

Relationships between reef fish communities and remotely sensed rugosity measurements in Biscayne National Park, Florida, USA

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Received: 3 February 2006 / Accepted: 29 April 2006
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Abstract The realization that coral reef ecosystem management must occur across multiple spatial scales and habitat types has led scientists and resource managers to seek variables that are easily measured over large areas and correlate well with reef resources. Here we investigate the utility of new technology in airborne laser surveying (NASA Experimental Advanced Airborne Research Lidar (EAARL)) in assessing topographical complexity (rugosity) to predict reef fish community structure on shallow (<10 m deep) patch reefs. Marine portions of Biscayne National Park, Florida, USA, were surveyed remotely using the EAARL, and reef fish populations were visually surveyed on 10 patch reefs at independent, randomly selected stations ($n = 10\text{--}13$ per reef). Rugosity at each station was

assessed in situ by divers using the traditional chain-transect method (10-m scale), and remotely using the EAARL submarine topography data at multiple spatial scales (2, 5, and 10 m). The rugosity and biological datasets were analyzed together to elucidate the predictive power of EAARL rugosity in describing the variance in reef fish community variables and to assess the correlation between chain-transect and EAARL rugosity. EAARL rugosity was not well correlated with chain-transect rugosity, or with species richness of fishes (although statistically significant, the amount of variance explained by the model was very low). Variance in reef fish community attributes was better explained in reef-by-reef variability than by physical variables. However, once the reef-by-reef variability was taken into account in a two-way analysis of variance, the importance of rugosity could be seen on individual reefs. Fish species richness and abundance were statistically higher at high rugosity stations compared to medium and low rugosity stations, as predicted by prior ecological research. The EAARL shows promise as an important mapping tool for reef resource managers as they strive to inventory and protect coral reef resources.

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Keywords Habitat · Mapping · Marine protected areas · Coral reef management · Remote sensing · Topographic complexity

Introduction

Recent advancements in remote sensing and mapping technology have resulted in detailed habitat maps of reef systems at multiple spatial scales (Mumby and Wabnitz 2002). Now that the success of ‘no-take’ conservation efforts is recognized (Halpern and Warner 2002), habitat maps are playing a central role in the planning of marine protected areas (MPAs) and designating essential fish habitat. Maps that show the spatial extent of each habitat type (e.g., seagrass bed, sand, reef) are useful, but maps containing information regarding the relative quality of those different habitats would be even more informative. Although in its infancy, mapping that assesses habitat quality may be based on biogeochemical function (Atkinson and Grigg 1984; Brock et al. in press) or physical structure that has ecological significance (Brock et al. 2004).

Rugosity is a measure of topographic complexity that provides an index of potential shelter for mobile (benthic and neritic) marine organisms, and measuring rugosity at a large spatial scale could serve as a valuable tool in conservation planning. In marine ecological studies, rugosity is an oft-measured parameter because it defines the physical structure of the reef and often correlates positively with the abundance, biomass, and/or species richness of reef fish (Luckhurst and Luckhurst 1978; Caley and St. John 1996; Friedlander and Parrish 1998; Chapman and Kramer 2001). Manipulative experiments have confirmed the importance of physical complexity for fish (Connell and Jones 1991; Syms and Jones 2000). However, one of the difficulties in assessing relationships between fish assemblages and habitat characteristics is the issue of scale. Depending upon the way that different fish species interact with habitat and ontogenetic shifts in this usage (Nagelkerken et al. 2000), species probably respond to reef characteristics on a range of scales throughout their life cycles.

Experimental Advanced Airborne Research Lidar (EAARL) is a novel method for remotely assessing shallow subtidal topography using lidar (light detection and ranging), which has recently been developed to assess coral reef resources

(Brock et al. 2004). The high-density bathymetry data resulting from the EAARL can be used to estimate the rugosity of the benthos at multiple spatial scales, thereby quantifying the physical complexity of the reef habitat. Using EAARL to measure rugosity allows for an objective, quantitative assessment of rugosity, and for a much greater level of coverage compared to traditional methods (e.g., the chain transect method), because entire swaths of reef can be assessed. Moreover, the EAARL airborne lidar datasets also present the opportunity to assess the importance of rugosity to fish and other organisms at multiple spatial scales.

Here we assess how EAARL rugosity measurements correlate with reef fish community structure in order to examine the utility of the EAARL in quantifying reef habitat quality with respect to fish populations. We surveyed 10 patch reefs within Biscayne National Park, measuring fish species richness and abundance, as well as substratum rugosity using the traditional chain transect method. We then combined the three data sets to assess possible relationships between them. Through this exercise, our goal was to assess the utility of EAARL as a quantitative mapping and evaluation tool for marine resources.

Materials and methods

Study area

The study was conducted on mid-shelf patch reefs within Biscayne National Park, Florida, U.S.A (Fig. 1). These reefs are generally dome-shaped, with ‘clusters’ of large coral heads (mainly *Montastrea* spp.) around the outer fringe, and flat rubble-strewn tops (‘campus’ zone) colonized by gorgonians and occasional small coral heads (Marszalek et al. 1977; Jaap 1984; Ginsburg et al. 2001). Benthic community structure on these reefs will be reported in another manuscript, but a summary of our data is provided here for descriptive purposes. The benthic community observed on the patch reefs was largely dominated by macrophytes and gorgonians. *Dictyota* spp. accounted for the majority of fleshy algae ($n = 16$ quadrats sampled per reef, % cover grand

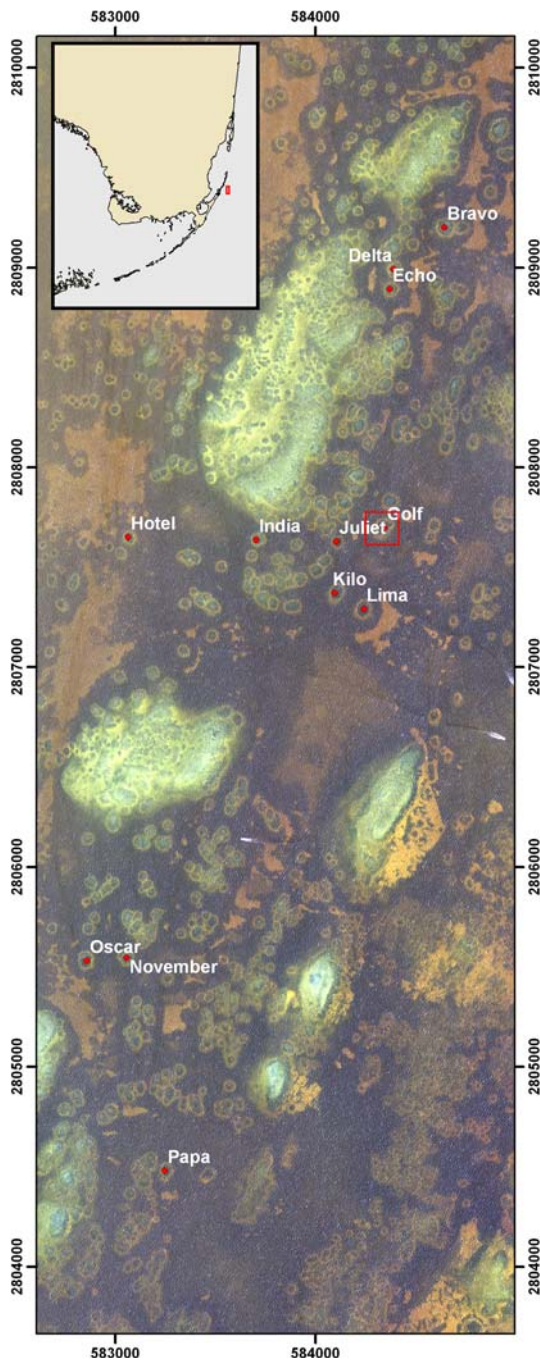


Fig. 1 Study area within Biscayne National Park depicted on a Quickbird satellite image. Patch reefs investigated are labeled 'Bravo' through 'Papa' (in alphabetical order from north to south)

mean $\pm$ 1 standard error = 15.4 ± 0.8), whereas *Halimeda tuna* was the main calcifying alga ($11.7 \pm 0.6\%$ cover), and cyanobacteria were also

fairly abundant ($7.8 \pm 0.7\%$ cover). The mean density of gorgonians on these patch reefs was 32.1 ± 0.9 individuals m^{-2} , and scleractinian corals only accounted for a mean of $5.8 \pm 0.6\%$ of the benthos. The remainder of the living community was mainly composed of encrusting invertebrates (Porifera, *Briareum asbestinum*, *Palythoa caribaeorum*, *Erythropodium caribaeorum*, gorgonian holdfasts, and *Millepora alcicornis*), contributing about 2–4% cover each. A mean of $20.8 \pm 1.1\%$ of the bottom was assigned to the category 'bare lithified substratum,' defined as hard substratum covered mostly in crustose coralline algae and lacking sediments > 1 mm deep, macroalgae, or thick turf algae (suitable settlement substratum for coral larvae).

EAARL data acquisition and processing

EAARL data were collected from an airborne platform during a 2-week period in August 2002 over a broad swath extending from north of Triumph Reef to south of Carysfort Reef off the upper Florida Keys. During operation at a nominal aircraft altitude of 300 m and 50% swath overlap, the NASA EAARL collected 10 cm diameter laser spot elevation soundings at a spatial density of 1 sounding per m^2 . The resulting voluminous dataset of EAARL laser reflections was stored as raw temporal waveforms that were analyzed by tailored algorithms that determine range to the sea surface and water-column thickness. These laser-range soundings were then combined with the instantaneous aircraft location derived by differential GPS techniques to yield spot submarine topographic elevations referenced to the NAVD88 vertical datum and the NAD83 horizontal datum. A validation study of the EAARL's capability to retrieve shallow submarine topography was recently conducted in Tampa Bay. Comparisons of geographically coincident elevation determinations from the EAARL and from a survey-grade Marimatech acoustic fathometer yielded a mean standard error for EAARL topographic soundings of less than 20 cm (A. Nayegandhi, personal communication).

Following creation of a regional substratum spot-elevation dataset based on the laser soundings, a random point gridding operation was

applied to generate a digital elevation model (DEM) at 1-m cell resolution. Using an approach loosely based upon Dahl's surface index, defined as the ratio of the actual surface area to that of a flat, horizontal two-dimensional plane with similar boundaries (Dahl 1973), rugosity was estimated at three different scales (2, 5, and 10 m kernel size) based on the lidar-derived DEM (e.g., Fig. 2). At each scale, the mean rugosity values for each digital map cell within the kernel were calculated. By definition, rugosity as determined from a lidar DEM must always be greater than or equal to 1. Higher values of this ratio correspond to greater departure from smooth flatness.

Selection of reefs and stations within reefs

Reefs were chosen based upon similarities in average depth, area, positioning across reef shelf, and other potentially confounding variables (Table 1). Further, the spatial density of August 2002 EAARL laser soundings for all of the selected reefs met or exceeded the survey target

value of 1 sounding per m^{-2} . Sampling stations within reefs were chosen randomly as follows. Elevation contours were generated from the EAARL DEM, and a QuickBird multispectral image acquired in April 2002 was used to help determine which contour defined the edge of each patch reef. The edge of the patch reef was defined to be where the sand halo touched the reef edge. Typically, this boundary was also the site of an abrupt topographic step that was clearly represented in the lidar DEM. We then selected topographic contours on the lidar DEM to represent the patch reef boundaries, converted these lines into polygons, and used a geographic information system (GIS) to generate random points in a polygon. Distances between each random point were determined, and points that were closer than 1 m to another point were removed and replaced by new random points until 20 were obtained. The latitude–longitude coordinates for the random points were loaded into a hand-held GPS unit and used to navigate a small vessel to deliver marker buoys to each station. The GPS unit used to deploy the marker buoys, a Garmin

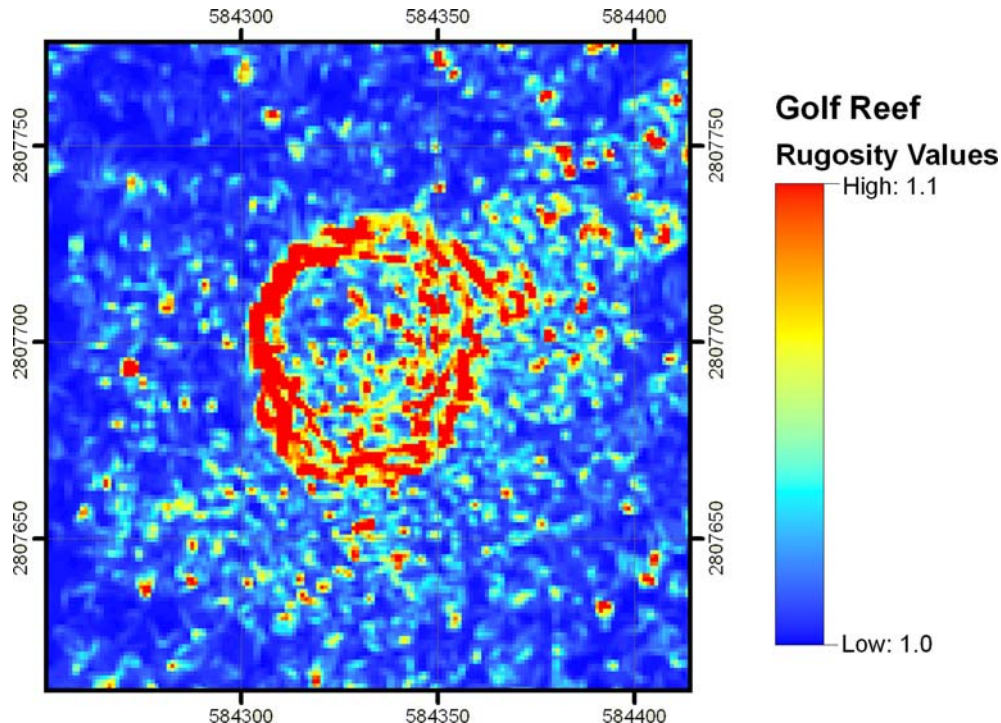


Fig. 2 Lidar rugosity map for the patch reef labeled 'Golf.' Rugosity data are calculated at the 2-m scale (2×2 m kernel), with 1-m map cells

Table 1 GPS locations and descriptive data for patch reefs surveyed by dive team from 9 to 16 September 2003

Reef	Northings	Eastings	Distance to next reef (m)	Depth (m (SE))	Area (m ²)
Bravo	2809202.30	584641.20	83.56	3.69 (0.11)	4748.6
Delta	2808991.35	584388.60	109.56	4.13 (0.17)	2814.0
Echo	2808892.40	584368.30	109.56	4.48 (0.15)	2590.3
Golf	2807699.95	584340.15	130.99	4.71 (0.30)	3633.6
Hotel	2807651.60	583061.90	88.41	4.37 (0.13)	1905.5
India	2807639.50	583703.30	86.84	3.86 (0.18)	2499.0
Juliet	2807629.65	584101.45	72.14	4.59 (0.22)	1691.5
Kilo	2807372.00	584094.60	144.16	4.07 (0.16)	3406.0
Lima	2807292.15	584239.60	163.13	5.33 (0.33)	3609.3
November	2805548.00	583056.85	148.97	3.71 (0.17)	3484.4
Oscar	2805533.50	582856.80	159.33	4.28 (0.25)	3379.8
Papa	2804483.40	583245.85	76.47	5.46 (0.24)	2350.3

No fish data were collected on reefs 'Hotel' or 'Kilo'

Map 76, provides a horizontal positioning accuracy of approximately 3 m while receiving corrections from the Wide Area Augmentation System (WAAS). Maps were prepared for each reef so that field personnel could use them to place marker buoys and navigate underwater from station to station.

Fish and chain rugosity surveys

SCUBA-diver surveys were conducted at the 12 chosen patch reefs from 9 to 16 September 2003. Four divers with specialist capabilities in the identification of coral, algae, reef fish, gorgonians, and geomorphic structure worked simultaneously, rotating from station to station while remaining underwater. Benthic and substratum data are reported in another manuscript (Kuffner et al. in preparation). All surveys were conducted between 0900 and 1800 EST. Fish surveys were conducted using the Bohnsack and Bannerot (1986) point-count method, wherein a diver sits stationary in the middle of a 7.5-m radius cylinder, recording fish of every species observed in a 5-min period and subsequently estimates length and abundance for each recorded species for the following 10 min. Total lengths of fishes were estimated to the nearest centimeter. Occasionally, a point-count cylinder included more than one station due to the random assignment of stations within reefs. When a cylinder contained more than one station, the fish data were randomly assigned to one of the stations, and the other station was left with missing values for fish

variables. Thus, the number of stations per reef varied from 10 to 13.

Chain-transect rugosity was measured using a traditional method (Risk 1972; Luckhurst and Luckhurst 1978). Divers placed a 10-m transect line across the reef in an east–west direction, with the 5-m mark over the station marker. The purpose of the east–west directional deployment of the line was to mimic the EAARL raster scanning (the plane flew along roughly north–south flight-lines, and the instrument scans were collected across-track in an approximately east–west orientation within 240 m-wide swaths). Using a 1-m chain with links 1 cm in length, the contoured distance was estimated by serially laying the chain across the substratum, following every topographical high and low underneath the transect line. Thus, chain-transect rugosity is the ratio of the contoured distance to the linear distance.

Statistical analyses

Simple linear regression was used to assess relationships among reef fish community variables and rugosity measures. When the assumptions of linear regression were violated (e.g., residuals not normally distributed), the data were transformed as reported in the results. For fish species richness, there was one station where only one species was observed (very unusual). For fish abundance, there was one station where an extremely large school of juvenile grunts was observed (over 1200 fish). We felt justified in removing these two outliers because they were not very influential

(i.e., did not change the results of the statistical tests), while removing them allowed the assumptions of the models to be met (residuals normally distributed). Two-factor analysis of variance (ANOVA) was used to assess patterns in reef fish distribution in relation to rugosity across reefs. For these analyses, the continuous variable of EAARL rugosity (at the 10-m scale) was collapsed into categories by dividing the ordered data into thirds (slightly unbalanced due to ties) so that each station was assigned to a low (1.012–1.037), medium (1.038–1.059), or high (1.060–1.171) rugosity category. Number of stations within each rugosity category ranged from 1 to 10, so unbalanced two-factor ANOVA was applied via the general linear model procedure using Statistix® 8 (Analytical Software, Tallahassee, Florida, USA) statistical software.

Results

Statistical analyses showed that EAARL rugosity measurements at all three spatial scales were significantly correlated with rugosity measurements made with the chain-transect method, though the amount of variance explained was extremely low (Fig. 3, 10-m scale, chain rugosity inverse-transformed $R^2 = 0.154$, $P < 0.0001$), especially at the smaller scales (5-m scale, chain rugosity inverse-transformed $R^2 = 0.106$, $P < 0.0001$; 2-m scale, chain rugosity inverse-transformed $R^2 = 0.043$, $P = 0.004$). EAARL rugosity at the 10-m scale was well correlated to distance from the edge of the patch reef (Fig. 4, $R^2 = 0.393$, $P < 0.0001$), and the relationship weakened with reduction in lidar scale (5-m scale, distance from edge square root-transformed $R^2 = 0.333$, $P < 0.0001$; 2-m scale, distance from edge square root-transformed $R^2 = 0.175$, $P < 0.0001$). However, the relationship is clearly not linear, which can be explained by the general flat-topped dome shape of the patch reefs (low rugosity stations were generally found on the flat tops). The ‘edge-effect’ is clearly seen on maps of patch reef lidar rugosity (Fig. 2) that typically depict elevated rugosity around the sloping margins of the patch reefs. In contrast, chain-transect

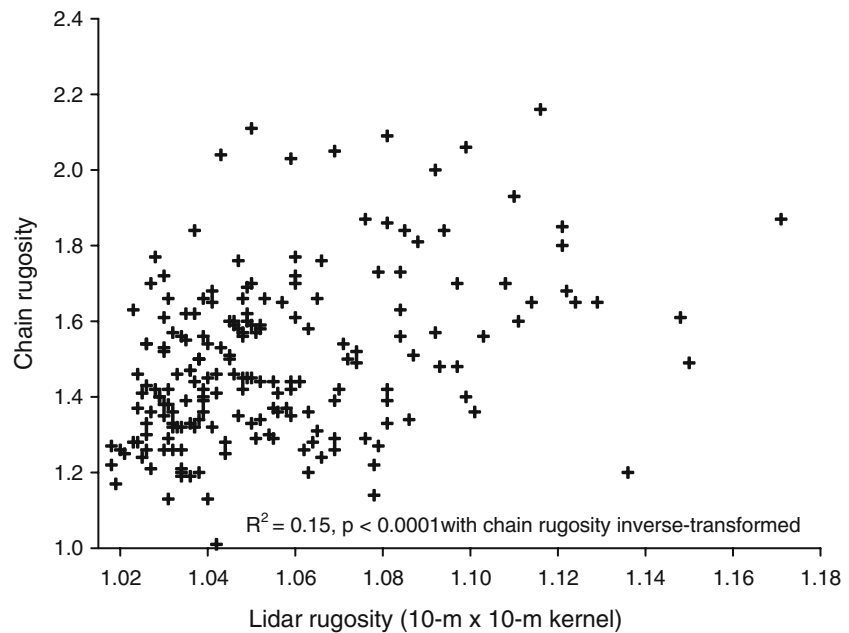
rugosity was not well related to distance from edge of the reef, although the relationship was statistically significant ($R^2 = 0.101$, $P < 0.0001$).

During our in situ observations, we counted 12,036 reef fish belonging to 80 species at the 119 stations where fish were surveyed. Haemulidae (grunts) and Scaridae (parrotfish) were the dominant families (Fig. 5), and most were juveniles, with 44.5% of the total fish observed being juvenile grunts, and 24.4% juvenile parrotfish. The three most abundant species were the white grunt, *Haemulon plumieri* (Lacepède, 1801), the tomtate, *Haemulon aurolineatum*; Cuvier, 1830, and the striped parrotfish, *Scarus iserti* (Bloch, 1789). The overall low abundance and lack of large specimens of economically important families (i.e., grouper, snapper) was conspicuous. Of all the fish observed, 33.7% were herbivores, whereas only 3.5% were piscivores (only 10 groupers were observed during the entire survey). We found man-made debris on all reefs except Golf, and debris specific to fishing (e.g., weights, line, leaders, and ghost traps) on 10 of the 12 reefs.

In a linear regression using data from 118 stations where fish were surveyed, EAARL rugosity was not a good predictor of fish species richness (number of species per census), although the relationship was statistically significant at the 5-m scale ($R^2 = 0.082$, $P = 0.002$). For comparison, the relationship was even weaker at the 2-m scale ($R^2 = 0.056$, $P = 0.010$), and 10-m scale ($P^2 = 0.052$, $P = 0.013$). The relationship between chain-transect rugosity and fish species richness was not significant ($R^2 = 0.019$, $P = 0.146$).

Total fish abundance was negatively correlated with distance from the edge of the patch reefs, but the amount of variance explained by the model was very low (data log-transformed $R^2 = 0.092$, $P = 0.0008$). When fish families were analyzed individually, Haemulidae (grunts) and Pomacentridae (damselfish) were the only families that displayed this pattern (grunts: data log-transformed, $R^2 = 0.203$, $P < 0.0001$, damselfish: data log-transformed $R^2 = 0.192$, $P < 0.0001$). There were too few grouper and snapper to assess this relationship, but most observations occurred at stations near the edges.

Fig. 3 Scatter plot showing a weak relationship between EAARL rugosity at the 10-m scale and rugosity measured with the traditional chain-transect method at 196 stations across 12 patch reefs in Biscayne National Park



Mean fish abundance was statistically different among reefs (Fig. 5; Kruskal–Wallis one-way ANOVA, $P < 0.0001$), and all pair-wise comparisons (family alpha = 0.05) showed that reef Lima had fewer fish compared to all reefs except Echo and Golf.

When the reef factor was included in a two-way ANOVA with the EAARL rugosity (10-m scale) factor broken down into three categories (low,

medium, and high), a statistically significant effect of rugosity on fish species richness was revealed (Table 2, Fig. 6). Within each reef, more species of fish were found at the high rugosity stations compared to medium and low (Tukey's honestly significant difference, $P < 0.05$). High rugosity stations had the greatest mean species richness of the three rugosity categories on 7 out of the 10 reefs. The same pattern was seen in the fish

Fig. 4 Scatter plot showing relationship between EAARL rugosity at the 10-m scale and distance to patch reef edge at 196 stations in Biscayne National Park. Regression line with 95% confidence (inner lines) and prediction (outer lines) intervals calculated using Sigma Plot

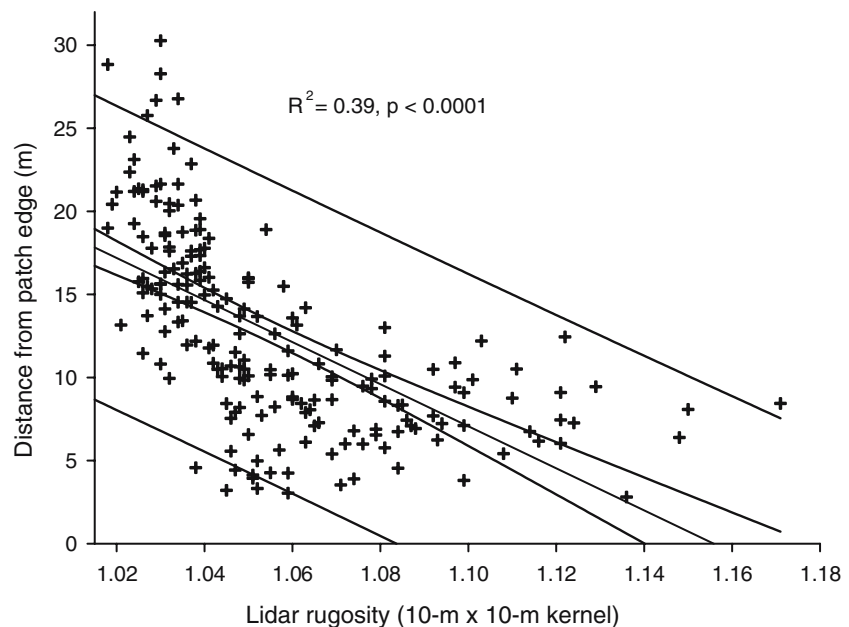
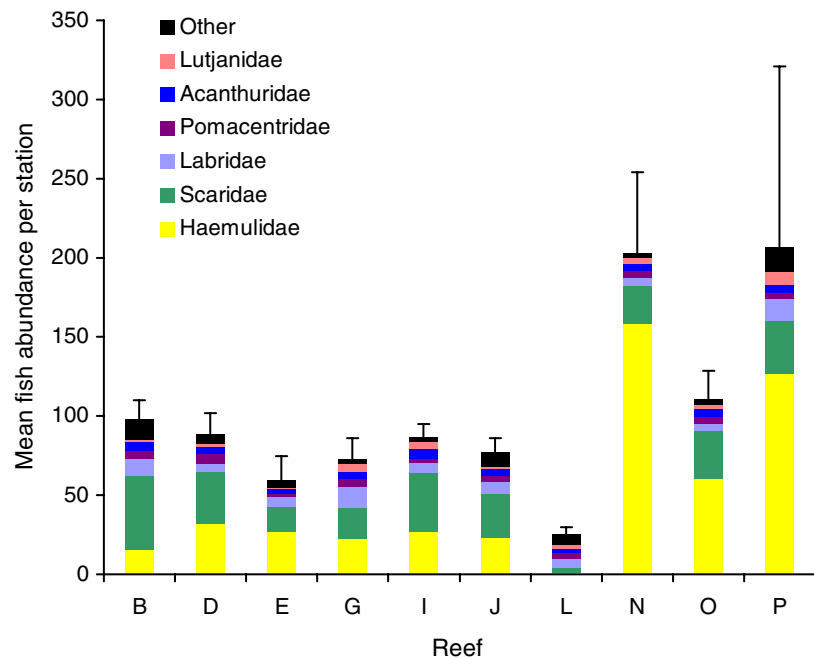


Fig. 5 Mean fish abundance (individuals per 7.5-m radius cylinder) by family on 10 patch reefs in Biscayne National Park showing reef-to-reef variability. Error bars (± 1 SE) presented for total fish abundance per reef



abundance data (Table 2, Fig. 7), with more fish found at high rugosity stations compared to medium and low (Tukey's honestly significant difference, $P < 0.05$). On 8 out of the 10 reefs, high rugosity stations had the greatest mean fish abundance of the three rugosity categories.

Discussion

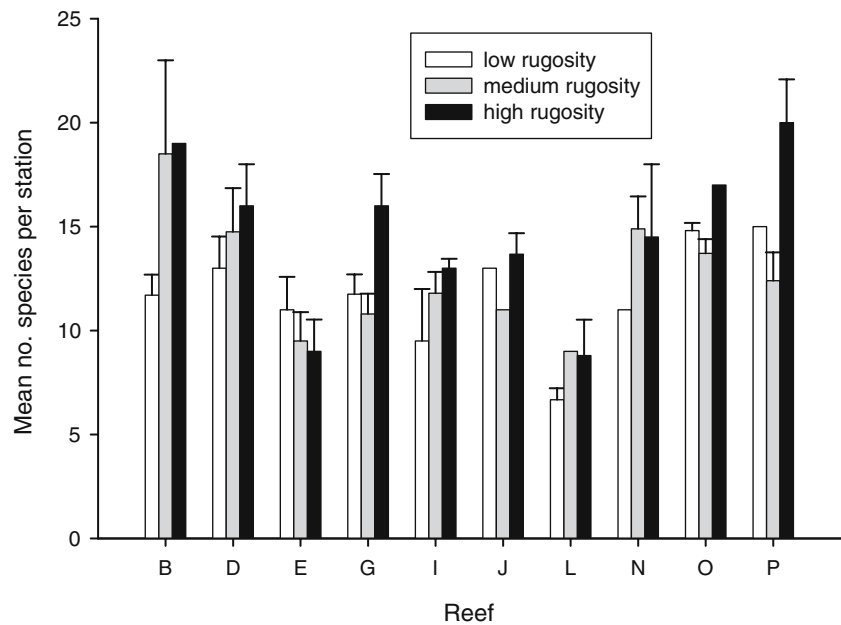
Fish community attributes were not well correlated with rugosity indices derived from the

EAARL data in this study. This was initially surprising given the results of past work (Luckhurst and Luckhurst 1978; Chabanet et al. 1997; Friedlander et al. 2003). However, other studies have reported a lack of relationship between habitat and fish variables (Sale and Douglas 1984). These disparate results could have to do with the range in habitat types included in the studies. The reefs we selected were all mid-shelf patch reefs, and thus do not incorporate the range in rugosity that would be apparent if different habitats (e.g., fore reef, sand plains, etc.) were

Table 2 Two-way ANOVA results for fish species richness and fish abundance (data rank-transformed), by EAARL rugosity (low, medium, and high) and reef (10 levels). Statistically significant P -values (< 0.05) are highlighted in bold

Factor	Df	SS	MS	F	P
<i>Fish species richness</i>					
Rugosity 10-m	2	101.26	50.63	5.27	0.0069
Reef	9	462.17	51.35	5.35	0.0000
Interaction term	18	231.96	12.89	1.34	0.1822
Error	88	844.65	9.60		
Total	117				
<i>Total fish abundance (ranks)</i>					
Rugosity 10-m	2	10368.1	5184.03	7.34	0.0011
Reef	9	35957.5	3995.28	5.66	0.0000
Interaction term	18	12541.9	696.77	0.99	0.4822
Error	88	62143.0	706.17		
Total	117				

Fig. 6 Bar graph showing relationship between fish species richness and patch reef, broken down into three categories of EAARL rugosity (low, medium, and high) calculated at the 10-m scale. Error bars are ± 1 SE, and are absent where $n = 1$

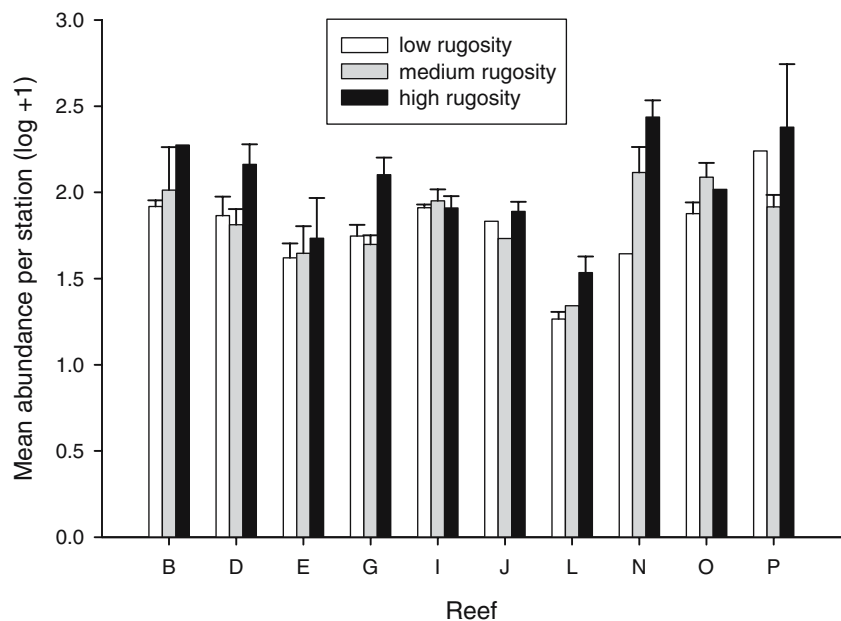


considered. Most studies that have concluded biologically relevant correlations between benthic variables and fish communities have included vastly different habitats and/or depths in their studies (Luckhurst and Luckhurst 1978; Chabanet et al. 1997; Friedlander et al. 2003; Gratwicke and Speight 2005). This distinction is important; it is well known that fish species have affinities for particular habitats (Christensen et al. 2003), but

fish distributions within the same habitat type are much more difficult to explain (Roberts and Ormond 1987).

In our study, the fish observed during a particular fish count had more to do with what reef we were sampling than any of the physical or benthic variables (data to be presented in another manuscript) that were measured. This strong 'reef' effect was observed in all of our analyses of

Fig. 7 Bar graph showing relationship between fish abundance (log-transformed) and patch reef, broken down into three categories of EAARL rugosity (low, medium, and high) calculated at the 10-m scale. Error bars are ± 1 SE, and are absent where $n = 1$



fish community attributes, in agreement with other studies on fish community structure conducted on patch reefs (Sale and Douglas 1984; Syms and Jones 2000; Chittaro and Sale 2003). The stochastic nature of larval dispersal and recruitment of most reef fishes is widely recognized as a contributing factor to the uniqueness of communities separated by space and time. Abundance of larval fish settling from the plankton is spatially and temporally heterogeneous and does not correlate strongly with winds, tides, or other environmental variables (Wilson and Meekan 2001).

In hindsight, the patch reef habitat was probably not a good choice of habitat type to focus on while in search of relationships between lidar rugosity and fish communities. Ault and Johnson (1998) found that fish populations found on isolated patch reefs are much more responsive to larval recruitment patterns than populations on contiguous reef. They suggest that post-settlement processes such as migration would be of little importance on patch reefs due to decreased connectivity with neighboring reef habitat (habitat characteristics explained less variance in fish assemblages on patch reefs compared to contiguous reef), especially in more site-attached species. On a contiguous reef, fishes are able to move without leaving shelter to areas of ecological significance, such as sites with greater food availability, or spawning sites. Another possible explanation for the lack of relationship between rugosity and fish attributes in this study could be the low abundance of large fish that typically use this habitat. Historical studies report that grouper (including red, black and Nassau), mutton snapper, and hogfish utilized the cavernous outer fringe of BNP patch reefs as habitat (Jaap 1984), whereas we did not see a single individual of these species. Perhaps this habitat is simply under saturated with fish due to recreational fishing (presently allowed in the park), thereby masking potential relationships.

However, further analysis of our data gave clues as to the potential of EAARL rugosity in predicting fish community attributes in future studies. Once the variation due to the 'reef' effect was taken out of the statistical models by applying two-way ANOVA, distribution of fishes and fish

species into rugose areas within individual reefs was observed (Figs. 6 and 7). Thus, reef fish do not seem to be arriving at or surviving on particular patch reefs for any specific reason that we can discern, but when the analysis is scaled down to look at distribution of fishes within reef, lidar rugosity explains a statistically significant amount of variance in fish community attributes. Given the isolation of these patch reefs, separated by a minimum of 72 m of open sand and seagrass habitat, resident fish may not be in control of what isolated patch reef they land and must persist on, but they do seem to be non-randomly selecting an area to reside within their home reef on the scale of tens of meters. Whereas our dataset can only be used to show relationships between EAARL rugosity and fish community attributes when reef-to-reef variability was removed and distributions analyzed within reefs, we believe that the detection of these patterns gives clues as to the utility of EAARL in habitats where the isolation of habitat patches is not the driving factor behind the assemblages observed there.

There was a statistically significant, though very weak, correlation between EAARL rugosity and rugosity measurements made with the chain method. Given that the latter method is labor-intensive, time consuming, and subject to observer bias (authors' personal observations), it would be extremely beneficial to reef scientists and managers to have a new tool for assessing substratum rugosity. Our results indicate that the chain-transect method and the EAARL are probably not measuring rugosity at the same scale. The good relationship between distance from reef edge and EAARL rugosity shown here indicates that EAARL may be better at detecting rugosity resulting from the sloping edges of the reefs ('broad' scale rugosity) than the chain transect (more appropriate for 'fine' scale rugosity), and the difficulty in using the chain method at the margins of the reef could help explain the lack of a good relationship between the two methods. It is very difficult to use the chain-transect method at reef edges because placing a transect line parallel to the water surface on a sloping reef edge is practically impossible, leading to an underestimation of rugosity at reef edges.

Also, none of the relationships between fish attributes and chain rugosity was statistically significant in this study, whereas relationships between fish and lidar rugosity were significant (though not explaining an ecologically relevant amount of variation due to the reef-by-reef variability as explained earlier). Thus, fish may be responding to rugosity on a larger scale than is detectable using the chain transect method. EAARL in this context may represent an improvement in coverage capability, as well as data acquisition at larger spatial scales.

The importance of conducting multi-scale surveys when assessing relationships between marine resources and the physical/geographical environment is increasingly being recognized (Syms 1995; Murdoch and Aronson 1999; Eagle et al. 2001). The EAARL is capable of measuring rugosity at multiple spatial scales over vast tracts of ocean in a single day, suggesting that the EAARL could make substantial contributions to multi-scale studies. Fish respond to habitat at a range of scales, depending upon species, life history stage, and reef zone (Lawson et al. 1999; Nagelkerken et al. 2000; Gust et al. 2001). Identifying the appropriate scales for examining interactions between the organisms of interest and their environment is critical for marine conservation planning. The spatial flexibility of the EAARL allows assessment of habitat rugosity at user-defined increments of scale. Map products that reflect an important ecological variable such as rugosity could add another dimension of value to the standard habitat maps so important to resource managers today.

Conclusions

EAARL lidar rugosity can be measured at multiple spatial scales across large areas of reef. The predictive relationships between fish variables and the EAARL rugosity were weak in this study, but we believe this was a result of stochastically assembled fish populations on patch reefs within BNP, rather than a failure of lidar to detect rugosity within the appropriate range. Once the inter-reef variability was

accounted for in our analyses, the importance of rugosity in determining fish community attributes was revealed on a broad (tens of meters) scale. The fact that the EAARL was sensitive enough to discern patterns in rugosity that explained habitat usage by fish within reefs is promising. Thus, we believe that the EAARL method of assessing substratum rugosity has the potential to help reef resource managers in assessing fish habitat, especially if a greater range of habitat types (e.g., back reef, fore reef) is considered.

Acknowledgments The U.S. Geological Survey (Geological Discipline – Coastal and Marine Geology Program, and Biological Resource Discipline – Terrestrial, Freshwater and Marine Ecosystems Program) was responsible for funding the project. We thank Richard Curry (Biscayne National Park) for in-kind support of our work, and B. Lidz, R. Halley, T. Kellison and V. Garrison for helpful comments on the manuscript. We also thank Capt. Barry Denton for keeping us safe and comfortable aboard his vessel ‘*Winning Ticket*.’ Any use of trade names herein was for descriptive purposes only and does not imply endorsement by the U.S. Government.

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