

1 Title: Abiotic and biotic controls on coral recovery 16 years after mass bleaching

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16

17 **Abstract**

18 As climate changes increase heat stress on tropical ecosystems, the long-term
19 persistence of coral reefs requires rapid coral recovery following coral bleaching events.
20 Using the extent of coral cover return to a pre-bleaching baseline as a benchmark, recovery of
21 fast-growing and stress-tolerant coral growth forms suggest that reefs can bounce back
22 between repeated disturbances if given adequate time and protection from anthropogenic
23 disturbances. However, long-term recovery dynamics of coral communities following severe
24 bleaching and mass mortality are limited, particularly for fringing reefs along inhabited
25 coastlines where human stressors may compromise recovery potential. Here, we examine the
26 dynamics and drivers of coral recovery in Seychelles, where 12 reefs returned to pre-
27 bleaching coral cover levels after a severe bleaching event caused >95% coral mortality. Six
28 reefs with initially low cover (<25%) recovered within 7-12 years and, after 16 years,
29 exceeded pre-bleaching cover levels by 132-305%. In contrast, six reefs with initially high
30 cover (20-60%) remained at 48-93% of pre-bleaching levels, with recovery projected to take
31 17-29 years. Abiotic and historic conditions constrained recovery rates, with the slowest
32 recovery times observed on deep and wave-exposed reefs with high pre-bleaching coral
33 cover. Reefs with high juvenile coral densities and low nitrogen levels recovered fastest,
34 possibly due to the interplay between nutrient enrichment, algal proliferation, and coral
35 recruitment. Our findings emphasize the importance of understanding small-scale variation in
36 recovery potential, whereby recovery times were governed by natural limits on growth rates
37 and modified by coral recruitment and nutrient enrichment. Ultimately, climate-impacted
38 reefs can recover to moderate coral cover levels but, if bleaching causes repeated high coral
39 mortality, short recovery windows will prevent a return to historic levels of coral dominance.

40

41

42 **Introduction**

43 Climate-driven thermal stress events that cause coral bleaching events are accelerating in
44 frequency, threatening the persistence of coral-dominated reefs across the tropics (Pandolfi et
45 al. 2003, Heron et al. 2016). As global temperatures have risen from 1980 to 2016, coral
46 bleaching recovery windows have shortened from 27 to 5.9 years (Hughes et al. 2018a), and
47 are likely to become even shorter as severe bleaching events are expected to occur annually
48 by 2050 (van Hooidonk et al. 2016). Although examples of resilient reefs that regenerate
49 coral cover suggest that certain conditions, such as isolation from human stressors, facilitate
50 recovery from bleaching (Sheppard et al. 2008, Gilmour et al. 2013), the conditions that
51 promote or depress recovery rates are not well understood, particularly for fringing reefs
52 along inhabited coastlines where chronic anthropogenic stressors are pervasive. As such, it is
53 unclear under what conditions reefs may be able to recover rapidly in the face of diminishing
54 recovery windows.

55 The ability of coral reefs to return to coral-dominated states following declines from acute
56 disturbances, including bleaching, is typically measured by the degree of recovery towards
57 pre-disturbance coral cover (Connell 1997, Osborne et al. 2011, Johns et al. 2014). Although
58 differential bleaching susceptibility and recovery potential of coral growth forms (Darling et
59 al. 2013) means that reassembly of community composition is expected to lag behind cover
60 recovery (Johns et al. 2014), return times to pre-disturbance coral cover (i.e. 100% recovery)
61 may be considered an early indicator of recovery. Short return times enhance the probability
62 of coral-dominated states under recurrent bleaching, but should also increase the potential for
63 a return to pre-bleaching functioning (Alvarez-Filip et al. 2013). However, return times can
64 vary considerably among reefs (Osborne et al. 2011, Johns et al. 2014) and regions (Connell
65 1997, Baker et al. 2008, Graham et al. 2011), implying that recovery potential is highly
66 context dependent. As such, our understanding of plausible recovery times under recurrent

67 bleaching scenarios requires analysis of long-term benthic changes according to local
68 conditions of resilient reefs.

69 Regional and local differences in coral recovery are likely due to reef-specific abiotic and
70 biotic conditions that are conducive to coral growth, and to degrading influences of local
71 anthropogenic stressors. For example, high wave energy limits coral growth and larval
72 settlement, thus placing natural constraints on coral cover (Gove et al. 2015) which likely
73 also influence recovery times. Ecological feedbacks between corals, algae, grazers and
74 nutrients underscore the importance of biotic processes in determining coral recovery, with
75 coral recruitment and survival dependent on grazing control of algal competitors (McCook et
76 al. 2001, Birrell et al. 2008), particularly under nutrient regimes that stimulate algal
77 productivity (Burkepile & Hay 2009, Burkepile et al. 2013). These feedbacks may be
78 disrupted by anthropogenic influences where, for example, sedimentation directly inhibits
79 coral growth (Fabricius et al. 2005) and nitrogen enrichment promotes macroalgal
80 overgrowth (Lapointe 1997). Overexploitation of grazers can promote algal overgrowth
81 (Mumby et al. 2006) and magnify nutrient effects (Burkepile & Hay 2006) and so, after
82 bleaching, may slow recovery rates by limiting coral recruitment (Elmhirst et al. 2009).
83 These factors imply that benthic recovery will vary spatially and thus impact ecosystem
84 functions in different ways among reefs and between regions, but that natural recovery
85 processes could be accelerated to increase the resilience of coral reefs within expected
86 recovery windows.

87 To date, empirical studies of coral recovery have typically contended with several types
88 of disturbance on reefs that are partially protected from human stressors. For example,
89 comparative analyses of reef recovery rates on the Great Barrier Reef (GBR) suggest that
90 water quality (Ortiz et al. 2018, MacNeil et al. 2019) and thermal heating (Osborne et al.
91 2017) have compromised GBR recovery potential. The GBR has suffered severe bleaching

92 following the 2016 El Niño (Hughes et al. 2018b) but previous studies have focused on
93 recovery following moderate coral decline by other disturbances (e.g. cyclones, crown-of-
94 thorns starfish), and the role of protection networks (Mellin et al. 2016). Furthermore,
95 detection of recovery mechanisms requires reef-scale ecological metrics (e.g. coral
96 recruitment, nutrient loads) that are often unavailable at the appropriate temporal and spatial
97 scale.

98 Here, we assess the factors that promote or depress long-term coral recovery following a
99 severe bleaching event. We utilize long-term monitoring data of reef sites in the inner
100 Seychelles that experienced >90% coral mortality after bleaching in 1998, where 12 reefs
101 gradually regained coral cover and habitat complexity over 2005-2014 (Graham et al. 2015).
102 These monitoring data identified reef-specific conditions that increased the likelihood of
103 regime shifts to macroalgal states (Graham et al. 2015), but equivalent reef-level variation in
104 recovery dynamics at resilient reefs has not yet been examined. We used logistic growth
105 models in a hierarchical Bayesian modelling framework to demonstrate variability in
106 recovery trajectories, and quantified variation in projected recovery times according to
107 historic reef states, abiotic and biotic influences, and anthropogenic stressors.

108

109 **Methods**

110 *Identification of recovering reefs*

111 We examined the benthic recovery dynamics at 12 reef sites in the inner Seychelles
112 (Fig. 1). Reefs were defined as recovering from the 1998 bleaching event by Graham et al.
113 (2015), based on the relative abundance and trajectories of hard coral and macroalgae from
114 1994-2014. Recovering reefs had greater cover of hard corals than macroalgae, increased in
115 hard coral cover from 2005 to 2011, and met one of the three following trajectory criteria: 1)
116 declining Euclidean distance between pre-disturbance (1994) and post-disturbance benthic

117 condition (2005, 2008, 2011); 2) the rate of hard coral cover increase was stable or greater
118 than that of macroalgal cover change; 3) the decline in coral cover between 1994-2011 was
119 lower than that of 1994-2005, and corresponding change in macroalgal cover was negligible
120 (Graham et al. 2015). Because Seychelles reefs experienced a second mass bleaching event in
121 2016 (Hughes et al. 2018a), our analysis focuses on the recovery period 2005-2014.

122

123 *Benthic community data*

124 Coral cover and structural complexity estimates were collected using visual point
125 counts. Surveys were conducted in 1994 (i.e. pre-bleaching) and, in the recovery period,
126 every three years from 2005-2014 (2005, 2008, 2011, 2014). At each reef site, one diver (SJ
127 in 1994, SW in all subsequent years) visually assessed benthic cover and structural
128 complexity in point counts of 7 m radius. Percent cover of major coral growth forms
129 (branching, massive, encrusting) was estimated in each point count, and structural complexity
130 was visually assessed on a 6-point scale (Polunin & Roberts 1993). Point counts were
131 repeated for eight (2011, 2014) or sixteen replicates (1994, 2005, 2008) at each reef site.
132 Coral visual assessments were supplemented with genera-level surveys conducted in 2008,
133 2011 and 2014. At each reef site, we used eight replicate 10 m line intercept transects to
134 record the percent cover of major coral genera.

135

136 *Predictors of benthic recovery*

137 We examined reef-level variation in benthic recovery dynamics using a suite of
138 abiotic, biotic and anthropogenic covariates that are thought to influence benthic recovery
139 dynamics. Abiotic processes place natural constraints on coral abundances (Williams et al.
140 2015) and, as such, may depress or promote recovery rates. For example, recovery may be
141 compromised in shallow water locations where corals are more vulnerable to bleaching

142 (Safaie et al. 2018). Locations subjected to high intensity wave action may have lower natural
143 cover of fast-growing branching corals (Gove et al. 2015) that are vulnerable to breakage and
144 dislodgement during severe storms (Madin & Connolly 2006) and, as such, may also require
145 longer recovery periods. To measure these processes, we used UVC survey depth (5 – 10 m)
146 and a long-term wave climatology metric as abiotic predictor covariates. Wave energy
147 (Joules) estimates were derived from hourly wind speed and direction values (Seychelles
148 National Meteorological Service) and accounted for the uninterrupted fetch distance across
149 which waves are generated (Ekeboom et al. 2003, Chollett & Mumby 2012). For each reef,
150 fetch distances were based upon a 55 m resolution map extending to 500 km for 32 compass
151 directions, and wind speed and direction values were averaged over 1998-2011 (Graham et
152 al. 2015). Thus, our wave energy metric represents reef-level variation in physical exposure
153 in the post-bleaching recovery period.

154 Abiotic constraints may be modified by herbivorous grazing pressure, which enhances
155 coral recruitment by clearing larval settlement space and suppressing growth of competing
156 turf and macroalgae (McCook et al. 2001, Mumby et al. 2006). In Seychelles, reefs with
157 higher herbivore biomass were also less likely to transition to macroalgal states after 1998
158 bleaching, but it is unclear if this effect also influenced recovery of resilient reefs. We used
159 observations of herbivorous fish biomass from diver surveys conducted at the same reef sites.
160 Before each benthic survey conducted in 2005, one diver (NAJ) surveyed the abundance and
161 length (cm) of 37 species of all diurnally active, reef-associated herbivorous fish (croppers,
162 scrapers, excavators and browsers), using point counts of 7 m radius. Abundances and
163 lengths were converted to biomass (kg ha^{-1}) using published length ~ weight relationships
164 (Froese and Pauly 2015), and averaged across replicates to give the mean herbivorous fish
165 biomass at each reef. As a measure of coral recruitment rates at each reef in the recovery
166 period, we estimated juvenile coral densities in 2011. Juveniles were corals <10 cm in

167 diameter, estimated using 33x33 cm quadrats for 8 replicates placed within each benthic
168 point count survey.

169 Recovery rates may be depressed on reefs nearby to sources of anthropogenic runoff,
170 owing to unbalanced nutrient loads which may indirectly impact coral recruitment through
171 proliferation of algal competitors (McCook et al. 2001, Fabricius et al. 2005, D'Angelo &
172 Wiedenmann 2014). We estimated the nitrogen concentration (%) of *Sargassum* fronds
173 collected at each reef site in 2014 (Graham et al. 2015). Nitrogen concentrations reflect
174 differences in nitrogen availability among reefs due to spatial variation in terrestrial nutrient
175 inputs.

176 Finally, we used pre-disturbance surveys to account for potential unmeasured reef-
177 level variation in the capacity of each reef to reach highly complex, coral-dominated states
178 (hereafter 'historic' predictors). Furthermore, because we defined recovery as a return to pre-
179 bleaching coral cover, we expected coral-dominated reefs to have the longest recovery times.
180 Initial benthic conditions were the pre-bleaching estimate of hard coral cover and structural
181 complexity (i.e. in 1994), averaged across replicates at each reef site. All predictor covariates
182 were scaled and centered to a mean of 0 and standard deviation of 1 and examined for
183 collinearity before model fitting.

184

185 *Coral recovery models*

186 We examined reef-level variation in hard coral recovery trajectories using a
187 hierarchical Bayesian logistic model. Observed hard coral cover (y) was modelled as a
188 logistic function where the recovery rate r , asymptote a_{max} , and the curve inflexion point
189 x_{mid} predict the coral cover in each post-disturbance survey year i . Survey year was rescaled
190 to represent recovery years following 1998 bleaching (e.g. first survey year 2005 = 7
191 recovery years).

192 We fitted two logistic model parameterizations, for either a standard 3-parameter
 193 logistic model with one maximum asymptote term (1) or a more flexible 4-parameter logistic
 194 with minimum (a_min) and maximum asymptote terms (a_max) (2). Furthermore, because
 195 the logistic asymptote may be defined by the observed recovery rate or fixed to the substrate
 196 area available for coral colonization, we also fitted models with either unconstrained
 197 asymptotes (i.e. a_max is estimated by the model) or asymptotes set to the amount of hard
 198 substrate area available for colonization at each reef in 1994 (i.e. $a_max = \text{total hard coral} +$
 199 $\text{rock} + \text{rubble}$). Reef-level recovery dynamics were modelled in a hierarchical structure that
 200 allowed r , a_min , and a_max to vary by each reef site s , for gamma-Poisson distributed
 201 observations (McElreath 2017),

$$202 \quad y_i \sim DPOIS(\mu, scale)$$

203 with mean models:

$$204 \quad \log(\mu_{i,s}) \sim \frac{a_max_r}{1 + e^{-\frac{(xmid-i)}{r_s}}} \quad (1)$$

$$205 \quad \log(\mu_{i,s}) \sim a_min_r + \frac{a_max_r - a_min_r}{1 + e^{-\frac{(xmid-i)}{r_s}}} \quad (2)$$

206 Models were estimated by Markov Chain Monte Carlo (MCMC) using the No-U-
 207 Turn-Sampler implemented in Stan, sampling for 3,000 iterations across 3 chains with
 208 warmup of 1,500. Prior values were drawn from a normal distribution with mean = 6 and
 209 standard deviation = 1 ($N(6, 1)$) for r , from $N(3.6, 1)$ for a_min and a_max (= 36% cover on
 210 linear scale), and $N(-0.9, 1)$ for $xmid$. We compared model fits among logistic models (1, 2)
 211 and asymptote values (unconstrained or fixed to available substrate area) with the Widely
 212 Applicable Information Criterion (WAIC) (McElreath 2017), which supported the four-
 213 parameter logistic model with a_max fixed to the available substrate area (Electronic
 214 Supplementary Material, ESM Table S1). We ensured chain convergence by assessing trace
 215 plots, and by checking that the Gelman-Rubin diagnostic (\hat{R}) was < 1.01 and the number of

216 effective samples was sufficiently high (Electronic Supplementary Material, ESM Table S2).
217 We also evaluated model fits by checking correspondence between fitted and observed values
218 (Electronic Supplementary Material, ESM Fig. S2). Finally, we sampled posterior predictions
219 of recovery year using a model of 7,000 iterations across 1 chain.

220

221 *Reef level variability in coral recovery*

222 We examined coral recovery trajectories at each reef by drawing predicted cover
223 values from the posterior distribution for each year in the recovery period 2005-2014.
224 Observed reef-level trajectories were visualized on a common scale by rescaling each
225 predicted coral cover value relative to its baseline (i.e. 1994), such that coral recovery was
226 expressed as a proportion of its pre-bleaching cover (e.g. coral recovery = 100% when
227 predicted coral cover = coral cover in 1994). We then examined variation in recovery times
228 by identifying, for each reef, the year when mean predicted coral recovery reached the pre-
229 bleaching baseline. For reefs that failed to recover by the last visual census (2014), we
230 projected coral recovery trajectories forward in time until the baseline was reached.

231 Next, we sought to understand variation in the expected year of recovery ($y_{recovery}$)
232 according to abiotic, biotic and anthropogenic covariates. We fitted a Bayesian linear model
233 to recovery year and eight fixed covariates,

$$234 \quad y_{recovery_s} \sim a_s + \beta_1 herb_{biomass} + \beta_2 depth + \beta_3 coral_{juveniles} + \beta_4 complexity_{1994} \\ 235 \quad \quad \quad + \beta_5 coral_{cover}_{1994} + \beta_6 wave + \beta_7 management + \beta_8 C : N$$

236 with prior values drawn from the distribution $N(0, 2)$ for fixed covariates and at the average
237 recovery year across reefs ($N(17, 5)$) for the intercept. Model parameters were estimated by
238 MCMC sampling of 7,000 iterations, with a warmup of 1,500 across 3 chains. Model
239 convergence was assessed with posterior predictive checks, effective samples, and \hat{R}
240 (Electronic Supplementary Material, ESM Table S3). We further ensured that parameter

241 effect sizes were robust to potential estimation biases caused by outlying predictor values at
242 individual reefs. Using a jackknife resampling approach, we compared parameter posterior
243 distributions across predictive models fitted to datasets that dropped each reef in turn (i.e. 12
244 models, each with $n = 11$). Possible overfitting of recovery year models fitted to relatively
245 few reefs ($n = 12$) and a high number of predictors (8) was minimized by use of weakly-
246 uninformative covariate priors and half-Cauchy variance prior (*Cauchy*(0, 2)) (McNeish
247 2016).

248 We assessed covariate influences with standardized effect sizes, represented by the
249 posterior distribution median with 95% (strong inference) and 50% (weak inference)
250 confidence intervals, and visualized median recovery times across the observed gradient of
251 each covariate. We also used heat maps to visualize the combined effect of any strong biotic
252 and human covariates on median coral recovery time, thus allowing us to assess how local
253 reef conditions might be manipulated to enhance coral recovery after bleaching.

254 All analyses were conducted in R 3.4.1 (R Development Core Team 2018), logistic
255 model parameterizations were provided by *SSlogis* and *SSfpl*, and Bayesian models were
256 fitted in Stan with the *rethinking* package (McElreath 2017). We provide our R code and
257 model predictions at github.com/jpwrobinson/coral-bleach-recovery.

258

259 **Results**

260 Of the 12 reefs that recovered from mass bleaching in 1998, pre-bleaching coral cover
261 averaged 26%, with seven low cover reefs (10-20%) and five high cover reefs (20-60%). In
262 2005, 7 years after bleaching, mean coral cover across all 12 reefs was 11%, which steadily
263 increased to return to mean pre-bleaching cover (27%) by 2014 (Fig. 1d). However, mean
264 trends obscured considerable variation in reef-level recovery trajectories. In 2005, four reefs
265 had recovered 72-127% of pre-bleaching coral cover, whereas eight reefs remained below

266 50% of pre-bleaching cover (Fig. 2a). From 2005 to 2014 (i.e. 7-16 years after bleaching),
267 reefs steadily recovered towards pre-bleaching conditions (Electronic Supplementary
268 Material, ESM Fig. S1). By 2014, six ‘overshoot’ reefs had exceeded baseline cover by 132 –
269 305% to reach fully recovered states within 7-12 years, while six reefs failed to recover to
270 1994 conditions and remained at 48-93% baseline cover, with recovery predicted to occur
271 within 17-29 years (Fig. 2b). Thus, despite recovery trajectories across reefs (Electronic
272 Supplementary Material, ESM Fig. S2) and return to average pre-bleaching coral cover (Fig.
273 1d), time to recovery was highly variable across reefs, ranging from 7 to 29 years. Recovery
274 was primarily driven by branching *Acropora* corals rather than massive or encrusting forms
275 (Fig. 1d; Electronic Supplementary Material, ESM Figs. S3, S4).

276

277 *Reef-level influences on recovery year*

278 Recovery years were strongly associated with reef-level explanatory covariates. For
279 abiotic and historic covariates, recovery was slowest at exposed and deep reefs with high pre-
280 bleaching coral cover (Figs. 3,4). For instance, recovery year was delayed by 1.8 years for
281 every 10% increase in historic coral cover, by 2.7 years for every 5 m increase in depth, and
282 by 2.4 years for every 0.5 J hr⁻¹ increase in wave energy (Fig. 4). Initial structural complexity,
283 which was relatively similar among reefs (3 – 3.7) relative to post-bleaching habitat structure
284 (1.9 – 3.2), was weakly associated with recovery year (effect size = 0.37; 95% CIs = -1.30,
285 2.08).

286 Coral juvenile densities and nitrogen load were the strongest positive influences on
287 recovery year, with recovery times minimized on reefs with low nutrient enrichment and high
288 juvenile coral density (Figs. 3, 5) (Electronic Supplementary Material, ESM Fig. S5). After
289 accounting for abiotic effects, recovery times <10 years were expected for reefs with both
290 low nitrogen load (nitrogen <0.7%) and high coral recruitment (>40 juveniles m⁻²) (Fig. 5).

291 Surveyed reefs, however, did not meet these criteria, with predicted relationships primarily
292 driven by slow recovery times of nutrient enriched reefs with low juvenile coral densities,
293 and by fast recovery times of one nutrient-poor reef (7 years, 0.6% nitrogen) and one high-
294 density juvenile coral reef (9 years, 58.8 juveniles m⁻²). Despite these outliers, covariate
295 effect sizes were not biased by observations from individual reefs (Electronic Supplementary
296 Material, ESM Fig. S7) and abiotic and biotic covariates were uncorrelated (Electronic
297 Supplementary Material, ESM Fig. S1), indicating that variability in recovery times was
298 attributable to the combined effect of several covariates rather than to collinearity or the
299 condition of outlying reefs. Recovery times were slower on protected reefs (effect size =
300 1.56; 95% CIs = -0.07, 3.18) and on those with abundant herbivores, with recovery extending
301 by 4.1 years from the lowest to highest levels of grazing biomass (42-509 kg ha⁻¹) (Electronic
302 Supplementary Material, ESM Fig. S5b).

303

304 **Discussion**

305 Over a decade after severe coral bleaching, recovering Seychelles reefs varied
306 substantially in their extent of coral recovery, with six reefs returning to pre-bleaching coral
307 cover within 7-12 years and six reefs failing to reach pre-bleaching cover before the next
308 major bleaching event in 2016. Projected recovery times ranged from 7-29 years and were
309 linked to reef-level variation in several abiotic, biotic and anthropogenic factors. Abiotic and
310 historic conditions placed natural constraints on recovery, with the fastest recovery times
311 predicted for shallow reefs with low initial coral cover and low daily wave exposure. After
312 accounting for abiotic limits, recovery times were also faster under conditions of high coral
313 recruitment and low nitrogen enrichment, implying that improving juvenile coral survival and
314 mitigation of nutrient runoff may enhance coral recovery.

315 Reef recovery was driven by regeneration of fast-growing branching *Acropora* corals,
316 which on most reefs have replaced massive growth forms (Wilson et al 2012, Wilson et al. in
317 revision). Such compositional turnover suggests that these reefs have not recovered their pre-
318 bleaching functions and, for example, recovery of structural complexity was incomplete by
319 2014. Other ecosystem functions, such as community calcification rates, have not fully
320 returned (Januchowski-Hartley et al. 2017). Although we were unable to examine long-term
321 abundance shifts among individual coral species, community turnover is expected to continue
322 after pre-bleaching cover levels have been reached (Johns et al. 2014). Studies which model
323 recovery trajectories for individual coral species will help to identify future community
324 compositions for heat-stressed reefs (Ortiz et al. 2018). Compositional shifts towards
325 branching *Acropora* corals, combined with either overshoot or failure to return to pre-
326 bleaching coral cover, mean that Seychelles reefs failed to resemble pre-bleaching states after
327 16 years of recovery. As bleaching events continue to accentuate boom-bust dynamics in the
328 keystone habitat structure of coral reefs (Wilson et al. in revision) the likelihood of full
329 recovery cycles is diminishing (Hughes et al. 2018a). In Seychelles, the 2016 coral bleaching
330 event caused extensive coral mortality (Wilson et al. in revision), meaning the recovery
331 dynamics we have documented in this study need to re-commence.

332 Recovery times did, however, vary predictably with natural abiotic limits, with the
333 slowest recovery times occurring on deep reefs with high wave exposure. Such influences
334 likely reflect constraints on coral growth rates where, for example, light attenuation at depth
335 slows coral growth rates (Huston 1985, Pratchett et al. 2015). However, the influence of
336 depth on bleaching responses is multifaceted, with evidence that shallow reefs often incur
337 great incidences of bleaching (Bridge et al. 2013) and are more likely to undergo regime
338 shifts to macroalgae after bleaching (Graham et al. 2015). Thus, deep cool water reefs may be
339 refuges to heat stress (Safaie et al. 2018). As such, the fast coral growth at shallow reefs may

340 only be realized under conditions which promote coral growth (e.g. high juvenile coral
341 density), while reduced stress in deeper waters may help reefs to retain high coral cover, at
342 the cost of slower recovery times. For wave energy, exposure gradients determine spatial
343 patterns in coral cover (Done 1982, Williams et al. 2015, Gove et al. 2015) and extreme
344 events can cause physical dislodgement of coral colonies (Madin & Connolly 2006). We
345 extend these concepts to show that wave energy may also negatively influence coral recovery
346 rates, with reefs exposed to high daily wave action also slower to recover. Such physical
347 constraints on coral recovery likely occurred because branching corals, which are most
348 susceptible to removal by wave action (Madin & Connolly 2006), dominated recovery
349 dynamics. Thus, abiotic filtering of community composition can enhance or retard reef
350 recovery rates. For example, reefs with highest wave exposure were characterized by low
351 levels of branching corals, and failed to reach pre-bleaching total coral cover (Mahe E Patch,
352 66% recovery; Ste Anne Patch, 62% recovery). Together, these predictions of abiotic
353 constraints can guide expectations of coral recovery after bleaching events, which are
354 particularly needed for reefs where *in-situ* monitoring data are unavailable. For example,
355 remote sensing of depth and wave energy could be paired with thermal stress maps and
356 predictors of bleaching vulnerability (e.g. Safaie et al. 2018) to forecast long-term resilience
357 to heat stress across large spatial scales.

358 Coral recruitment and nutrient enrichment exceeded abiotic limits on coral recovery
359 times, likely due to their opposing influences on competition between calcifiers and algal
360 taxa. High rates of coral recruitment (i.e. juvenile coral densities) should positively correlate
361 with future adult coral abundances (Birrell et al. 2008) and thus shorten recovery times. In
362 Seychelles, reef-level variation in coral recruitment appears to be driven by benthic habitat
363 properties rather than larval supply. Survivorship of juvenile corals to adults is lower on
364 unstable rubble reefs that are frequently disturbed by wave action (Chong-Seng et al. 2014),

365 and juvenile coral recovery from severe bleaching is moderated by habitat complexity (Dajka
366 et al. 2019). Nitrogen enrichment, however, may have had an additional, indirect influence on
367 recovery times by stimulating algal growth. Nutrients may exert bottom-up control of benthic
368 composition through animal excretion (Graham et al. 2018), seasonal and upwelling sources
369 (Williams et al. 2015), and by anthropogenic-driven eutrophication (Fabricius et al. 2005).
370 Our results demonstrate that high nutrient loads attributable to terrestrial run-off also slowed
371 coral recovery, which is consistent with previous observations that low C:N ratios (i.e. high
372 nitrogen concentrations) increased the probability of a macroalgal regime shift on Seychelles
373 reefs (Graham et al. 2015). Indeed, juvenile coral densities decreased with increasing nutrient
374 enrichment at 10 of 12 reefs (though were uncorrelated in our predictive models), possibly
375 because high nutrient loads inhibit coral recruitment (Koop et al. 2001) and promote growth
376 of competing algal organisms (Burkepile & Hay 2009), which likely combine to raise post-
377 recruitment coral mortality (Chong-Seng et al. 2014). Nutrient concentrations can also benefit
378 coral growth, though this is contingent on high herbivory levels (Burkepile & Hay 2006) and
379 the ratio of nitrogen to phosphorus (D'Angelo & Wiedenmann 2014). Given that several
380 nutrient-based mechanisms potentially underpin considerable reef-level variability in
381 recovery times, experimental investigation of the relationships between coral recruitment,
382 nutrient enrichment, and bleaching recovery is urgently needed. Such research will help to
383 unravel biotic feedbacks and thus identify conditions that accelerate coral recovery.

384 Local biotic and anthropogenic influences on recovery times should anchor expectations
385 according to abiotic constraints and reveal potential processes that might be manipulated to
386 enhance recovery after bleaching. Across regions, large-scale oceanographic influences such
387 as temperature and productivity constrain natural baselines of coral cover (Williams et al.
388 2015) and so may contribute to regional differences in recovery times (Baker et al. 2008,
389 Graham et al. 2011). At smaller spatial scales, biotic processes that promote coral recruitment

390 may be enhanced by manipulation of ecological feedbacks to enhance coral recovery
391 (Nystrom et al. 2012, Ladd et al. 2018), such as reducing terrestrial run-off. However, the
392 influences of nutrient enrichment on coral condition are complex, owing to confounding
393 sources from terrestrial inputs (Fabricius et al. 2005), upwellings and animal excretion
394 (Graham et al. 2018), variable impacts according to the type and balance of nutrients
395 (D'Angelo & Wiedenmann 2014), and uncertainties surrounding nutrient cycling and their
396 long-term persistence in seawater (Fabricius et al. 2005). Isolation of nutrient pathways
397 which enhance coral growth and recruitment is a critical avenue for further research.

398 Herbivore biomass had a weak, positive effect on recovery year, contradicting
399 expectations that high grazing pressure will enhance recovery through top-down control of
400 algae. Given that reefs with herbivore biomass $>177 \text{ kg ha}^{-1}$ were less likely to regime shift in
401 Seychelles (Graham et al. 2015), grazing pressure may be a relatively weak influence on
402 coral recovery as herbivore biomass has increased on Seychelles reefs since the 1998
403 bleaching event (Robinson et al. 2019), and thus thresholds that prevent macroalgal
404 overgrowth have been exceeded on many reefs. Alternatively, because grazing effects on
405 benthic communities are tightly linked to the size structure and functional composition of
406 herbivore assemblages (Nash et al. 2015, Steneck et al. 2018), grazing influences on coral
407 recovery may not be detectable with coarse biomass metrics which combine distinct
408 functional groups. The longer recovery times on reefs protected from fishing was also
409 unexpected. Both herbivore and management effects may, however, be somewhat
410 confounded by pre-bleaching coral cover. Compared to fished reefs, protected reefs
411 supported 65 kg ha^{-1} greater herbivore biomass and 15.5% higher pre-bleaching coral cover,
412 meaning that protected reefs require longer recovery times to reach coral-dominated states.
413 Extending our recovery analyses to other regions will help resolve uncertainties around
414 management and herbivory effects.

415 Recovery times from severe bleaching events inform expectations for the long-term
416 persistence of coral-dominated reefs in a warming climate. Here, similar recovery trajectories
417 meant that reefs that recovered before the next mass bleaching event (i.e. within 16 years)
418 were those with pre-bleaching cover <25%. Reefs that failed to recover were generally those
419 with exceptional coral cover (>30%). Such patterns are consistent with evidence that
420 recurring mass bleaching events, particularly those that occur within 16 years of each other
421 and cause severe coral mortality, will prevent coral reefs returning to historic coral-
422 dominated states (Birkeland 2004, Hughes et al. 2018a). Furthermore, given that pre-
423 bleaching cover was highly variable (11-55%), our findings underscore the uncertainty
424 associated with using historic conditions as a recovery benchmark. For example, pre-
425 bleaching disturbances may have limited potential coral cover, which would explain why
426 overshoot reefs were able to far exceed their baseline cover after bleaching.

427 Our long-term analysis of coral recovery dynamics uncovered substantial reef-scale
428 variability in recovery times after mass bleaching, whereby reefs either failed to recover or
429 exceeded their baseline state and recovery ranged from 7 to 29 (projected) years. The number
430 of recovery years were strongly constrained by abiotic conditions (depth, wave energy) and
431 pre-bleaching coral cover, indicating that predictions of bleaching recovery times can be
432 informed by abiotic and historic conditions at the scale of individual reefs. The strongest
433 influences on recovery times were post-bleaching juvenile coral densities and nitrogen
434 concentrations, suggesting that recovery might be enhanced by limiting nutrient run-off and
435 promoting coral recruitment and survivorship. However, coral-dominated reefs are unlikely
436 to persist under recurrent bleaching events that cause extensive coral mortality, if recovery
437 windows from such severe bleaching shorten to less than 10 years (Hughes et al. 2018a).
438 Further investigation of feedbacks between nutrients, algal growth, and coral recruitment is

439 necessary to understand how manipulation of biotic processes can accelerate reef recovery
440 after climate-driven bleaching events.

441

442 **Competing interests**

443 We have no competing interests.

444

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451

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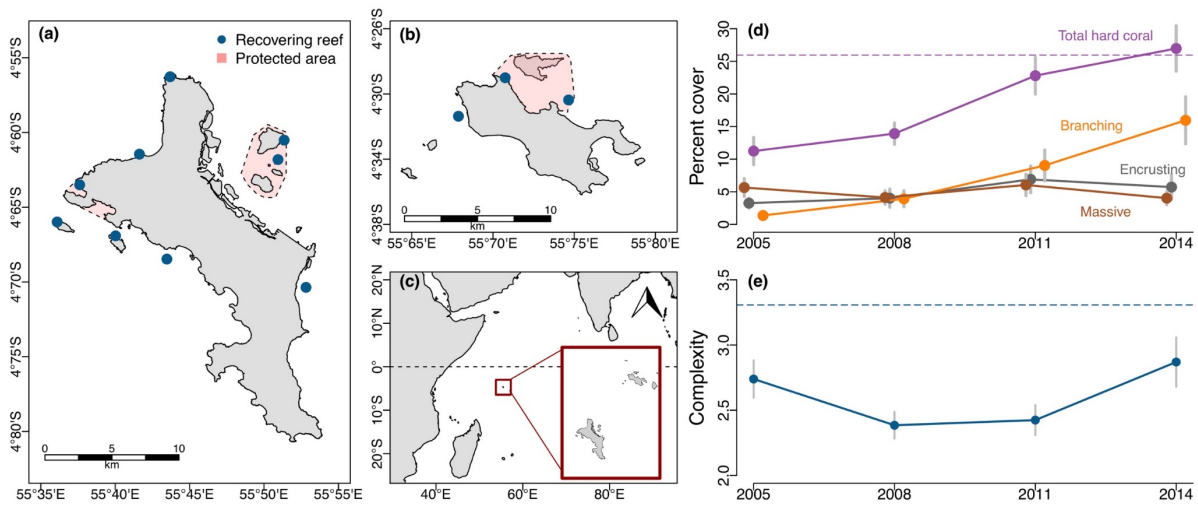
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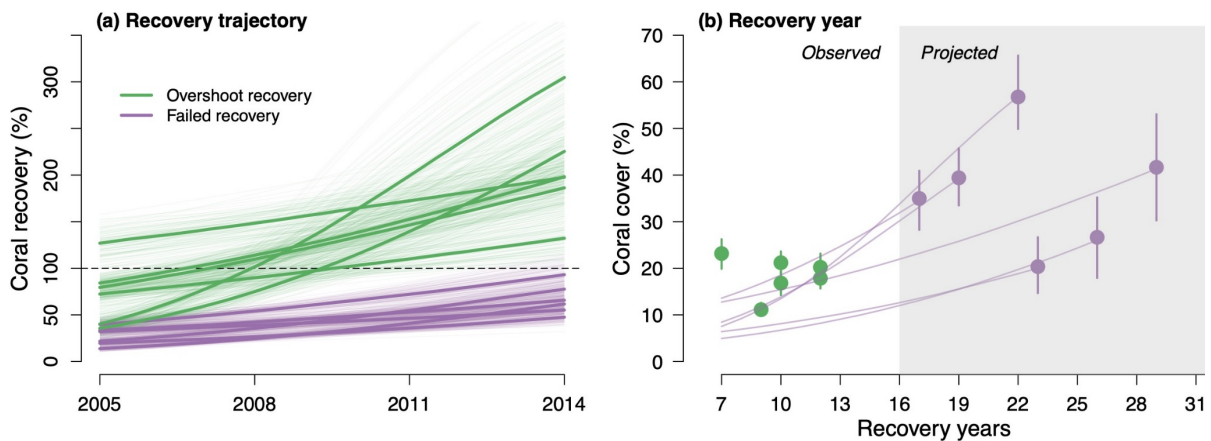
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655 **List of Figures**



656

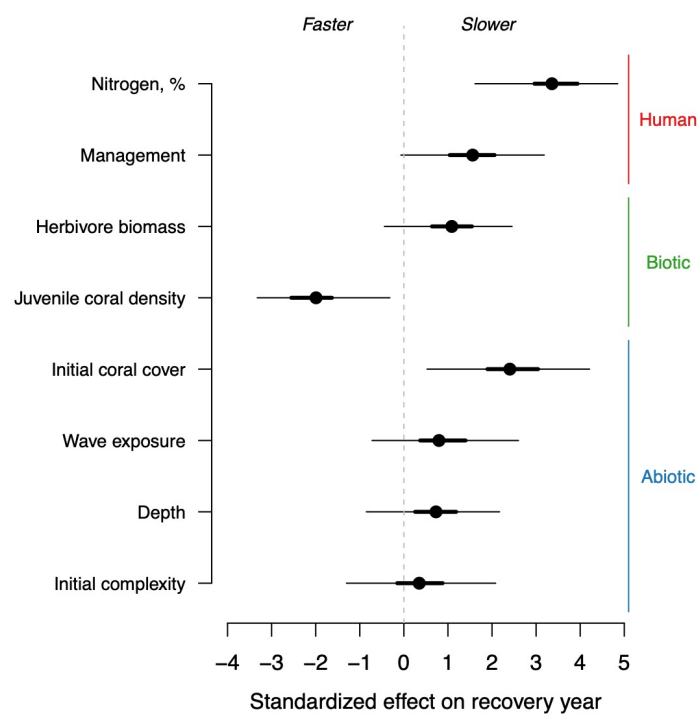
657 **Figure 1** Map of recovering reef sites on Mahe (a) and Praslin (b) in Seychelles, with Indian
 658 Ocean location (c) and change in benthic habitat composition over 2005-2014 (d,e). Points
 659 are mean percent cover of coral growth forms (d) and structural complexity (e) across all
 660 recovering reefs (± 2 standard errors). 1994 pre-bleaching baseline total coral cover and
 661 structural complexity indicated as dashed lines.



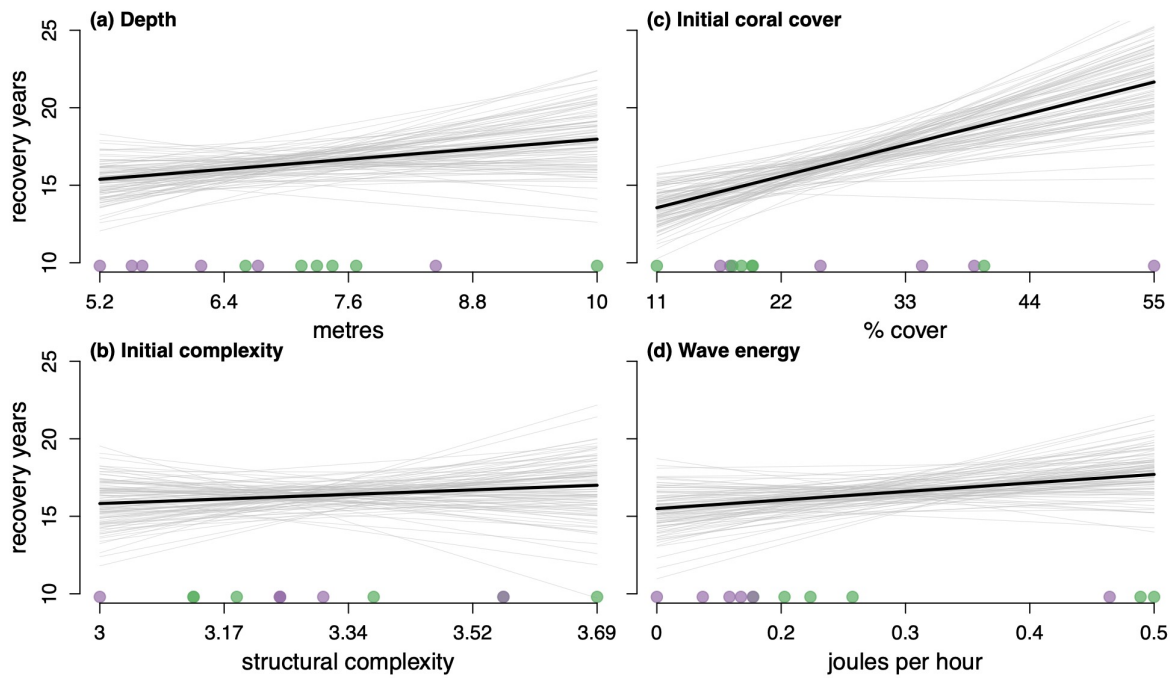
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663 **Figure 2** Reef-level variability in the extent and timing of coral recovery. (a) Hard coral
 664 cover as a proportion of the pre-bleaching coral cover at each reef in 1994, for overshoot
 665 (green) and failed (purple) recovery trajectories. Lines are posterior predictions of hard coral
 666 at each reef from 2005-2014 conditioned on reef-specific predictor covariates, for the median
 667 prediction (solid lines) and 100 draws (thin lines) from the posterior distribution. (b) Time to

668 recovery for each reef, defined as the year at which predicted coral cover equaled pre-
 669 bleaching cover (i.e. 1994). Points are median recovery year with 95% credible intervals,
 670 with lines indicating median recovery trajectories. Corresponding percent cover trajectories
 671 are displayed in Electronic Supplementary Material, ESM Fig. S2. Recovery models assume
 672 no further mortality to corals, but we note that the 2016 mass bleaching event caused mass
 673 mortality at these reefs (Wilson et al., in revision) and therefore visualized recovery
 674 trajectories were not completed.



675
 676 **Figure 3** Abiotic, biotic, human and historic influences on recovery year. Effect sizes are the
 677 median of the posterior distribution for each parameter, with 95% and 50% credible intervals
 678 drawn from 1,000 samples. Predictors were standardized to the same scale and effect sizes
 679 were robust to jackknife resampling (Electronic Supplementary Material, ESM Fig. S5).



680

681

Figure 4 Predicted change in recovery year across gradients in abiotic and historic

682

conditions, for (a) depth, (b) initial complexity, (c) initial coral cover, and (d) wave energy.

683

Thick lines are median posterior estimate sampled across the range of each abiotic covariate,

684

holding all other covariate effects to their means (0), with uncertainty represented with by

685

100 samples from the posterior distribution (thin lines). Observed data distribution is

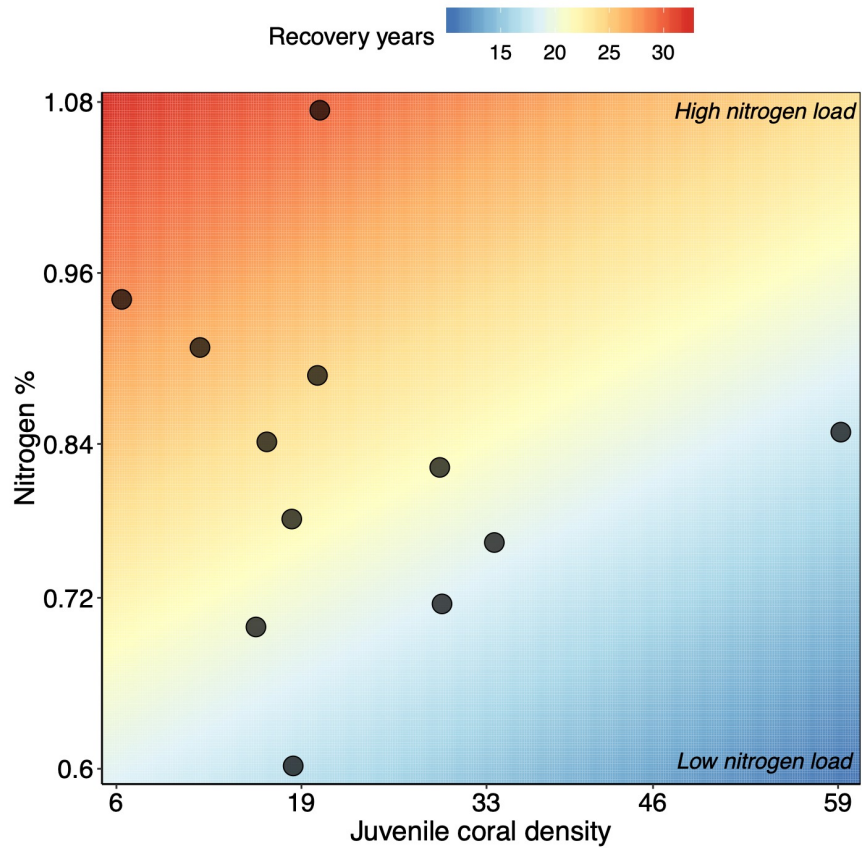
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indicated along the x-axis with points colored by their recovery trajectory (overshoot = green,

687

failed = purple).

688



689

690 **Figure 5** Combined influence of juvenile coral density and nitrogen concentration on
 691 recovery year. Colors indicate the median recovery year across the range of each predictor
 692 covariate, holding all other influences to their means (0). The range of observed coral
 693 densities and nitrogen concentrations are represented by grey points. Note that additional
 694 abiotic and historic influences on recovery times mean that points do not necessarily
 695 correspond with predicted recovery year.

696

697 **Electronic Supplementary Material, Appendix 1.**