Relationships between structural complexity, coral traits, and reef fish assemblages

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Abstract

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

Keywords: Habitat diversity, species traits, functional ecology, reef architecture, Scleractinian corals, coral reef fish
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
cover and reef fish assemblages have been weaker than structural complexity 
(Holbrook et al. 2008; Wilson et al. 2012), field experiments suggest that 
microhabitat (i.e., coral) diversity and some coral species can have a positive effect 
on fish diversity and community structure (Messmer et al. 2011; Holbrook et al. 
2015). Recently, trait-based approaches have outlined important characteristics of 
coral assemblage beyond total coral cover or taxonomic composition (Darling et al. 
2012; Madin et al. 2016a,b), which may provide insights for predicting the structure 
and diversity of reef fish communities. Traits that describe coral morphology, 
growth rate and colony size may be expected to predict structural complexity, and 
thus the structure and composition of fish assemblages. As such, coral traits may 
provide a means of quantifying structural complexity and predicting fish 
assemblage properties from benthic surveys where direct measures of 
macrocomplexity were not taken, particularly in combination with the availability of 
open-access trait information (Madin et al. 2016a,b). For example, traits that 
describe branching, corymbose or plating growth forms can provide keystone 
structures for reef fishes, which can preferentially select specific structural traits of 
corals for shelter (Noonan et al. 2012; Kerry and Bellwood 2012, 2015; Wilson et al. 
2016). A range of other explicit links can be made for other coral traits (Table 1). 
To the best of our knowledge, this study presents the first large-scale 
empirical test of trait-based relationships among coral communities, structural 
complexity and reef fish assemblages. We use surveys across a large gradient of fish 
biomass in the Indian and Pacific Oceans ranging from exploited sites to those 
within one of the world’s most pristine reef systems, the Chagos archipelago
(Graham and McClanahan 2013). Our objectives were to, 1) evaluate which aspects of the physical and biological characteristics of benthic habitats best explain the structure of reef fish assemblages, in particular how well do coral traits describe fish assemblages relative to physical measures of reef structure, and 2) investigate the relationships between hard coral cover, life histories and species traits with structural complexity.

Methods

Study sites

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

Coral assemblages

Coral assemblages were surveyed using two methods: four x 50 m point intercept transects in Chagos, Maldives and Australia, and eight x 10m line intercept transects in the Seychelles. For point intercept transects, the substrate directly below the transect tape was surveyed every 50 cm. For line intercept transects, the length of
each substrate type was measured along the entire 10 m distance. For each method, we recorded major benthic categories (e.g., hard coral, soft coral, sand, rubble, pavement, algae, sponge, etc.) and identified hard corals to genus and growth form using standard morphological genus names. These methods are typically comparable (Facon et al. 2016) and here, we directly compared these methods by conducting a sensitivity analysis where we re-ran our entire analysis without the line intercept transects from the Seychelles and reached similar overall conclusions (see Appendix 1).

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

We derived 17 metrics of coral communities based on benthic surveys, including total cover of scleractinian corals, genera richness, percent cover of life
histories, and abundance-weighted trait means and functional diversity (Table 1). Total coral cover was estimated as the average percent of living hard coral at each site, and genera richness was estimated as the average number of coral genera on replicate transects. Richness was estimated from raw estimates and not adjusted by rarefaction after a post-hoc sensitivity analysis of two underwater survey methods revealed similar conclusions (Appendix 1). Life histories were evaluated based on the abundance (percent cover) of four life-history groups – competitive, stress-tolerant, weedy and generalist corals – proposed by Darling et al. (2012), which have revealed community shifts in response to various disturbances on coral reefs (Darling et al. 2013; Graham et al. 2014; Sommer et al. 2014). The functional structure of coral assemblages was evaluated by five traits that define the life histories reported in Darling et al. (2012): colony growth form (branching, plating or domed), maximum colony size, growth rate (measured as annual linear extension, mm year⁻¹), reproductive mode (brooding or broadcast spawning) and fecundity. These five coral traits were selected because they had tangible links to reef fish assemblages; see Table 1 for detailed justification. A full list of observed hard corals, growth forms and their associated traits can be found in Supporting Table S1; trait information is also freely available online at https://coraltraits.org (Madin et al. 2016a). To estimate genus-level trait values, we averaged available trait information for species that occurred in the appropriate Indo-Pacific faunal province, based on Keith et al. (2013) (Africa-India province: Chagos, Maldives and Seychelles; Australian province: Great Barrier Reef). For categorical traits (colony growth form and reproductive mode), we calculated the proportion of species in
each genus with the trait (see Table S1). Six genera (*Heliopora, Millepora, Oulaphyllia, Polyphyllia, Tubastrea, Tubipora*) were removed from life history and trait analyses because of limited trait information (and these genera had limited abundances within our surveyed coral communities).

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

**Reef fish assemblages**

We estimated the density and individual sizes of all species of diurnally active, non-cryptic, reef associated fish >8 cm total length at each site using two comparable...
methods. In the Seychelles, eight replicate 7 m radius point counts were conducted at each site (154 m²/replicate); all other locations used four replicate 50 m x 5 m belt transects (250 m²/replicate) for large and mobile fishes, while smaller and site-attached, territorial species (e.g., pomacentrids) were recorded using four replicate 50 m x 2 m belt transects (100 m²/replicate). For each transect, we calculated the total numerical abundance, biomass and species richness of reef fish assemblages and averaged these values at each site. All estimates were standardized to estimates/250m² for comparison across sites. As described in the benthic analyses, we conducted a sensitivity analysis to account for these different methodologies by re-running analyses with and without the Seychelles dataset, which revealed very similar findings to the full dataset analysis; while there is some influence of survey methods on the list of variables in the top models, overall our main findings and conclusions are supported (Appendix 1). We also included fish method (point count vs. belt transect) as a variance-covariate in the model framework to account for uneven variation across methods (see Data Analysis below). Total reef fish abundance was strongly correlated to the numerical abundance of small fish (< 20 cm; general linear model $R^2 = 0.85$, $p < 0.001$), and we modelled both total abundance and the abundance of small fish < 20 cm in separate analyses. This allowed us to model the abundance of both the overall fish assemblage and juvenile or small-bodied fish that are often more associated with the reef habitat (Beets and Hixon 1989; Bergman et al. 2000; Graham et al. 2007; Wilson et al. 2010). Reef fish biomass was calculated using standard length-weight conversions and diversity was estimated from species richness as the total number of species observed at each site.
Fish species were assigned to the following trophic (feeding) groups, following Graham et al. (2006): corallivores, herbivores, invertivores, mixed-diet feeders, piscivores and planktivores. The link between these feeding groups and specific characteristics of the coral assemblage may be expected to be stronger than for total biomass.

Data analysis

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

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

For the analysis of reef fish assemblages, we applied the following model
structure to reef fish abundance, biomass, species richness and trophic groups:
Fish response\(_{ij}\) = \(\beta_0 + \beta_1 \times \text{Reef zone}_{ij} + \beta_2 \times \text{Depth}_{ij} + \beta_3 \times \text{Management}_{ij}\) + \(\beta_4 \times \text{Complexity}_{ij} + \beta_5 \times \text{GeneraRichness}_{ij} + \beta_6 \times \text{FunctionalRao}_{ij}\) + \(\beta_7 \times \text{CoralBranching}_{ij} + \beta_8 \times \text{CoralMaxSize}_{ij}\) + \(\beta_9 \times \text{CoralBrooding}_{ij} + \beta_{10} \times \text{CoralFecundity}_{ij}\) + \(\beta_{11} \times \text{Competitive}_{ij} + \beta_{12} \times \text{Generalist}_{ijk} + \beta_{13} \times \text{StressTolerant}_{ik} + \beta_{14} \times \text{Weedy}_{ij}\) + \(\varepsilon_{ij}\) 

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

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

\(\varepsilon_{ij} \sim N(0, \sigma^2 \times |\text{Complexity}|^{28})\) 

Prior to analysis, all input variables were centered to a mean of zero and standardized to a standard deviation of ± 1, in order to allow for direct comparisons of variable effect sizes (in R, function ‘rescale’ in package arm; Gelman 2008). For each fish response, we evaluated 3473 models by completing every combination of variables (up to 5 variables per model) and comparing models using Akaike’s Information Criteria corrected for small sample size (AIC\(_c\)) (Akaike 1974). Within a top model set of 4 \(\Delta\text{AIC}\(_c\) of the best model, we calculated model-averaged coefficients and 95% confidence intervals; significant coefficients were identified from confidence intervals that did not overlap zero. We also calculated the variable importance for each coefficient as the sum of Akaike weights across all models, which provided a rank for each variable, where a relative variable importance of 1.0 identifies the highest ranked input variable (Burnham and Anderson 2002). For model validation we assessed the heterogeneity and normality of residuals across the top 95% set of candidate models. We fit all models in the package nlme (Pinheiro
et al. 2015) with multi-model averaging using the package *MuMin* (Bartoń 2016); all analyses were conducted in R (R Core Team 2015).

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

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

\[ + \beta_4 \times \text{GeneraRichness}_{ij} + \beta_5 \times \text{FunctionalRao}_{ij} \]

\[ + \beta_7 \times \text{CoralBranching}_{ij} + \beta_8 \times \text{CoralMaxSize}_{ij} \]

\[ + \beta_9 \times \text{CoralBrooding}_{ij} + \beta_{10} \times \text{CoralFecundity}_{ij} \]

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

\[ + \epsilon_{ij} \]

\[ \epsilon_{ij} \sim N(0, \sigma^2_l) \quad l = \text{Management}, \]

\[ \epsilon_{ij} \sim N(0, \sigma^2_m) \quad m = \text{Coral Method} \]

As described above, all input variables were centered and standardized to a mean of zero ± 1 standard deviation prior to analysis, and we conducted the same multi-model inferences using Akaike’s information criteria.

**Results**

Structural complexity and reef zone were the strongest predictors of reef fish abundance, biomass, diversity and trophic structure across ~38,000 mixed-effects models. Structural complexity was a consistently top-ranked predictor in all models of reef fish assemblages (i.e., with a maximum relative variable importance of 1.0 in
all model comparisons (Table 2; Appendices 3-6). Characteristics of reef zone and depth also revealed high variable importance for abundance and diversity, but not biomass; slope and crest zones were typically associated with more abundant and diverse reef fish communities than reef flats (Table 2; Fig. 2a-c).

Management (marine reserve vs. open access), coral cover and genera richness, functional diversity, species traits of colony size and branching and some life histories were also associated with different characteristics of reef fish assemblages, including the abundance of small fishes and trophic groups (Table 2; Fig. 2; Fig. 3; Appendices 3-6). Total reef fish abundance decreased with depth and functional diversity, and increased with more complex habitats, cover of stress-tolerant corals and slope zones (Fig. 2a); these patterns were consistent for the abundance of smaller fish < 20cm, which also included weaker effects of life histories, coral traits, genera richness and management variables in the top models (Appendix 4), although complexity only appeared in two of the top 11 models for smaller fish abundance and had a lower relative importance than aforementioned variables. Reef fish biomass increased with structural complexity within no-take reserves and, across all management types, with greater cover of stress-tolerant corals, and decreased cover of weedy corals (Fig. 2b). Species richness was greater at sites within slope and crest habitats, with higher complexity, and characterized by larger maximum colony size. In addition, a suite of life histories, traits, depth and management had weaker influences, i.e., with 95% confidence intervals overlapping zero and lower relative variable importance (Table 2; Fig. 2c). Overall, total abundance and biomass were predicted by fewer variables (5-6 in top models) than
the abundance of smaller fish and diversity, which included 15 variables in each top model set (Appendix 4).

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

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

Structural complexity was predicted by a large suite of benthic and habitat characteristics, including hard coral traits and life histories (Fig. 4). Habitat and the abundance of competitive, stress-tolerant and generalist life histories, genera richness, and traits of colony size, branching and fecundity were the strongest predictors of structural complexity and had the highest relative variable importance in the top 95% model set after evaluating ~3,000 mixed-effects models (Fig. 4, Table...
Structural complexity was typically higher on the reef slope and crest than reef flat and increased with percent cover of competitive and generalist corals, genera richness, and maximum colony size; structural complexity was lower on reefs with a high abundance of corals with branching traits and high fecundity (Fig. 3b). Coral cover was also a significant and positive predictor of structural complexity; sites with higher coral cover were associated with higher structural complexity (Appendix 3).

Discussion

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

The consistent influence of structural complexity and reef zone emphasize the importance of both living and non-living components of the reef that can structure reef fish assemblages. For examples, we show that the living ‘veneer’ provided by live hard corals and their associated traits, diversity and life histories can also influence reef fish assemblages and contributes critically to structural complexity. Interestingly, different characteristics of the coral assemblage contributed to different components of the reef fish assemblage. Coral genera richness and functional diversity appeared in the top model sets for total biomass and diversity, the abundance of small fish, and the biomass of herbivores, piscivores and planktivores, yet were mainly weak variables compared to the influence of complexity and habitat. Similarly, coral life histories and traits influenced total abundance, biomass and diversity, the abundance of small fish, and the biomass of corallivores, mixed-diet feeders, piscivores and planktivores but were also typically weaker predictors (Figs. 2-3, Appendices 4-5). Thus, we conclude that the mechanistic hypotheses that coral diversity, life histories and traits support the structure of reef fish assemblages is only weakly supported (e.g., Table 1), compared to the stronger influences of overall structural complexity and reef zone. It should be noted, however, that the reef fish community was only surveyed >8cm in length. It is possible that smaller fishes would show a stronger relationship with some coral growth forms, such as branching corals.
We also found that some components of reef fish assemblages were influenced by more variables than others: notably species richness, the abundance of smaller individuals (between 8 and 20cm) and the biomass of piscivores and planktivores, with >10 variables in the top model set (Fig. 2-3, Appendix 4). This suggests that different types of living corals and their traits influence different components of reef fish assemblages, as well as provide important habitat for the abundance of all fishes and smaller juvenile fish recruits even when adults of their species may have less affinity for live corals (Jones et al. 2004). Clearly, there are many complex and indirect interdependencies between reef corals and reef fishes that require further investigation (Pratchett et al. 2015), and a combination of structural complexity and living corals is likely required for optimal reef fish productivity and diversity.

Overall, the strong influence of seascape-level structural complexity on reef fish assemblages may be because this index integrates both living hard corals and non-living features of the reef matrix such as caves, crevices or overhangs that can reflect reef growth and erosion processes accumulated over decades, centuries or even millennia (Kleypas et al. 2001; Appendix 2). Thus, the reef matrix can provide some resilience to disturbances that directly confer mortality to living corals (e.g., bleaching and outbreaks of crown-of-thorns starfish), which may also explain why fish diversity can be maintained following extensive coral mortality on inherently complex reefs (Wilson et al 2009; Graham et al. 2015). However, we have shown that various aspects of the living corals are critical to providing structural complexity, and likely maintaining it in the long run. However, the seascape metric
of structural complexity we used does not capture small-scale complexity, such as
the presence of small holes <10cm (Wilson et al. 2007), and our surveys focus on
fish > 8cm, which limits our ability to make inferences about the how smaller fish
use finer-scale structural complexity (e.g., smaller spaces within branching coral
colonies).

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

Here, our analysis of reef fish assemblages focused on site-level variables of
habitat zonation and exposure and not broad biogeographic gradients of wave
exposure or other environmental variables (e.g., currents, bleaching or cyclone
disturbances). For example, wave-induced water motion and flow velocity has been
shown to structure the distribution and functional structure of reef fishes on Lizard
Island (Fulton & Bellwood 2005). Similarly, our correlative study did not consider
how reef fish behavior – e.g., swimming ability and the use of flow or habitat refuges
might affect these patterns (Johansen et al. 2008). However, our findings are in agreement with experimental studies on how reef fish use benthic habitat space, for example the finding that *Acropora* table corals can provide keystone structure for large reef fishes (Kerry & Bellwood 2012; 2015) and field observations that show tight links between specific coral and fish species (Cocker et al 2014). Clearly, controlled experimental studies will be necessary to understand the relationships between coral traits, life histories and diversity that we have investigated here using field-based surveys and correlative analyses.

Hard coral assemblages strongly influenced structural complexity – sites with higher coral cover, greater genera richness, more abundant competitive and generalist life histories, and traits of larger colony sizes and higher growth rates were associated with more complex reefs (Table 3; Fig. 4; Supporting Appendix 3). Surprisingly, the abundance of corals with branching traits was negatively associated with structural complexity (Fig 3). This is a contrasting finding to studies that have found a positive association between the abundance of branching corals and fish assemblages via structural complexity (Chabanet et al. 1997; Messmer et al. 2011; Graham and Nash 2013). This may, perhaps, be because the refuge spaces associated with many fine branching corals are small (<10cm) and this scale of complexity is not well captured by the visual assessments of structural complexity used here (Wilson et al. 2007). In addition, the dominance of corals with branching traits may also create a homogeneous habitat that might reduce the overall structural complexity of a reef. Alternatively, coral identities (i.e., specific genera) or life histories may be a better predictor of structural complexity than the individual
coral traits investigated in this analysis. For example, the cover of competitive life histories (typically branching and plating acroporiids, Darling et al. 2012) was positively associated with structural complexity, as was the number of coral genera. Previous studies have also found strong relationships between specific genera with structural complexity; for example, large, massive *Montastrea* (now *Orcibella*) colonies are associated with greater structural complexity (Alvarez-Filip et al. 2011) while the cover of branching *Pocillopora* was negatively related to reef complexity (Perry et al. 2015). However, as the new systematics of Scleractinia continue to inform and revise morphological classifications (e.g., Kitiha et al. 2016), trait selection and inference must carefully consider how traits are matched to genera observed on monitoring surveys.

While structural complexity and reef zonation are known to be major drivers of reef fish assemblages (Wilson et al. 2009; Graham and Nash 2013), here we show that coral traits and diversity can also have subtle effects on these relationships, as well as being key variables in determining structural complexity. This suggests that the long term maintenance and production of future structural complexity on carbonate reefs will rely on living hard corals continuing to build the carbonate framework of reefs since dead corals inevitably break down and erode. Furthermore, this emphasizes the importance of past disturbance histories and recovery trajectories, particularly as disturbed coral assemblages shift in composition towards smaller weedier or opportunistic species that may provide less complexity overall (Darling et al. 2013; Alvarez-Filip et al. 2013).
As trait-based approaches move to advance coral reef science (Madin et al. 2016a,b), our study highlights two important caveats and considerations for future trait-based investigations. First, coral traits may have weak associations with reef fish assemblages, even if these traits are mechanistically associated with ecosystem processes of interest (e.g., growth forms, colony size or growth rates). Here, the five traits used in this analysis had general relevance for fish community structure, although considering different traits, such as inter-colony volume, actual colony size, or volume under colonies, may have resulted in stronger relationships and different conclusions. Traits might also be explicitly tied to reef fish processes through specific links to energy production or shelter provisioning, however empirical data on these processes is typically limited and may require additional experimental (e.g., Kerry & Bellwood 2012; 2015) or modeling approaches (e.g., biomass spectrum models or size-based theory; Trebilco et al. 2013). Second, most species-level coral trait information is largely available only as global averages, which does not reflect regional or intra-specific variation in coral traits. Given that intraspecific variation in coral morphology influences associations between fishes and host corals (e.g., Noonan et al. 2012), this will limit the usefulness of trait information when averaged up to the genera level (the common taxonomic resolution of most underwater coral surveys). Here, we used genus-level trait averages estimated from regionally appropriate species lists (the Indo-Pacific faunal provinces of Keith et al. 2013), yet we still find relatively weak associations between traits and coral reef fish assemblages. Evaluating the coral traits of specific colonies (vs. species or genus-level averages) may yield stronger relationships, although this
requires significantly more field effort which is logistically challenging for regional or global comparisons (Coker et al. 2014). However, we also find that simple life history groups based on species traits (from Darling et al. 2012) are useful predictors of structural complexity, which suggests that even coarse groupings of life history traits may have some utility in describing reef functions, such as structural complexity and the trophic structure of reef fish assemblages. Overall, the availability of new, open-access databases can aggregate and provide trait information online to test these hypotheses in the future (Madin et al. 2016a).

Conclusions

An obvious symptom of reef degradation is the transition towards net erosion, due to declines in reef accretion caused by declines in abundance and/or growth of calcifying organisms, and especially scleractinian corals (Kleypas et al. 2001; Alvarez-Filip et al. 2009; Perry et al. 2013). Maintaining key demographic processes of coral growth and carbonate accretion will be increasingly important to maintain structural complexity and habitat diversity for reef fishes and invertebrates. However, this is a challenging recommendation for managers and decision makers in the context of increasing local stressors, ocean warming and acidification, and sea level rise (Hoegh-Guldberg et al. 2007; Manzello et al. 2008; DeCarlo et al. 2015). Identifying relationships and thresholds between key demographic processes and specific management actions (like water clarity or the biomass of herbivorous fishes) remains a key focus for future research. Furthermore, ongoing coral community shifts towards stress-tolerant, weedy and
low complexity species may superficially maintain coral cover while silently
masking declines in complexity, coral accretion, and ecosystem services (Alvarez-
Filip et al. 2013; Rogers et al. 2014).

Monitoring reef condition requires indicators that capture key processes and
early signs of decline (Hughes et al. 2010; McClanahan et al. 2011). Here, we show
that seascape visual estimates of structural complexity can be easily incorporated
into monitoring and management programs (see Appendix 2 for more details).
Interestingly, this method could also be calculated retrospectively from underwater
images that provide a panoramic view about transects (Wilson et al. 2009), or with
machine-learning methods applied to satellite images or digital reef terrain maps,
which would allow this methodology to scale up beyond SCUBA-based surveys to
larger temporal and spatial scales (e.g., Pittman et al. 2009). For example, including
a panoramic assessment at the start and end of the transect line that includes
geomorphological reef features like caves or overhangs can provide important
assessments of structural complexity relevant to fishes (e.g., Collins et al. 2016).
Further, while our study is based on observations, our results are supported by
experimental studies that have manipulated structural complexity and specific
habitats (e.g., the space below tabulate corals) to reveal the importance of
complexity for reef fishes (Beets and Hixon 1989; Syms and Jones 2000; Gratwicke
and Speight 2005; Kerry and Bellwood 2012, 2015). Overall, incorporating a
standard measure of structural complexity into long-term monitoring programs
may provide useful information on the loss of reef architecture and knock-on effects
for coral reef ecosystems (e.g. Graham et al. 2015).
Continued declines in the three-dimensional complexity and coral diversity of tropical reefs will have consequences for reef fishes, fisheries and the human societies that depend on these ecosystem services (Alvarez-Filip et al. 2013; Hicks & Cinner 2014; Rogers et al. 2014). Here, we highlight the importance of structural complexity as well as the more nuanced and subtle influences of coral traits and functional diversity on reef fishes. Maintaining structural complexity and coral diversity should be a key focus for managers, because it can help reefs recover to a coral-dominated state after mass bleaching (McClanahan et al. 2012; Graham et al. 2015) and supports fish diversity and fisheries productivity (Rogers et al. 2014; Holbrook et al. 2015). Managing for structural complexity may include prioritizing conservation and no-take reserves to, i) reefs with high existing complexity and abundant live corals, such as including reef slopes with high complexity, or ii) reefs where the underlying complexity is not so reliant on the accretion of reef by living corals (e.g. granitic reefs) (Harris et al. 2014). Management should also reduce activities that directly damage reef structural complexity or coral functional diversity, such as destructive fishing gears (dynamite, drag nets, some traps), physical damage by tourists, and boat anchoring. Here, we have highlighted the utility of a simple and standardized methodology for assessing large-scale patterns of reef complexity, as well as the need to understand the subtler effects of hard coral traits and diversity, to meet the future challenges of monitoring a changing ecosystem.

Acknowledgements
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FIGURES

Figure 1 Map of 157 coral reef study sites surveyed between 2010 and 2013 in the Seychelles, Maldives, Chagos Archipelago and Australia's Great Barrier Reef. Underwater visual censuses of both benthic and fish assemblages occurred at each site and points are slightly jittered to reveal sampling effort.

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

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

Figure 4 Structural complexity is predicted by coral traits and life histories. (a) Multi-model averaged parameter estimates and 95% confidence intervals for
predictors of structural complexity. (b) Relationships between significant coral characteristics and structural complexity; blue lines are linear model fits and red lines are LOESS locally weighted smoothers with standard error. The fit in the bottom-right plot between coral cover and structural complexity is from model results presented in Appendix 3.
Table 1 Structural complexity and coral assemblage variables of total cover, richness and functional diversity, life histories, and community-weighted trait values considered as predictors of reef fish abundance, biomass and species richness. A description and justification is provided for each variable, as well as the Variance Inflation Factor (VIF) used to assess independence of variables.

<table>
<thead>
<tr>
<th>Group</th>
<th>Variable</th>
<th>Description</th>
<th>VIF</th>
<th>Justification</th>
</tr>
</thead>
<tbody>
<tr>
<td>Structural complexity</td>
<td>Habitat complexity</td>
<td>A visual score from 0 (flat) to 5 (highly complex)</td>
<td>1.60</td>
<td>More complex reefs offer greater structure for reef fishes.</td>
</tr>
<tr>
<td>Coral cover</td>
<td>Hard coral cover, %</td>
<td>Total % cover of live hard corals</td>
<td>&gt;5</td>
<td>Reefs with higher cover of hard corals provide more habitat for reef fishes.</td>
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<td></td>
<td>Coral cover models are presented in Appendix 3 given high multicollinearity.</td>
</tr>
<tr>
<td>Richness and diversity</td>
<td>Genera richness</td>
<td>Number of hard coral genera</td>
<td>4.69</td>
<td>Assemblages with greater hard coral richness and functional diversity are</td>
</tr>
<tr>
<td></td>
<td>Functional richness</td>
<td>Number of functional groups of hard corals</td>
<td>&gt;5</td>
<td>hypothesized to provide more functional resources that can be used by reef</td>
</tr>
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<td></td>
<td>Rao's Functional diversity, Q</td>
<td>Abundance-weighted variance of the dissimilarities between all hard coral</td>
<td>1.67</td>
<td>Greater habitat diversity typically supports a greater diversity of</td>
</tr>
<tr>
<td></td>
<td></td>
<td>species pairs in multivariate functional space</td>
<td></td>
<td>fishes because there are more available niches.</td>
</tr>
<tr>
<td>Life history¹</td>
<td>Competitive, %</td>
<td>Absolute % cover of hard corals in competitive life history</td>
<td>2.87</td>
<td>Coral life histories are trait-based groupings of species that are</td>
</tr>
<tr>
<td></td>
<td>Stress tolerant, %</td>
<td>Absolute % cover of hard corals in stress-tolerant life history</td>
<td>4.49</td>
<td>proposed to describe community successional patterns and responses to</td>
</tr>
<tr>
<td></td>
<td>Generalist, %</td>
<td>Absolute % cover of hard corals in generalist life history</td>
<td>2.10</td>
<td>disturbances; we hypothesize that life histories associated with more</td>
</tr>
<tr>
<td></td>
<td>Weedy, %</td>
<td>Absolute % cover of hard corals in weedy life history</td>
<td>2.42</td>
<td>disturbed environments can influence reef fish communities. For example,</td>
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<td>coral life history traits relate to disturbance response of corals and will</td>
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<td>influence response of different fish functional groups based on their</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>susceptibility to disturbance.</td>
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<tr>
<td>Branching</td>
<td></td>
<td>Mean value of branching trait (0 - not branching, 1 - branching), weighted</td>
<td>3.01</td>
<td>Morphological traits can influence the size, and shape of habitat refugia</td>
</tr>
<tr>
<td></td>
<td></td>
<td>by abundance, across all species present at each site</td>
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<td>for fishes. For example, branching morphologies provide fine-scale</td>
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<td>structural complexity for small-bodied fishes, and for fishes specialized</td>
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<td></td>
<td>on live coral for habitat or diet (e.g., corallivores).</td>
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<tr>
<td>Growth rate</td>
<td></td>
<td>Mean value of growth rate trait (linear extension, mm year⁻¹), weighted</td>
<td>&gt;5</td>
<td>Coral assemblages with fast-growing corals might provide more structure</td>
</tr>
<tr>
<td></td>
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<td>by abundance, across all species present at each site</td>
<td></td>
<td>and living coral for reef fishes.</td>
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<tr>
<td>Maximum colony size</td>
<td></td>
<td>Mean value of maximum colony size trait (cm), weighted by</td>
<td>3.20</td>
<td>Larger colonies provide more space and living cover that can be used by</td>
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<td></td>
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<td>abundance, across all species present at each site</td>
<td></td>
<td>reef fish assemblages by providing more structural complexity and shelter</td>
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<td></td>
<td>space.</td>
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<tr>
<td>Brooding</td>
<td></td>
<td>Mean value of brooding trait (0 - not brooding, 1 - brooding), weighted</td>
<td>1.66</td>
<td>Coral assemblages with brooding corals suggest a more disturbed or</td>
</tr>
<tr>
<td></td>
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<td>by abundance, across all species present at each site</td>
<td></td>
<td>opportunistic community that provide less suitable habitat for reef fishes.</td>
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<td>Reproductive traits might also influence the availability of food from</td>
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<td></td>
<td>propagules or polyps.</td>
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<tr>
<td>Fecundity</td>
<td></td>
<td>Mean value of fecundity trait, weighted by abundance, across all</td>
<td>2.22</td>
<td>Coral assemblages with more fecund species may be able to persist or</td>
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<td></td>
<td></td>
<td>species present at each site</td>
<td></td>
<td>recover from disturbances to maintain live coral habitat for reef fishes.</td>
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<td>More fecund corals might also influence the availability of food from</td>
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<td></td>
<td>propagules or polyps.</td>
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</tbody>
</table>

¹Life history classifications and trait values are provided in Table S1.
Table 2 Top models describing reef fish assemblages, a) total abundance, b) biomass and c) species richness. Check marks indicate presence of variables in the 95% top model candidate set. Model characteristics (degrees of freedom, df; log Likelihood, logLik; AIC scores corrected for small sample sizes, AICc; and model weight, Weight) are also presented for each model.
Table 3 Top models describing structural complexity of 157 sites in Seychelles, Maldives, Chagos and the Great Barrier Reef. Check marks indicate presence of variables in the 95% top model candidate set. Model characteristics (degrees of freedom, df; log Likelihood, logLik; AIC scores corrected for small sample sizes, AICc; and model weight, Weight) are also presented for each model.
ELECTRONIC SUPPLEMENTARY MATERIAL


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

Appendix 3. Model comparisons using total coral cover.


Appendix 5. Analysis of six reef fish functional groups.

Appendix 6. Comparison across marine reserves and fished reefs.

Table S1. List of coral genera with life history classifications and trait values.