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

Introduction

Scleractinian corals – the foundation species of tropical reef ecosystems – have long

been recognized to provide essential habitat for reef associated organisms

(Luckhurst and Luckhurst 1978; Roberts and Ormond 1987; Stella et al. 2011).

Similarly, structural complexity, defined as the physical three-dimensional

configuration of a reef, can shape the abundance and diversity of reef fish

assemblages across both large and small spatial scales (McCormick 1994; Nash et al.

2012; Ferrari et al. 2016). Several ecological hypotheses are proposed to underlie

these relationships, notably that structural complexity and habitat diversity can

mediate competition and predation, and facilitate co-habitation of an increased

number of species (Hutchinson 1959; Hixon and Beets 1993; Beukers and Jones

1997).

Structural complexity is often positively associated with abundance and

diversity of fishes across both temperate and tropical ecosystems (Friedlander et al.

2003; Graham and Nash 2013). Moreover, reductions in structural complexity and

habitat diversity can result in reduced abundance, local extinctions, diversity loss

(Graham et al. 2006; Holbrook et al. 2015; Newman et al. 2015), and declining

fisheries productivity (Rogers et al. 2014); all outcomes with profound implications

for reef biodiversity and associated ecosystem services.

Despite important relationships between structural complexity and reef

fishes, coral reef monitoring programs typically focus on measuring total live cover

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^{-1}), 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^2/replicate); all other locations used four replicate 50 m x 5 m

187   belt transects (250m^2/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^2/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^2 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 $$\text{Fish response}_{ij} = \beta_0 + \beta_1 \times \text{Reef zone}_{ij} + \beta_2 \times \text{Depth}_{ij} + \beta_3 \times \text{Management}_{ij}$$

253 $$+ \beta_4 \times \text{Complexity}_{ij} + \beta_5 \times \text{GeneraRichness}_{ij} + \beta_6 \times \text{FunctionalRao}_{ij}$$

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 $$+ \varepsilon_{ij}$$

258 $$\varepsilon_{ij} \sim N(0, \sigma^2_l) \; l = \text{Management},$$

259 $$\varepsilon_{ij} \sim N(0, \sigma^2_m) \; m = \text{Fish Method},$$

260 $$\varepsilon_{ij} \sim N(0, \sigma^2 \times |\text{Complexity}|^{2\delta})$$

261 Prior to analysis, all input variables were centered to a mean of zero and

262 standardized to a standard deviation of ± 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$_c$) (Akaike 1974). Within a

267 top model set of 4 ΔAIC$_c$ 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:

282 $$\text{Complexity}_{ij} = \beta_0 + \beta_1 \times \text{Habitat}_{ij} + \beta_2 \times \text{Depth}_{ij} + \beta_3 \times \text{Management}_{ij}$$

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 $$+ \beta_{11} \times \text{Competitive}_{ij} + \beta_{12} \times \text{Generalist}_{ijk} + \beta_{13} \times \text{StressTolerant}_{ik} + \beta_{14} \times \text{Weedy}_{ij}$$

287 $$+ \varepsilon_{ij}$$

288 $$\varepsilon_{ij} \sim N\,(0, \sigma^2_l)\ l = \text{Management},$$

289 $$\varepsilon_{ij} \sim N\,(0, \sigma^2_m)\ m = \text{Coral Method}$$

290 As described above, all input variables were centered and standardized to a mean of

291 zero ± 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

14

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 'veneer'

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

570   ecosystem.

571

572   **Acknowledgements**

582

583

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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[1]	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[1]	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-1), 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 [1]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.

						aits	Coral life histories		
Rank	Depth	Reef zone	Management	Complexity	Genera richness				

837
838

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		Coral life histories
					Genera richness		

843
844

845   **ELECTRONIC SUPPLEMENTARY MATERIAL**

846

847   **Appendix 1.** Sensitivity analysis of survey methods.

848

849   **Appendix 2.** Description of method to visually estimate structural complexity.

850

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**.**