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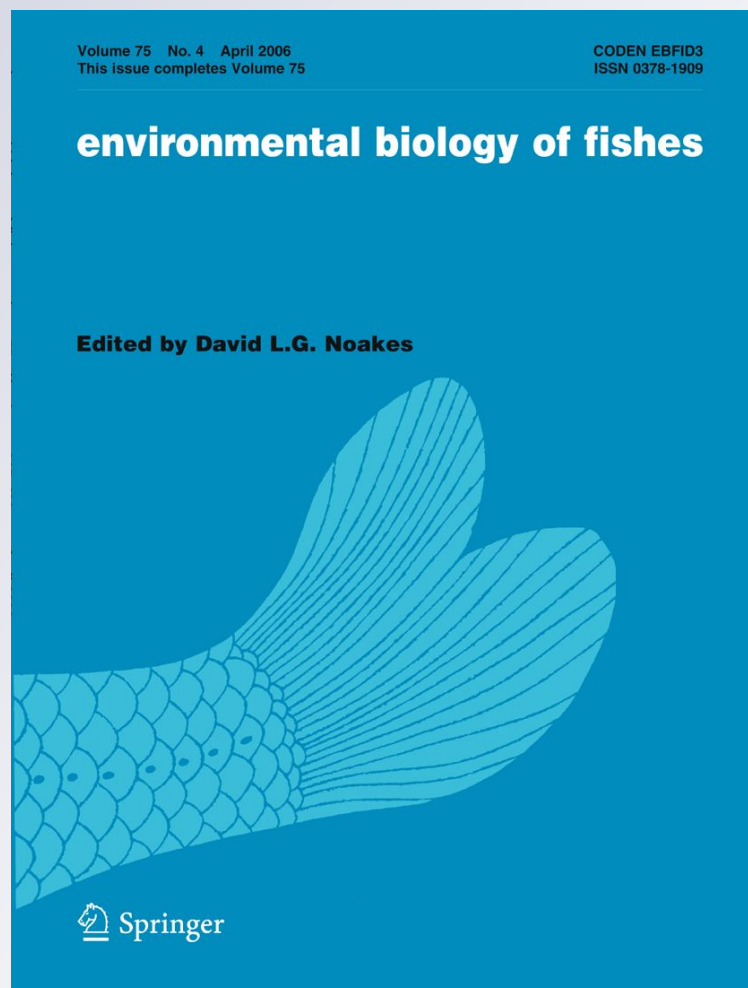
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The effectiveness of different meso-scale rugosity metrics for predicting intra-habitat variation in coral-reef fish assemblages

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Abstract Habitat structure is frequently an important variable affecting species' abundances and diversity, and identifying the key aspects and spatial scales of habitat complexity is critical for understanding the ecology and conservation of a range of communities. Many coral-reef fishes are intimately linked with benthic habitat structure, and previous research has demonstrated rugosity as an important predictive variable of assemblage parameters. However, these studies typically consider rugosity at small scales, amalgamate multiple habitat features, or are semi-quantitative. This study considers meso-scale rugosity (within 51 plots of 25 m² on a Belizean forereef) generated by varying coral densities, heights, and complexities. Seven rugosity metrics were calculated for each plot, and were regressed against each of 11

fish assemblage parameters. Intra-habitat variability of each fish parameter was significantly positively or curvilinearly correlated to at least one metric of meso-scale rugosity, but the metric generating the strongest correlation varied. The abundance of small fishes, and consequently most of the assemblage statistics (e.g., total fish abundance and diversity) were best predicted by the number of tall (>50 cm) corals. The abundance of damselfishes, parrotfish biomass, the abundances of medium-sized and large fishes, and total fish biomass were curvilinearly related to mean coral height. The abundances of wrasses and surgeonfishes were most strongly correlated with the number of corals within a plot. Because coral-generated meso-scale rugosity is an important factor influencing intra-habitat variation in fishes, it should be explicitly considered when investigating fish-habitat relationships and predicting the impacts of coral mortality on ecosystem processes and services.

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Introduction

The quantity and quality of habitat structure are critical influences on the abundance and population dynamics of species in a range of ecosystems (e.g., Bell et al. 1991). Therefore, documenting the most functionally important aspects and spatial scales of

habitat complexity is vital for understanding the ecology and conservation of communities (e.g., Hewitt et al. 2005). On coral reefs, habitat structure has repeatedly been demonstrated as a key factor influencing reef-fish assemblages. For example, coral growth creates small-scale crevices that provide foraging, spawning, and nesting sites (Robertson and Sheldon 1979), affect patterns of recruitment (Sale 1991), can help fishes maintain themselves in high-flow environments (Johansen et al. 2008), and sheltering in refuges reduces the high risk of predation on reefs (Hixon 1991). This multitude of functions for habitat complexity has led to well-established links between the abundance and diversity of reef fishes and coral cover (e.g., Bell and Galzin 1984; Jones et al. 2004) or rugosity (e.g., Luckhurst and Luckhurst 1978; Friedlander and Parrish 1998). Furthermore, following mortality from stressors such as bleaching and hurricanes, loss of coral cover has dramatic effects on coral-associated fish species (Jones and Syms 1998; Jones et al. 2004; Wilson et al. 2006; Pratchett et al. 2008).

Despite numerous studies demonstrating that reef rugosity is an important predictor of the characteristics of reef-fish assemblages, a comprehensive understanding of the importance of different aspects of topographic complexity is still lacking. This limited understanding is largely caused by the use of techniques that are well suited to overall assessments of the complexity of a habitat patch, but do not allow different aspects of rugosity to be resolved. For example, the commonest technique for quantifying rugosity on reefs involves use of a chain, a few metres in length, which is draped across the reef and allows complexity to be expressed as the ratio of chain length to horizontal distance it actually covers across the reef (Risk 1972). Values generated by chain transects are a function of multiple aspects of rugosity including the number of crevices within corals, spaces within the carbonate framework, and the abundance of benthic organisms. Consequently, determining whether each of these aspects contributes equally to the abundances of different fish species is problematic. Similar problems occur when using maximum relief within a sampling unit (Wilson et al. 2007; Harborne et al. 2008b), statistics calculated from profile gauges (McCormick 1994), or metrics of change of height within quadrats (Nanami et al. 2005).

Elucidating the importance of different aspects of reef rugosity is also limited by the majority of studies

considering specific aspects of rugosity, such as the size and abundance of holes in the substratum (Roberts and Ormond 1987; Friedlander and Parrish 1998; Nemeth 1998), are focused on relatively small-scale aspects of habitat complexity. Along with small-scale rugosity on reefs, spatially variable coral recruitment and survival leads to changing densities of colonies across reefs. The influence of this larger-scale complexity on reefs (tens of square metres, subsequently termed 'meso-scale') is poorly understood, but is a potentially important scale of complexity lying between coral colony-scale habitat structure and macro-scale indices of seascape complexity. For example, meso-scale complexity may affect the hunting efficiency of predators that actively chase prey (Eklöv and Diehl 1994), decrease agonistic encounters between territorial and non-territorial species (Levin et al. 2000), and increase fish recruitment rates (Stier and Osenberg 2010). Meso-scale complexity is implicitly measured by the range of visual estimates of overall habitat complexity used by some researchers (Polunin and Roberts 1993; Jennings et al. 1996; Spalding and Jarvis 2002; Russ et al. 2005; Mellin et al. 2007; Wilson et al. 2007; Emslie et al. 2008). However, these techniques are typically semi-quantitative, such as the 6-point scale of Polunin and Roberts (1993). Furthermore, like smaller-scale protocols, these techniques are designed to summarise complexity at a survey site and amalgamate multiple aspects of meso-scale rugosity [but see Gratwicke and Speight (2005) for a meso-scale study considering multiple aspects of complexity]. This mixing of habitat characteristics limits more detailed analyses of the relative effects of factors such as coral colony complexity, density, and size on fish assemblages.

In this study we quantify meso-scale rugosity within 25 m² reef plots using seven different metrics incorporating different aspects of coral density, height, and complexity. This range of metrics is used because of the absence of previous data on this scale of rugosity that could be used for guidance on the most appropriate indices. We then assume that the metrics best reflecting the functional interaction between meso-scale rugosity and reef fishes will be those that have strongest correlations with fish abundances and diversity. This study explicitly examines intra-habitat variability in fish abundances and diversity because there are very clear inter-habitat patterns in fish zonation (Alevizon et al. 1985;

Harborne et al. 2006), which will be correlated with most measures of rugosity. Intra-habitat variation is significant in Caribbean fish assemblages, particularly in the habitat considered here (coral-rich forereef), but is more subtle than inter-habitat variation and less well described (Harborne et al. 2008a). Therefore, we conduct an exacting assessment of the importance of different meso-scale rugosity metrics on fish assemblages. In summary, the two key aims of the study are to conduct exploratory analyses to provide guidance for other researchers wishing to quantify meso-scale rugosity of reefs, and to investigate how meso-scale rugosity affects the intra-habitat variation of reef-fish assemblages. Furthermore, the study aims to complement earlier studies of micro-scale rugosity, and aid building a more holistic understanding of the relationship between the structure of fish assemblages and habitat structure. We hypothesised that the density of tall, complex, reef-building corals within a reef plot would be the most important factor influencing the abundance and diversity of reef fishes.

Methods

Study site

The study was conducted on a section (<3 km) of the Mesoamerican Barrier Reef, just south of Carrie Bow Cay in Belize (16°48.173' N, 88°4.928' W). Using a small section of reef for the entire study minimised the variation in potentially confounding factors such as larval supply and fishing pressure. All surveys were conducted within the species-rich '*Montastraea* reef' habitat (forereef visually dominated by *Montastraea* corals) at a depth of ≈10 m and <100 m from the escarpment. Within this biophysical environment, *Montastraea annularis* is the primary reef-builder in the Caribbean (Weil and Knowlton 1994). Individual *M. annularis* colonies were separated by areas of reef framework covered by a thin layer of carbonate sand and rubble [see Rützler and Macintyre (1982) for a full description of the reefs of this area].

Plot-scale surveys

A total of 51 plots of 5 x 5 m were haphazardly chosen, delineated by tape measures, and their position recorded with a GPS. A plot of 25 m² is appropriate for the

home ranges of fishes less than ~8 cm (Kramer and Chapman 1999). Although 25 m² is smaller than the home ranges of many larger fishes, it captures a scale of rugosity appreciably larger than that quantified by chain transects. We also do not focus on explaining intra-habitat variation in large-bodied, wide-ranging fish families such as groupers, jacks, and snappers. Furthermore, each plot is small enough that two researchers can survey the dimensions of each coral colony and census the fish assemblage in ~20 min, allowing the documentation of multiple replicate plots within a single SCUBA dive. In this study, with the exception of the first dive (one plot), five plots were surveyed during each dive and every plot was a minimum of 25 m away from any other plot. The maximum distance among plots was ~2.6 km.

During a period of 10 min within each plot, all fishes were identified, assigned a life phase (determined by colouration or a size of <4 cm for species without distinct colour phases), counted, and sized to the nearest centimetre. The biomass of each fish was calculated using allometric relationships (Bohnsack and Harper 1988). Following each fish survey, all coral colonies were identified, counted, and their heights recorded. Colony area was strongly positively correlated with colony height (Pearson product-moment correlation coefficient, $r=0.502$, $P<0.001$) and was not considered in this study because coral height is likely to be more functionally important to fishes. For example, there is some evidence that tall colonies provide fishes with a better view of approaching predators (Nemeth 1998). Furthermore, areal data is more time consuming to gather, and the aim was to suggest meso-scale metrics that are relatively easy for researchers to quantify in the field. Finally, each plot was videoed in five, 1 m wide swaths. Subsequently, three 1 m² areas of each plot were analysed with the Vidana software [freely available from <http://www.marinespatialecologylab.org/resources/vidana>] to estimate coral and macroalgal cover.

Meso-scale rugosity metrics

Seven different metrics were developed to quantify meso-scale rugosity (Table 1). 'Complex' corals were defined as those with morphologies offering multiple refuges for fishes, such as *Montastraea annularis* and *Agaricia tenuifolia*, and branching species such as *Acropora cervicornis* and *Porites porites*. 'Simple'

Table 1 Description and characteristics of the seven meso-scale rugosity metrics used in this study

Metric	Characteristics
Mean coral height	Increases with increasing mean coral height, but is independent of coral density or complexity.
Variance of coral height	Increases with increasing variation in coral heights, and will tend to increase with increasing mean height and coral density.
Number of corals	Represents coral density, but is independent of coral heights and complexities.
Number of tall corals (>50 cm)	Incorporates aspects of both coral density and height, but is independent of coral complexities.
Number of complex corals	Represents the density of complex corals that may be particularly functionally important on reefs, but is independent of coral heights.
Sum of coral heights	Incorporates both coral heights and densities, but is independent of coral complexity.
Sum of heights of complex corals	Incorporates both the heights and densities of complex corals that may be particularly functionally important on reefs.

corals were typically those with encrusting or massive morphologies, such as *Agaricia agaricites*, *Diploria strigosa*, and *Montastraea cavernosa* (see Online Resource 1 for the complexity values of all species). Tall corals were defined as those >50 cm, which was 25% of the tallest colony. The metrics were generally significantly correlated with each other (20 of 21 correlations $P < 0.03$, Pearson product-moment correlation coefficients, $0.97 > r > 0.15$, mean 0.70). However, the metrics were not strongly correlated with coral cover (mean Pearson product-moment correlation coefficient = 0.39), demonstrating that they are functionally different assessments of rugosity than a simple measure of the abundance of live corals. Differences between meso-scale rugosity and coral cover can be caused by factors such as a plot being dominated by low-relief corals (high coral cover but low meso-scale rugosity) and disturbances such as bleaching that can dramatically reduce the amount of live coral tissue at a site but have little short-term effect on meso-scale rugosity.

Data analysis

Each metric was regressed against a series of statistics derived from the fish assemblage data. These were four summary statistics: total biomass (log transformed), total abundance, species richness, and Shannon-Wiener diversity. Species richness was calculated using Margalef's species richness: $d = (S-1)/\text{Log}(N)$, where S = the number of species present and N = the number of individuals. Rugosity metrics were also regressed against the abundance of: adult territorial damselfishes (*Stegastes adustus*, *S. diencaeus*, *S. planifrons*,

and *S. variabilis*), surgeonfishes (Acanthuridae), and wrasses (Labridae), and the biomass of parrotfishes (Scaridae, square-root transformed). Territorial damselfishes pugnaciously defend territories against intruders in order to maintain both food resources and egg masses (Robertson 1996), and have been described as keystone species in reef-fish assemblages (Hixon and Brostoff 1983). Surgeonfishes and parrotfishes are key grazers on reefs, reducing the abundances of macroalgae that have a number of detrimental effects on corals (e.g., Burkepile and Hay 2008). The biomass of parrotfishes was used because it is closely correlated to their grazing impact (Mumby 2006). Wrasses are frequently the most abundant family on Caribbean reefs. Finally, each metric was regressed against the abundance of small (1–10 cm), medium (11–20 cm), and large (21–30 cm) fishes to investigate whether particular sizes of fishes were affected by different aspects of meso-scale rugosity.

Linear regression was used for examining the relationship between biomass and fish summary statistics (total biomass, species richness, Shannon diversity, and parrotfish biomass) and each meso-rugosity metric, including quadratic terms to investigate any curvilinear relationships. Although Mantel tests (Mantel 1967) showed no evidence of spatial autocorrelation ($P > 0.05$), the distance between each plot was also included in the regression models to account for any spatial structure in the data. If insignificant ($P > 0.05$), terms were removed (least significant variable first) and then models were compared to ensure that term removal did not lead to a significant increase in deviance, and leading to a minimal adequate model (Crawley 2007). Models for each metric were

compared using coefficient of determination (R^2) values. Because abundance values were count data they were analysed using generalised linear models with Poisson error structures and the log link function. As for the other fish assemblage parameters, linear and quadratic terms and distance were the explanatory variables. However, all models were overdispersed and the Poisson assumptions were replaced with a negative binomial model (Ver Hoef and Boveng 2007). As for the linear regression, terms were removed if not significant and the significance of the removal tested. Models generated from each rugosity metric were compared using the Akaike Information Criterion (AIC, best model has the lowest AIC, Crawley 2007). Despite the multiple regression analyses for each fish assemblage parameter, no corrections were applied to P values because the primary aim of the study was to compare the strengths of the correlations among meso-scale rugosity metrics using R^2 and AIC. Generalised linear models generate measures of null and residual deviance that can be used to calculate a 'pseudo R^2 ' for the model using Eq. 1 (Dobson and Barnett 2008; Zuur et al. 2009). Pseudo R^2 values were calculated for the generalised linear model with the strongest correlation to each fish parameter.

$$\frac{\text{Null deviance} - \text{residual deviance}}{\text{Null deviance}} \times 100 \quad (1)$$

Finally, species-level data for seven of the fish assemblage statistics (biomasses of each species, abundances of each species, abundances of each adult territorial damselfish, abundances of each surgeonfish, and abundance of each small, medium, or large fish) were used for multivariate analyses. Because of their complex life histories, life phase-level data was used for the abundances of each wrasse species and the biomass of each parrotfish species. The BEST routine within the PRIMER software was used correlate the species- or life phase-level data to every combination of the seven rugosity metrics. The optimal combination of rugosity variables was determined by calculating a Spearman rank correlation coefficient (ρ), and calculating its significance using a permutation test.

Results

Coral cover in the plots varied between 1.0 and 25.3%, with a mean of 7.4% (S.E. = 0.8%). The range

of macroalgal cover in the plots was 2.6–37.0% (mean 12.7%, S.E. = 1.0%). Like most reefs in the Caribbean, coral cover has decreased and macroalgal abundance has increased because of a range of stressors including coral bleaching, disease of corals and the herbivorous urchin *Diadema antillarum*, and fishing of key grazers (Gardner et al. 2003). Specifically, reefs in Belize were affected by bleaching episodes in 1995, 1998, and 2005, and by a category 5 hurricane (Mitch) in 1998 (Wilkinson 2008). A 2006 assessment of coral and macroalgal cover in Belize suggested that the national means were 11% and 12% respectively, indicating that the site used for this study is typical of many reefs within the country, and the Mesoamerican region generally (Wilkinson 2008).

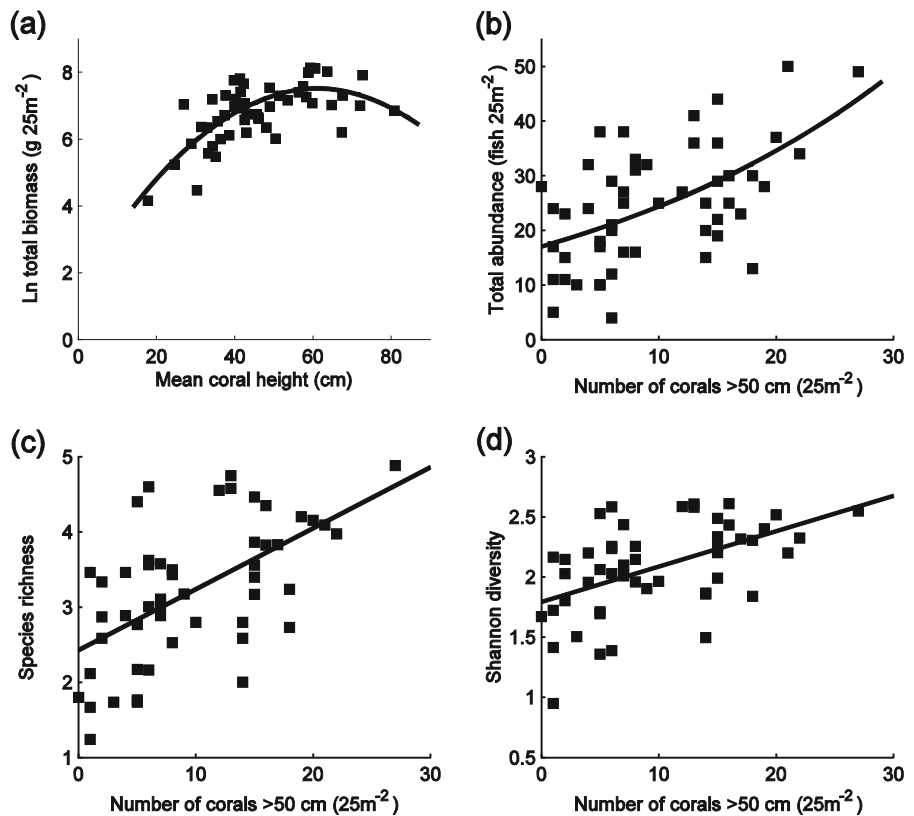
A total of 1450 individuals from 63 species were recorded in the 51 plots (see Online Resource 2 for a list of species and their mean abundances). The most abundant species were *Scarus iseri*, *Stegastes partitus*, *Halichoeres garnoti*, *Stegastes planifrons*, and *Sparisoma aurofrenatum* (≥ 100 individuals). The most abundant families were Pomacentridae (431 individuals), Scaridae (384), and Labridae (349), accounting for >80% all fishes. Small fishes (1080 individuals) were more abundant than medium (261) and large (98) fishes, and an additional 11 fishes were >30 cm.

The 11 strongest relationships between individual fish assemblage parameters and the seven meso-scale rugosity metrics included three different rugosity metrics (Table 2; Figs. 1, 2 and 3; Online Resource 3). Three of the four fish assemblage summary statistics (total abundance, species richness, and Shannon diversity), and the abundance of small fishes, were most strongly correlated with the number of tall coral colonies, and the relationships were positive and linear or slightly curvilinear. In contrast, the biomass of parrotfishes and the abundances of territorial damselfishes, medium-sized fishes, and large fishes were best predicted by a curvilinear relationship to mean coral height. Total biomass, which is dominated by the abundance of larger individuals, also had a strong curvilinear relationship with mean coral height. The best rugosity metric for predicting the abundance of surgeonfishes was the number of corals within the 25 m² plot, and the relationship was curvilinear. Typically, the curvilinear relationships were convex and tending towards an asymptote, or decreasing at

Table 2 Summary of regression analyses between meso-scale rugosity metrics and fish assemblage parameters. For clarity only sign of model coefficients shown, and intercept is omitted. The inter-plot distance term was also not significant ($P>0.05$) in each model has been omitted for clarity. Within cells first sign is DIRECTION OF SIGNIFICANT linear term and second sign is quadratic term. ***= $P<0.001$, **= $P<0.01$, *= $P<0.05$, ns=not significant ($P>0.05$). Figure is coefficient of determination (R^2) or AIC. Figure in parentheses is the pseudo R^2 . Best model is highlighted in bold. Full details of coefficients for best model in Online Resource 3. Multivariate analysis shows metrics chosen by the BEST routine as being the optimal predictors of assemblage structure

	Assemblage data			Family data			Size-specific data			
	Total biomass (g)	Species richness	Shannon diversity	Territorial damselfish abundance	Parrotfish biomass (g)	Wrasse abundance	Surgeonfish abundance	Abundance of small fishes	Abundance of medium-sized fishes	Abundance of large fishes
Mean coral height (MCH)	+ *** - *** 0.50	+ ** - * 0.29	+ ** - * 0.25	+ *** ns 215.75 (0.22)	+ ** - * 0.26	ns ns 301.94	ns ns 158.27	+ ** ns 357.97	+ ** - ** 261.45 (0.21)	+ * - * 182.47 (0.21)
Variance of coral height (VCH)	+ *** - ** 0.41	+ *** ns 0.25	+ *** ns 0.24	+ ** ns 220.75	+ ** ns 0.16	ns ns 301.94	+ * ns 155.47	+ ** ns 358.39	ns ns 270.20	+ ** - * 185.17
Number of corals (NOC)	+ * ns 0.12	+ ** ns 0.18	+ ** ns 0.14	ns ns 227.78	+ * - * 0.15	- ** + * 299.79 (0.11)	+ * - * 154.27 (0.13)	ns ns 363.36	ns ns 270.20	+ * ns 189.53
Number of tall corals (>50 cm) (NTC)	+ *** - * 0.39	+ *** ns 0.34	+ *** ns 0.26	+ *** ns 217.57	+ ** ns 0.16	ns ns 301.94	+ * ns 155.38	+ ** ns 356.69 (0.14)	+ ** ns 263.76	+ ** ns 184.48
Number of complex corals (NCC)	+ ** - * 0.19	+ ** ns 0.13	+ * ns 0.09	ns ns 227.78	+ ** ns ** 0.20	ns ns 301.94	ns ns 158.27	ns ns 363.36	+ * ns 267.99	+ * - * 189.97
Sum of coral heights (SCH)	+ *** - ** 0.43	+ *** ns 0.33	+ *** ns 0.25	+ ** ns 222.75	+ ** ns 0.18	- ** + * 299.95	+ * ns 154.42	+ ** ns 357.64	+ ** ns 265.56	+ *** ns 182.58
Sum of heights of complex corals (SHCC)	+ *** - ** 0.40	+ *** ns 0.29	+ *** ns 0.21	+ ** ns 221.28	+ ** ns 0.17	ns ns 301.94	+ * ns 154.58	- * ns 357.67	+ ** ns 264.25	+ ** ns 185.20
Multivariate analysis (BEST)	ns	MCH NCC -	-	MCH	ns	ns	ns	ns	ns	NCC SCH
		$\rho=0.167$		$\rho=0.139$						$\rho=0.132$
		$P=0.040$		$P=0.040$						$P=0.050$

Fig. 1 Scatter plots of the meso-rugosity metric that had the strongest correlation with (a) log total fish biomass (b) total fish abundance (c) fish species richness and (d) fish Shannon diversity. Regression lines fitted using models described in Online Resource 3, with back-transformation of response data to account for negative binomial error structure where necessary. $n=51$ plots of 25 m²



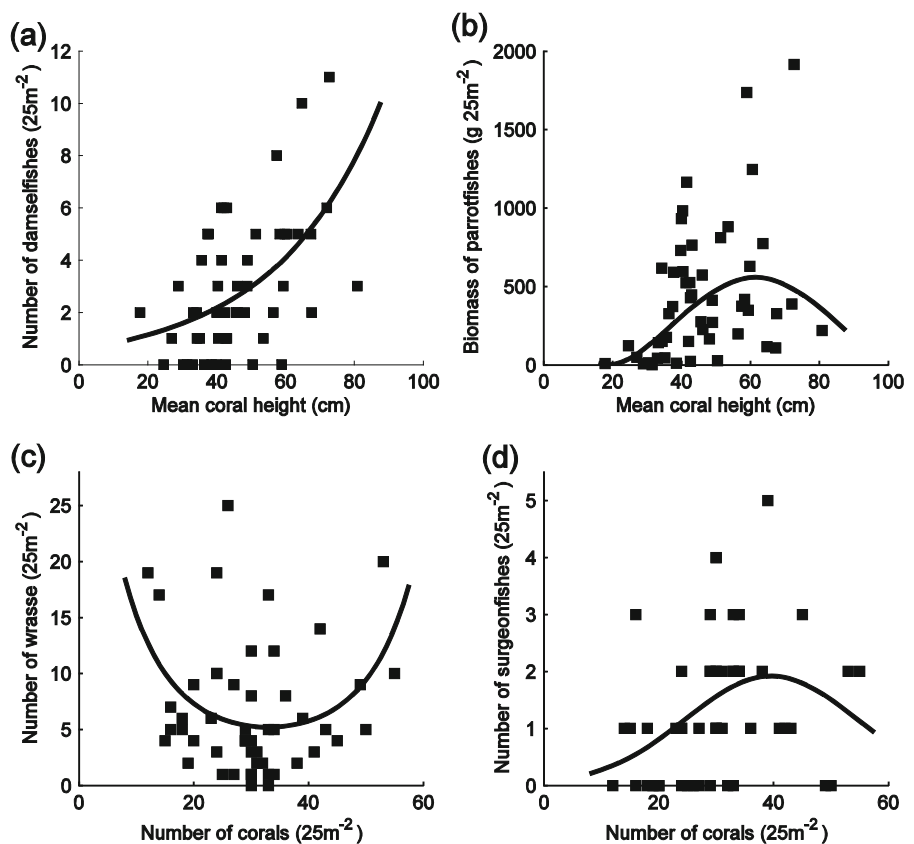
the highest values of meso-scale rugosity for total biomass and the number of medium and large fishes. However, the relationship between the number of damselfishes and mean coral height was a concave curvilinear relationship. More strikingly, the abundance of wrasses was best explained by a u-shaped concave curvilinear relationship with the total number of coral colonies within each 25 m² plot. The model for total biomass had the highest coefficient of determination (0.50). The R^2 or pseudo R^2 was ≤ 0.34 for all other models. The distance term was non-significant in every model.

The rugosity metrics were generally poor predictors of multivariate assemblage structure, although a combination of mean coral height and the number of complex corals was a significant predictor of the entire assemblage structure using abundance data. Mean coral height was a significant predictor of the multivariate structure of damselfish assemblages, and the number of complex corals and the sum of coral heights was significantly correlated with the assemblage structure of large fishes using abundance data (Table 2). Although these associations were significant ($P < 0.05$), the correlation coefficients were low (< 0.17).

Discussion

This study demonstrates both that meso-scale rugosity is a significant predictor of the intra-habitat variation in fish assemblages, and that different meso-scale rugosity metrics are the best predictors of different aspects of intra-habitat variation in fish assemblages. The importance of tall coral colonies for the abundance and diversity of fish assemblages is likely to be multifaceted. Firstly, many of the tall corals were *Montastraea annularis*, which is one of the most structurally complex corals in the Caribbean (Ebersole 1985), and provides a range of refuges for fishes. Furthermore, the number of refuges provided by *M. annularis* increases with colony size. The abundance of refuges is particularly beneficial to small fishes that are most susceptible to predation on reefs (Almany and Webster 2006), and the provision of refuges by tall *M. annularis* colonies is likely to be a key factor explaining the relationship between the abundance of small fishes and the number of tall corals within a plot. Furthermore, because small fishes were the most abundant and diverse component of the fish assemblages in each plot, this relationship

Fig. 2 Scatter plots of the meso-rugosity metric that had the strongest correlation with (a) number of territorial adult damselfishes (b) biomass of parrotfishes (c) number of wrasses and (d) number of surgeonfishes. Regression lines fitted using models described in Online Resource 3, with back-transformation of response data to account for negative binomial error structure where necessary. $n=51$ plots of 25 m^2



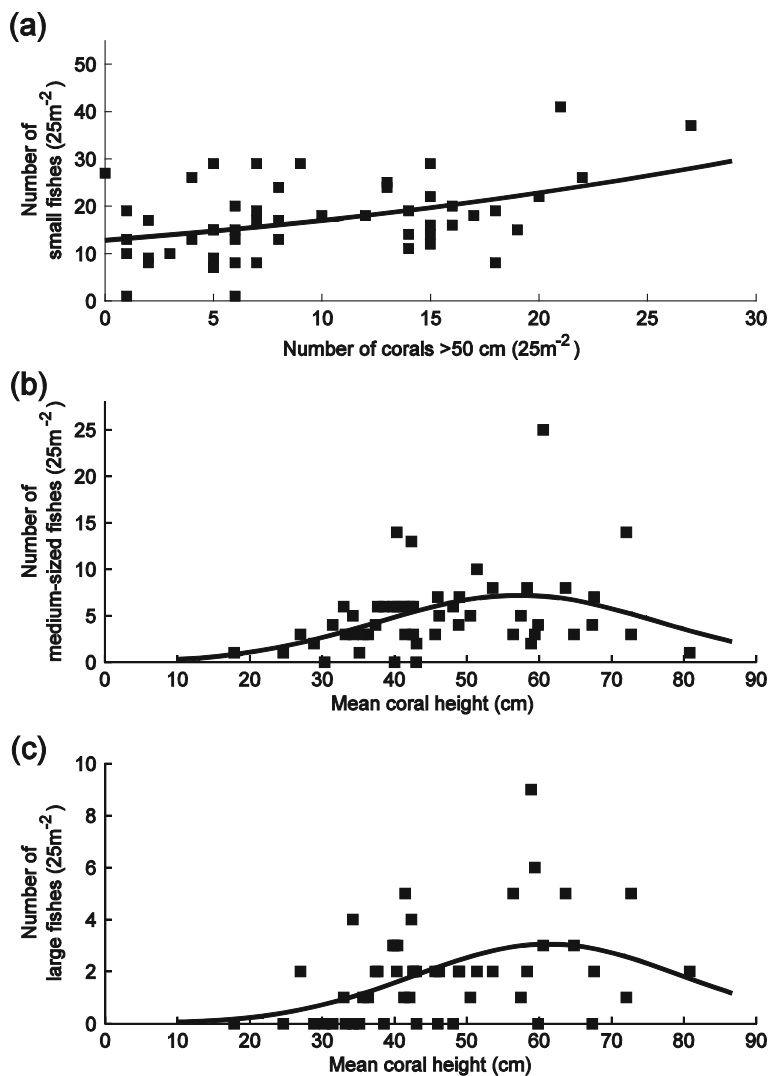
is likely to be a key driver of the relationship between the number of tall corals and the fish assemblage summary statistics. Secondly, there is some evidence that tall colonies provide fishes with a better view of approaching predators (Nemeth 1998). Thirdly, taller colonies offer a better chance for fishes to observe mates and maximise the effectiveness of courtship displays (Rilov et al. 2006). Fourthly, planktivorous food is more abundant higher in the water column, and can affect the distribution of planktivores (Clarke 1992). Finally, settlement may simply scale with colony size and, unless post-settlement mortality is strongly density dependent, larger colonies will subsequently support more fishes. Plots with more coral colonies are also likely to provide greater opportunities for foraging, mating, and predator refuges as fishes move about the reef.

Wrasses constitute a significant component of the small-fish assemblage on reefs, but appear to be responding to different aspects of meso-scale rugosity compared to other small fishes. The link between their abundance and the number of coral colonies in a plot was weak, but surprisingly more wrasses were found in plots

with low and high coral colony densities compared to medium-density plots. This pattern may reflect factors such as wrasses using refuges and schooling for protection from predators (White and Warner 2007) and juveniles acting as cleaners (Randall 1967), allowing them to use a wide range of reef patches. Use of a range of reef patches is also facilitated by adult wrasses having relatively large home ranges (Jones 2005) and all wrasses having broad diets (Randall 1967). Surgeonfish were also most strongly related to the number of corals within a plot, but again this relationship was weak and the range of fish abundances was low. Adult surgeonfishes are more abundant in more complex habitats, but their distribution is affected by their varied schooling behaviour with fish occurring as individuals, small groups, or large mixed-species schools (Lawson et al. 1999; Semmens et al. 2005). However, the curvilinear relationship for this taxon indicates that coral mortality may have significant implications for the abundance of these functionally important species.

Mean coral height was not expected to be a useful metric of meso-scale rugosity because it is independent

Fig. 3 Scatter plots of the meso-rugosity metric that had the strongest correlation with (a) small (b) medium-sized and (c) large fishes. Regression lines fitted using models described in Online Resource 3, with back-transformation of response data to account for negative binomial error structure. $n=51$ plots of 25 m^2



of coral density, indicating that fish would be just as abundant in plots with a single coral of a particular height as they are in plots with many corals of that height, or indeed a plot with a variety of corals with that mean height. However, mean coral height was the best predictor of total fish biomass, apparently driven by the abundance of medium-sized and large fishes that dominate the assemblage biomass parameter, and the highest abundances of these fishes was at a mean coral height of ~ 60 cm. We can only suggest explanations for this pattern that could direct future research, but it is clear that the underlying mechanisms will be varied because of the range of species, spanning multiple trophic categories, grouped within the metric of

medium-sized and large fishes. For example, most of the piscivores are >10 cm and hunting efficiency can be significantly affected by variations in habitat structure (Eklöv and Diehl 1994). Reef piscivores may hunt optimally among medium to large-sized corals that offer sufficient cover to approach prey but fewer refuges to prey than are provided by the tallest corals. Medium-sized corals may also have characteristics, such as optimum-sized daytime refuges, which make them preferable to fish that are predominantly active at night. Nocturnally active fishes such as grunts and squirrelfishes (Burke 1995; Ménard et al. 2008) were mainly in the larger size groups, and the squirrelfish *Holocentrus rufus* uses refuges with specific characteristics (Ménard et al. 2008).

Many of the parrotfishes recorded within this study were also medium-sized or large, and indeed the relationship between their total biomass and mean coral height was qualitatively similar to those for all medium-sized or large fishes. Adult parrotfishes prefer to feed on the top of *Montastraea annularis* colonies (Mumby pers. obs.), and corals with a mean height of ~60 cm may represent a trade-off between taller corals having more optimal algal food but being too high in the water column increasing the visibility of fishes to predators. Such a trade-off does not appear to be important to territorial damselfishes, as their abundance increases rapidly with mean coral height. The preference of damselfish for tall corals is likely to be a function of refuge availability, viewing predators, observing mates, the availability of planktivorous food, and settlement preferences as for other small fishes. However, because they hold territories on a single coral it is less important that this colony is surrounded by other tall corals, and it seems that mean height alone is a better predictor than the abundance of tall corals. However, this pattern may be relatively recent as damselfishes increasingly inhabit taller *Montastraea annularis* colonies following the disease-induced loss of their preferred *Acropora cervicornis* microhabitat (Precht et al. 2010).

Clearly there are a range of additional factors driving intra-habitat variation on this forereef habitat because the explanatory power of the models was $\leq 50\%$, and was particularly weak for predicting multivariate structure of the fish assemblages. Other factors influencing intra-habitat variation at the spatial scale considered in this study are likely to include recruitment preferences of fishes (Tolimieri 1998), home ranges of larger fishes being bigger than our 25 m² plots (Kramer and Chapman 1999), variations in the distribution of invertebrate prey across reefs (e.g., Stoner 1985), and competitive interactions among species (e.g., Robertson 1996). A fuller understanding of these factors will be necessary to fully elucidate the role of intra-habitat heterogeneity in meso-scale rugosity for maintaining fish abundances and diversity. Studies are also required from other reef systems, such as the Indo-Pacific, where a greater range of coral morphologies may lead to very different metrics being most appropriate for quantifying meso-scale rugosity. Furthermore, while this study demonstrates that fish abundances and diversity typically increase with increasing meso-scale rugosity, it is not clear whether

patches of low complexity reef within the habitat have important functional roles for particular fish species. Thus we cannot currently answer the question of whether all fish species would have maximum densities throughout a homogenous reef area of high complexity, or whether some species require that the high complexity patches be interspersed with low complexity patches for functions such as feeding. Equally, the magnitude and implications of any reductions in the heterogeneity of reef rugosity following decreases in Caribbean coral cover are unclear. However, while the importance of reef heterogeneity is poorly understood, it is clear that the number of critical patches of high meso-scale complexity habitat have been dramatically reduced on reefs by factors such as size-specific mortality rates that cause a long-term shift towards smaller coral colonies on reefs (Edmunds and Elahi 2007), shifts towards communities increasingly dominated by low complexity corals (Green et al. 2008), and more severe hurricanes that reduce the densities of coral colonies on reefs (Woodley et al. 1981). The effect on fishes of the general flattening of coral reefs has been highlighted repeatedly (e.g., Alvarez-Filip et al. 2009), but a fuller, multi-scale understanding of the interactions between reef complexity and fish assemblages is critical for predicting the effects of declining reef health on key ecosystem processes and services.

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