

1 **Boom and bust of keystone structure on coral reefs**

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3 Shaun K Wilson^{1,2*}, James PW Robinson³, Karen Chong-Seng⁴, Jan Robinson⁵,
4 Nicholas AJ Graham³

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6 1 Department of Biodiversity, Conservation and Attractions: Marine Science Program,
7 Kensington, WA 6151, Australia

8 2 Oceans Institute, University of Western Australia, Crawley, WA 6009, Australia

9 3 Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK

10 4 ARC Centre of Excellence for Coral Reef Studies, James Cook University,
11 Townsville, QLD 4811, Australia

12 5 Ministry of Finance, Trade, Investment and Economic Planning, Victoria, Mahe,
13 Seychelles

14

15 *Communicating author. Email: shaun.wilson@dbca.wa.gov.au

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18

19 **Abstract**

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

43

44 **Introduction**

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

54 The physical structure, occurrence and life history traits of corals are variable, which may
55 make some components of the coral assemblage of greater importance to reef associated
56 fauna than others. For example, the types of corals with which fish associate varies among
57 fish species and life history stages. Some fish feed or dwell with specific coral taxa, whilst
58 others may associate with a broader group of corals (Cole et al. 2008; Coker et al. 2014).
59 Branching corals appear especially important for fish as the structural complexity provided
60 by this diverse group of corals provides refuges of numerous dimensions (Komyakova et al.
61 2018).

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

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

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

87

88 **Methods**

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

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 154m² 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

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, 154m²). 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 cyanobacteria 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

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 $((\text{Cover}_{2014} - \text{Cover}_{2017})/\text{Cover}_{2014})$. 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 154m² 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.

198

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),

214 though changes are not as dramatic as for branching corals, and average cover of massive
215 corals remained at 5 ± 1 (SE)% on recovering reefs, even after the 2016 bleaching event.

216 Temporal changes in the cover of different coral growth forms were associated with changes
217 in coral genera between 2011 and 2017 ($F_{3,62} = 3.66$, $P=0.005$) and among reef types ($F_{1,62} =$
218 15.33 , $P<0.001$). Recovery on granitic reefs was associated with an increase in the abundance
219 of branching *Pocillopora* and encrusting *Favia*, *Acanthastrea* and *Montipora* between 2008
220 and 2014. However, the recovery on carbonate and patch reefs was characterised by
221 *Acropora*, *Echinopora*, massive *Lobophyllia* / *Goniopora*, and encrusting *Galaxea* (Fig. 3).
222 Coral cover on regime-shifted reefs was low and characterised by *Fungia* and branching
223 *Porites*, especially on carbonate reefs.

224 Like coral cover, the structural complexity of Seychelles reefs has declined since 1994,
225 though temporal trajectories differed between reef states (Fig 1d). On regime-shifted reefs
226 structure gradually declined between 2005 and 2011, whilst on recovering reefs it has
227 remained relatively stable. On both recovering and regime-shifted reefs structural complexity
228 did not change greatly between 2014 and 2017.

229 *2016 bleaching event*

230 Plan view assessments of bleaching at 16 reefs around Seychelles' granitic islands in May-
231 June 2016 found that 80% of coral had bleached or recently died, and on 15 of these reefs
232 >50% of the estimated coral cover had bleached (Fig 4a). Coverage of branching corals was
233 high compared to other growth forms (28%), however 63% of these corals were bleached
234 and 30% had recently died (Fig 4b). Similarly, almost all tabular corals had bleached or died
235 and only 2% of these corals appeared healthy. Conversely, although 68% of the massive coral
236 coverage (10%) had bleached few of these corals had recently died and the majority of
237 encrusting corals were healthy. Assessments of bleaching at the colony level were similar to

238 those from plan views with 82% of the 1194 colonies being bleached or recently dead (Fig
239 4c). Of the *Acropora* (369) and *Pocillopora* (99) colonies surveyed more than 94% were
240 bleached or recently dead, whilst 26% of *Porites* colonies (255), which were among the most
241 common massive genera, were considered healthy.

242 Spatial variation in the extent of coral bleaching in 2016 was best explained by a model that
243 included susceptibility of the coral community to heat stress, water quality and wave
244 exposure (Table 1). Sites with low to medium wave exposure, a high proportion of genera
245 susceptible to bleaching, and higher nitrogen content in macroalgal samples tended to have a
246 higher percentage of bleached corals (Fig 5a). The extent of coral loss between 2014 and
247 2017 was also related to bleaching susceptibility, changes in coral cover being less
248 pronounced on reefs with high abundance of thermally resistant taxa (Fig 5b).

249 *Branching coral and fish assemblages*

250 Changes in branching coral cover affected fish from all dietary categories, particularly those
251 that are small-bodied. Indeed abundance of fish with estimated total lengths 8 to 11 cm was
252 positively correlated with branching coral cover for all dietary categories, although this
253 relationship was weaker among larger fish (Fig 6). The relationship was especially strong
254 among small-bodied corallivores, changes in percent cover of branching corals accounting for
255 50% of the variation in coral feeding fish 8 to 11 cm. Accordingly abundance of small-bodied
256 corallivores declined during periods when coral bleaching had caused loss of branching
257 corals (1994 to 2005 and 2014 to 2017), but increased during the intermediate period (2005 to
258 2014), when branching coral cover increased on some reefs.

259 Decline in small corallivore abundance was greatest between 2014 and 2017, following the
260 2016 bleaching event, However, declines in abundance of small planktivores and herbivores
261 (8 to 11 cm) was greatest between 1994 and 2005, seven years after the 1998 bleaching event,

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.

268

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)

286 *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

311 al. 2008). Fish that increased in abundance between 1998 and 2005 were those of medium
312 body size with a mixed diet, which is consistent with theories that generalists benefit from
313 disturbance (Bellwood et al. 2006). Conversely, a year after the 2016 bleaching, coral cover
314 had declined by 70% yet only the smaller bodied fish were negatively affected. Indeed,
315 abundance of medium-sized predators had increased during this short time frame, suggesting
316 these meso-predators have contributed to the demise of smaller bodied prey. The apparent
317 short-term increase in predators is unlikely to be sustainable, especially if reef structure
318 collapses and there is a shift to macroalgal dominated states (Hempson et al. 2018).

319 *Conclusion*

320 Increased frequency of heat stress events may have dire consequences for the persistence of
321 branching corals. In Seychelles, coral cover fell by 90% soon after the 1998 event (Goreau et
322 al. 2000) and although some of these reefs recovered, others underwent a regime shift and are
323 now dominated by fleshy macroalgae (Graham et al. 2015). It took more than 10 years for
324 those reefs that recovered to attain levels of coral cover similar to that recorded pre-
325 bleaching. Severe bleaching events are now expected every 6 years (Hughes et al. 2018a),
326 seriously compromising the capacity of corals to recover and leading to a gradual ratchetting
327 down of coral cover (Birkeland 2004). This will gradually diminish the amplitude of boom
328 bust cycles in branching coral cover and the influence they have on reef ecosystems.

329 The sensitivity of branching taxa to bleaching has led to suggestions that coral assemblages
330 will be increasingly characterised by thermally tolerant taxa (van Woesik et al. 2011). Indeed,
331 we found both coral bleaching and mortality were directly related to the susceptibility of the
332 coral community to heat stress. The prominence of massive coral colonies on Seychelles reefs
333 in surveys after bleaching indicates that some corals have persisted through the 1998 and
334 2016 events. Although relatively slow growing compared to branching growth forms

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.

354

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361

362 **Conflicts of interest**

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

364

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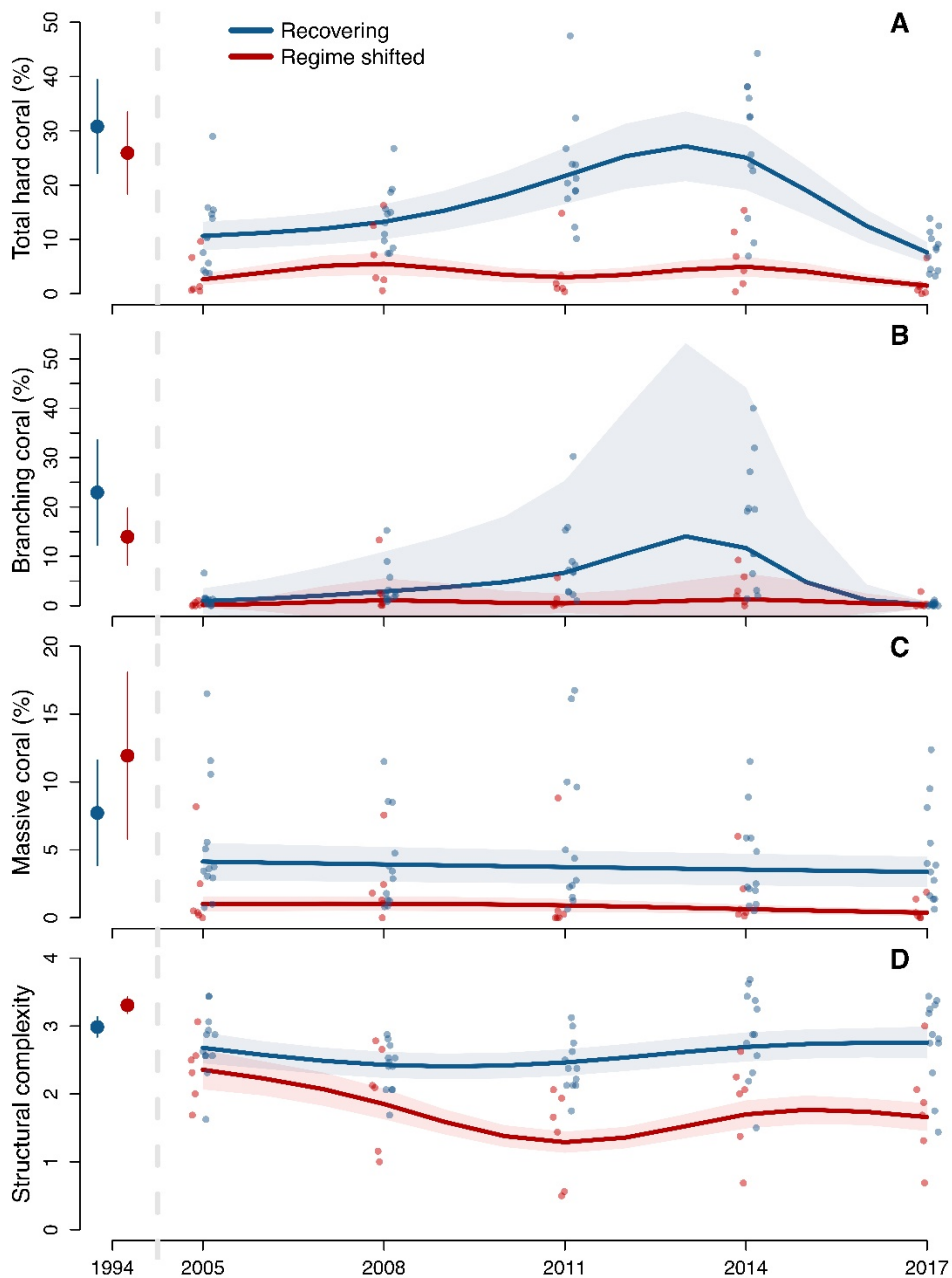
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505 Table 1. Best models for predicting bleaching and mortality of corals following heat stress in
 506 2016. Variables considered in models were: *Susceptibility* of the coral community to
 507 bleaching in 2014 based on bleaching response of different 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	Δ AIC	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

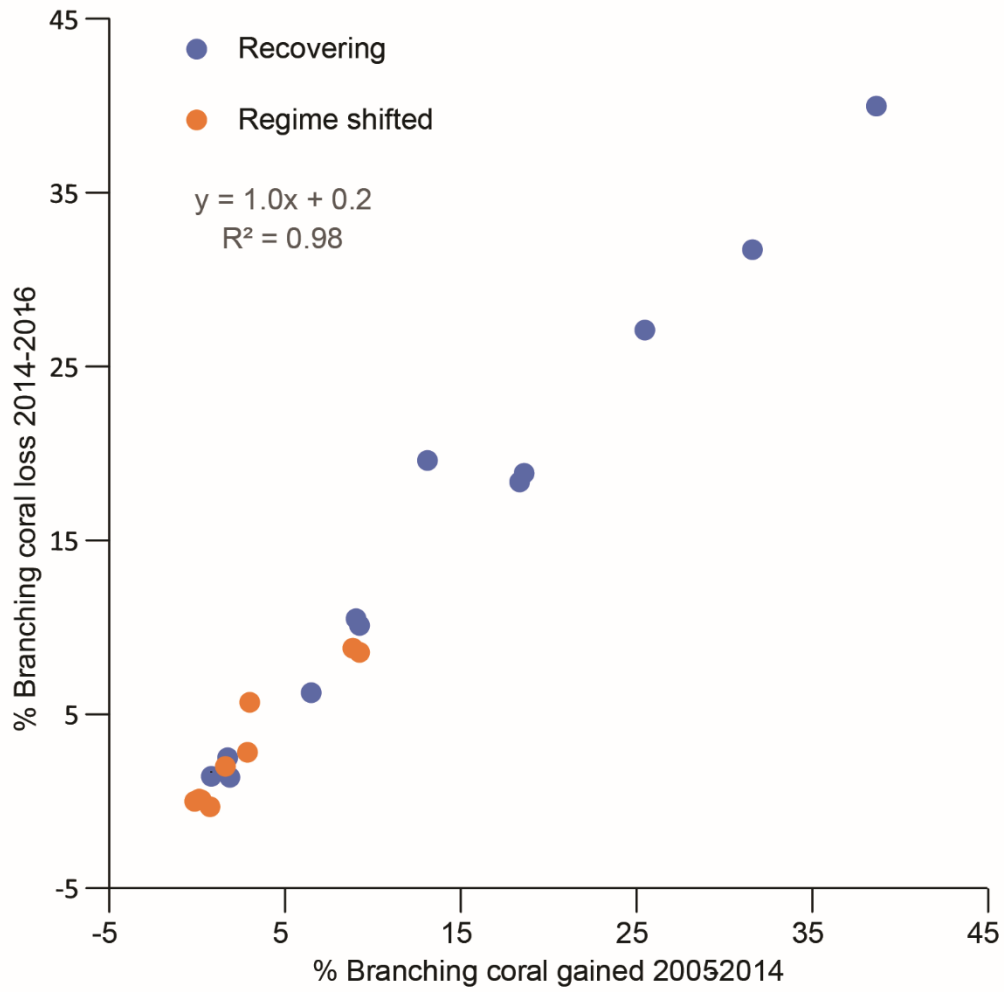
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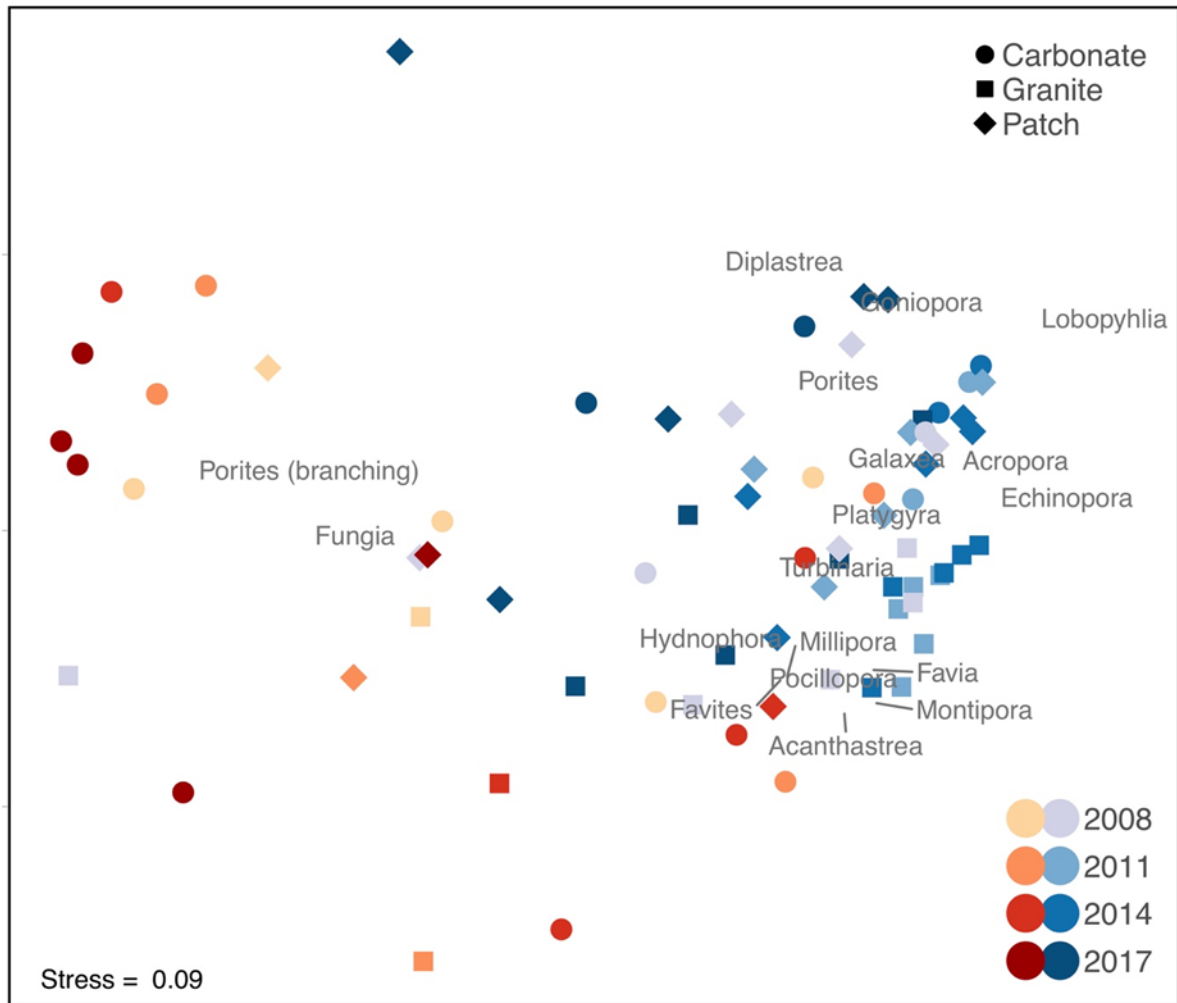
515 Fig 1. Temporal change in coral cover and structural complexity from 1994-2017. Lines are
 516 predictions from GAMs of total coral cover (A), branching cover (B), massive cover (C), and
 517 structural complexity (D), shaded with 2 standard errors (SE). Points are mean cover
 518 estimates (± 2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



521

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

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

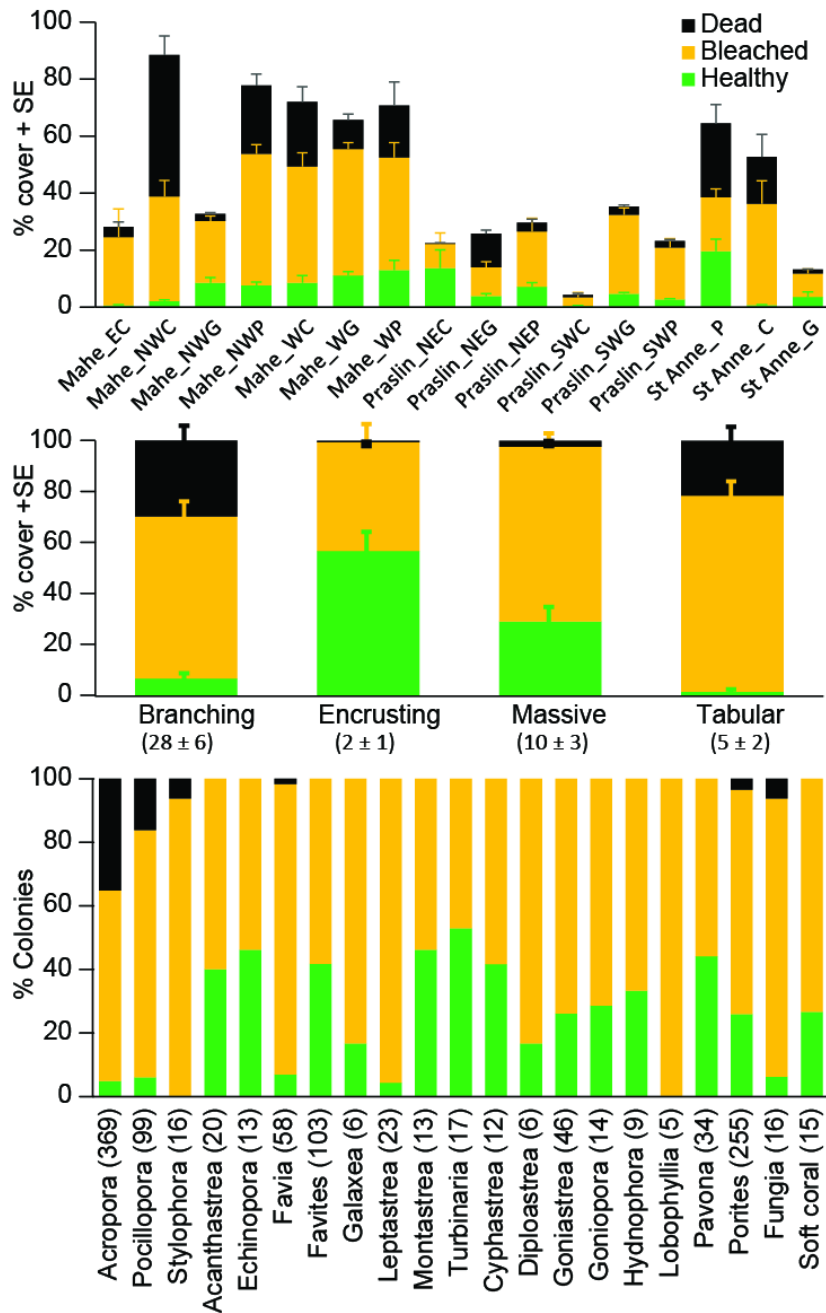
528 Seychelles reefs surveyed between 2008 and 2017 displayed. Red reefs have undergone a

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).

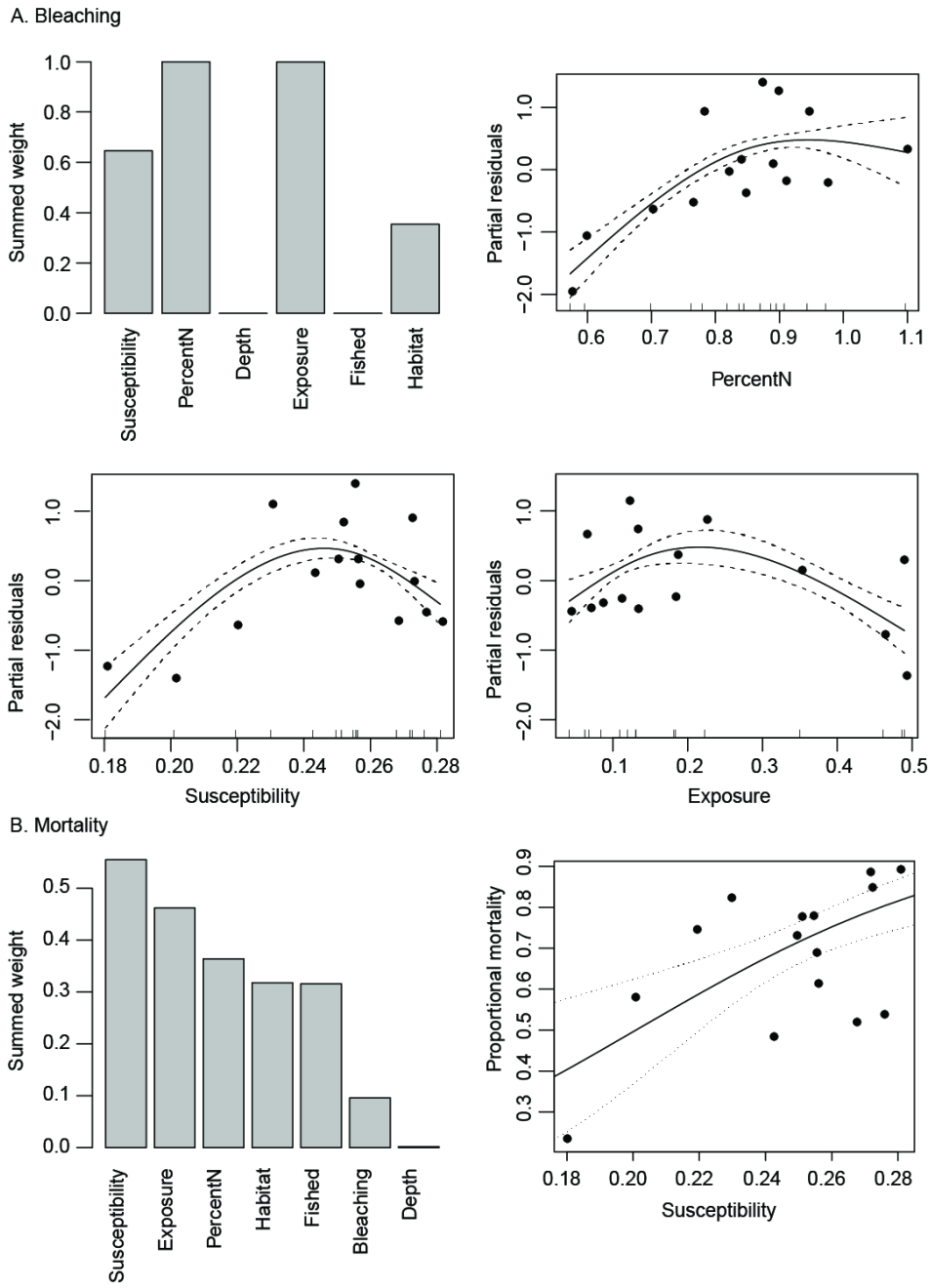
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534 Fig 4. Extent of coral bleaching on 16 Seychelles reefs in May-June 2016. Means and
 535 standard errors calculated from 8 replicate counts at each reef. Likelihood ratio tests indicated
 536 significant spatial variation in bleaching ($P < 0.001$), dead coral ($P < 0.001$), and healthy
 537 coral ($P < 0.001$). Bleaching also varied among corals of different morphology and genera.
 538 The number of colonies surveyed within each genera is in parentheses.

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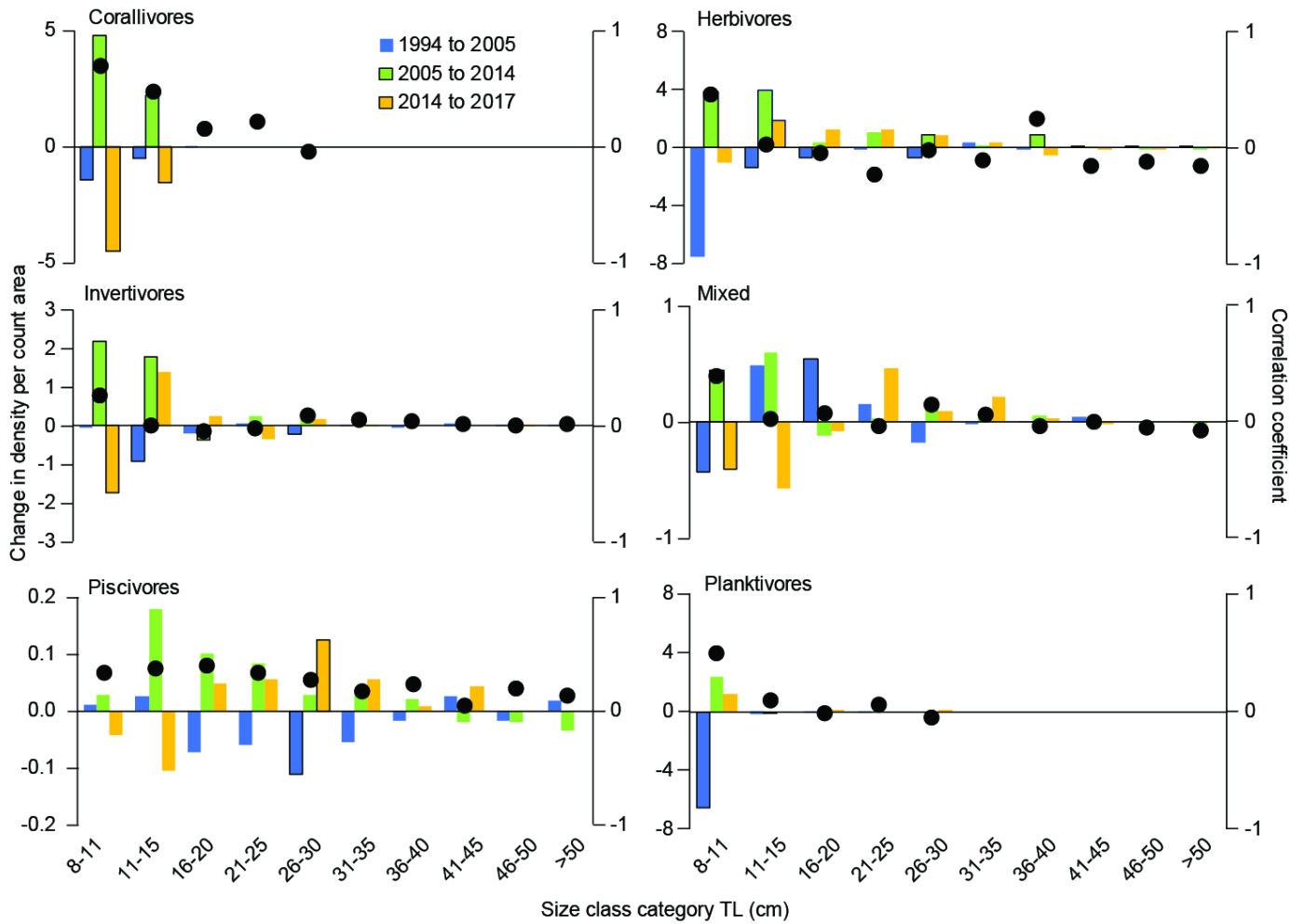
541 Fig 5. Relative importance of environmental variables in predicting the extent of coral A.

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

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

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547 Fig 6. Shifts in fish abundance during periods of branching coral cover decline (1994 to 2005
 548 and 2014 to 2017) and recovery (2005 to 2014). Each bar represents the average change in
 549 fish density (left axis) per count area (154m²) from 18 reefs consistently surveyed over the
 550 three time periods. Bars with a black outline denote significant changes in density based on
 551 95% confidence intervals. Dots are correlation coefficients for the relationship between
 552 abundance of fish within each dietary size category and percent cover of branching coral
 553 (right axis).

554