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

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16

Abstract

17

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

Introduction

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

The ability of coral reefs to return to coral-dominated states following declines from acute disturbances, including bleaching, is typically measured by the degree of recovery towards pre-disturbance coral cover (Connell 1997, Osborne et al. 2011, Johns et al. 2014). Although differential bleaching susceptibility and recovery potential of coral growth forms (Darling et al. 2013) means that reassembly of community composition is expected to lag behind cover recovery (Johns et al. 2014), return times to pre-disturbance coral cover (i.e. 100% recovery) may be considered an early indicator of recovery. Short return times enhance the probability of coral-dominated states under recurrent bleaching, but should also increase the potential for a return to pre-bleaching functioning (Alvarez-Filip et al. 2013). However, return times can vary considerably among reefs (Osborne et al. 2011, Johns et al. 2014) and regions (Connell 1997, Baker et al. 2008, Graham et al. 2011), implying that recovery potential is highly 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 (Ekebom 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 *xmid* 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* = total hard coral +

199   rock + 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    $$y_i \sim DPOIS(\mu, scale)$$

203   with mean models:

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

205    $\log(\mu_{i,s}) \sim a\_min_r + \dfrac{a\_max_r - a\_min_r}{1 + e^{\frac{(xmid-i)}{r_s}}}$ (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   $y\_recovery_s \sim a_s + \beta_1 herbbiomass + \beta_2 depth + \beta_3 coraljuveniles + \beta_4 complexity_{1994}$

235         $+ \beta_5 coralcover_{1994} + \beta_6 wave + \beta_7 management + \beta_8 C{:}N$

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

50% of pre-bleaching cover (Fig. 2a). From 2005 to 2014 (i.e. 7-16 years after bleaching),

reefs steadily recovered towards pre-bleaching conditions (Electronic Supplementary

Material, ESM Fig. S1). By 2014, six 'overshoot' reefs had exceeded baseline cover by 132 –

305% to reach fully recovered states within 7-12 years, while six reefs failed to recover to

1994 conditions and remained at 48-93% baseline cover, with recovery predicted to occur

within 17-29 years (Fig. 2b). Thus, despite recovery trajectories across reefs (Electronic

Supplementary Material, ESM Fig. S2) and return to average pre-bleaching coral cover (Fig.

1d), time to recovery was highly variable across reefs, ranging from 7 to 29 years. Recovery

was primarily driven by branching *Acropora* corals rather than massive or encrusting forms

(Fig. 1d; Electronic Supplementary Material, ESM Figs. S3, S4).

Reef-level influences on recovery year

Recovery years were strongly associated with reef-level explanatory covariates. For

abiotic and historic covariates, recovery was slowest at exposed and deep reefs with high pre-

bleaching coral cover (Figs. 3,4). For instance, recovery year was delayed by 1.8 years for

every 10% increase in historic coral cover, by 2.7 years for every 5 m increase in depth, and

by 2.4 years for every 0.5 J hr^{-1} increase in wave energy (Fig. 4). Initial structural complexity,

which was relatively similar among reefs (3 – 3.7) relative to post-bleaching habitat structure

(1.9 – 3.2), was weakly associated with recovery year (effect size = 0.37; 95% CIs = -1.30,

2.08).

Coral juvenile densities and nitrogen load were the strongest positive influences on

recovery year, with recovery times minimized on reefs with low nutrient enrichment and high

juvenile coral density (Figs. 3, 5) (Electronic Supplementary Material, ESM Fig. S5). After

accounting for abiotic effects, recovery times <10 years were expected for reefs with both

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 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

445 **Acknowledgements**

451

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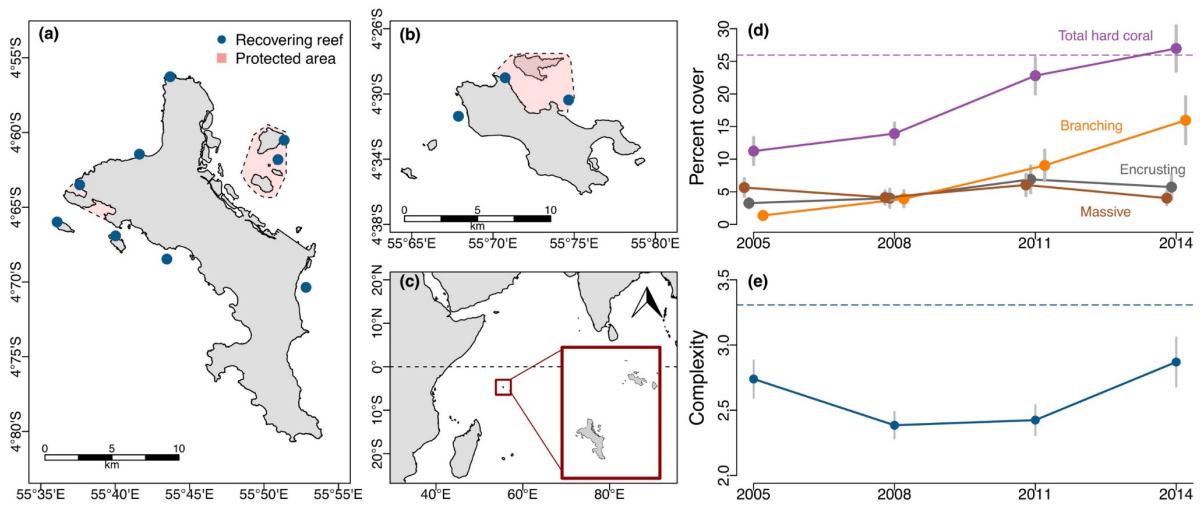
657 **Figure 1** Map of recovering reef sites on Mahe (a) and Praslin (b) in Seychelles, with Indian

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.
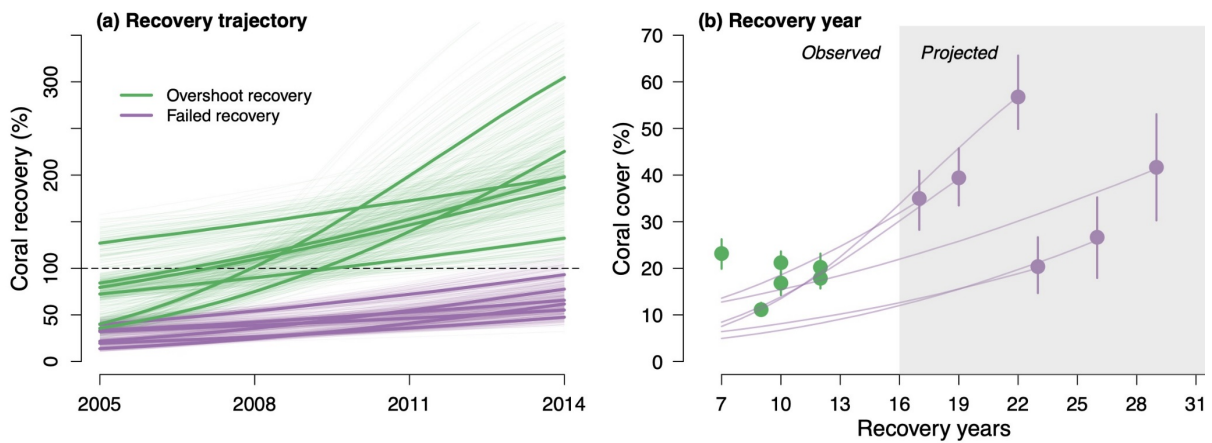
663 **Figure 2** Reef-level variability in the extent and timing of coral recovery. (a) Hard coral

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

24

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.
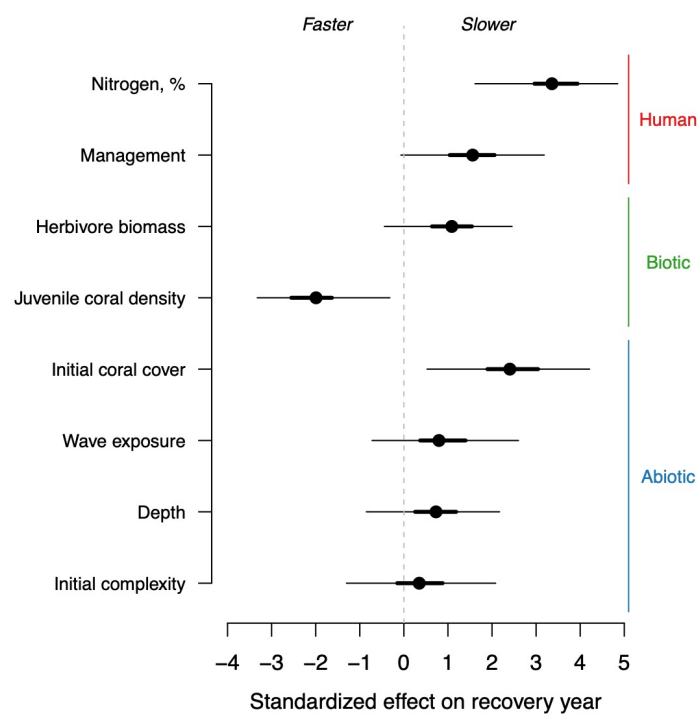
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676   **Figure 3** Abiotic, biotic, human and historic influences on recovery year. Effect sizes are the

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).
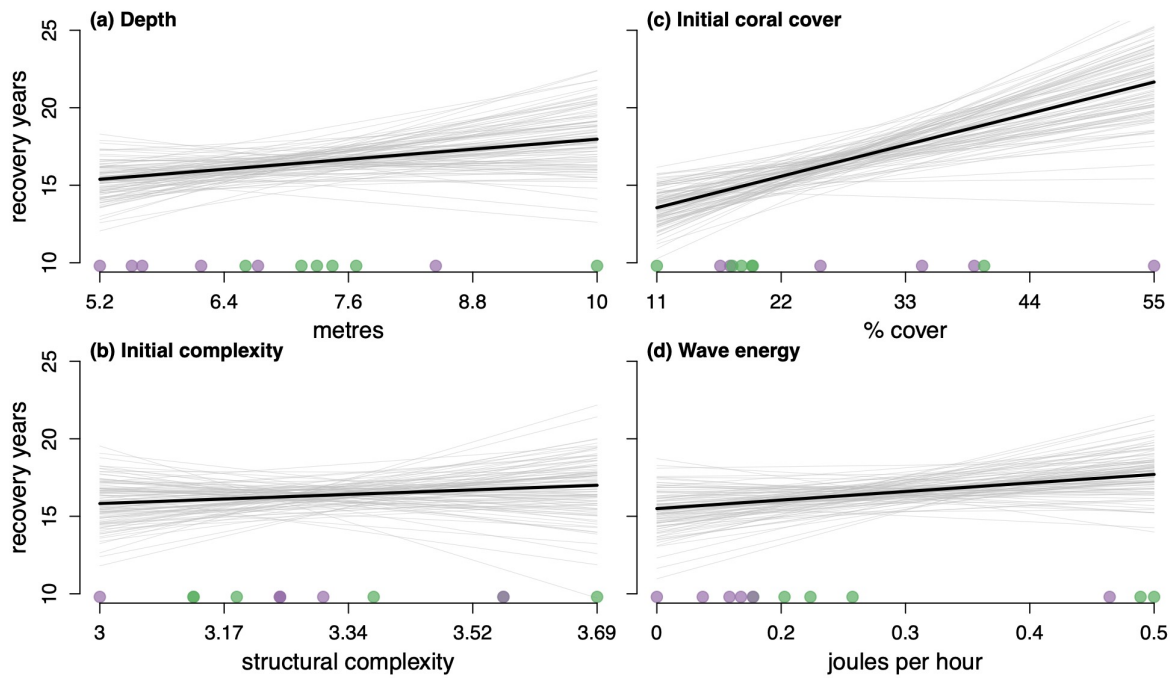
680

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

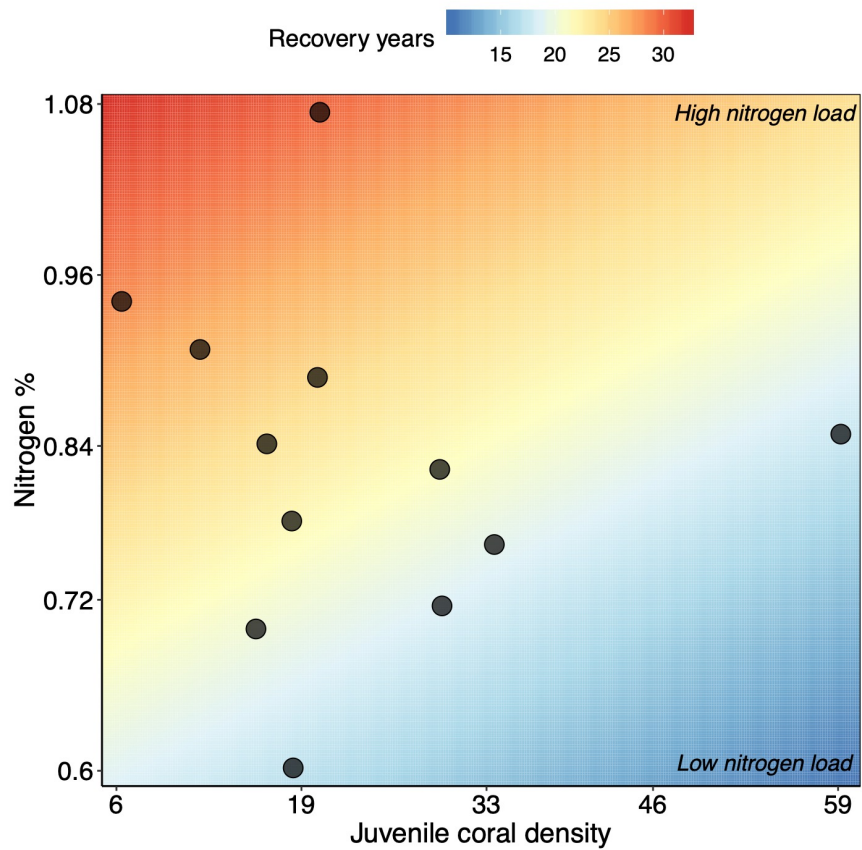685　100 samples from the posterior distribution (thin lines). Observed data distribution is

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

687　failed = purple).

688

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

Electronic Supplementary Material, Appendix 1.