Boom and bust of keystone structure on coral reefs

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Abstract

Repeated bouts of coral bleaching threaten the long-term persistence of coral reefs and associated communities. Here we document the short- and long-term impacts of heatwave events on coral and fish assemblages, based on regular surveys of 18 reefs of the granitic islands of Seychelles over 23 years. Extreme heat events in 1998 and 2016 led to bleaching associated declines in coral cover, whilst between these years there was an interim period of coral recovery on some reefs. Coral decline and recovery were primarily due to changes in the cover of branching coral, particularly those from the families Acroporidae and Pocilloporidae. Surveys during the 2016 bleaching, found that 95% of the 484 *Acropora* and *Pocillopora* colonies observed were either bleached or recently dead. The extent of bleaching and subsequent mortality were best explained by a priori assessments of community susceptibility to heat stress. One year later (2017) coral cover had fallen by 70% and average coverage across the 18 reefs was at 6%, similar to levels recorded in 2005, seven years after the 1998 bleaching. Decline in coral following the 2016 bleaching coincided with reduced abundance of fish <11cm TL, particularly corallivores, invertivores and mixed diet feeders. These changes are likely to foreshadow more widespread loss once the habitat structure erodes. Accordingly, seven years after the 1998 bleaching, when coral skeletons and reef structure had collapsed on some reefs, abundance of both large and small bodied fish had declined. We show that fluctuation in the cover of branching coral is positively associated with changes in the abundance of small-bodied fish which contribute to ecological processes and high diversity, suggesting branching corals are a keystone structure. Increased frequency of bleaching threatens the capacity of branching corals to fully recover after disturbances, reducing the amplitude of boom bust cycles of these corals and the keystone habitat structure they provide reef fish.

Introduction

Like many high diversity ecosystems in the tropics, coral reefs are threatened by a range of anthropogenic disturbances (Barlow et al. 2018). Of particular concern is the increasing frequency of marine heat waves that cause extensive mass bleaching and mortality of corals (Hughes et al. 2018a). These corals create the reef framework, underpinning ecological processes and services. For example, corals provide food and habitat for many of the reef associated species including highly diverse assemblages of fish (Wilson et al. 2006). These fish have crucial functional roles in terms of herbivory and bioerosion, and multispecies fisheries provide food and livelihoods for coastal communities around the world (Moberg and Folke 1999; Bellwood et al. 2004).

The physical structure, occurrence and life history traits of corals are variable, which may make some components of the coral assemblage of greater importance to reef associated fauna than others. For example, the types of corals with which fish associate varies among fish species and life history stages. Some fish feed or dwell with specific coral taxa, whilst others may associate with a broader group of corals (Cole et al. 2008; Coker et al. 2014). Branching corals appear especially important for fish as the structural complexity provided by this diverse group of corals provides refuges of numerous dimensions (Komyakova et al. 2018).

When a group of habitat forming taxa have a disproportionate contribution to ecological diversity and processes relative to their abundance, they may be considered keystone structures (Tews et al. 2004). This terminology has been used to highlight the ecological importance of large trees in terrestrial landscapes (Manning et al. 2006), and has recently been used to describe corals with specific growth forms (Kerry and Bellwood 2015). It is however difficult to definitively identify keystones as their influence may vary in different ecological settings (Menge et al. 1994). Large scale perturbations that remove candidate

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keystones, combined with temporal assessments of changes in the community, provide an
opportunity to identify keystone structures. Coral reefs regularly experience disturbances, and
fast-growing coral taxa may represent a 'boom' growth form that can recover habitat
structure relatively quickly.

Since the 1980s there have been several global scale marine heatwaves that have caused
widespread bleaching and mortality of corals. The granitic islands of Seychelles, in the Indian
Ocean, have a history of exposure to severe bleaching over this time. Previous research has
described the impact of mass bleaching on coral and fish assemblages on reefs in Seychelles
following the 1998 heatwave (Graham et al. 2006). Subsequent surveys of the same reefs
identified environmental and ecological factors that promote coral recovery and prevent reefs
undergoing regime shifts (Graham et al. 2015). Here we provide detailed assessments of how
the 2016 El Niño associated heatwave affected corals and associated fish on reefs in
Seychelles. Based on long-term assessments of reef communities that span the major
bleaching events in 1998 and 2016, and an intervening period of recovery, we identify the
change in abundance of branching corals as the major cause of temporal change in coral
cover and habitat structure. We then assess how periods of decline and increase in branching
coral cover have influenced fish assemblages to investigate whether these corals are keystone
structures on coral reefs.

Methods

Benthic and fish surveys of 18 Seychelles reefs were initially undertaken in 1994, with
subsequent surveys in 2005, 2008, 2011, 2014 and 2017. The 18 reefs were founded on
habitats of either granitic, contiguous carbonate or patches surrounded by sand or rubble. Six

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92   of the reefs were within no-take marine reserves, that have been in place since the 1970s and

93   are managed by the government in Seychelles (Jennings et al. 1996).

94   At each of the 18 reefs the abundance and size (total length, TL) of fish >7cm was recorded

95   from 134 non-cryptic, diurnally active species observed within 154m^2 replicate areas (7m

96   radius). The diver conducting fish surveys calibrated size estimates of fish by estimating and

97   confirming the size of plastic pipes at the start of each survey day, with mean error within

98   ~3% (Graham et al. 2007). All large mobile fish were recorded first, before a systematic

99   search of smaller site attached species. Count areas were located at the base of reef slopes at

100   2-9m depth. In 1994, 2005 and 2008 there were 16 replicate areas surveyed at each of the 18

101   reefs and in 2011, 2014 and 2017 eight replicate areas per reef. Average values were

102   calculated from the number of areas surveyed at each reef to account for differences in

103   sampling intensity over time.

104   The structural complexity of each replicate area was scored on a scale between 0 and 5,

105   where areas with 0 structure were sandy or rubble substrate with no vertical relief and areas

106   that scored 5 were exceptionally complex, with numerous caves and overhangs (Polunin and

107   Roberts 1993). The percent cover of coral and coral growth forms (branching, massive,

108   encrusting, tabular) within each replicate area was estimated from a plan view of the area, the

109   coral forms being based on broad growth forms described by Veron (1986). In addition to

110   plan view surveys, 10m line intercept transects were carried out in each area from 2008. Line

111   intercept transects recorded percent cover of coral to the genera level and comparisons

112   between this technique with plan view surveys found estimates of coral cover from the two

113   techniques were very similar (Wilson et al. 2007, 2012).

114   Reefs were also categorised as either recovering or regime shifted based on temporal trends

115   in coral and macroalgal cover (Graham et al. 2015). Recovering reefs had higher coral than

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116 macroalgal cover in 2011, and an increase in coral cover between 2005 and 2011. Conversely

117 regime shifted reefs had higher macroalgal than coral cover in 2011, with increasingly

118 dissimilar benthic communities from 1994, characterised by rising coverage of macroalgae.

119 Heat stress around Seychelles reefs reached 4 degree heat weeks (DHW) in January 2016,

120 rapidly increased in April and peaked at 11.4 DHW in May

121 (http://coralreefwatch.noaa.gov/vs/index.php). The extent of coral bleaching was assessed at

122 16 of the 18 regularly surveyed reefs between May 19th and 1st June 2016, at the height of

123 thermal stress in the region. At each reef the plan view technique was used to estimate the

124 percent cover of healthy, bleached and recently dead corals within eight areas of the same

125 dimensions used to regularly monitor benthic cover (7m radius, 154m^2). Within each

126 replicate area all coral colonies along a 10m line intercept transect were also identified to

127 genus and status recorded as either healthy, bleached or recently dead. For both plan view

128 and transect assessments recently dead colonies were those where the structure of corallites

129 and growth form had not visibly eroded, there were no polyps or coral tissue visible and there

130 was a thin film of cyanobacateria or turf algae growing over the colony.

131 *Statistical analyses*

132 We assessed spatial variation in coral bleaching and temporal variation in coral community

133 composition using generalized linear models (GLMs). Using site-level estimates of

134 bleaching, mortality, and healthy coral cover from surveys conducted in 2016, we fitted

135 separate GLMs for coral bleaching, coral mortality and healthy coral cover, each with site as

136 a covariate and quasibinomial distributed errors. We assessed evidence for spatial variation in

137 bleaching impacts using likelihood ratio tests which weighed model support for the site-

138 covariate model relative to a null, intercept-only model. For all three bleaching models, fits

139 were considerably improved by inclusion of the site covariate ($p < 0.001$). Next, we

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140 examined temporal trends in coral cover from 2005-2017 for each regime state (regime-

141 shifted or recovering). GLMs were fit separately to total hard coral cover, massive cover,

142 branching cover, and structural complexity estimates (4 total models), and we assessed

143 support for linear or non-linear relationships by comparing GLMs with generalised additive

144 models (GAMs) with similar model structures. Temporal trends were modelled with survey

145 year and regime state (recovering or regime shifted) as interacting fixed effects, and random

146 effect structures which accounted for covariance with sites. Models were fitted with Poisson

147 error distributions, except structural complexity which was fitted with Gamma error

148 distributions. For GAMs, we also evaluated support for the degree of smoothness in temporal

149 trends by fitting different knot values and selecting the model with lowest AIC value to

150 interpret temporal relationships (Table S1) (Burnham and Anderson 2003; Wood 2017). Our

151 approach ensured that smoothers adequately represented non-linear temporal trends but

152 minimized potential overfitting of relationships. For each benthic variable, we visualized

153 predicted coral cover and structural complexity from 2005-2017 in each regime state,

154 excluding random effects. All model fits were inspected for normality using residual plots.

155 Temporal and spatial changes in the abundance of coral genera were examined using

156 PERMANOVA, where survey year (2008, 2011, 2014, 2017) and regime state (shifted or

157 recovering) were considered fixed factors and habitat (granitic, carbonate or patch) a random

158 factor. The analysis was based on a resemblance matrix constructed from Euclidean distances

159 and 9999 permutations. Non-metric multidimensional scaling (nMDS) was used to visualise

160 and interpret differences in coral communities with respect to survey years, habitat and

161 regime state. nMDS fitted with four dimensions produced a high goodness-of-fit according to

162 the Shepard plot and stress value (0.09).

163 GAMs were used to identify which environmental variables best predicted the extent of coral

164 bleaching and mortality following the 2016 event. Percent bleaching was based on surveys in

165   2016 and mortality calculated as $((Cover_{2014} - Cover_{2017})/Cover_{2014})$. Reef level variables

166   included in analyses were: susceptibility of the coral community to heat stress, water quality,

167   depth, wave exposure, percent coral cover in 2014, if the reef was in a no-take marine reserve

168   and habitat type (patch, carbonate or granite). Analyses where mortality was the dependant

169   variable also included the extent of bleaching in May 2016. Coral susceptibility for each reef

170   was based on the coral community composition in 2014 and genera-specific bleaching

171   response data from the western Indian Ocean (McClanahan et al. 2007). Coral communities

172   with a high susceptibility to bleaching had values close to 1 whilst those with low bleaching

173   susceptibilities had values approaching 0. Water quality was measured as the mean

174   percentage of nitrogen in 10 *Sargassum* fonds collected from each reef in 2014 (Graham et al.

175   2015), higher values being indicative of poorer water quality and greater propensity of corals

176   to bleaching (Wooldridge 2016). The extent of coral bleaching is linked to water depth

177   (McClanahan et al. 2007; Moore et al. 2012), which we measured as the mean depth across

178   replicate reef areas within a reef. Wave exposure was considered in analyses as it may

179   increase flushing of reefs, ameliorating the effects of heat stress (Shedrawi et al. 2017).

180   Exposure at each reef (measured in Joules) was calculated from fetch, wind speed and

181   direction between 1998 and 2011 (Graham et al. 2015). Finally, we considered the effect of

182   no-take areas, which reduce other anthropogenic pressures and thereby potentially increase

183   reef resilience (Mellin et al. 2016). All combinations of three or fewer explanatory variables

184   were considered in analyses and the best models selected based on lowest AIC scores and

185   fewest variables (Fisher et al. 2018). The relative importance of variables was also calculated

186   by summing AIC weights (Burnham and Anderson 2003). The analysis was restricted to the

187   15 reefs where information on all variables was available.

188   To assess the effect of coral loss on fish assemblages we examined the relationship between

189   percent cover of branching coral and abundance of fish of different size and diet. Fish were

190   placed into 5cm size classes and broad diet categories (Corallivores, Herbivores, Invertivores

191   Piscivores, Planktivores and Mixed) based on information in Fishbase (Froese and Pauly

192   2012). Changes in abundance of different sized fish from each dietary category were also

193   assessed with respect to periods of coral decline (1994 to 2005 and 2014 to 2017) and coral

194   increase (2005 to 2014). For these assessments, the average density of fish per 154m^2 count

195   area was calculated for each dietary size class at each reef over each time period. Temporal

196   changes in fish abundance were then calculated using reefs as replicates and significant

197   declines or increases of each fish group were determined by 95% confidence intervals.

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199   **Results**

200   *Long-term trends in coral*

201   A year after the 2016 bleaching event the average coral cover across 18 reefs, that had been

202   consistently monitored since 1994, was 6 ± 1 (SE) % (Fig 1a). This represented a decline of

203   70% in total coral cover from 2014 ($20 \pm 3\%$), which was similar on both recovering (70%)

204   and regime-shifted (74%) reefs. The decline in coral cover between 2014 and 2017 is also

205   similar to the 68% change in coral cover between 1994 and 2005 following the 1998

206   bleaching. In both instances the loss of coral following bleaching was primarily due to

207   mortality of corals with a branching growth form. Temporal trends of branching and total

208   coral cover were very similar, particularly on recovering reefs where cover gradually

209   increased between 2005 and 2014, before the rapid fall in 2017 (Fig 1b). Indeed, major

210   fluctuations in coral cover between 2005 and 2017 can be directly attributed to changes in the

211   percent cover of branching corals. The gain in cover of branching cover between 2005 and

212   2014 was effectively nullified by decline of these corals after bleaching in 2016 (Fig 2).

213   Percent cover of massive corals has also declined since surveys began in 1994 (Fig 1c),

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though changes are not as dramatic as for branching corals, and average cover of massive

corals remained at 5 ± 1 (SE)% on recovering reefs, even after the 2016 bleaching event.

Temporal changes in the cover of different coral growth forms were associated with changes

in coral genera between 2011 and 2017 ($F_{3,62} = 3.66$, P=0.005) and among reef types ($F_{1,62} =$

15.33, P<0.001). Recovery on granitic reefs was associated with an increase in the abundance

of branching *Pocillopora* and encrusting *Favia*, *Acanthastrea* and *Montipora* between 2008

and 2014. However, the recovery on carbonate and patch reefs was characterised by

Acropora, *Echinopora,* massive *Lobophylia* /*Goniopora*, and encrusting *Galaxea* (Fig. 3).

Coral cover on regime-shifted reefs was low and characterised by *Fungia* and branching

Porites, especially on carbonate reefs.

Like coral cover, the structural complexity of Seychelles reefs has declined since 1994,

though temporal trajectories differed between reef states (Fig 1d). On regime-shifted reefs

structure gradually declined between 2005 and 2011, whilst on recovering reefs it has

remained relatively stable. On both recovering and regime-shifted reefs structural complexity

did not change greatly between 2014 and 2017.

2016 bleaching event

Plan view assessments of bleaching at 16 reefs around Seychelles' granitic islands in May-

June 2016 found that 80% of coral had bleached or recently died, and on 15 of these reefs

>50% of the estimated coral cover had bleached (Fig 4a). Coverage of branching corals was

high compared to other growth forms (28%), however 63% of these corals where bleached

and 30% had recently died (Fig 4b). Similarly, almost all tabular corals had bleached or died

and only 2% of these corals appeared healthy. Conversely, although 68% of the massive coral

coverage (10%) had bleached few of these corals had recently died and the majority of

encrusting corals were healthy. Assessments of bleaching at the colony level were similar to

those from plan views with 82% of the 1194 colonies being bleached or recently dead (Fig

4c). Of the *Acropora* (369) and *Pocillopora* (99) colonies surveyed more than 94% were

bleached or recently dead, whilst 26% of *Porites* colonies (255), which were among the most

common massive genera, were considered healthy.

Spatial variation in the extent of coral bleaching in 2016 was best explained by a model that

included susceptibility of the coral community to heat stress, water quality and wave

exposure (Table 1). Sites with low to medium wave exposure, a high proportion of genera

susceptible to bleaching, and higher nitrogen content in macroalgal samples tended to have a

higher percentage of bleached corals (Fig 5a). The extent of coral loss between 2014 and

2017 was also related to bleaching susceptibility, changes in coral cover being less

pronounced on reefs with high abundance of thermally resistant taxa (Fig 5b).

Branching coral and fish assemblages

Changes in branching coral cover affected fish from all dietary categories, particularly those

that are small-bodied. Indeed abundance of fish with estimated total lengths 8 to 11cm was

positively correlated with branching coral cover for all dietary categories, although this

relationship was weaker among larger fish (Fig 6). The relationship was especially strong

among small-bodied corallivores, changes in percent cover of branching corals accounting for

50% of the variation in coral feeding fish 8 to 11cm. Accordingly abundance of small-bodied

corallivores declined during periods when coral bleaching had caused loss of branching

corals (1994 to 2005 and 2014 to 2017), but increased during the intermediate period (2005 to

2014), when branching coral cover increased on some reefs.

Decline in small corallivore abundance was greatest between 2014 and 2017, following the

2016 bleaching event, However, declines in abundance of small planktivores and herbivores

(8 to 11 cm) was greatest between 1994 and 2005, seven years after the 1998 bleaching event,

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262   whilst changes in small piscivores were negligible following both bleaching events. There

263   were however significant changes in medium sized (26 to 30 cm) piscivores, their numbers

264   increasing a year after the 2016 bleaching, but this same size category declined seven years

265   after the 1998 bleaching. Similarly, many medium sized herbivores declined in abundance

266   between 1994 and 2005, yet the abundance of these medium sized herbivores increased

267   following the bleaching in 2016.

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269   **Discussion**

270   Over the past 20 years the granitic islands of Seychelles have experienced two major heat

271   stress events that have caused widespread coral bleaching and mortality. The decline in

272   percent coral cover following these two events, and recovery during the intervening years,

273   has been predominantly driven by fluctuations in the cover of branching corals. Many of the

274   taxa that have branching morphology have life history traits that favour wide dispersal and

275   rapid growth (Pratchett et al. 2015), characteristics that allow rapid recovery following

276   disturbance (Darling et al. 2012). However, these taxa are also highly susceptible to a range

277   of environmental pressures including heat stress (Hoey et al. 2016). As a consequence,

278   coverage of branching corals on reefs can undergo dramatic and rapid changes (Goreau et al

279   2000), reflecting periods of boom and bust, that have concomitant impacts on reef associated

280   fish assemblages. This affords some level of stability in cover over longer time frames and

281   branching corals have dominated reef assemblages over the past 1.8 million years (Renema et

282   al. 2016). The onset of the Anthropocene has however coincided with the decline of these

283   corals over large parts of the Caribbean (Greenstein et al. 1998; Cramer et al. 2012) and an

284   inshore reef on the GBR (Roff et al. 2013). Recent bleaching at global scales has extended

285   this effect to many of the world's reefs (Hughes et al. 2018a, 2018b)

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Ecological significance of branching corals

287 Long-term data from the Seychelles, through two major disturbances and an extended period

288 of recovery, highlight the potential role of branching coral as a keystone structure on coral

289 reefs. Declines in coral and the flow-on impacts to associated communities affect the

290 ecosystems services provided by reefs (Pratchett et al. 2014; Robinson et al. 2018). For

291 example, branching corals are especially important for maintaining high rates of reef growth

292 and protecting coastlines from rising sea levels (Perry et al. 2015, 2018). Percent cover of

293 branching corals is also positively correlated with structural complexity; an important

294 determinant of reef fish diversity (Graham and Nash 2013). Here we clearly demonstrate that

295 these corals are especially important habitat for a trophically diverse group of small bodied

296 fish, whose abundance closely tracks changes in branching coral cover. Accordingly loss of

297 coral following the 1998 bleaching was associated with a decline in both small-bodied taxa

298 and species richness of fish in the Seychelles (Graham et al. 2006). Moreover, loss of

299 branching corals is associated with changes in prey availability and predator diets that alter

300 how energy is transferred within coral reef food webs (Hempson et al. 2018). Many larger

301 bodied predators are also closely associated with the reef during the early stages of their

302 benthic lives, often sheltering among the branches of coral colonies (Wen et al. 2013). These

303 species are often important to reef fisheries, and changes in branching coral cover is likely to

304 have flow-on implications for future stocks of these taxa (Graham et al. 2007).

305 The timing of our post-bleaching surveys allowed assessments of both long and short-term

306 changes to branching coral cover to fish assemblages. In 2005, seven years after declines of

307 live branching coral, the reef structure had started to collapse on many reefs (Graham et al.

308 2006). Accordingly, we documented declines in both small and medium sized fish from

309 piscivorous and herbivorous feeding guilds. Many fish in these guilds have no obvious

310 reliance on live coral but may take shelter or feed among the branching skeletons (Pratchett et

al. 2008). Fish that increased in abundance between 1998 and 2005 were those of medium

body size with a mixed diet, which is consistent with theories that generalists benefit from

disturbance (Bellwood et al. 2006). Conversely, a year after the 2016 bleaching, coral cover

had declined by 70% yet only the smaller bodied fish were negatively affected. Indeed,

abundance of medium-sized predators had increased during this short time frame, suggesting

these meso-predators have contributed to the demise of smaller bodied prey. The apparent

short-term increase in predators is unlikely to be sustainable, especially if reef structure

collapses and there is a shift to macroalgal dominated states (Hempson et al. 2018).

Conclusion

Increased frequency of heat stress events may have dire consequences for the persistence of

branching corals. In Seychelles, coral cover fell by 90% soon after the 1998 event (Goreau et

al. 2000) and although some of these reefs recovered, others underwent a regime shift and are

now dominated by fleshy macroalgae (Graham et al. 2015). It took more than 10 years for

those reefs that recovered to attain levels of coral cover similar to that recorded pre-

bleaching. Severe bleaching events are now expected every 6 years (Hughes et al. 2018a),

seriously compromising the capacity of corals to recover and leading to a gradual ratchetting

down of coral cover (Birkeland 2004). This will gradually diminish the amplitude of boom

bust cycles in branching coral cover and the influence they have on reef ecosystems.

The sensitivity of branching taxa to bleaching has led to suggestions that coral assemblages

will be increasingly characterised by thermally tolerant taxa (van Woesik et al. 2011). Indeed,

we found both coral bleaching and mortality were directly related to the susceptibility of the

coral community to heat stress. The prominence of massive coral colonies on Seychelles reefs

in surveys after bleaching indicates that some corals have persisted through the 1998 and

2016 events. Although relatively slow growing compared to branching growth forms

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335 (Pratchett et al. 2015) these massive corals are important for maintaining positive reef

336 accretion post-bleaching (Januchowski-Hartley et al. 2017) and are an important component

337 of reef structure at seascape scales (Darling et al. 2017). The gradual decline of massive

338 corals is of concern, as these corals are expected to take much longer to recover than

339 branching morphologies (Pratchett et al. 2015). Massive coral colonies are however unlikely

340 to shelter the same abundance and diversity of fish as branching colonies of similar size

341 (Holbrook et al. 2002a), emphasizing the importance of branching corals to fish assemblages.

342 Branching corals are clearly important habitat for many fish on reefs within the Seychelles,

343 and other parts of the world (Holbrook et al. 2002b; Wilson et al. 2008; Coker et al. 2014;

344 Komyakova et al. 2018). Moreover, diversity of coral associated invertebrates is highest in

345 colonies with complex branching morphology, with many species inhabiting branching

346 pocilloporids and acroporids (Stella et al. 2011). As a consequence, spatial and temporal

347 variation in the cover of branching corals is a key determinant of diversity, size structure and

348 trophodynamics on coral reefs. That branching corals are also major contributors to reef

349 growth and accretion emphasises their ecological and geomorphological roles across multiple

350 processes and suggests these corals are keystone structures. Boom and bust fluctuations in the

351 amount of branching corals are therefore expected to alter ecological and physical processes,

352 their long-term demise having flow-on effects for the ecosystem services provide by coral

353 reefs.

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Conflicts of interest

On behalf of all authors, the corresponding author states that there is no conflict of interest.

References

Barlow J, França F, Gardner TA, Hicks CC, Lennox GD, Berenguer E, Castello L, Economo EP, Ferreira J, Guenard B (2018) The future of hyperdiverse tropical ecosystems. Nature 559:517–526

Bellwood DR, Hoey AS, Ackerman JL, Depczynski M (2006) Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. Glob Change Biol 12:1587–1594

Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. Nature 429:827–833

Birkeland C (2004) Ratcheting down the coral reefs. BioScience 54:1021–1027

Brandl SJ, Goatley CH, Bellwood DR, Tornabene L (2018) The hidden half: ecology and evolution of cryptobenthic fishes on coral reefs. Biol Rev 93:1846–1873

Burnham KP, Anderson DR (2003) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer Science & Business Media,

Coker DJ, Wilson SK, Pratchett MS (2014) Importance of live coral habitat for reef fishes. Rev Fish Biol Fish 24:89–126

Cole AJ, Pratchett MS, Jones GP (2008) Diversity and functional importance of coral-feeding fishes on tropical coral reefs. Fish Fish 9:286–307

Cramer KL, Jackson JBC, Angioletti CV, Leonard-Pingel J, Guilderson TP (2012) Anthropogenic mortality on coral reefs in Caribbean Panama predates coral disease and bleaching. Ecol Lett 15:561–567

Darling ES, Alvarez-Filip L, Oliver TA, McClanahan TR, Côté IM (2012) Evaluating life-history strategies of reef corals from species traits. Ecol Lett 15:1378–1386

Darling ES, Graham NAJ, Januchowski-Hartley FA, Nash KL, Pratchett MS, Wilson SK (2017) Relationships between structural complexity, coral traits, and reef fish assemblages. Coral Reefs 36:561–575

Fisher R, Wilson SK, Sin TM, Lee AC, Langlois TJ (2018) A simple function for full-subsets multiple regression in ecology with R. Ecol Evol 8:6104–6113

Froese R, Pauly D (2012) FishBase. http://www.fishbase.org,

Goreau T, McClanahan T, Hayes R, Strong A (2000) Conservation of Coral Reefs after the 1998 Global Bleaching Event. Conserv Biol 14:5–15

Graham NA, Wilson SK, Jennings S, Polunin NV, Bijoux JP, Robinson J (2006) Dynamic fragility of oceanic coral reef ecosystems. Proc Natl Acad Sci 103:8425–8429

16

Graham NAJ, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature 518:94–97

Graham NAJ, Nash KL (2013) The importance of structural complexity in coral reef ecosystems. Coral Reefs 32:315–326

Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Robinson J, Bijoux JP, Daw TM (2007) Lag Effects in the Impacts of Mass Coral Bleaching on Coral Reef Fish, Fisheries, and Ecosystems. Conserv Biol 21:1291–1300

Greenstein BJ, Curran HA, Pandolfi JM (1998) Shifting ecological baselines and the demise of Acropora cervicornis in the western North Atlantic and Caribbean Province: a Pleistocene perspective. Coral Reefs 17:249–261

Hempson TN, Graham NA, MacNeil MA, Hoey AS, Wilson SK (2018) Ecosystem regime shifts disrupt trophic structure. Ecol Appl 28:191–200

Hoey A, Howells E, Johansen J, Hobbs J-P, Messmer V, McCowan D, Wilson S, Pratchett M (2016) Recent advances in understanding the effects of climate change on coral reefs. Diversity 8:12

Holbrook SJ, Brooks AJ, Schmitt RJ (2002a) Variation in structural attributes of patch-forming corals and in patterns of abundance of associated fishes. Mar Freshw Res 53:1045–1053

Holbrook SJ, Brooks AJ, Schmitt RJ (2002b) Predictability of fish assemblages on coral patch reefs. Mar Freshw Res 53:181–188

Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC (2018a) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359:80–83

Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey AS, Hoogenboom MO, Liu G, McWilliam MJ, Pears RJ, Pratchett MS, Skirving WJ, Stella JS, Torda G (2018b) Global warming transforms coral reef assemblages. Nature 556:492

Januchowski-Hartley FA, Graham NAJ, Wilson SK, Jennings S, Perry CT (2017) Drivers and predictions of coral reef carbonate budget trajectories. Proc R Soc B Biol Sci 284:20162533

Jennings S, Marshall SS, Polunin NV (1996) Seychelles' marine protected areas: comparative structure and status of reef fish communities. Biol Conserv 75:201–209

Kerry JT, Bellwood DR (2015) Do tabular corals constitute keystone structures for fishes on coral reefs? Coral Reefs 34:41–50

Komyakova V, Jones GP, Munday PL (2018) Strong effects of coral species on the diversity and structure of reef fish communities: A multi-scale analysis. PLOS ONE 13:e0202206

Manning AD, Fischer J, Lindenmayer DB (2006) Scattered trees are keystone structures–implications for conservation. Biol Conserv 132:311–321

McClanahan TR, Ateweberhan M, Graham NAJ, Wilson SK, Sebastian CR, Guillaume MM, Bruggemann JH (2007) Western Indian Ocean coral communities: bleaching responses and susceptibility to extinction. Mar Ecol Prog Ser 337:1–13

433 Mellin C, Aaron MacNeil M, Cheal AJ, Emslie MJ, Julian Caley M (2016) Marine protected areas
434 increase resilience among coral reef communities. Ecol Lett 19:629–637

435 Menge BA, Berlow EL, Blanchette CA, Navarrete SA, Yamada SB (1994) The keystone species
436 concept: variation in interaction strength in a rocky intertidal habitat. Ecol Monogr 64:249–
437 286

438 Moberg F, Folke C (1999) Ecological goods and services of coral reef ecosystems. Ecol Econ 29:215–
439 233

440 Moore JAY, Bellchambers LM, Depczynski MR, Evans RD, Evans SN, Field SN, Friedman KJ, Gilmour JP,
441 Holmes TH, Middlebrook R, Radford BT, Ridgway T, Shedrawi G, Taylor H, Thomson DP,
442 Wilson SK (2012) Unprecedented Mass Bleaching and Loss of Coral across 12° of Latitude in
443 Western Australia in 2010–11. PLoS ONE 7:e51807

444 Perry CT, Alvarez-Filip L, Graham NA, Mumby PJ, Wilson SK, Kench PS, Manzello DP, Morgan KM,
445 Slangen AB, Thomson DP (2018) Loss of coral reef growth capacity to track future increases
446 in sea level. Nature 558:396–400

447 Perry CT, Murphy GN, Graham NAJ, Wilson SK, Januchowski-Hartley FA, East HK (2015) Remote coral
448 reefs can sustain high growth potential and may match future sea-level trends. Sci Rep
449 5:18289

450 Polunin NVC, Roberts CM (1993) Greater biomass and value of target coral-reef fishes in two small
451 Caribbean marine reserves. Mar Ecol-Prog Ser 100:167–167

452 Pratchett M, Anderson K, Hoogenboom M, Widman E, Baird A, Pandolfi J, Edmunds P, Lough J (2015)
453 Spatial, Temporal and Taxonomic Variation in Coral Growth?Implications for the Structure
454 and Function of Coral Reef Ecosystems. In: Hughes R., Hughes D., Smith I., Dale A. (eds)
455 Oceanography and Marine Biology. CRC Press, pp 215–296

456 Pratchett MS, Hoey AS, Wilson SK (2014) Reef degradation and the loss of critical ecosystem goods
457 and services provided by coral reef fishes. Curr Opin Environ Sustain 7:37–43

458 Pratchett MS, Munday P, Wilson SK, Graham NA, Cinner JE, Bellwood DR, Jones GP, Polunin NV,
459 McClanahan TR (2008) Effects of climate-induced coral bleaching on coral-reef fishes. Ecol
460 Econ Consequences Oceanogr Mar Biol Annu Rev 46:251–296

461 Renema W, Pandolfi JM, Kiessling W, Bosellini FR, Klaus JS, Korpanty C, Rosen BR, Santodomingo N,
462 Wallace CC, Webster JM (2016) Are coral reefs victims of their own past success? Sci Adv
463 2:e1500850

464 Robinson JPW, Wilson SK, Robinson J, Gerry C, Lucas J, Assan C, Govinden R, Jennings S, Graham NAJ
465 (2018) Productive instability of coral reef fisheries after climate-driven regime shifts. Nat
466 Ecol Evol 1

467 Roff G, Clark TR, Reymond CE, Zhao J, Feng Y, McCook LJ, Done TJ, Pandolfi JM (2013)
468 Palaeoecological evidence of a historical collapse of corals at Pelorus Island, inshore Great
469 Barrier Reef, following European settlement. Proc R Soc B 280:20122100

470 Shedrawi G, Falter JL, Friedman KJ, Lowe RJ, Pratchett MS, Simpson CJ, Speed CW, Wilson SK, Zhang
471 Z (2017) Localised hydrodynamics influence vulnerability of coral communities to
472 environmental disturbances. Coral Reefs 36:861–872

473   Stella J, Pratchett MS, Hutchings P, Jones GP (2011) Coral-associated invertebrates: diversity,
474   ecological importance and vulnerability to disturbance. Oceanogr Mar Biol Annu Rev 49:43–
475   104

476   Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species
477   diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J
478   Biogeogr 31:79–92

479   Veron JEN (1986) Corals of Australia and the Indo-pacific. Angus & Robertson Sydney,

480   Wen CKC, Pratchett MS, Almany GR, Jones GP (2013) Patterns of recruitment and microhabitat
481   associations for three predatory coral reef fishes on the southern Great Barrier Reef,
482   Australia. Coral Reefs 32:389–398

483   Wilson SK, Fisher R, Pratchett MS, Graham NAJ, Dulvy NK, Turner RA, Cakacaka A, Polunin NVC,
484   Rushton SP (2008) Exploitation and habitat degradation as agents of change within coral reef
485   fish communities. Glob Change Biol 14:2796–2809

486   Wilson SK, Graham NAJ, Fisher R, Robinson J, Nash K, Chong-Seng K, Polunin NVC, Aumeeruddy R,
487   Quatre R (2012) Effect of Macroalgal Expansion and Marine Protected Areas on Coral
488   Recovery Following a Climatic Disturbance: *Macroalgae, MPAs, and Coral Recovery*. Conserv
489   Biol 26:995–1004

490   Wilson SK, Graham NAJ, Polunin NVC (2007) Appraisal of visual assessments of habitat complexity
491   and benthic composition on coral reefs. Mar Biol 151:1069–1076

492   Wilson SK, Graham NAJ, Pratchett MS, Jones GP, Polunin NVC (2006) Multiple disturbances and the
493   global degradation of coral reefs: are reef fishes at risk or resilient? Glob Change Biol
494   12:2220–2234

495   van Woesik R, Sakai K, Ganase A, Loya Y (2011) Revisiting the winners and the losers a decade after
496   coral bleaching. Mar Ecol Prog Ser 434:67–76

497   Wood SN (2017) Generalized additive models: an introduction with R. Chapman and Hall/CRC,

498   Wooldridge SA (2016) Excess seawater nutrients, enlarged algal symbiont densities and bleaching
499   sensitive reef locations: 1. Identifying thresholds of concern for the Great Barrier Reef,
500   Australia. Mar Pollut Bull

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505 Table 1. Best models for predicting bleaching and mortality of corals following heat stress in

506 2016. Variables considered in models were: *Susceptibility* of the coral community to

507 bleaching in 2014 based on bleaching response of different genera (McClanahan et al. 2007);

508 Water Quality measured as *%N* of macroalgae collected in 2014; *Depth*; *Exposure* based on

509 fetch, wind speed and direction (Graham et al. 2015); *Cover* of coral in 2014; if reefs were

510 *Fished* or no-take reserves; and *Habitat* type. *Bleaching* of corals in 2016 was also

511 considered in analyses to predict coral mortality.

|	Predictors	ΔAIC	AIC wt	edf	R^2
Bleaching	Susceptibility + %N+ Exposure	0.00	0..65	6.9	0.63
	%N + Exposure + Habitat	1.20	0.35	7.0	0.46
Mortality	%N + Exposure + Habitat	0.00	0.23	5.0	0.71
	Susceptibility + Fished	0.57	0.18	3.0	0.37
	Susceptibility	0.89	0.15	2.0	0.34
	Susceptibility + Exposure	2.10	0.08	3.1	0.35

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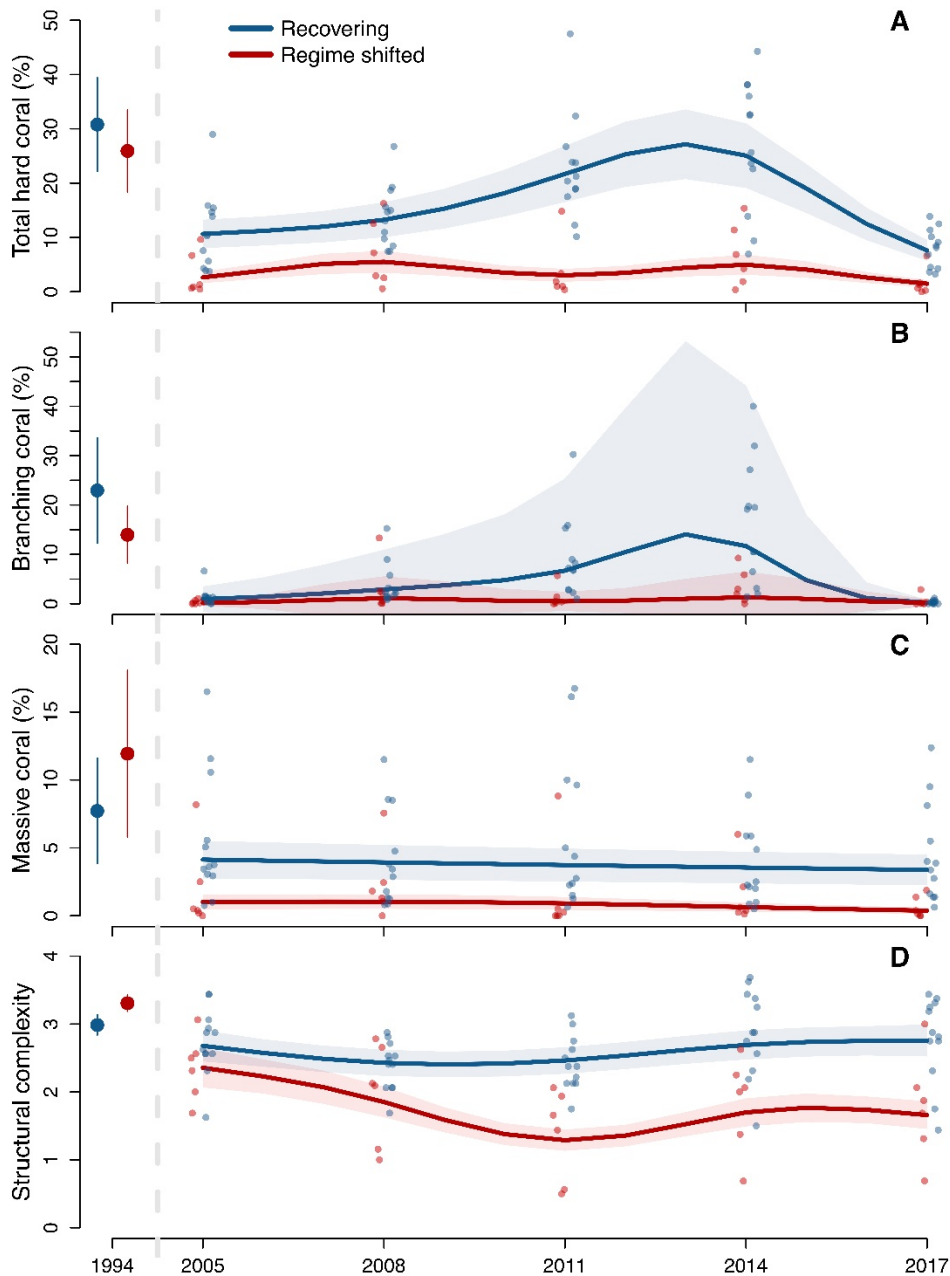
Fig 1. Temporal change in coral cover and structural complexity from 1994-2017. Lines are predictions from GAMs of total coral cover (A), branching cover (B), massive cover (C), and structural complexity (D), shaded with 2 standard errors (SE). Points are mean cover estimates (± 2 SE), jittered to separate regime shifted (red) from recovering (blue) reefs. Models were fitted with interacting survey year and regime state covariates, and random effect terms for reef site.

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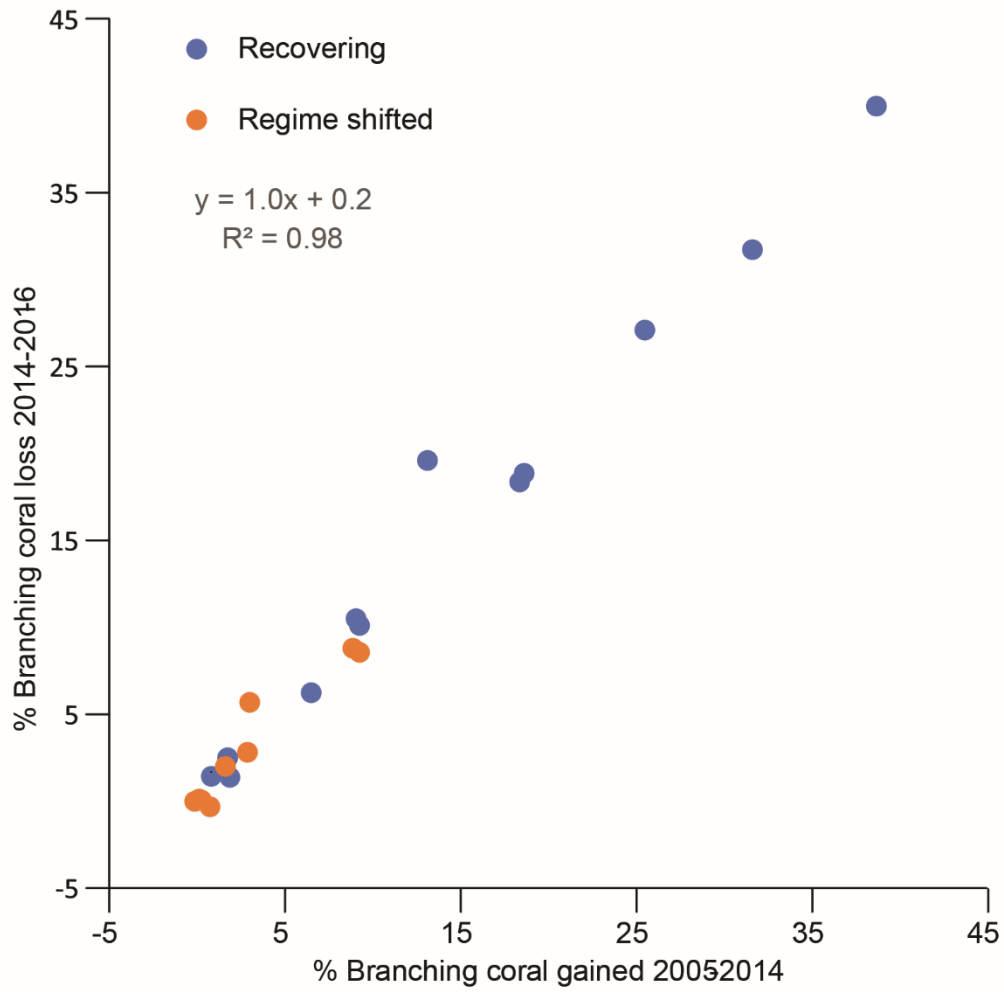
Fig 2. Extent of change in branching coral cover during periods of recovery (2005-2014) and
decline (2014-2017). Correlation co-efficient calculated from six regime shifted (orange) and
twelve recovering (blue) reefs.

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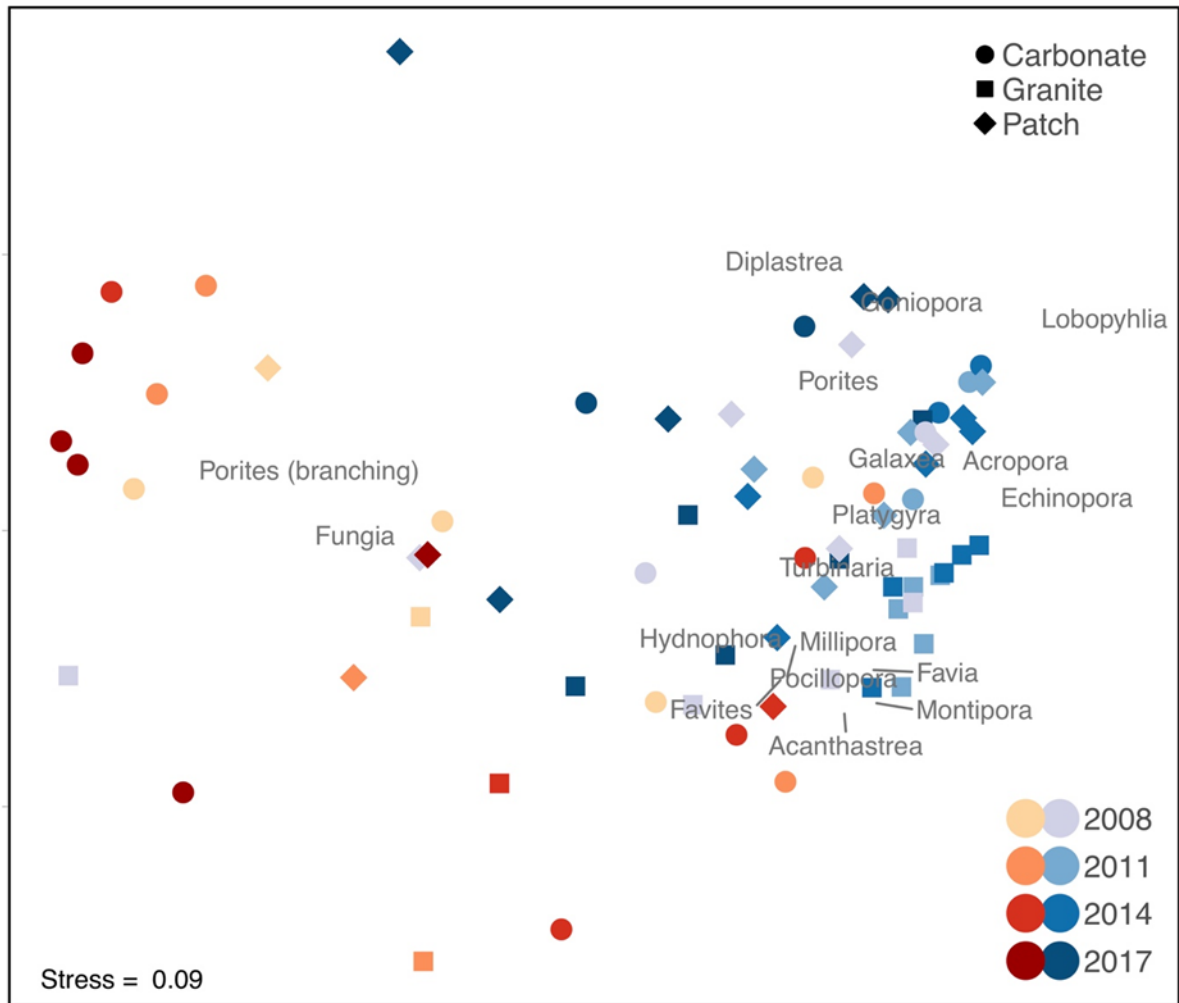
527   Fig 3. Spatial and temporal variation in coral communities. Non-metric MDS analysis of 18

528   Seychelles reefs surveyed between 2008 and 2017 displayed. Red reefs have undergone a

529   regime shift and blue reefs are recovering (Graham et al. 2015). Shading indicates survey

530   year (lightest = 2008, darkest = 2017) and symbol shape indicates habitat type (carbonate =

531   circles, granite = squares, patch = diamonds).

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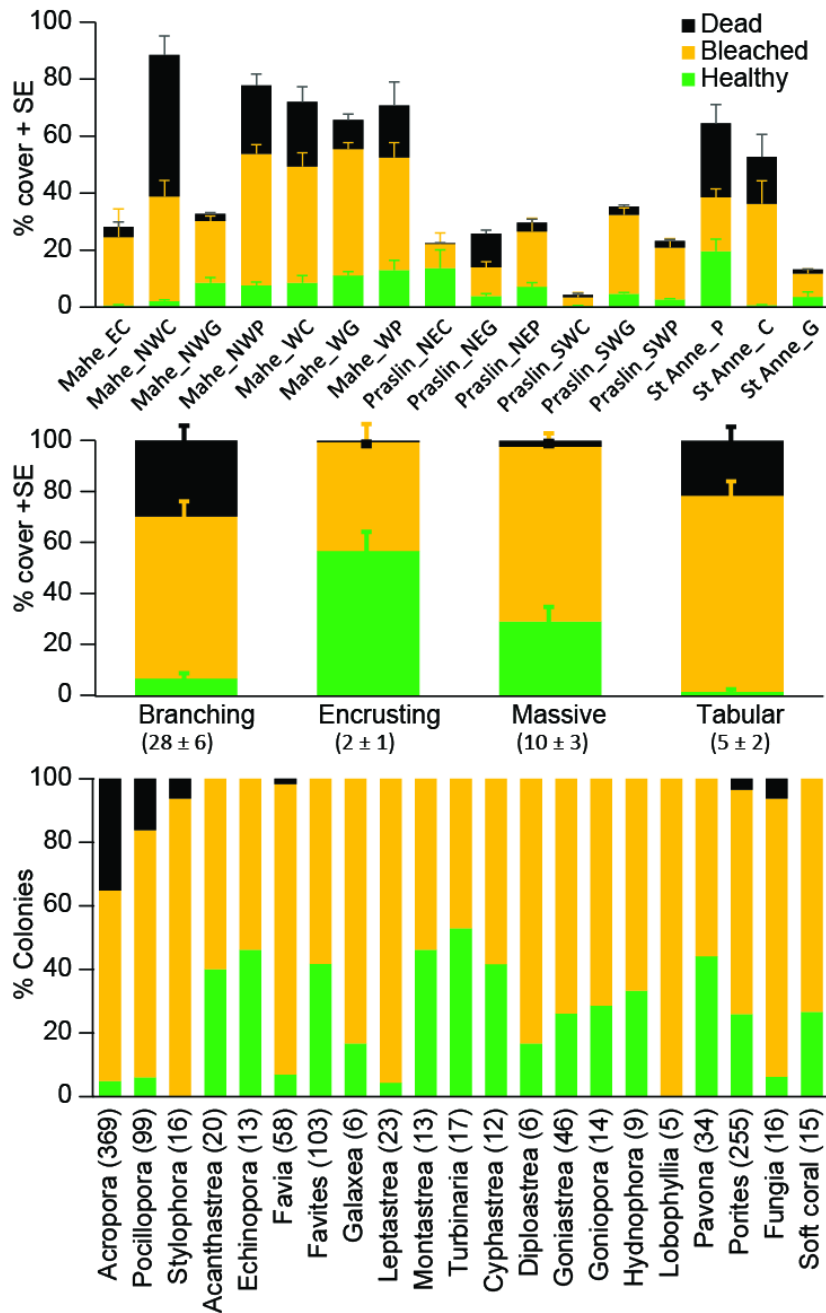
Fig 4. Extent of coral bleaching on 16 Seychelles reefs in May-June 2016. Means and

standard errors calculated from 8 replicate counts at each reef. Likelihood ratio tests indicated

significant spatial variation in bleaching (P < 0.001), dead coral (P < 0.001), and healthy

coral (P < 0.001). Bleaching also varied among corals of different morphology and genera.

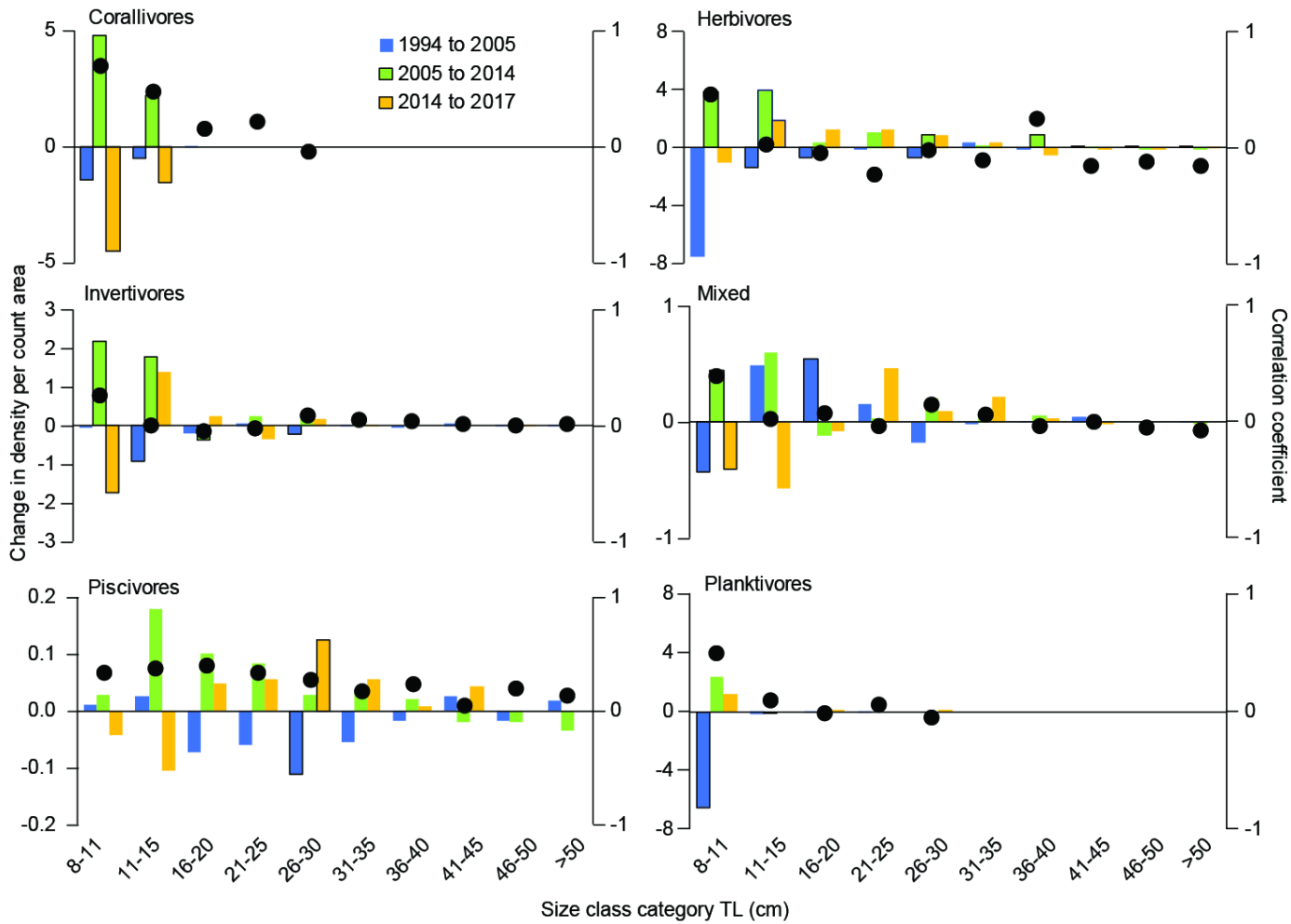The number of colonies surveyed within each genera is in parentheses.

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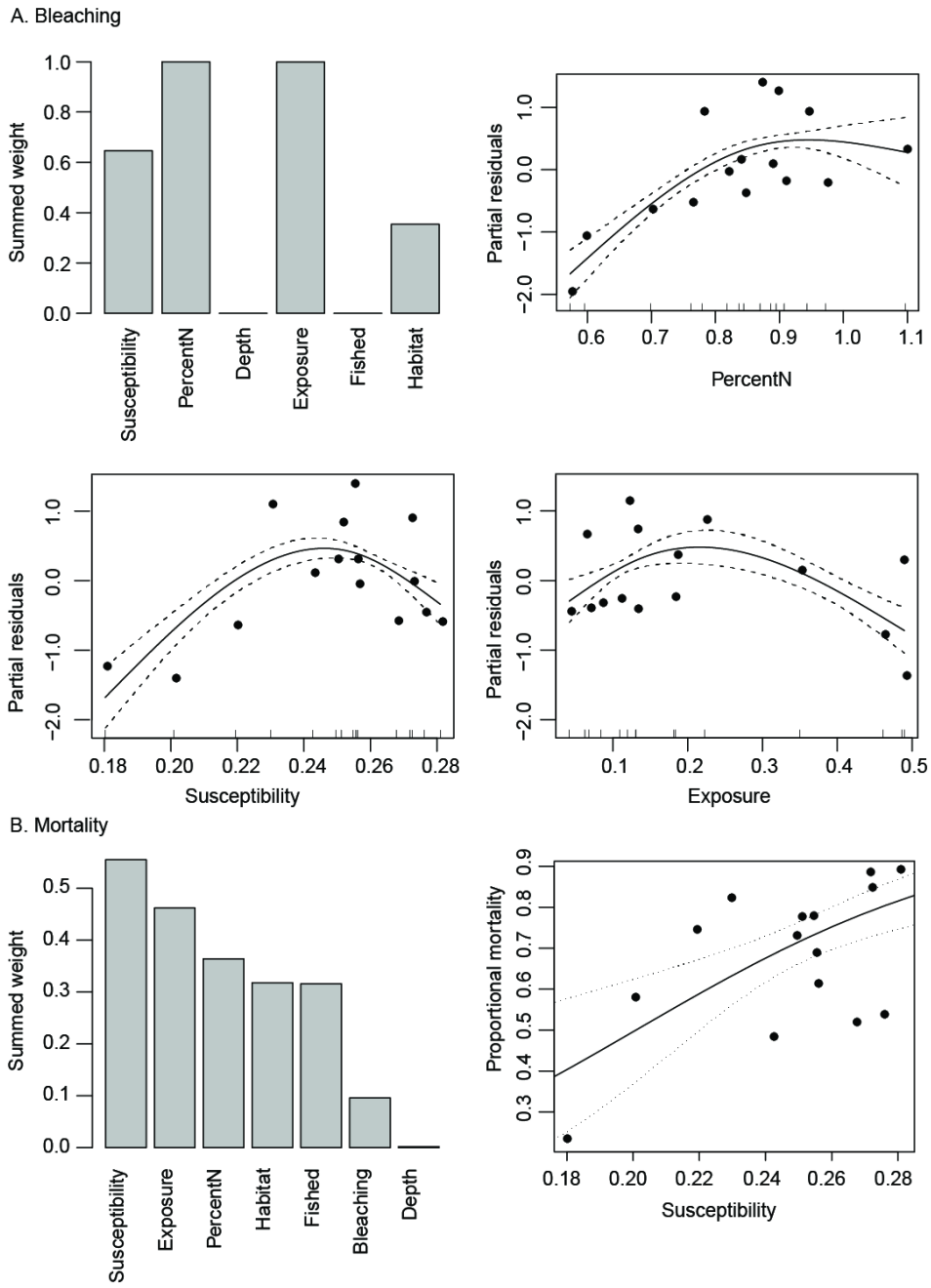
Fig 5. Relative importance of environmental variables in predicting the extent of coral A.

bleaching and B. mortality at 15 Seychelles reefs following 2016 heat stress. The

relationships for the best models, with 95% confidence intervals (dotted lines), are plotted.

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Fig 6. Shifts in fish abundance during periods of branching coral cover decline (1994 to 2005

and 2014 to 2017) and recovery (2005 to 2014). Each bar represents the average change in

fish density (left axis) per count area ($154m^2$) from 18 reefs consistently surveyed over the

three time periods. Bars with a black outline denote significant changes in density based on

95% confidence intervals. Dots are correlation coefficients for the relationship between

abundance of fish within each dietary size category and percent cover of branching coral

(right axis).

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