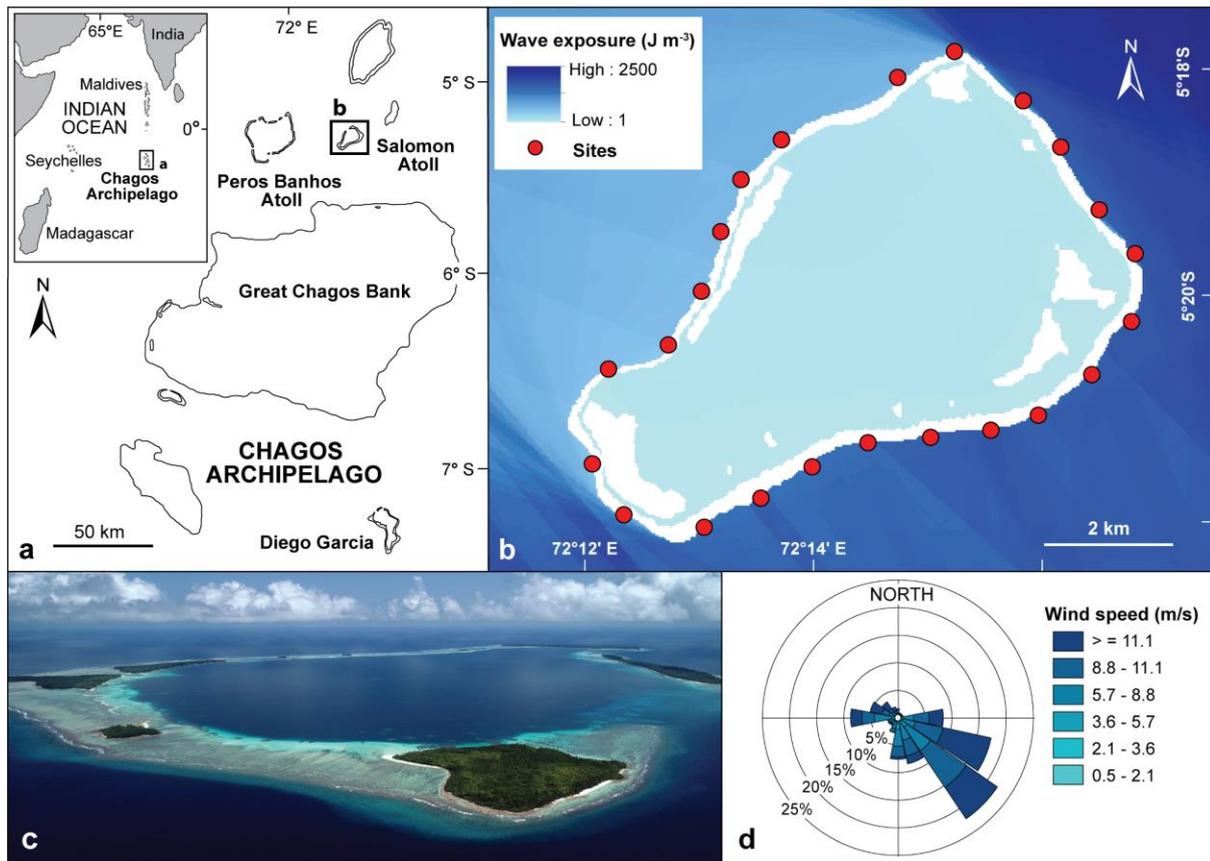
493 Wedding LM, Lecky J, Gove JM, Walecka HR, Donovan MK, Williams GJ, Jouffray J-B, Crowder LB, Erickson A,
494 Falinski K, Friedlander AM, Kappel CV, Kittinger JN, McCoy K, Norström A, Nyström M, Oleson KLL,
495 Stamoulis KA, White C, Selkoe KA (2018) Advancing the integration of spatial data to map human and natural
496 drivers on coral reefs. *PLoS One* 13:e0189792

497 Williams GJ, Gove JM, Eynaud Y, Zgliczynski BJ, Sandin SA (2015) Local human impacts decouple natural biophysical
498 relationships on Pacific coral reefs. *Ecography* 38:751-761

499 Williams GJ, Smith JE, Conklin EJ, Gove JM, Sala E, Sandin SA (2013) Benthic communities at two remote Pacific coral
500 reefs: effects of reef habitat, depth, and wave energy gradients on spatial patterns. *PeerJ* 1:e81

501 Yadav S, Rathod P, Alcoverro T, Arthur R (2016) "Choice" and destiny: the substrate composition and mechanical stability
502 of settlement structures can mediate coral recruit fate in post-bleached reefs. *Coral Reefs* 35:211-222

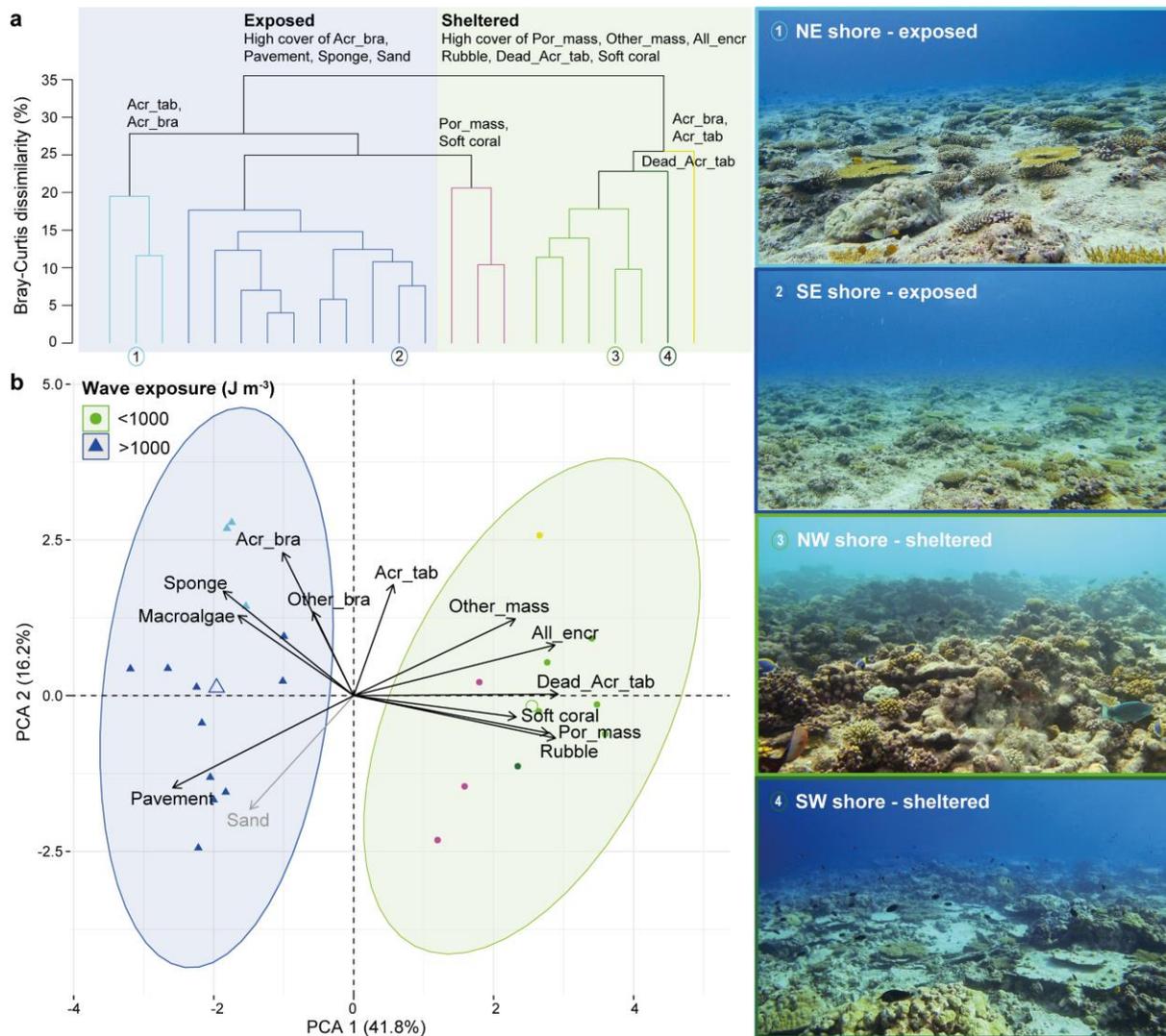
503



504

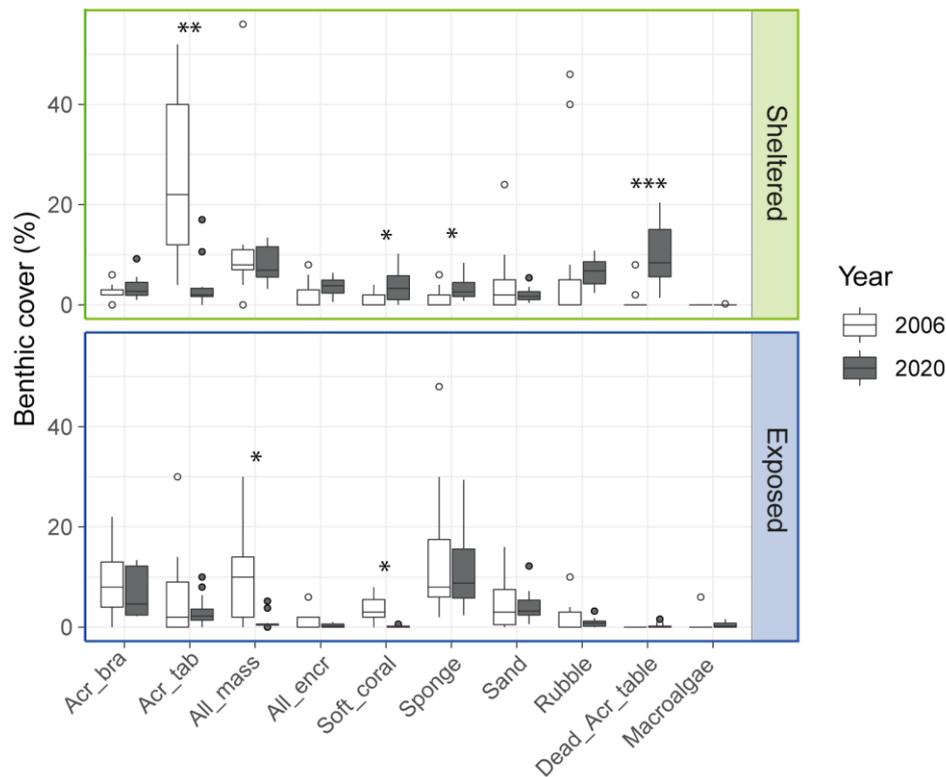
505 **Figure 1: Location of study sites.** a) Location of Salomon atoll in the Chagos Archipelago and in the
 506 central Indian Ocean (inset); b) Modelled wave exposure around Salomon atoll with locations of 23
 507 surveyed fore reef sites (in red); Blue shading indicates magnitude of wave exposure; c) Drone image
 508 of Salomon atoll from the most northern point looking south (channel into the lagoon on the right),
 509 photo courtesy of Robert Dunbar; d) Rose diagram showing annual wind direction, frequency and
 510 speed based on hourly wind measurements obtained from Diego Garcia airport (adapted from Perry et
 511 al. 2015).

512



513

514 **Figure 2: Reef community composition around Salomon atoll.** a) CLUSTER/SIMPROF Analysis
 515 indicating significant differences in community composition among sites at a significance level of
 516 $p=0.05$ (colored lines). Wave exposure (blue box: exposed $>1000 \text{ J m}^{-3}$, green box: sheltered $<1000 \text{ J}$
 517 m^{-3}) and categories driving the differences were added post analysis; b) Principal Component
 518 Analysis (PCA) showing similarities in community composition in a two-dimensional space with sites
 519 colored according to SIMPROF Cluster Analysis and symbols and ellipses denoting the gradient in
 520 wave exposure (at $p=0.001$; blue: exposed, green: sheltered; empty symbols represent center points of
 521 ellipses). All benthic vectors except ‘Sand’ significantly drive the displayed differences between sites
 522 (at $p<0.05$); Abbreviations: Acr – Acropora, Por – Porites, bra – branching, tab – table, mass –
 523 massive, encr – encrusting. Photographs in the right panel show reef community and structure at
 524 exposed and sheltered sites indicated by colored frames and numbers 1-4.



525

526 **Figure 3: Percent cover of main benthic categories** at sheltered and exposed sites in 2006 and 2020.

527 Note that All_mass includes Porites_mass and Other_mass and that Pavement was not plotted (2006:

528 $36\pm 5\%$ (mean \pm SE) at sheltered and $45\pm 4\%$ at exposed sites; 2020: $53\pm 8\%$ at sheltered and $71\pm 10\%$ at

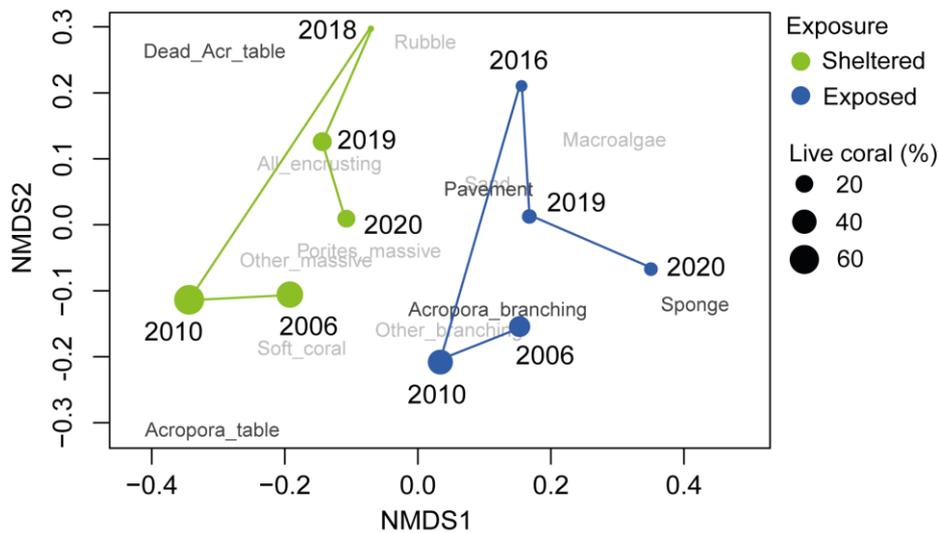
529 exposed sites). Abbreviations: Acr – Acropora, Por – Porites, bra – branching, tab – table, mass –

530 massive, encr – encrusting. Boxes depict 25th and 75th percentiles with median line, whiskers and

531 points extend to the smallest and largest values. Results of Welch’s t-tests are stated if significant

532 (***) <0.001 , (**) <0.01 , (*) <0.05).

533



534

535 **Figure 4: Non-metric multidimensional scaling (nMDS) of benthic communities** between 2006
 536 and 2020 at sheltered ($<1000 \text{ J m}^{-3}$; green) and exposed ($>1000 \text{ J m}^{-3}$; blue) fore reefs around Salomon
 537 atoll. Vectors connecting years display directional change of coral community composition. Benthic
 538 groups driving differences among locations and years are displayed in grey (dark grey $p < 0.05$, light
 539 grey $p > 0.05$). Scaled points indicate mean percent hard coral cover per year.

540