

Measuring Structural Complexity on Coral Reefs

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Abstract

Structural complexity on coral reefs has been shown to positively influence several measures of biodiversity, and is thus an important ecological variable. The dominant field method used by reef scientists to measure structural complexity is the chain-and-tape method, which produces a measure of rugosity calculated as the ratio of contour-following vs. straight distance between two points on the reef. Expanding on this method, we developed simple and easy-to-use tools to measure rugosity at four spatial scales for a range of typical coral reef structures, and also used the data to calculate fractal dimensions at three intermediate scales. We show that measures of structural complexity change unpredictably across spatial scales, and illustrate that typical coral reef structures are too complex for any single measure to function as a comprehensive index of structure over a range of scales. This illustrates that considerations of spatial scale are important when measuring structural complexity, and that the smallest scale obtainable with current remote sensing technology and methods is not directly related to the scale used in most studies of fish ecology. We also illustrate that the fractal dimension measure is more closely related to human intuitive perception of structural complexity than is rugosity, though we are unable to test its value in fish ecology with our current dataset. Future research will relate fish body size to the scale of reef structural complexity, and develop remote sensing-based methods to map structural complexity over large spatial extents.

Introduction

The influence of structural complexity on the biodiversity of fish assemblages has received much attention in the fish ecology literature (McCormick 1994; Szmant 1997). Most studies have concluded that high structural complexity is spatially correlated with overall fish species richness (Chabanet *et al.*, 1997), or the abundance of specific trophic guilds (Hixon and Beets 1993) or mobility guilds (Friedlander and Parrish 1998). Other studies have found that the fish biodiversity variables are temporally correlated with structural complexity, declining as reef frameworks disintegrate after mass bleaching events (Jones *et al.*, 2004; Wilson *et al.*, 2006) or experimental manipulation (Syms and Jones 2000). However, the *in-situ* quantification of structural complexity has received surprisingly little attention, and there is neither consensus on the best measure of structural complexity, nor on the most relevant spatial scale at which to measure or assess it. Table 1 illustrates approaches taken to quantify structural complexity in studies of coral reefs and other near-shore environments, and the different scales at which the complexity has been measured. The variety of methods seen in the table exists despite the acknowledged importance of structural complexity for coral reef biodiversity and ecology.

Few studies have investigated what measure of structural complexity best predicts a positive effect on fish biodiversity (McCormick, 1994; Gratwicke and Speight, 2005), and none have determined the best spatial scale at which to measure it. In this study, we investigated the influence of spatial scale on measures of structural complexity. We did this by measuring rugosity, the most commonly used

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measure of structural complexity, at four spatial scales for six characteristic substrate types on coral reefs.

Table 1: A review of methods for assessment of structural complexity of coral reefs and other near-shore environments.

Source	Environment	Organism(s)	Chain length (m)	Link length (cm)
Friedlander and Parrish, 1998	Coral reefs	Fishes	3	1.3
Chabanet <i>et al.</i> , 1997	Coral reefs	Fishes	Coverage of branching corals	
McCormick, 1994	Coral reefs	Fishes	3	10 and Unknown
Hixon and Beets 1993	Coral reefs	Fishes	Holes of varying size and number	
Ormond <i>et al.</i> , 1996	Coral reefs	Pomacentrids	Geomorphologic zones, microhabitats	
Luckhurst and Luckhurst, 1978	Coral reefs	Territorial fishes	3	1.5
Garpe and Ohman, 2003	Coral reefs	Fishes	Unknown	Unknown
McClanahan, 1999	Patch reefs	<i>Echinometra</i>	10	Nylon line
Chapman and Kramer, 1999	Coral reefs	Fishes	14	?
Kostylev <i>et al.</i> , 2005	Rocky shore	Macrofauna	0.15	0.1
Gratwicke and Speight, 2005	Artificial reefs	Fishes	1-3.64	Unknown
Syms and Jones, 2000	Coral reefs	Fishes	Vertical relief	
McClanahan, 1988	Coral reefs	Sea urchins	10	Unknown
Kohn, 1968	Multiple types	Gastropods	No quantification	
Lara and Gonzalez, 1998	Coral Reefs	Fishes	6-point scale (visual estimation)	
Sleeman <i>et al.</i> , 2005	Model coral reef	None	18	10
Brock <i>et al.</i> , 2004	Patch reefs	None	Variable, ~60	80
Rogers <i>et al.</i> , 1991	Coral reefs	None	10 (transect)	1.3
Bainbridge and Reichelt, 1988	Coral reefs	None	Vertical relief	

Methods

To measure rugosity at four spatial scales we constructed four simple chains, each with a different link length. Chains with the two longest link lengths (82 and 12 cm respectively) links were constructed of cut pieces of PVC pipe pulled over a rope, with knots separating each link. Chains with shorter link lengths (3.1 and 0.2 cm) were ready-made metal chains. All chains were five meters long, and negatively buoyant.

We chose our smallest scale (0.2 cm) as similar to the smallest of those reported in the literature to ensure coverage of the scales that fish ecologists have found to correlate with fish biodiversity variables (see Table 1). We chose our largest spatial scale (82 cm) to simulate the best available resolution of current large-coverage remote sensing instruments (Brock *et al.*, 2004) to assess the possibility of measuring structural complexity remotely. We also chose two intermediate scales (3.1 and 12 cm) that are closer to the body sizes of most reef fish to create some continuity between the smallest and largest scales.

In April and May of 2006, on Ngederrak forereef in Palau, we measured rugosities for six distinct substrate types: sand, rubble, coarse branching coral, tabulate coral, foliose coral, and fine branching *Millepora* coral. These substrate types were chosen because they were distinct, easily identifiable, and

could be found in patches five metres across. A typical example of each substrate is illustrated in Figure 1.

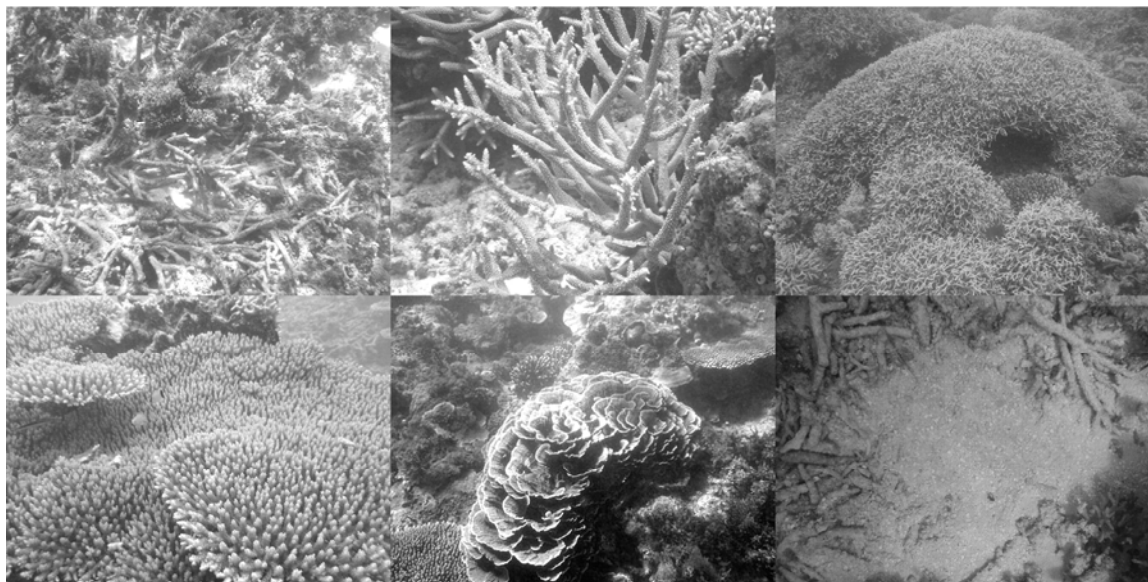


Figure 1: The six substrate types measured in this study. Top row from left: rubble, coarse branching coral, fine branching *Millepora* coral. Bottom row from left: tabulate coral, foliose coral, sand.

Each measurement consisted of draping the chain as closely as possible in a straight line over the substrate, then measuring the straight-line distance between the two end points with a tape measure. When end points were located in depressions, the straight-line distance was estimated by holding the tape measure over the opening of the depression. For each substrate type, using each of the four chains, this measurement was repeated at least seven times over different areas. The mean and standard deviation of rugosity could then be calculated for each substrate, at each spatial scale. Figure 2 illustrates the four chains, and the tape measure, draped over a rubble substrate. Rugosity is calculated by dividing the known length of the chain (five meters) by the measured distance between the end points (Risk, 1972).

Using the mean rugosities we calculated the fractal dimensions (D) of the six substrates, at three intermediate spatial scales. The fractal dimension is a measure of the change in rugosity with changing scale of measurement, and can be calculated as $D = 1 - S$, where S is the slope of rugosity values on a log-log plot with rugosity on the y-axis and spatial scale on the x-axis (Mandelbrot, 1977).



Figure 2: Four chains draped over a rubble substrate.

Results

Figure 3 presents the mean rugosities of each substrate type, at each scale. As expected, each substrate type shows variation in rugosity with variation in the scale of measurement (one-way ANOVA, $p < 0.001$). T-tests were used to confirm that sand substrates had the lowest rugosity values at all scales ($p < 0.001$) and that coarse branching coral substrates had the highest rugosity values at the 0.2 cm and 3.1 cm scales ($p = 0.007$ and $p < 0.001$, respectively). At the largest scale, tabulate coral substrates had the highest mean rugosity, though not significantly higher than that of foliose coral substrates ($p = 0.142$).

At each spatial scale, the six substrate types demonstrated significant differences in rugosity (one-way ANOVA, $p < 0.001$), though not all substrate types are distinguishable at all scales (e.g., tabulate and fine branching *Millepora* coral has similar rugosity when measured at the 3.1 cm scale).

As expected, branching coral substrates have high rugosities at the smaller spatial scales, at which the complexity of the branching network plays a role. At the larger spatial scales, coral colonies with tabulate form have high rugosity, due to the overall shape of the colonies.

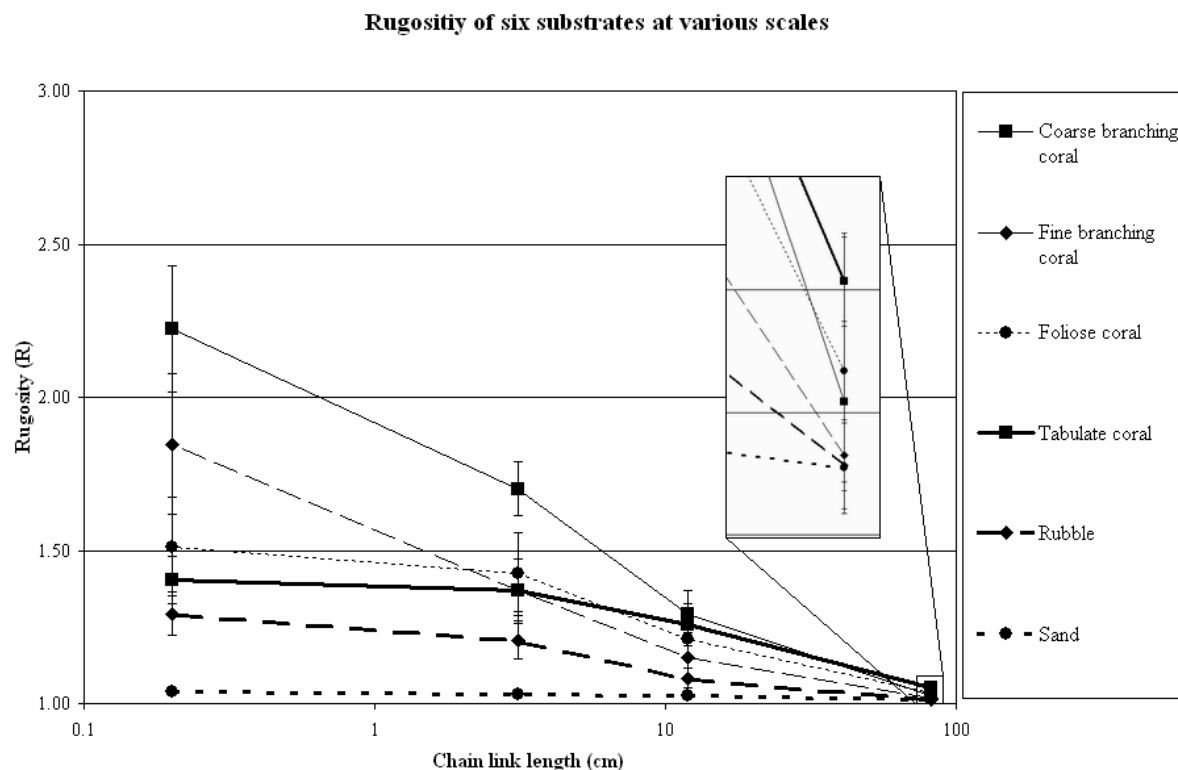


Figure 3: Mean rugosity for the six substrate types - at the four scales of measurement.

Figure 4 presents the mean fractal dimension values of each substrate type, at each scale. T-tests confirmed that the two branching coral substrates had the highest fractal dimension at the smallest scale ($p < 0.001$), coarse branching coral had the highest fractal dimension at the intermediate scale ($p = 0.006$), and non-significantly at the largest scale ($p = 0.157$). Sand substrates had the lowest fractal dimension at any scale ($p < 0.001$). As for rugosity values, the six substrate types demonstrated significant differences in fractal dimension (one-way ANOVA, $p < 0.001$), though not all substrate types are distinguishable at all scales.

For individual substrate types, the fractal dimension varies significantly between scales. Fine branching *Millepora* coral and coarse branching coral have their highest fractal dimensions at the intermediate scale, and tabulate coral has its highest fractal dimension at the largest scale. Sand is the only substrate type with a near-constant fractal dimension. The highly varying fractal dimensions of all substrate types other than sand stand in contrast to the near-constant fractal dimensions reported for individual coral polyps (Basillais, 1997) and for larger reefscapes (Reichelt and Bradbury, 1984; Purkis *et al.*, 2005).

Fractal dimensions of substrates at various scales

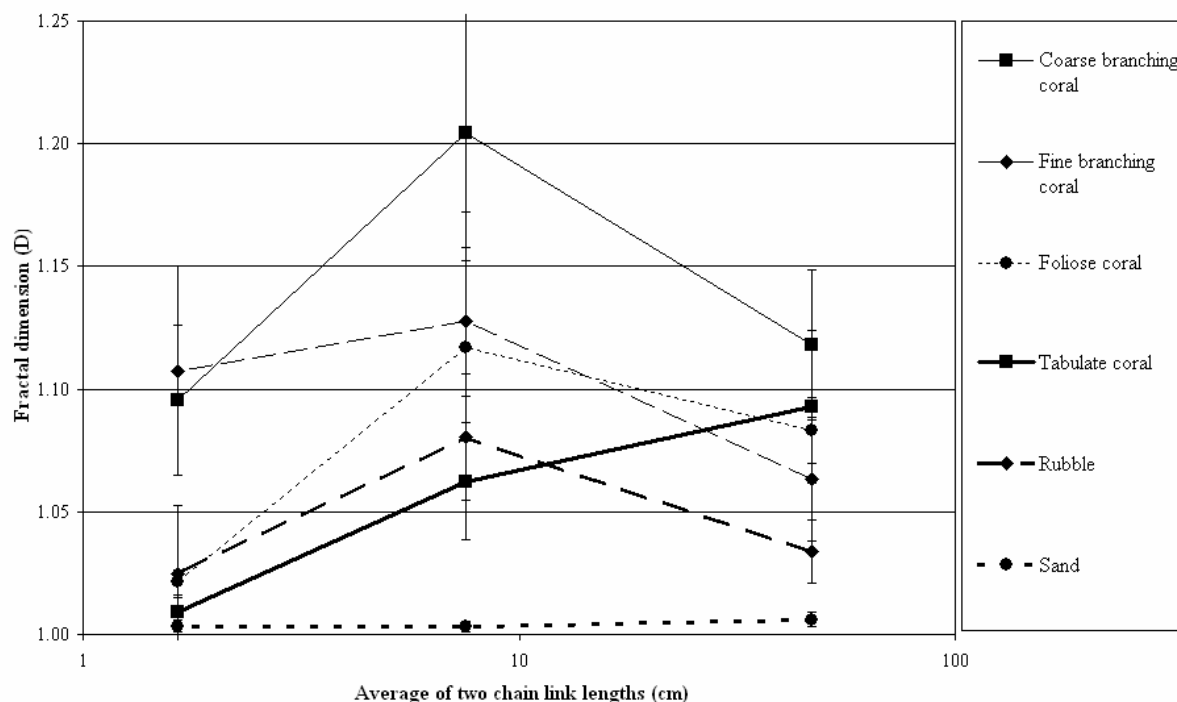


Figure 4: Mean fractal dimension for the six substrate types, at the three scales of measurement.

Discussion

For each substrate type, the spatial scale at which rugosity is measured significantly influences the resulting values of both rugosity and fractal dimension (one-way ANOVA, $p=0.0014$). The structural complexity of a substrate relative to other substrates also changes with scale, and with measure. Several conclusions can be drawn:

1. Structural complexity at the smallest scale, a scale similar to that used in the fish ecology literature, cannot be directly inferred by measurements of structural complexity at a larger scale. Structural complexity, as measured by either rugosity or fractal dimension, does not vary with scale in a straight-forward or predictable manner, but is highly dependent on substrate type. Information about structural complexity at one scale therefore does not enable predictions about structural complexity at another scale unless the substrate type, and hence the scaling relationship, is known.

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2. Fish and other organisms respond to the structural complexity of their habitat at a scale similar to that of their own body size (Gratwicke and Speight, 2005). The spatial scale at which rugosity is measured is therefore important for studies of fish ecology. More careful considerations when selecting the appropriate spatial scale to measure structural complexity is likely to yield stronger relationships between fish biodiversity and structural complexity variables. The scale of measurement should preferably match the typical body size of the organisms whose habitat is being investigated.
3. Because of the scale-dependency of the two measures of structural complexity, rugosity measurements based on the best available remote sensing technology (equal to the largest scale measured in this study) cannot be related directly to rugosity measured *in situ* at the smaller scales, as typically measured in the literature.
4. For each substrate type, the measure of fractal dimension is more similar to an intuitive perception of structural complexity than rugosity. The branching coral types, arguably having the most complex structure at the smallest scale, has the highest fractal dimension of any measured substrate at the smallest scale. At the intermediate scale, only the coarse branching coral has the highest fractal dimension, because at this scale the small spaces between individual fine branches are not registered, whereas the larger spaces between the coarse branches are. At the largest scale, coarse branching coral still has the highest fractal dimension as a result of the 'valleys' between individual colonies, but does not differ significantly from tabulate and foliose coral substrates which also have high fractal dimensions at this scale. Fine branching *Millepora* coral colonies often form continuous and relatively flat surfaces, and therefore have a low fractal dimension at the largest scale. Measuring and calculating fractal dimensions thus give a picture of structural complexity at several spatial scales that is easily interpretable.
5. It is well documented that reef fishes have specific substrate preferences (Myers, 1999). These preferences are likely to influence the normally positive relationship between rugosity and the diversity of a fish assemblage (see Table 1). However, given the scale-based variation in the relative rugosity of the observed substrate types, the scale of measurement will influence the nature and strength of this relationship, and therefore the accuracy with which the diversity of fish assemblages can be predicted from the rugosity measurements. Given that efforts are being made to operationalize such predictions using airborne lidar measurements of rugosity at several scales (Kuffner *et al.*, 2007), further insight into the influence of spatial scale is needed.
6. Given the variation between substrate types in relative values of both structural complexity measures, no one measure at one scale can adequately describe the structural complexity of a substrate. However, measuring rugosity at multiple scales, as required for the calculation of the fractal dimension, is time-consuming. It requires more time spent under water than standard rugosity measurements, which can already be time-consuming and cumbersome. Handling multiple five-metre chains of varying buoyancy on a coral reef, without severely damaging the substrates being measured, requires patience, especially when working in a current of surf environment. Efficient measurement of structural complexity on a coral reef will remain dependent on the objective of the study, and particularly on the relevant spatial scale.

Future Research

Future research will include collection of data on fish biodiversity variables, and establish guidelines for choosing the best spatial scale at which to measure structural complexity in fish ecology studies. It will also explore remote sensing methods to obtain information on coral reef structural complexity at the relevant spatial scales, with a view to ultimately replace in-situ measurements.

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