

1 **Relationships between structural complexity, coral traits, and reef fish**  
2 **assemblages**

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25 **Abstract**

26 With the ongoing loss of coral cover and the associated flattening of reef  
27 architecture, understanding the links between coral habitat and reef fishes is of  
28 critical importance. Here, we investigate whether considering coral traits and  
29 functional diversity provides new insights into the relationship between structural  
30 complexity and reef fish communities, and whether coral traits and community  
31 composition can predict structural complexity. Across 157 sites in Seychelles,  
32 Maldives, the Chagos archipelago and Australia's Great Barrier Reef, we find that  
33 structural complexity and reef zone are the strongest and most consistent  
34 predictors of reef fish abundance, biomass, species richness, and trophic structure.  
35 However, coral traits, diversity and life histories provided additional predictive  
36 power for models of reef fish assemblages, and were key drivers of structural  
37 complexity. Our findings highlight that reef complexity relies on living corals – with  
38 different traits and life histories – continuing to build carbonate skeletons, and that  
39 these nuanced relationships between coral assemblages and habitat complexity can  
40 affect the structure of reef fish assemblages. Seascape-level estimates of structural  
41 complexity are rapid and cost-effective with important implications for the  
42 structure and function of fish assemblages, and should be incorporated into  
43 monitoring programs.

44

45 **Keywords:** Habitat diversity, species traits, functional ecology, reef architecture,  
46 Scleractinian corals, coral reef fish

47

48

49 **Introduction**

50 Scleractinian corals – the foundation species of tropical reef ecosystems – have long  
51 been recognized to provide essential habitat for reef associated organisms  
52 (Luckhurst and Luckhurst 1978; Roberts and Ormond 1987; Stella et al. 2011).  
53 Similarly, structural complexity, defined as the physical three-dimensional  
54 configuration of a reef, can shape the abundance and diversity of reef fish  
55 assemblages across both large and small spatial scales (McCormick 1994; Nash et al.  
56 2012; Ferrari et al. 2016). Several ecological hypotheses are proposed to underlie  
57 these relationships, notably that structural complexity and habitat diversity can  
58 mediate competition and predation, and facilitate co-habitation of an increased  
59 number of species (Hutchinson 1959; Hixon and Beets 1993; Beukers and Jones  
60 1997).

61       Structural complexity is often positively associated with abundance and  
62 diversity of fishes across both temperate and tropical ecosystems (Friedlander et al.  
63 2003; Graham and Nash 2013). Moreover, reductions in structural complexity and  
64 habitat diversity can result in reduced abundance, local extinctions, diversity loss  
65 (Graham et al. 2006; Holbrook et al. 2015; Newman et al. 2015), and declining  
66 fisheries productivity (Rogers et al. 2014); all outcomes with profound implications  
67 for reef biodiversity and associated ecosystem services.

68       Despite important relationships between structural complexity and reef  
69 fishes, coral reef monitoring programs typically focus on measuring total live cover  
70 and composition of reef-building corals. While many relationships between coral

71 cover and reef fish assemblages have been weaker than structural complexity  
72 (Holbrook et al. 2008; Wilson et al. 2012), field experiments suggest that  
73 microhabitat (i.e., coral) diversity and some coral species can have a positive effect  
74 on fish diversity and community structure (Messmer et al. 2011; Holbrook et al.  
75 2015). Recently, trait-based approaches have outlined important characteristics of  
76 coral assemblage beyond total coral cover or taxonomic composition (Darling et al.  
77 2012; Madin et al. 2016a,b), which may provide insights for predicting the structure  
78 and diversity of reef fish communities. Traits that describe coral morphology,  
79 growth rate and colony size may be expected to predict structural complexity, and  
80 thus the structure and composition of fish assemblages. As such, coral traits may  
81 provide a means of quantifying structural complexity and predicting fish  
82 assemblage properties from benthic surveys where direct measures of  
83 macrocomplexity were not taken, particularly in combination with the availability of  
84 open-access trait information (Madin et al. 2016a,b). For example, traits that  
85 describe branching, corymbose or plating growth forms can provide keystone  
86 structures for reef fishes, which can preferentially select specific structural traits of  
87 corals for shelter (Noonan et al. 2012; Kerry and Bellwood 2012, 2015; Wilson et al.  
88 2016). A range of other explicit links can be made for other coral traits (Table 1).

89         To the best of our knowledge, this study presents the first large-scale  
90 empirical test of trait-based relationships among coral communities, structural  
91 complexity and reef fish assemblages. We use surveys across a large gradient of fish  
92 biomass in the Indian and Pacific Oceans ranging from exploited sites to those  
93 within one of the world's most pristine reef systems, the Chagos archipelago

94 (Graham and McClanahan 2013). Our objectives were to, 1) evaluate which aspects  
95 of the physical and biological characteristics of benthic habitats best explain the  
96 structure of reef fish assemblages, in particular how well do coral traits describe fish  
97 assemblages relative to physical measures of reef structure, and 2) investigate the  
98 relationships between hard coral cover, life histories and species traits with  
99 structural complexity.

100

## 101 **Methods**

### 102 *Study sites*

103 We surveyed 157 sites in the Seychelles, Maldives, Chagos archipelago and the Great  
104 Barrier Reef in Australia between 2010 and 2013 (Figure 1). Sites were  
105 haphazardly sampled across three reef zones (reef crest, flat and slope; also referred  
106 to as reef habitat) and include fished sites and sites within no-take marine reserves.  
107 Depth was recorded for each site and ranged from 1.5 m to 10 m. At each site,  
108 benthic and coral reef fish surveys were conducted using underwater visual census  
109 methods to evaluate coral communities, habitat complexity and reef fish  
110 assemblages.

111

### 112 *Coral assemblages*

113 Coral assemblages were surveyed using two methods: four x 50 m point intercept  
114 transects in Chagos, Maldives and Australia, and eight x 10m line intercept transects  
115 in the Seychelles. For point intercept transects, the substrate directly below the  
116 transect tape was surveyed every 50 cm. For line intercept transects, the length of

117 each substrate type was measured along the entire 10 m distance. For each method,  
118 we recorded major benthic categories (e.g., hard coral, soft coral, sand, rubble,  
119 pavement, algae, sponge, etc.) and identified hard corals to genus and growth form  
120 using standard morphological genus names. These methods are typically  
121 comparable (Facon et al. 2016) and here, we directly compared these methods by  
122 conducting a sensitivity analysis where we re-ran our entire analysis without the  
123 line intercept transects from the Seychelles and reached similar overall conclusions  
124 (see Appendix 1).

125 We estimated structural complexity on each transect using a visual six-point  
126 scale, following Polunin & Roberts (1993). The scale ranges from 0 (no vertical  
127 relief) to 5 (exceptionally complex habitats with numerous caves and overhangs);  
128 for a full description of this scale and pictures, see Appendix 2. This measure of  
129 structural complexity has been shown to correlate well with a range of other  
130 structural complexity measurement techniques (Wilson et al. 2007), to strongly  
131 predict coral and reef fish diversity (Polunin and Roberts 1993; Chong-Seng et al.  
132 2012; Newman et al. 2015), and reef recovery following mass bleaching events  
133 (Graham et al. 2015). All visual observations of structural complexity were recorded  
134 by one observer, NAJG. This method has also been shown to quickly provide a  
135 reliable and effective estimate of habitat complexity, with regular training of  
136 multiple observers limiting observer bias (Wilson et al. 2007).

137 We derived 17 metrics of coral communities based on benthic surveys,  
138 including total cover of scleractinian corals, genera richness, percent cover of life

139 histories, and abundance-weighted trait means and functional diversity (Table 1).  
140 Total coral cover was estimated as the average percent of living hard coral at each  
141 site, and genera richness was estimated as the average number of coral genera on  
142 replicate transects. Richness was estimated from raw estimates and not adjusted by  
143 rarefaction after a post-hoc sensitivity analysis of two underwater survey methods  
144 revealed similar conclusions (Appendix 1). Life histories were evaluated based on  
145 the abundance (percent cover) of four life-history groups – competitive, stress-  
146 tolerant, weedy and generalist corals – proposed by Darling et al. (2012), which  
147 have revealed community shifts in response to various disturbances on coral reefs  
148 (Darling et al. 2013; Graham et al. 2014; Sommer et al. 2014). The functional  
149 structure of coral assemblages was evaluated by five traits that define the life  
150 histories reported in Darling et al. (2012): colony growth form (branching, plating  
151 or domed), maximum colony size, growth rate (measured as annual linear  
152 extension, mm year<sup>-1</sup>), reproductive mode (brooding or broadcast spawning) and  
153 fecundity. These five coral traits were selected because they had tangible links to  
154 reef fish assemblages; see Table 1 for detailed justification. A full list of observed  
155 hard corals, growth forms and their associated traits can be found in Supporting  
156 Table S1; trait information is also freely available online at <https://coraltraits.org>  
157 (Madin et al. 2016a). To estimate genus-level trait values, we averaged available  
158 trait information for species that occurred in the appropriate Indo-Pacific faunal  
159 province, based on Keith et al. (2013) (Africa-India province: *Chagos, Maldives and*  
160 *Seychelles*; Australian province: Great Barrier Reef). For categorical traits (colony  
161 growth form and reproductive mode), we calculated the proportion of species in

162 each genus with the trait (see Table S1). Six genera (*Heliopora*, *Millepora*,  
163 *Oulaphyllia*, *Polyphyllia*, *Tubastrea*, *Tubipora*) were removed from life history and  
164 trait analyses because of limited trait information (and these genera had limited  
165 abundances within our surveyed coral communities).

166 To derive multivariate measures of functional diversity, we conducted a  
167 principal components analysis (PCoA) on the five coral traits using a Gower  
168 dissimilarity matrix. We then estimated two measures of functional diversity:  
169 functional richness and Rao's quadratic entropy. Functional richness was derived  
170 from the number of distinct functional groups in a community based on a Ward's  
171 clustering analysis, and Rao's quadratic entropy was measured from the average  
172 distance of abundance-weighted maximum pairwise-distances in functional space at  
173 each site (Mouillot et al. 2013). At each site, we calculated a community-weighted  
174 trait mean for each of the five traits by weighting the values of each trait by the  
175 relative abundance of corals (Mouillot et al. 2013). Overall, our approaches estimate  
176 three unique components of traits and functional diversity to consider, a) functional  
177 richness of trait combinations (FunctionalRichness), b) functional entropy of a  
178 community (FunctionalRao), and c) abundance-weighted trait values for five traits.  
179 We used the package "FD" in R for all functional analyses (Laliberté and Legendre  
180 2010).

181

### 182 *Reef fish assemblages*

183 We estimated the density and individual sizes of all species of diurnally active, non-  
184 cryptic, reef associated fish >8 cm total length at each site using two comparable



185 methods. In the Seychelles, eight replicate 7 m radius point counts were conducted  
186 at each site (154m<sup>2</sup>/replicate); all other locations used four replicate 50 m x 5 m  
187 belt transects (250m<sup>2</sup>/replicate) for large and mobile fishes, while smaller and site-  
188 attached, territorial species (e.g., pomacentrids) were recorded using four replicate  
189 50 m x 2 m belt transects (100m<sup>2</sup>/replicate). For each transect, we calculated the  
190 total numerical abundance, biomass and species richness of reef fish assemblages  
191 and averaged these values at each site. All estimates were standardized to  
192 estimates/ 250m<sup>2</sup> for comparison across sites. As described in the benthic analyses,  
193 we conducted a sensitivity analysis to account for these different methodologies by  
194 re-running analyses with and without the Seychelles dataset, which revealed very  
195 similar findings to the full dataset analysis; while there is some influence of survey  
196 methods on the list of variables in the top models, overall our main findings and  
197 conclusions are supported (Appendix 1). We also included fish method (point count  
198 vs. belt transect) as a variance-covariate in the model framework to account for  
199 uneven variation across methods (see Data Analysis below). Total reef fish  
200 abundance was strongly correlated to the numerical abundance of small fish (< 20  
201 cm; general linear model  $R^2 = 0.85$ ,  $p < 0.001$ ), and we modelled both total  
202 abundance and the abundance of small fish < 20 cm in separate analyses. This  
203 allowed us to model the abundance of both the overall fish assemblage and juvenile  
204 or small-bodied fish that are often more associated with the reef habitat (Beets and  
205 Hixon 1989; Bergman et al. 2000; Graham et al. 2007; Wilson et al. 2010). Reef fish  
206 biomass was calculated using standard length-weight conversions and diversity was  
207 estimated from species richness as the total number of species observed at each site.

208 Fish species were assigned to the following trophic (feeding) groups, following  
209 Graham et al. (2006): corallivores, herbivories, invertivores, mixed-diet feeders,  
210 piscivores and planktivores. The link between these feeding groups and specific  
211 characteristics of the coral assemblage may be expected to be stronger than for total  
212 biomass.

213

#### 214 *Data analysis*

215 For all analyses, we used multi-model averaging of mixed-effects linear models with  
216 maximum likelihood estimation to evaluate relationships between coral  
217 assemblages, structural complexity and reef fish communities. We evaluated all  
218 variables described above for multicollinearity, and found, not surprisingly, that  
219 coral life histories were strongly correlated with coral cover. Therefore we  
220 conducted two similar analyses: one with life histories and one with coral cover (see  
221 Appendix 3). Our final variable set consisted of independent predictors with  
222 variance inflation factors  $< 5$ , following Zuur et al. (2010)(Table 1) – notably growth  
223 rate was removed from the candidate set of traits due to multicollinearity ( $VIF > 5$ ;  
224 Table 1). Using mixed-effects general linear models, we first evaluated the effects of  
225 coral diversity (genera richness), traits, life histories and structural complexity on  
226 reef fish abundance, biomass and diversity, followed by a second analysis that  
227 evaluated the effects of coral diversity, traits and life histories on structural  
228 complexity. All models were repeated by replacing the four coral life histories with  
229 total coral cover, to address issues of multicollinearity between life histories and

230 coral cover, as discussed above. Total biomass and biomass for the six trophic  
231 groups of fishes were log-transformed in all models.

232 All models included a random effect of country, whereby sites were nested  
233 within country to account for biogeographic differences of latitude, large-scale  
234 environmental conditions, and differences in fishing pressure among the countries  
235 studied (see equation: site  $j$  in country  $i$ ). We also applied residual variance  
236 structures to account for identifiable structure in the error residuals of our full  
237 model. Variance structures are variables used to model the structure of the  
238 residuals, without a penalty of adding more model parameters (Zuur et al. 2009).  
239 We used AIC to compare variance structures and identify which one performed  
240 better in all models. For all models, a varIdent variance structure was applied to  
241 account for uneven residual error within management groups (marine reserve vs.  
242 open access) and fish methods (belt transect vs. point count). For fish abundance,  
243 we also applied a varPower variance structure to habitat complexity that accounted  
244 for greater observed residual variation in more complex habitats; this error  
245 structure was not required for the biomass or diversity models, although we did  
246 apply it in models for the six trophic groups. We also tested a varIdent variance  
247 structure for coral method (point count vs. line intercept), which did not improve  
248 model fit in the fish models, but did improve fit in the analysis of structural  
249 complexity.

250 For the analysis of reef fish assemblages, we applied the following model  
251 structure to reef fish abundance, biomass, species richness and trophic groups:

252 Fish response<sub>ij</sub> =  $\beta_0 + \beta_1 \times \text{Reef zone}_{ij} + \beta_2 \times \text{Depth}_{ij} + \beta_3 \times \text{Management}_{ij}$   
 253 +  $\beta_4 \times \text{Complexity}_{ij} + \beta_5 \times \text{GeneralRichness}_{ij} + \beta_6 \times \text{FunctionalRao}_{ij}$   
 254 +  $\beta_7 \times \text{CoralBranching}_{ij} + \beta_8 \times \text{CoralMaxSize}_{ij}$   
 255 +  $\beta_9 \times \text{CoralBrooding}_{ij} + \beta_{10} \times \text{CoralFecundity}_{ij}$   
 256 +  $\beta_{11} \times \text{Competitive}_{ij} + \beta_{12} \times \text{Generalist}_{ijk} + \beta_{13} \times \text{StressTolerant}_{ik} + \beta_{14} \times \text{Weedy}_{ij}$   
 257 +  $\epsilon_{ij}$   
 258  $\epsilon_{ij} \sim N(0, \sigma^2_l) \quad l = \text{Management},$   
 259  $\epsilon_{ij} \sim N(0, \sigma^2_m) \quad m = \text{Fish Method},$   
 260  $\epsilon_{ij} \sim N(0, \sigma^2 \times |\text{Complexity}|^{2\delta})$   
 261 Prior to analysis, all input variables were centered to a mean of zero and  
 262 standardized to a standard deviation of  $\pm 1$ , in order to allow for direct comparisons  
 263 of variable effect sizes (in R, function ‘rescale’ in package *arm*; Gelman 2008). For  
 264 each fish response, we evaluated 3473 models by completing every combination of  
 265 variables (up to 5 variables per model) and comparing models using Akaike’s  
 266 Information Criteria corrected for small sample size (AIC<sub>c</sub>) (Akaike 1974). Within a  
 267 top model set of  $4 \Delta \text{AIC}_c$  of the best model, we calculated model-averaged  
 268 coefficients and 95% confidence intervals; significant coefficients were identified  
 269 from confidence intervals that did not overlap zero. We also calculated the variable  
 270 importance for each coefficient as the sum of Akaike weights across all models,  
 271 which provided a rank for each variable, where a relative variable importance of 1.0  
 272 identifies the highest ranked input variable (Burnham and Anderson 2002). For  
 273 model validation we assessed the heterogeneity and normality of residuals across  
 274 the top 95% set of candidate models. We fit all models in the package *nlme* (Pinheiro

275 et al. 2015) with multi-model averaging using the package *MuMin* (Bartoń 2016); all  
276 analyses were conducted in R (R Core Team 2015).

277 We applied the same statistical approach to model structural complexity  
278 using characteristics of coral diversity, traits and life histories. Here, 2380 models  
279 were evaluated using every possible combination (up to 5 variables) with a random  
280 effect of country and a variance-covariate varIdent structure applied to  
281 management and coral method. The model structure was defined as:

$$\begin{aligned} 282 \quad \text{Complexity}_{ij} = & \beta_0 + \beta_1 \times \text{Habitat}_{ij} + \beta_2 \times \text{Depth}_{ij} + \beta_3 \times \text{Management}_{ij} \\ 283 & + \beta_4 \text{GeneraRichness}_{ij} + \beta_6 \times \text{FunctionalRao}_{ij} \\ 284 & + \beta_7 \times \text{CoralBranching}_{ij} + \beta_8 \times \text{CoralMaxSize}_{ij} \\ 285 & + \beta_9 \times \text{CoralBrooding}_{ij} + \beta_{10} \times \text{CoralFecundity}_{ij} \\ 286 \quad & + \beta_{11} \times \text{Competitive}_{ij} + \beta_{12} \times \text{Generalist}_{ijk} + \beta_{13} \times \text{StressTolerant}_{ik} + \beta_{14} \times \text{Weedy}_{ij} \\ 287 & + \varepsilon_{ij} \\ 288 & \varepsilon_{ij} \sim N(0, \sigma^2_l) \quad l = \text{Management}, \\ 289 & \varepsilon_{ij} \sim N(0, \sigma^2_m) \quad m = \text{Coral Method} \end{aligned}$$

290 As described above, all input variables were centered and standardized to a mean of  
291 zero  $\pm$  1 standard deviation prior to analysis, and we conducted the same multi-  
292 model inferences using Akaike's information criteria.

293

## 294 **Results**

295 Structural complexity and reef zone were the strongest predictors of reef fish  
296 abundance, biomass, diversity and trophic structure across ~38,000 mixed-effects  
297 models. Structural complexity was a consistently top-ranked predictor in all models  
298 of reef fish assemblages (i.e., with a maximum relative variable importance of 1.0 in

299 all model comparisons (Table 2; Appendices 3-6). Characteristics of reef zone and  
300 depth also revealed high variable importance for abundance and diversity, but not  
301 biomass; slope and crest zones were typically associated with more abundant and  
302 diverse reef fish communities than reef flats (Table 2; Fig. 2a-c).

303 Management (marine reserve vs. open access), coral cover and genera  
304 richness, functional diversity, species traits of colony size and branching and some  
305 life histories were also associated with different characteristics of reef fish  
306 assemblages, including the abundance of small fishes and trophic groups (Table 2;  
307 Fig. 2; Fig. 3; Appendices 3-6). Total reef fish abundance decreased with depth and  
308 functional diversity, and increased with more complex habitats, cover of stress-  
309 tolerant corals and slope zones (Fig. 2a); these patterns were consistent for the  
310 abundance of smaller fish < 20cm, which also included weaker effects of life  
311 histories, coral traits, genera richness and management variables in the top models  
312 (Appendix 4), although complexity only appeared in two of the top 11 models for  
313 smaller fish abundance and had a lower relative importance than aforementioned  
314 variables. Reef fish biomass increased with structural complexity within no-take  
315 reserves and, across all management types, with greater cover of stress-tolerant  
316 corals, and decreased cover of weedy corals (Fig. 2b). Species richness was greater  
317 at sites within slope and crest habitats, with higher complexity, and characterized  
318 by larger maximum colony size. In addition, a suite of life histories, traits, depth and  
319 management had weaker influences, i.e., with 95% confidence intervals overlapping  
320 zero and lower relative variable importance (Table 2; Fig. 2c). Overall, total  
321 abundance and biomass were predicted by fewer variables (5-6 in top models) than

322 the abundance of smaller fish and diversity, which included 15 variables in each top  
323 model set (Appendix 4).

324 The biomass of reef fish trophic groups also included structural complexity  
325 as a main driver in each analysis, whereby sites with more complex reef structure  
326 were associated with greater biomass of each trophic group (Fig. 3; Appendix 5).  
327 Each trophic group was predicted by a different suite of traits, life histories and  
328 other variables; for example, the biomass of corallivores increased with the  
329 abundance of competitive branching and plating corals and with depth (Fig. 3a),  
330 while the biomass of piscivores increased with depth and management, in addition  
331 to a suite of weaker trait and life history variables (Fig. 3e).

332 We also separated out the effects of management in these relationships by  
333 conducting separate analyses of total reef fish biomass within no-take marine  
334 reserves vs. open access fished reefs (Appendix 6). This revealed that the influence  
335 of complexity, life histories, traits and habitat on total biomass within marine  
336 reserves was more complex (i.e., 7 top variables) than on fished reefs, where  
337 biomass was predicted by complexity and a weaker influence of coral genera  
338 richness (Fig. S6-1).

339 Structural complexity was predicted by a large suite of benthic and habitat  
340 characteristics, including hard coral traits and life histories (Fig. 4). Habitat and the  
341 abundance of competitive, stress-tolerant and generalist life histories, genera  
342 richness, and traits of colony size, branching and fecundity were the strongest  
343 predictors of structural complexity and had the highest relative variable importance  
344 in the top 95% model set after evaluating ~3,000 mixed-effects models (Fig. 4, Table

345 3). Structural complexity was typically higher on the reef slope and crest than reef  
346 flat and increased with percent cover of competitive and generalist corals, genera  
347 richness, and maximum colony size; structural complexity was lower on reefs with a  
348 high abundance of corals with branching traits and high fecundity (Fig. 3b). Coral  
349 cover was also a significant and positive predictor of structural complexity; sites  
350 with higher coral cover were associated with higher structural complexity  
351 (Appendix 3).

352

### 353 **Discussion**

354 Understanding the associations between habitat structure and reef fishes and  
355 mobile invertebrates has been a key focus of coral reef ecology for decades  
356 (Luckhurst and Luckhurst 1978; Roberts and Ormond 1987; Stella et al. 2011).  
357 Recently, trait-based metrics for both corals (Darling et al. 2012; Madin et al. 2016b)  
358 and reef fishes (Mouillot et al. 2013) have been proposed to offer new insights into  
359 patterns of diversity and function on coral reefs in order to provide a more  
360 mechanistic understanding of associations between benthic characteristics and fish  
361 assemblages. Here, we show that the abundance, biomass, diversity, and trophic  
362 structure of diurnal, non-cryptic reef fishes were strongly and consistently  
363 predicted by structural complexity and reef zone while characteristics of hard coral  
364 traits, total cover, life histories, and functional diversity added subtle, if weaker,  
365 effects to these relationships (Table 2; Fig. 2). Importantly, hard coral  
366 characteristics of total cover, traits and life histories, strongly influenced structural  
367 complexity (Table 3; Fig. 3), which highlights the indirect relationships by which



368 living hard corals can provide structural complexity and habitat diversity for reef  
369 fishes.

370         The consistent influence of structural complexity and reef zone emphasize  
371 the importance of both living and non-living components of the reef that can  
372 structure reef fish assemblages. For examples, we show that the living ‘vener’  
373 provided by live hard corals and their associated traits, diversity and life histories  
374 can also influence reef fish assemblages and contributes critically to structural  
375 complexity. Interestingly, different characteristics of the coral assemblage  
376 contributed to different components of the reef fish assemblage. Coral genera  
377 richness and functional diversity appeared in the top model sets for total biomass  
378 and diversity, the abundance of small fish, and the biomass of herbivores, piscivores  
379 and planktivores, yet were mainly weak variables compared to the influence of  
380 complexity and habitat. Similarly, coral life histories and traits influenced total  
381 abundance, biomass and diversity, the abundance of small fish, and the biomass of  
382 corallivores, mixed-diet feeders, piscivores and planktivores but were also typically  
383 weaker predictors (Figs. 2-3, Appendices 4-5). Thus, we conclude that the  
384 mechanistic hypotheses that coral diversity, life histories and traits support the  
385 structure of reef fish assemblages is only weakly supported (e.g., Table 1), compared  
386 to the stronger influences of overall structural complexity and reef zone. It should  
387 be noted, however, that the reef fish community was only surveyed >8cm in length.  
388 It is possible that smaller fishes would show a stronger relationship with some coral  
389 growth forms, such as branching corals.

390 We also found that some components of reef fish assemblages were  
391 influenced by more variables than others: notably species richness, the abundance  
392 of smaller individuals (between 8 and 20cm) and the biomass of piscivores and  
393 planktivores, with > 10 variables in the top model set (Fig. 2-3, Appendix 4). This  
394 suggests that different types of living corals and their traits influence different  
395 components of reef fish assemblages, as well as provide important habitat for the  
396 abundance of all fishes and smaller juvenile fish recruits even when adults of their  
397 species may have less affinity for live corals (Jones et al. 2004). Clearly, there are  
398 many complex and indirect interdependencies between reef corals and reef fishes  
399 that require further investigation (Pratchett et al. 2015), and a combination of  
400 structural complexity and living corals is likely required for optimal reef fish  
401 productivity and diversity.

402 Overall, the strong influence of seascape-level structural complexity on reef  
403 fish assemblages may be because this index integrates both living hard corals and  
404 non-living features of the reef matrix such as caves, crevices or overhangs that can  
405 reflect reef growth and erosion processes accumulated over decades, centuries or  
406 even millennia (Kleypas et al. 2001; Appendix 2). Thus, the reef matrix can provide  
407 some resilience to disturbances that directly confer mortality to living corals (e.g.,  
408 bleaching and outbreaks of crown-of-thorns starfish), which may also explain why  
409 fish diversity can be maintained following extensive coral mortality on inherently  
410 complex reefs (Wilson et al 2009; Graham et al. 2015). However, we have shown  
411 that various aspects of the living corals are critical to providing structural  
412 complexity, and likely maintaining it in the long run. However, the seascape metric

413 of structural complexity we used does not capture small-scale complexity, such as  
414 the presence of small holes <10cm (Wilson et al. 2007), and our surveys focus on  
415 fish > 8cm, which limits our ability to make inferences about the how smaller fish  
416 use finer-scale structural complexity (e.g., smaller spaces within branching coral  
417 colonies).

418 No-take marine reserves were also, unsurprisingly, a key factor in predicting  
419 total reef fish biomass (e.g, MacNeil et al. 2015). This suggests that strategically  
420 locating marine reserves or fisheries management (e.g., gear restrictions) in areas  
421 with structurally complex reefs may provide greater returns on investments for  
422 biomass recovery than if focused on low complexity reefs (McClanahan et al. 2011;  
423 MacNeil et al. 2015). Piscivore biomass was greater in reserves and there were more  
424 complex associations between habitat and coral traits in reserves compared to  
425 fished reefs, which showed much simpler relationships. This supports well-  
426 described evidence that overexploitation of fish can weaken predator-prey  
427 processes, and decouple biophysical relationships (Madin 2010; Houk & Musburger  
428 2013; Williams et al. 2015).

429 Here, our analysis of reef fish assemblages focused on site-level variables of  
430 habitat zonation and exposure and not broad biogeographic gradients of wave  
431 exposure or other environmental variables (e.g., currents, bleaching or cyclone  
432 disturbances). For example, wave-induced water motion and flow velocity has been  
433 shown to structure the distribution and functional structure of reef fishes on Lizard  
434 Island (Fulton & Bellwood 2005). Similarly, our correlative study did not consider  
435 how reef fish behavior – e.g., swimming ability and the use of flow or habitat refuges

436 – might affect these patterns (Johansen et al. 2008). However, our findings are in  
437 agreement with experimental studies on how reef fish use benthic habitat space, for  
438 example the finding that *Acropora* table corals can provide keystone structure for  
439 large reef fishes (Kerry & Bellwood 2012; 2015) and field observations that show  
440 tight links between specific coral and fish species (Cocker et al 2014). Clearly,  
441 controlled experimental studies will be necessary to understand the relationships  
442 between coral traits, life histories and diversity that we have investigated here using  
443 field-based surveys and correlative analyses.

444         Hard coral assemblages strongly influenced structural complexity – sites  
445 with higher coral cover, greater genera richness, more abundant competitive and  
446 generalist life histories, and traits of larger colony sizes and higher growth rates  
447 were associated with more complex reefs (Table 3; Fig. 4; Supporting Appendix 3).  
448 Surprisingly, the abundance of corals with branching traits was negatively  
449 associated with structural complexity (Fig 3). This is a contrasting finding to studies  
450 that have found a positive association between the abundance of branching corals  
451 and fish assemblages via structural complexity (Chabanet et al. 1997; Messmer et al.  
452 2011; Graham and Nash 2013). This may, perhaps, be because the refuge spaces  
453 associated with many fine branching corals are small (<10cm) and this scale of  
454 complexity is not well captured by the visual assessments of structural complexity  
455 used here (Wilson et al. 2007). In addition, the dominance of corals with branching  
456 traits may also create a homogeneous habitat that might reduce the overall  
457 structural complexity of a reef. Alternatively, coral identities (i.e., specific genera) or  
458 life histories may be a better predictor of structural complexity than the individual

459 coral traits investigated in this analysis. For example, the cover of competitive life  
460 histories (typically branching and plating acroporiids, Darling et al. 2012) was  
461 positively associated with structural complexity, as was the number of coral genera.  
462 Previous studies have also found strong relationships between specific genera with  
463 structural complexity; for example, large, massive *Montastrea* (now *Orbicella*)  
464 colonies are associated with greater structural complexity (Alvarez-Filip et al. 2011)  
465 while the cover of branching *Pocillopora* was negatively related to reef complexity  
466 (Perry et al. 2015). However, as the new systematics of Scleractinia continue to  
467 inform and revise morphological classifications (e.g., Kitihara et al. 2016), trait  
468 selection and inference must carefully consider how traits are matched to genera  
469 observed on monitoring surveys.

470         While structural complexity and reef zonation are known to be major drivers  
471 of reef fish assemblages (Wilson et al. 2009; Graham and Nash 2013), here we show  
472 that coral traits and diversity can also have subtle effects on these relationships, as  
473 well as being key variables in determining structural complexity. This suggests that  
474 the long term maintenance and production of future structural complexity on  
475 carbonate reefs will rely on living hard corals continuing to build the carbonate  
476 framework of reefs since dead corals inevitably break down and erode.  
477 Furthermore, this emphasizes the importance of past disturbance histories and  
478 recovery trajectories, particularly as disturbed coral assemblages shift in  
479 composition towards smaller weedier or opportunistic species that may provide  
480 less complexity overall (Darling et al. 2013; Alvarez-Filip et al. 2013).

481 As trait-based approaches move to advance coral reef science (Madin et al.  
482 2016a,b), our study highlights two important caveats and considerations for future  
483 trait-based investigations. First, coral traits may have weak associations with reef  
484 fish assemblages, even if these traits are mechanistically associated with ecosystem  
485 processes of interest (e.g., growth forms, colony size or growth rates). Here, the five  
486 traits used in this analysis had general relevance for fish community structure,  
487 although considering different traits, such as inter-colony volume, actual colony  
488 size, or volume under colonies, may have resulted in stronger relationships and  
489 different conclusions. Traits might also be explicitly tied to reef fish processes  
490 through specific links to energy production or shelter provisioning, however  
491 empirical data on these processes is typically limited and may require additional  
492 experimental (e.g., Kerry & Bellwood 2012; 2015) or modeling approaches (e.g.,  
493 biomass spectrum models or size-based theory; Trebilco et al. 2013). Second, most  
494 species-level coral trait information is largely available only as global averages,  
495 which does not reflect regional or intra-specific variation in coral traits. Given that  
496 intraspecific variation in coral morphology influences associations between fishes  
497 and host corals (e.g., Noonan et al. 2012), this will limit the usefulness of trait  
498 information when averaged up to the genera level (the common taxonomic  
499 resolution of most underwater coral surveys). Here, we used genus-level trait  
500 averages estimated from regionally appropriate species lists (the Indo-Pacific faunal  
501 provinces of Keith et al. 2013), yet we still find relatively weak associations between  
502 traits and coral reef fish assemblages. Evaluating the coral traits of specific colonies  
503 (vs. species or genus-level averages) may yield stronger relationships, although this

504 requires significantly more field effort which is logistically challenging for regional  
505 or global comparisons (Coker et al. 2014). However, we also find that simple life  
506 history groups based on species traits (from Darling et al. 2012) are useful  
507 predictors of structural complexity, which suggests that even coarse groupings of  
508 life history traits may have some utility in describing reef functions, such as  
509 structural complexity and the trophic structure of reef fish assemblages. Overall, the  
510 availability of new, open-access databases can aggregate and provide trait  
511 information online to test these hypotheses in the future (Madin et al. 2016a)

512

### 513 ***Conclusions***

514         An obvious symptom of reef degradation is the transition towards net  
515 erosion, due to declines in reef accretion caused by declines in abundance and/ or  
516 growth of calcifying organisms, and especially scleractinian corals (Kleypas et al.  
517 2001; Alvarez-Filip et al. 2009; Perry et al. 2013). Maintaining key demographic  
518 processes of coral growth and carbonate accretion will be increasingly important to  
519 maintain structural complexity and habitat diversity for reef fishes and  
520 invertebrates. However, this is a challenging recommendation for managers and  
521 decision makers in the context of increasing local stressors, ocean warming and  
522 acidification, and sea level rise (Hoegh-Guldberg et al. 2007; Manzello et al. 2008;  
523 DeCarlo et al. 2015). Identifying relationships and thresholds between key  
524 demographic processes and specific management actions (like water clarity or the  
525 biomass of herbivorous fishes) remains a key focus for future research.

526 Furthermore, ongoing coral community shifts towards stress-tolerant, weedy and

527 low complexity species may superficially maintain coral cover while silently  
528 masking declines in complexity, coral accretion, and ecosystem services (Alvarez-  
529 Filip et al. 2013; Rogers et al. 2014).

530 Monitoring reef condition requires indicators that capture key processes and  
531 early signs of decline (Hughes et al. 2010; McClanahan et al. 2011). Here, we show  
532 that seascape visual estimates of structural complexity can be easily incorporated  
533 into monitoring and management programs (see Appendix 2 for more details).  
534 Interestingly, this method could also be calculated retrospectively from underwater  
535 images that provide a panoramic view about transects (Wilson et al. 2009), or with  
536 machine-learning methods applied to satellite images or digital reef terrain maps,  
537 which would allow this methodology to scale up beyond SCUBA-based surveys to  
538 larger temporal and spatial scales (e.g., Pittman et al. 2009). For example, including  
539 a panoramic assessment at the start and end of the transect line that includes  
540 geomorphological reef features like caves or overhangs can provide important  
541 assessments of structural complexity relevant to fishes (e.g., Collins et al. 2016).  
542 Further, while our study is based on observations, our results are supported by  
543 experimental studies that have manipulated structural complexity and specific  
544 habitats (e.g., the space below tabulate corals) to reveal the importance of  
545 complexity for reef fishes (Beets and Hixon 1989; Syms and Jones 2000; Gratwicke  
546 and Speight 2005; Kerry and Bellwood 2012, 2015). Overall, incorporating a  
547 standard measure of structural complexity into long-term monitoring programs  
548 may provide useful information on the loss of reef architecture and knock-on effects  
549 for coral reef ecosystems (e.g. Graham et al. 2015).



550 Continued declines in the three-dimensional complexity and coral diversity  
551 of tropical reefs will have consequences for reef fishes, fisheries and the human  
552 societies that depend on these ecosystem services (Alvarez-Filip et al. 2013; Hicks &  
553 Cinner 2014; Rogers et al. 2014). Here, we highlight the importance of structural  
554 complexity as well as the more nuanced and subtle influences of coral traits and  
555 functional diversity on reef fishes. Maintaining structural complexity and coral  
556 diversity should be a key focus for managers, because it can help reefs recover to a  
557 coral-dominated state after mass bleaching (McClanahan et al. 2012; Graham et al.  
558 2015) and supports fish diversity and fisheries productivity (Rogers et al. 2014;  
559 Holbrook et al. 2015). Managing for structural complexity may include prioritizing  
560 conservation and no-take reserves to, i) reefs with high existing complexity and  
561 abundant live corals, such as including reef slopes with high complexity, or ii) reefs  
562 where the underlying complexity is not so reliant on the accretion of reef by living  
563 corals (e.g. granitic reefs) (Harris et al. 2014). Management should also reduce  
564 activities that directly damage reef structural complexity or coral functional  
565 diversity, such as destructive fishing gears (dynamite, drag nets, some traps),  
566 physical damage by tourists, and boat anchoring. Here, we have highlighted the  
567 utility of a simple and standardized methodology for assessing large-scale patterns  
568 reef complexity, as well as the need to understand the subtler effects of hard coral  
569 traits and diversity, to meet the future challenges of monitoring a changing  
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571

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582

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799 **FIGURES**

800 **Figure 1** Map of 157 coral reef study sites surveyed between 2010 and 2013 in the  
801 Seychelles, Maldives, Chagos Archipelago and Australia's Great Barrier Reef.

802 Underwater visual censuses of both benthic and fish assemblages occurred at each  
803 site and points are slightly jittered to reveal sampling effort.

804

805 **Figure 2** Benthic characteristics explain variation in reef fish assemblages. Multi-  
806 model averaged parameter coefficients and 95% confidence intervals are shown for  
807 (a) reef fish abundance, (b) biomass and (c) species richness. Positive coefficients  
808 indicate a positive relationship between coral and fish characteristics, and negative  
809 coefficients indicate a negative relationship. (d), (e), (f) The relationships between  
810 structural complexity and reef fish abundance, biomass and diversity, respectively.  
811 Blue lines are linear model fits and red lines are LOESS locally weighted smoothers  
812 with standard error for each. Shaded points show significant predictors of reef zone  
813 and management, as labeled in each legend.

814

815 **Figure 3** Influence of structural complexity and coral traits on the functional  
816 structure of reef fish assemblages: a) corallivores, b) herbivores, c) invertivores, d)  
817 mixed-diet feeders, e) piscivores and f) planktivores. Model-averaged coefficients  
818 are shown with 95% confidence intervals.

819

820 **Figure 4** Structural complexity is predicted by coral traits and life histories. (a)

821 Multi-model averaged parameter estimates and 95% confidence intervals for

822 predictors of structural complexity. (b) Relationships between significant coral  
823 characteristics and structural complexity; blue lines are linear model fits and red  
824 lines are LOESS locally weighted smoothers with standard error. The fit in the  
825 bottom-right plot between coral cover and structural complexity is from model  
826 results presented in Appendix 3.  
827

828 **Table 1** Structural complexity and coral assemblage variables of total cover, richness and functional diversity, life histories,  
 829 and community-weighted trait values considered as predictors of reef fish abundance, biomass and species richness. A  
 830 description and justification is provided for each variable, as well as the Variance Inflation Factor (VIF) used to assess  
 831 independence of variables.

Group	Variable	Description	VIF	Justification
Structural complexity	Habitat complexity	A visual score from 0 (flat) to 5 (highly complex)	1.60	More complex reefs offer greater structure for reef fishes.
Coral cover	Hard coral cover, %	Total % cover of live hard corals	>5	Reefs with higher cover of hard corals provide more habitat for reef fishes. Coral cover models are presented in Appendix 3 given high multicollinearity with life histories.
Richness and diversity	Genera richness	Number of hard coral genera	4.69	Assemblages with greater hard coral richness and functional diversity are hypothesized to provide more functional resources that can be used by reef fishes. Greater habitat diversity typically supports a greater diversity of fishes because there are more available niches.
	Functional richness	Number of functional groups of hard corals	>5	
	Rao's Functional diversity, Q	Abundance-weighted variance of the dissimilarities between all hard coral species pairs in multivariate functional space	1.67	
Life history <sup>1</sup>	Competitive, %	Absolute % cover of hard corals in competitive life history	2.87	Coral life histories are a trait-based groupings of species that are proposed to describe community successional patterns and responses to disturbances; we hypothesize that life histories associated with more disturbed environments can influence reef fish communities. For example, coral life history traits relate to disturbance response of corals and will influence response of different fish functional groups based on their susceptibility to disturbance
	Stress tolerant, %	Absolute % cover of hard corals in stress-tolerant life history	4.49	
	Generalist, %	Absolute % cover of hard corals in generalist life history	2.10	
	Weedy, %	Absolute % cover of hard corals in weedy life history	2.42	
Coral traits <sup>1</sup>	Branching	Mean value of branching trait (0 - not branching, 1 - branching), weighted by abundance, across all species present at each site	3.01	Morphological traits can influence the size, and shape of habitat refugia for fishes. For example, branching morphologies provide fine-scale structural complexity for small-bodied fishes, and for fishes specialized on live coral for habitat or diet (e.g., corallivores).
	Growth rate	Mean value of growth rate trait (linear extension, mm year <sup>-1</sup> ), weighted by abundance, across all species present at each site	>5	Coral assemblages with fast-growing corals might provide more structure and living coral for reef fishes.
	Maximum colony size	Mean value of maximum colony size trait (cm), weighted by abundance, across all species present at each site	3.36	Larger colonies provide more space and living cover that can be used by reef fish assemblages by providing more structural complexity and shelter space.
	Brooding	Mean value of brooding trait (0 - not brooding, 1 - brooding), weighted by abundance, across all species present at each site	1.86	Coral assemblages with brooding corals suggest a more disturbed or opportunistic community that provide less suitable habitat for reef fishes. Reproductive traits might also influence the availability of food from propagules or polyps.
	Fecundity	Mean value of fecundity trait, weighted by abundance, across all species present at each site	2.22	Coral assemblages with more fecund species may be able to persist or recover from disturbances to maintain live coral habitat for reef fishes. More fecund corals might also influence the availability of food from propagules or polyps.

832 <sup>1</sup>Life history classifications and trait values are provided in Table S1.

833 **Table 2** Top models describing reef fish assemblages, a) total abundance, b) biomass and c) species richness. Check marks  
834 indicate presence of variables in the 95% top model candidate set. Model characteristics (degrees of freedom, df; log  
835 Likelihood, logLik; AIC scores corrected for small sample sizes, AICc; and model weight, Weight) are also presented for each  
836 model.

Rank	Depth	Reef zone	Management	Complexity	Genera richness	aits	Coral life histories
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839 **Table 3** Top models describing structural complexity of 157 sites in Seychelles, Maldives, Chagos and the Great Barrier Reef.  
840 Check marks indicate presence of variables in the 95% top model candidate set. Model characteristics (degrees of freedom, df;  
841 log Likelihood, logLik; AIC scores corrected for small sample sizes, AICc; and model weight, Weight) are also presented for  
842 each model.

Rank	Depth	Reef zone	Management	Diversity Genera richness	Coral life histories
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845 **ELECTRONIC SUPPLEMENTARY MATERIAL**  
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847 **Appendix 1.** Sensitivity analysis of survey methods.  
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849 **Appendix 2.** Description of method to visually estimate structural complexity.  
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851 **Appendix 3.** Model comparisons using total coral cover.  
852  
853 **Appendix 4.** Multi-model analysis of small fish abundance.  
854  
855 **Appendix 5.** Analysis of six reef fish functional groups.  
856  
857 **Appendix 6.** Comparison across marine reserves and fished reefs.  
858  
859 **Table S1.** List of coral genera with life history classifications and trait values.