

TROPICAL COASTAL HABITATS AS SURROGATES OF FISH COMMUNITY STRUCTURE, GRAZING, AND FISHERIES VALUE

ALASTAIR R. HARBORNE,^{1,6} PETER J. MUMBY,¹ CARRIE V. KAPPEL,^{2,3} CRAIG P. DAHLGREN,⁴ FIORENZA MICHELI,³
KATHERINE E. HOLMES,⁵ AND DANIEL R. BRUMBAUGH⁵

¹Marine Spatial Ecology Lab, School of Biosciences, Hatherly Laboratory, University of Exeter, Prince of Wales Road, Exeter EX4 4PS United Kingdom

²National Center for Ecological Analysis and Synthesis, University of California Santa Barbara, 735 State St, Suite 300, Santa Barbara, California 93101 USA

³Hopkins Marine Station, Stanford University, Oceanview Boulevard, Pacific Grove, California 93950-3094 USA

⁴Perry Institute for Marine Science, 100 N. U.S. Highway 1, Suite 202, Jupiter, Florida 33477-5112 USA

⁵Center for Biodiversity and Conservation, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024-5192 USA

Abstract. Habitat maps are frequently invoked as surrogates of biodiversity to aid the design of networks of marine reserves. Maps are used to maximize habitat heterogeneity in reserves because this is likely to maximize the number of species protected. However, the technique's efficacy is limited by intra-habitat variability in the species present and their abundances. Although communities are expected to vary among patches of the same habitat, this variability is poorly documented and rarely incorporated into reserve planning. To examine intra-habitat variability in coral-reef fishes, we generated a data set from eight tropical coastal habitats and six islands in the Bahamian archipelago using underwater visual censuses. Firstly, we provide further support for habitat heterogeneity as a surrogate of biodiversity as each predefined habitat type supported a distinct assemblage of fishes. Intra-habitat variability in fish community structure at scales of hundreds of kilometers (among islands) was significant in at least 75% of the habitats studied, depending on whether presence/absence, density, or biomass data were used. Intra-habitat variability was positively correlated with the mean number of species in that habitat when density and biomass data were used. Such relationships provide a proxy for the assessment of intra-habitat variability when detailed quantitative data are scarce. Intra-habitat variability was examined in more detail for one habitat (forereefs visually dominated by *Montastraea* corals). Variability in community structure among islands was driven by small, demersal families (e.g., territorial pomacentrid and labrid fishes). Finally, we examined the ecological and economic significance of intra-habitat variability in fish assemblages on *Montastraea* reefs by identifying how this variability affects the composition and abundances of fishes in different functional groups, the key ecosystem process of parrotfish grazing, and the ecosystem service of value of commercially important finfish. There were significant differences in a range of functional groups and grazing, but not fisheries value. Variability at the scale of tens of kilometers (among reefs around an island) was less than that among islands. Caribbean marine reserves should be replicated at scales of hundreds of kilometers, particularly for species-rich habitats, to capture important intra-habitat variability in community structure, function, and an ecosystem process.

Key words: Bahamas; beta diversity; ecosystem goods and services; ecosystem processes; functional groups; intra-habitat variability; marine reserve networks; reef-fish communities; spatial variability.

INTRODUCTION

The protection of biodiversity, often through the use of protected areas, is a core aim of conservation (Margules and Pressey 2000, Lovejoy 2006) in order to maintain ecosystem functions, goods, and services (Solan et al. 2004, Worm et al. 2006). However, the focus of many conservation efforts is on species, even

though the term “biodiversity” is defined to cover biotic variation at levels from genes to ecosystems (Purvis and Hector 2000). This presents a major problem to researchers because conducting sufficient sampling to establish the number and distribution of species across an area of interest is frequently impractical (Roberts et al. 2003, Turner et al. 2003). Furthermore, the problem is growing as these data are increasingly recognized as a key input into systematic and cost-effective conservation planning (Balmford and Gaston 1999, Margules and Pressey 2000). There are a few examples where excellent spatial data are available for bird (Williams et al. 1996)

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⁶ E-mail address: a.r.harborne@ex.ac.uk

and temperate marine species (Ward et al. 1999), but most conservation planning has to be accomplished with an incomplete map of species distributions.

Given the almost inevitable limitations of available data, the use of surrogates for species diversity is attractive, although there are significant limitations (Ferrier 2002, Brooks et al. 2004). Generally, surrogates may be taxonomic, where known patterns of one taxa are used to infer patterns in other taxa, or environmental, where abiotic and biotic variables are believed to provide information on the spatial distribution of species (Oliver et al. 2004). Environmental surrogacy is commonly used synonymously with the consideration of landscape patches (e.g., habitats or land classes), but also incorporates approaches such as environmental diversity (Faith and Walker 1996). Landscape patches are a particularly attractive surrogate for species diversity because they embody variation in biophysical properties that affect the distribution and abundance of species, and are detectable through the use of remote sensing (Turner et al. 2003). Furthermore, the decreasing costs of remotely sensed imagery and increasing ease of data analysis mean that habitat types within many land and seascapes can be mapped relatively quickly and accurately (Mumby et al. 2004b, McDermid et al. 2005). Because there is frequently an either explicit or implicit link between habitats and distinct groups of species ("coherence within classes"; Mac Nally et al. 2002), habitat maps represent a key surrogate of biodiversity for conservation planning (Margules and Pressey 2000). Consequently, there is now an extensive literature on the subject of the assessment and monitoring of biodiversity through the use of remote sensing in terrestrial systems (e.g., Stoms and Estes 1993, Nagendra and Gadgil 1999). Subsequent application of this work to reserve planning seems clear: Habitat heterogeneity generally positively correlates with the cumulative number of species in the area, and should be a prime factor for choosing among alternative sites for reserves (Roberts et al. 2003).

Despite the appeal of the assessment of biodiversity by remote sensing of habitat types, a number of problems remain; in particular, extensive information on species-habitat associations is required, and inference may be limited by high beta diversity (Nagendra 2001). Beta diversity (or species turnover) incorporates a range of concepts, but is generally regarded as referring to some component of how two or more sampling units vary across spatial or temporal axes (e.g., Magurran 2004). If beta diversity is high, species assemblages may vary both among and within habitats. While inter-habitat differences, such as the species present or the abundances of species, among ecological communities are assumed when mapping habitats, intra-habitat heterogeneity (i.e., differences among patches of the same habitat) will reduce the efficacy of habitat maps as surrogates of biodiversity. Despite its importance when habitats are used as surrogates, intra-habitat beta

diversity is rarely quantified empirically (but see Oliver et al. 2004 for an exception including multiple taxa), and conservation planners are forced to consider different patches of the same habitat as identical (Ferrier 2002). Intra-habitat variation was, therefore, the focus of this study. We both document intra-habitat variability in tropical coastal habitats and aim to identify a proxy of this variability that could be used to suggest which habitats should be represented more frequently in networks of reserves.

Coral reefs, mangroves, and seagrass beds represent high-diversity systems (e.g., Karlson and Cornell 1998) that provide a range of important ecological and economic goods and services, such as seafood production and shoreline protection (Moberg and Folke 1999). However, these goods and services are threatened by a suite of stressors, and conservation efforts, such as limiting exploitation and increasing recruitment of key functional groups through the use of marine reserves, are imperative (Hughes et al. 2003, Pandolfi et al. 2003, Bellwood et al. 2004). Tropical marine ecosystems typically have exceptionally high levels of water clarity, and remote-sensing methods have been applied to map habitats with great accuracy (Mumby et al. 1998). Despite the relative ease of habitat mapping tropical marine habitats, and the need to quantify biodiversity for marine reserve selection algorithms (e.g., Sala et al. 2002, Leslie et al. 2003), few empirical studies evaluate the adequacy of remotely sensed habitat maps as biodiversity surrogates. Friedlander et al. (2003a) used habitat maps and the distinct inter-habitat differences in coral and fish communities to aid the design of an effective marine protected area in Colombia. In Panama, there was only a weak positive correlation between benthic diversity and the number of geomorphological zones in an area, regardless of the taxa considered, and this suggested that habitat types would be a better surrogate (Andréfouët and Guzman 2005).

Here, we evaluated the use of habitats as a surrogate of reef-fish community structure through the use of a large-scale data set on coral-reef fishes from eight habitats that range from coral-rich forereefs to seagrass communities. The study had three major aims, all of which have implications for marine reserve design. Firstly, we sought to show that each habitat contains distinct fish communities, through the consideration of the species present or the species present and their abundances, and justifies the approach of the assessment of biodiversity from such seascape surrogates. This inter-habitat beta diversity is only described briefly as variability in fish community structure with habitat zonation is relatively well established on reefs (e.g., Alevizon et al. 1985, McGehee 1994, Bouchon-Navaro et al. 2005). We then focus on beta diversity among patches of the same habitat type, and tested the hypothesis that the number of species in a habitat can be used as a proxy of its intra-habitat variation in community structure. Higher numbers of species poten-

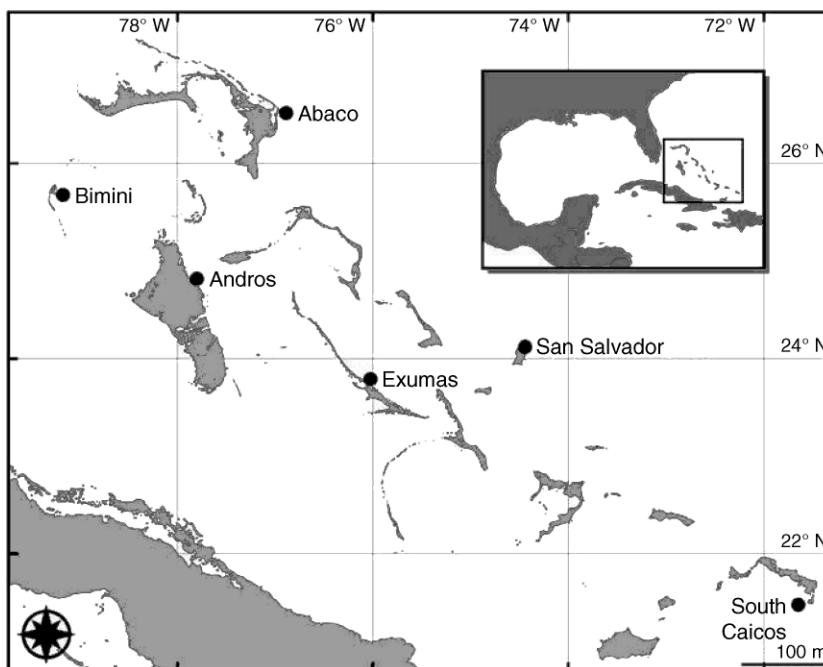


FIG. 1. Location of survey sites within the Bahamian archipelago.

tially leads to greater scope for variation because more species can exhibit local absence or stochastic or deterministic variation along biophysical gradients. Our final aim was to consider the ecological and economic significance of intra-habitat variations in community structure (i.e., is such beta diversity really important?). To address this question, we analyzed how variability in fish community structure affects ecological function (composition and abundance of different trophic groups), an ecosystem process (grazing by parrotfishes), and an ecosystem service (value of commercially important finfish). These analyses considered variation in *Montastraea* reefs (forereef habitats visually dominated by *Montastraea* corals) at both inter-island and inter-reef scales. *Montastraea* reef is the most species-rich habitat on Caribbean reefs and is hypothesized to have the greatest intra-habitat variability. Because reefs on the same island are likely to have more similar abiotic, biotic, and hydrodynamical conditions than reefs on different islands, we hypothesized that reef-scale variability will be less than that observed at island scales. The increasing dissimilarity of communities within habitats, or increasing beta diversity, with increasing distance has been documented for both marine and terrestrial ecosystems (e.g., Condit et al. 2002, Ellingsen and Gray 2002).

METHODS

Study sites and sampling design

Data were collected from around six islands in the Bahamian archipelago (Fig. 1): Abaco, Andros, Bimini, Exumas, San Salvador, and South Caicos (Turks and

Caicos Islands). The focal habitats were forereefs visually dominated by corals from the genus *Montastraea*, gorgonian and algae-dominated forereef, reef crest visually dominated by living or dead *Acropora palmata*, lagoonal patch reefs (subsequently “*Montastraea* reef,” “gorgonian plain,” “reef crest,” and “patch reef”), sparse, medium density, and dense seagrass beds, and mangroves. Seagrass habitats were defined as those visually assessed as having standing crops of 1 or 2 (sparse), 3 or 4 (medium-density), and 5 or 6 (dense) on the six-point scale defined by Mumby et al. (1997). Additional details of the hard-bottom habitats can be found in Mumby and Harborne (1999). These habitats represent communities that can typically be mapped through the use of IKONOS satellite imagery that is increasingly popular for remote-sensing applications in tropical coastal habitats (Maeder et al. 2002, Mumby and Edwards 2002, Andréfouët et al. 2003). Not all habitats were surveyed around each island (Table 1). Furthermore, sampling intensity varied among habitats; habitats were sampled at every island where they were found and, if possible, with two or three replicates separated by 5–10 km. This facilitated inter-island comparisons. However, *Montastraea* reefs, where they occurred, were also sampled with intra-reef replication (two or three replicates, <1 km apart). This sampling gave three sets of two or three closely spaced replicates with each set separated by 5–10 km, and allowed inter-reef analyses. Hence intra-habitat variation in fish community structure could be quantified at among-island and among-reef scales in a nested sampling design

TABLE 1. Sampling effort for each habitat type around the six islands visited in the Bahamian archipelago.

Habitat type	Abaco	Andros	Bimini	Exumas	San Salvador	South Caicos
Dense seagrass	3	2	3	3	1	2
Gorgonian plain	3	3	3	3	4	4
Mangrove	3	2	3	3	4	2
Medium-density seagrass	3	1	3	3	2	3
<i>Montastraea</i> reef	—	9	—	6	8	7
Patch reef	3	3	—	3	3	3
Reef crest	—	3	—	—	3	3
Sparse seagrass	3	3	3	—	1	4

Notes: All habitats were surveyed with island-scale replication, but only *Montastraea* reef was sampled with reef-scale replication (three sets of two or three closely spaced replicates with each set separated by 5–10 km). Values reported are the number of sites surveyed, and “—” indicates that habitat was not surveyed around that island.

for *Montastraea* reefs, but only at the former scale for the other seven habitats.

Fish community characterization

At each site, all but nocturnal (e.g., Apogonidae) and highly cryptic (Clinidae and Gobiidae) fish species were surveyed through the use of discrete group visual fish census (Green and Alevizon 1989). Species were divided into three groups and their density and size (to nearest centimeter) estimated along belt transects at each island system. Transect size and number was optimized through the use of data from equivalent surveys within the Caribbean (Mumby et al. 2004a). The following list of families surveyed by each diver is indicative rather than exhaustive, but transect dimensions and number were: 30×2 m ($n = 4$) for Pomacentridae, Labridae, Holocentridae, and small Serranidae; 30×4 m ($n = 10$) for Scaridae, Acanthuridae, Pomacanthidae, Chaetodontidae Diodontidae, and Monacanthidae; 50×4 m ($n = 5$) for Haemulidae, Lutjanidae, Carangidae, Balistidae, planktivorous Labridae, large Serranidae, and other large predators.

Statistical analyses

Fish data from each site were analyzed through the use of the following three metrics of abundance: (1) each species was recorded as being present or absent; (2) the density of each species was calculated as the total number of individuals seen at a site divided by the number of transects surveyed at that site and standardized to an area of 200 m^2 ; or (3) the mean biomass of each species was calculated as the total mass of individuals at a site divided by the number of transects surveyed at that site and standardized to an area of 200 m^2 . Inter-habitat differences and comparisons of intra-habitat variability among the eight habitat types were examined through the use of fish species' presence/absence and density and biomass data. Presence/absence analyses reflect traditional approaches to conservation where marine reserves simply aim to include all species found in an area, irrespective of their abundance (e.g., Sala et al. 2002). In contrast, biomass data are important for the consideration of ecosystem structure, trophic

relationships, and fisheries exploitation, but are heavily influenced by large, common species (Bohnsack and Harper 1988). Density data represent an intermediate metric of community composition between these two extremes. Detailed analyses of intra-habitat variation on *Montastraea* reefs were conducted through the use of biomass and density data alone, because some of the measures of variability used (e.g., grazing pressure) cannot be applied to presence/absence data. Fish lengths were converted to biomass using allometric relationships (Bohnsack and Harper 1988). Fish masses were calculated by using

$$\log(M) = \log(a) + b[\log(L)] \quad (1)$$

where M is the mass in grams, L is the length in millimeters, and a and b are constants. The values for $\log a$ and b for the parrotfish *Sparisoma viride* are -4.5223 and 2.9214 , respectively, so that the mass of a 300 mm fish is: $\log(M) = -4.5223 + 2.9214 \times \log(300) = 2.71$, and gives a value for M of 518 g. The equation was applied to every fish recorded (using the appropriate constant values) to allow mean biomass to be calculated.

Tests of inter- and intra-habitat variation in community structure across all habitats of presence/absence data and biomass and density data with a square-root transformation were conducted with one-way ANOSIM (Clarke 1993). ANOSIM returns a statistic R , which is a measure of separation among groups where 0 indicates complete mixing and 1 represents full clustering in which all samples within groups are more similar to one another than to any sample in another group. In order to compare variation in *Montastraea* reefs to the other seven habitats, a single site from each set of replicates separated by 5–10 km on each island was randomly chosen to test only island-scale differences. The use of data from a single site from each set of replicates removed reef-scale variation from the *Montastraea* reef habitat data. Subsequent analyses of intra-habitat variation in *Montastraea* reefs utilized the entire data set. Nested ANOSIM (entire community, individual family, and functional group structure) and nested ANOVA (number of species, Shannon diversity, grazing intensity, and fishery value; with square root or Box-Cox

transformations where necessary to meet the assumptions of normality) were used to analyze variation at island and reef scales. Bartlett's test was used to ensure homogeneity of variances. Shannon diversity was calculated according to

$$\text{Diversity } H = -\sum_{i=1}^S P_i \ln(P_i) \quad (2)$$

where S is the number of species present in the community, and P_i is the proportional abundance of the i th species.

Island-scale variation in mean biomass and density of functional groups (groups of species sharing a feeding strategy, such as piscivory or planktivory), grazing intensity, and fishery values were also quantified by (1) the coefficient of variation (standard deviation of mean values from each island divided by the mean of those values) and (2) the maximum difference between a pair of islands, expressed as a percentage of the mean calculated from all islands. Equivalent metrics were calculated for reef-scale variation; a coefficient of variation and maximum percentage difference was calculated for each island and then summarized as mean coefficient of variation and mean maximum percentage difference. Species were allocated to a functional group through the use of FishBase (*available online*),⁷ along with Bohlke and Chaplin (1993), Claro et al. (2001), and Randall (1967) (see Appendix A). Functional groups were assumed to be constant across survey sites because the groupings are broadly defined, and we are unaware of any data that suggest fish exhibit inter- or intra-habitat variation in their guilds. Parrotfish grazing was calculated using the model described in Mumby et al. (2006), which integrates fish densities and sizes with species-specific data on bite rates and mouth sizes. Fisheries values were calculated by multiplying standing stock with current market prices. Significance levels for multiple comparisons of families and functional groups within the data set for *Montastraea* reefs were adjusted through the use of the unweighted Bonferroni method of α/n (Shaffer 1995). However, any results where $P < 0.05$ are highlighted, because the use of Bonferroni corrections can be overly conservative (Gotelli and Ellison 2004).

RESULTS

Inter-habitat variation

A total of 153 species from 40 families were recorded from the 134 sites and eight habitats, and reflected the relatively depauperate Caribbean fish fauna (Bellwood and Wainwright 2002). Different habitats clearly had distinct fish communities, irrespective of whether these differences were assessed with univariate or multivariate statistics. There was significant inter-habitat variation in

the number of species and diversity per site (Kruskal-Wallis; $P < 0.001$). There was also significant variation in multivariate community structure among habitats with presence/absence data (ANOSIM, $R = 0.748$; $P = 0.001$), density (ANOSIM, $R = 0.705$; $P = 0.001$), or biomass data (ANOSIM, $R = 0.656$; $P = 0.001$). Furthermore, subsequent pairwise comparisons of biomass data showed that every habitat was significantly different from every other (ANOSIM, $P \leq 0.03$), with the exception of patch reef vs. reef crest (ANOSIM, $R = 0.096$; $P = 0.092$) and medium-density seagrass vs. dense seagrass (ANOSIM, $R = 0.004$; $P = 0.389$). Only 4.6% of the species were seen in all habitats compared to >27% that were in only one habitat.

Number of species as a proxy of intra-habitat variability

The mean (\pm SE) number of species recorded in a habitat per survey varied from 2.9 ± 0.8 in sparse seagrass beds to 41.5 ± 1.4 on *Montastraea* reefs (Table 2). Island-scale intra-habitat variation in community structure, based on fish biomass data, was significant in all habitats, except medium-density and dense seagrass beds (Fig. 2, Table 2). Variation in mean number of species was highly and positively correlated to island-scale variation in community structure (quantified as ANOSIM R ; Pearson product-moment correlation coefficient, $r = 0.895$, $P = 0.003$; Fig. 2, Table 2). Furthermore, intra-habitat variation was positively correlated with the mean number of genera and families ($r = 0.891$, $P = 0.003$ and $r = 0.885$, $P = 0.004$, respectively; Table 2). Density data also gave significant positive correlations between number of species, genera, or families in a habitat and island-scale variation in community structure in that habitat (Table 2). Intra-habitat variation was significant in all eight habitats. Correlations were only marginally significant if species' presence/absence were used instead of biomass data ($0.083 \geq P \geq 0.059$; Table 2), but intra-habitat variation was significant in six of the eight habitats ($P < 0.05$), excepting mangroves and sparse seagrass.

Intra-habitat variation of Montastraea reefs and consequences for community function and an ecosystem process and service

Number of species and Shannon diversity did not vary at island or reef scales (nested ANOVA: $P > 0.05$) in the *Montastraea* reef habitat, and intra-habitat variability appears negligible using these simple metrics of fish community structure. However, density and biomass data did detect significant inter-island and reef-scale variation in the community structure of different families and functional groups. Density and biomass data gave quantitatively very similar results for family and functional group analyses, and for clarity the density results are contained in Appendix B. The following results refer to analyses with biomass data. Following a Bonferroni correction, significant inter-island variation occurred in the entire community and

⁷ <http://www.fishbase.org>

TABLE 2. (a) Mean number of species, genera, and families per sampling unit in each of the habitats surveyed and the results of ANOSIM tests of island-scale intra-habitat variability using presence/absence, density, and biomass data and (b) Pearson product-moment correlation coefficients between the mean number of taxa in each habitat and the amount of intra-habitat variability.

Habitat type or sampling unit	Mean number of taxa per sampling unit (\pm SE)				ANOSIM of intra-habitat variability using different abundance metrics					
	n	Species	Genera	Families	Presence/absence		Density		Biomass	
					R	P	R	P	R	P
a) Habitat										
Montastraea reef	11	41.5 (1.4)	26.5 (0.9)	17.5 (0.6)	0.502	0.004	0.938	0.001	0.760	0.001
Patch reef	15	36.3 (2.2)	21.1 (1.3)	14.6 (0.8)	0.848	0.001	0.837	0.001	0.781	0.001
Reef crest	9	29.1 (1.8)	17.9 (1.0)	12.4 (0.8)	0.609	0.004	0.317	0.039	0.350	0.018
Gorgonian plain	20	25.0 (2.2)	17.3 (1.4)	12.5 (0.7)	0.529	0.001	0.669	0.001	0.595	0.001
Mangroves	17	13.1 (1.2)	9.1 (0.7)	7.1 (0.4)	0.159	0.123	0.259	0.033	0.285	0.025
Dense seagrass	14	6.1 (0.9)	5.1 (0.6)	4.7 (0.5)	0.333	0.031	0.391	0.010	0.157	0.149
Medium-density seagrass	15	3.2 (0.5)	2.9 (0.4)	2.7 (0.4)	0.485	0.002	0.372	0.012	0.151	0.137
Sparse seagrass	14	2.9 (0.8)	2.6 (0.7)	2.2 (0.5)	0.228	0.064	0.318	0.043	0.304	0.030
b) Sampling unit										
Species					0.689	0.059	0.797	0.018	0.895	0.003
Genus					0.646	0.083	0.804	0.016	0.891	0.003
Family					0.650	0.081	0.798	0.018	0.885	0.004

Note: Significant results ($P < 0.05$) are shown in boldface type.

for acanthurids, labrids, territorial pomacentrids, scarids, and small serranids (nested ANOSIM, $P < 0.0045$; Table 3). Without the Bonferroni correction, there was evidence of island-scale variation for all families ($P < 0.05$), except lutjanids and large groupers ($P > 0.05$). No group exhibited reef-scale variation, except in the absence of the Bonferroni correction when the commu-

nity structure of the entire community, lutjanids, territorial pomacentrids, and scarids varied at scales of 5–10 km within a reef complex ($P < 0.05$). Community structure can be considered more homogeneous at this scale than among islands.

Of the eight functional groups, the community structure of four varied significantly at the island scale

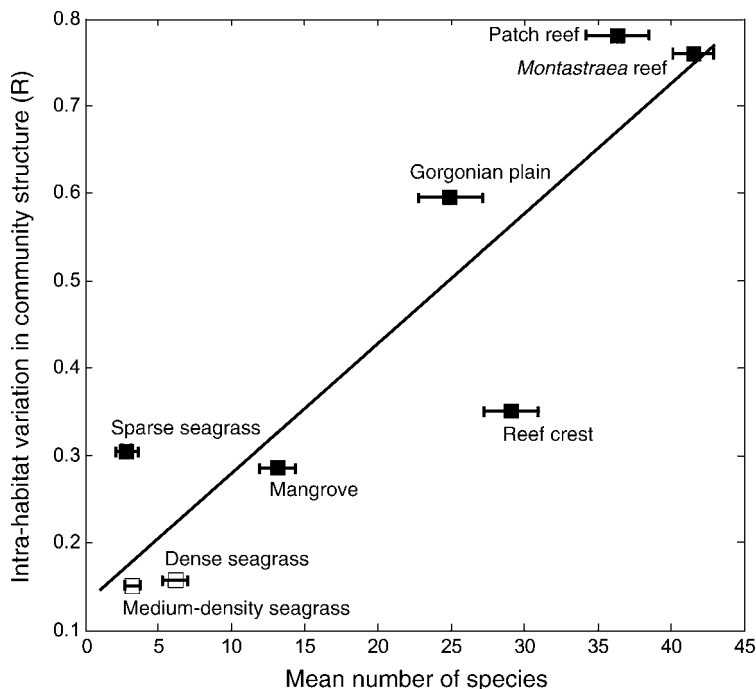


FIG. 2. Mean number of species per sample in each habitat vs. island-scale variation in community structure (ANOSIM global R for that habitat using biomass data). The Pearson product-moment correlation coefficient was 0.895 ($P = 0.003$). Filled squares indicate that the R value is significantly greater than 0; open squares indicate that R is not significantly different from 0. Error bars represent standard error. The solid line indicates linear regression. Raw data are reported in Table 2.

TABLE 3. Intra-habitat variation (assessed by nested ANOSIM of biomass data) within the entire fish community and individual families at island and reef scales for *Montastraea* reefs.

Taxon	Island-scale variation		Reef-scale variation	
	R	P	R	P
Entire community	0.849	0.001	<i>0.240</i>	<i>0.012</i>
Acanthuridae	0.644	0.004		0.230
Balistidae	<i>0.609</i>	<i>0.005</i>		0.256
Chaetodontidae	<i>0.387</i>	<i>0.007</i>		0.599
Haemulidae	<i>0.307</i>	<i>0.012</i>		0.119
Labridae	0.636	0.001		0.698
Lutjanidae		0.096	<i>0.159</i>	<i>0.045</i>
Territorial Pomacentridae†	0.689	0.003	<i>0.361</i>	<i>0.005</i>
Scaridae	0.564	0.002	<i>0.248</i>	<i>0.025</i>
Large Serranidae‡		<i>0.134</i>		0.843
Small Serranidae§	0.533	0.001		0.286

Notes: Boldface values are significant results following a Bonferroni correction of 0.05/11 ($P < 0.0045$), and italicized values show significance values of $0.05 > P > 0.0045$. Remaining values are not significant ($P > 0.05$). Missing R values correspond to results that were not significant ($P > 0.05$).

† *Stegastes* and *Microspathodon* only.

‡ Large, commercially important only (*Mycteroperca bonaci*, *M. tigris*, *M. venenosa*, *M. interstitialis*, and *Epinephelus striatus*).

§ *Cephalopholis fulvus*, *C. cruentatus*, *Epinephelus guttatus*, and *E. adscensionis*.

(nested ANOSIM with Bonferroni correction, $P < 0.0063$; Table 4), namely invertivores of small, mobile prey, planktivores, grazers of turf algae, and grazers of turf and macroalgae. Invertivores of large, mobile prey, and piscivores also exhibited significant variation in community structure in the absence of the Bonferroni correction ($P < 0.05$). This variability in multivariate community structure among islands represented a deviation in total biomass of up to 1.19 (coefficient of variation across all four islands), and a maximum difference between a pair of islands of ~250% of the mean for planktivorous fishes (Table 4). The community structure of only three functional groups varied significantly at reef scale (invertivores of large, mobile prey, grazers of turf algae, and grazers of turf and macroalgae), with the latter only significant without the Bonferroni correction ($P < 0.05$). Invertivores of large,

mobile prey had the highest mean coefficient of variation (0.83) and mean maximum difference of biomass (the maximum difference between a pair of sites on a given island was, on average, ~135% of the mean). Coefficients of variation and maximum percentage differences were generally lower at the reef scale than at the island scale (Table 4), and were consistent with the multivariate results that suggest reef-scale variation was less than at island scales.

Mean (\pm SE) grazing intensity by parrotfishes was estimated to be 1.08% \pm 0.21% of the reef/hour, but varied significantly among islands (nested ANOVA, $F_{3,19} = 9.17$, $P = 0.001$), with up to a threefold difference between maximum and minimum values (Fig. 3). The coefficient of variation among islands was 0.39, and the maximum difference between a pair of islands was ~90% of the mean. Variation was detected at reef scales,

TABLE 4. Intra-habitat variation of fish functional groups at island and reef scales for *Montastraea* reef.

Functional group	No. species recorded	Island-scale biomass data					Reef-scale biomass data			
		Mean (\pm SE)	Nested ANOSIM		Maximum difference (%)	Nested ANOSIM		Mean maximum difference (%)		
			R	P		R	P		CoV	
Iv/Pi	14	2065.52 (426.64)		0.100	0.41	79.10		0.159	0.35	61.08
Iv LM	41	3515.07 (1264.44)	<i>0.293</i>	<i>0.014</i>	0.72	145.55	0.327	0.005	0.83	135.35
Iv S	6	65.16 (18.91)		0.126	0.58	135.25		0.267	0.46	75.31
Iv SM	11	38.63 (7.09)	0.722	0.002	0.37	89.64		0.709	0.30	46.71
Pi	14	1524.06 (304.80)	<i>0.336</i>	<i>0.011</i>	0.40	97.56		0.102	0.52	91.46
Pk	8	1702.78 (1010.34)	0.724	0.002	1.19	250.87		0.098	0.38	91.47
Tu	12	377.94 (98.63)	0.742	0.001	0.52	117.22	0.332	0.003	0.38	58.95
Tu/Ma	8	1581.68 (197.05)	0.511	0.005	0.25	49.16	<i>0.222</i>	<i>0.042</i>	0.29	54.07

Notes: Differences in community structure were tested by nested ANOSIM, and variation of total biomass was quantified as coefficient of variation (CoV). The maximum difference between two islands (or reefs) is expressed as a percentage of the mean. Functional category abbreviations are: Iv/Pi, invertivore/piscivore; Iv LM, invertivore of large, mobile prey; Iv S, invertivore of sessile prey; Iv SM, invertivore of small, mobile prey; Pi, piscivore; Pk, planktivore; Tu, grazer of turf algae; and Tu/Ma, grazer of turf and macroalgae. Boldface values are significant results following a Bonferroni correction of 0.05/8 ($P < 0.0063$), and italicized values show significance values of $0.05 > P > 0.0063$. Remaining values are not significant ($P > 0.05$). Missing R values correspond to results that were not significant ($P > 0.05$).

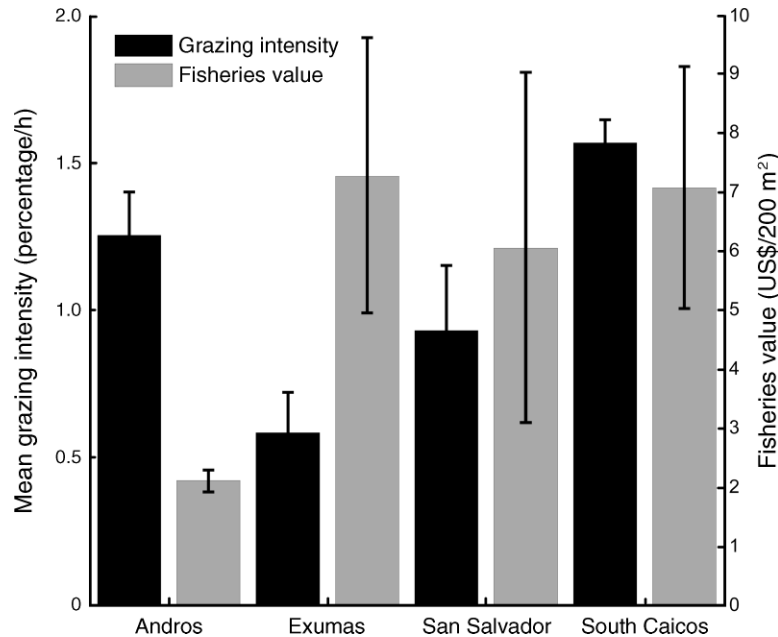


FIG. 3. Plot of intra-habitat variation in grazing intensity and fisheries value at island scale for *Montastraea* reef. Error bars represent \pm SE.

but was less significant than among islands (nested ANOVA, $F_{7,19} = 2.86$, $P = 0.032$). Considerable reef-scale variation in grazing intensity was also reflected in a coefficient of variation of 0.33. Mean fisheries value at the survey sites was 5.63 ± 1.21 U.S. dollars per 200 m², but did not vary significantly at either spatial scale (nested ANOVA, island scale $P = 0.127$ and reef scale $P = 0.653$; Fig. 3). However, the coefficients of variation and maximum differences between a pair of islands or reefs were similar to those for grazing intensity (coefficient of variations ~ 0.45 ; maximum differences $\sim 90\%$ of the means).

DISCUSSION

This study has highlighted significant inter-habitat variation in fish communities and intra-habitat variation in community structure, ecological function, and grazing intensity among islands and, to a lesser degree, among reefs around the same island. This high beta diversity has important implications for conservation planning. Remote sensing of tropical coastal ecosystems through the use of high-resolution sensors such as IKONOS and Quickbird can generate relatively accurate maps of the nature, size, and distribution of habitat patches (Mumby et al. 2004b). It is clear from published data that different habitats contain different assemblages of species, and conservation planners aiming to conserve biodiversity are routinely advised to maximize habitat heterogeneity within reserves (Roberts et al. 2003). Our data on reef fishes supports this principle; different habitats support significantly different fish communities whether considered with biomass or density data, or just species' presence/absence. Furthermore, over a quarter

of species were only found in one of the habitats. More importantly, our data provide insight into the additional "hidden" variability occurring among patches of the same habitat that should be captured by networks of marine reserves, and that the amount of intra-habitat variability can be estimated in different habitats when data are scarce by considering the species richness of each habitat.

Intra-habitat variation at island scales was significant in at least 75% of the habitats studied, irrespective of whether presence/absence, density, or biomass data were used. Intra-habitat variation in tropical coastal habitats is caused by many factors including substratum type, relief, rugosity, depth, food availability, current flow, water quality, wave action, diel and ontogenetic migration, and larval recruitment (e.g., Williams 1991, McGehee 1994, Friedlander et al. 2003b, Gratwicke and Speight 2005). Note that in this study we did not attempt to match pattern to process because of the diverse range of habitats, species, and processes concerned. The use of abundance data, either species' biomass or density, meant that the level of intra-habitat variation, comprised of both alterations of the species present and the abundances of species, was strongly and positively correlated to the mean number of species derived from sampling in that habitat. The correlation between number of species in a habitat and the magnitude of inter-island variation in community structure may be usefully incorporated, along with other economic, social, scientific, and feasibility considerations, within selection algorithms for siting marine reserves. We envisage a situation where conservation planners have a habitat map and some data on species-habitat

associations, either collected from fieldwork or derived from the literature. Our results show that, for reef fishes, habitats that support a high number of species will have the highest intra-habitat variability in community structure among islands (hundreds of kilometer scale). Therefore, it is arguably more important to replicate reserves of species-rich habitats at island scales than habitats supporting fewer species in order to represent the full range of community structure and function. Focusing on replicating species-rich habitats improves many current reserve planning approaches where the protection of a fixed proportion of each habitat is a key target (e.g., 20% of each of 23 habitats in the Florida Keys; Leslie et al. 2003). In terms of incorporating biodiversity into reserve networks, including all habitats, but weighting the amount of each habitat protected by its species richness, is likely to be more effective than aiming for a fixed proportion of its area. Furthermore, this principle will be especially beneficial in the high-diversity tropics where differences in intra-habitat variability are particularly problematic when surrogates are considered (Nagendra 2001).

In contrast to the correlations with density and biomass data, the number of species in a habitat sample was not a very effective proxy of intra-habitat variability in that habitat when presence/absence data were used. When considering only presence/absence data, inter-island variability will be increased in soft-bottom habitats, with otherwise depauperate fish faunas and low variability, by sightings of fishes such as transient predators that occasionally cross these habitats when moving among reefs (Hixon and Carr 1997). Similarly, a single coral head in a seagrass bed will lead to sightings of species, such as pomacentrids, that are normally absent (A. R. Harborne, *personal observation*). Recording species with highly patchy distributions will have lesser effects in species-rich habitats, and inter-island variability will not increase linearly with increasing mean number of species per sample. Abundance data provide a more detailed insight into intra-habitat variability in community structure, and reduces the effects of rarely seen fishes. However, although the mean number of species in a habitat will underestimate variability in the species present around different islands in soft-bottom habitats, these differences are of very limited importance when designing networks of marine reserves because they are driven by transient species or a few individual fishes. Therefore, the representation of species-rich habitats more frequently in networks of marine reserves is still an appropriate method to try to maximize the amount of biodiversity within the reserves. For example, having multiple representations of the *Montastraea* reef habitat around multiple islands in marine reserves will capture more significant intra-habitat differences in species composition than multiple representations of a seagrass habitat. Clearly, during conservation planning, the desire to maximize biodiversity within reserves will have to be balanced with

considerations such as the important nursery function of habitats with relatively depauperate faunas and floras (Mumby et al. 2004a).

That intra-habitat variability also positively correlates with the mean number of genera and families, particularly when density of biomass data are used, reflects a growing literature indicating that recording data at lower resolutions loses relatively little information when compared to species data (e.g., Dethier and Schoch 2006, Marshall et al. 2006). The ability to assess intra-habitat variability with data on genera or families could be particularly useful where taxonomic expertise is not available, such as in projects that utilize nonprofessional researchers (Wells 1995). However, the effectiveness of this approach will vary depending on the ratio of species to higher taxonomic levels. If each species represents a single family, the use of family- and species-level data will be identical, and the relationship will generally weaken with increasing numbers of species in each family. There were 3.8 species per family in this study, although this may be lower than other parts of the Caribbean where the ratio may be as high as 6.2 (Bellwood and Wainwright 2002). Therefore, the use of higher taxa as a proxy of intra-habitat variability may be more effective on reefs such as those in the Caribbean, Hawaii (ratio of 4.4 species per family; Friedlander and Parrish 1998), or the Indian Ocean (ratio of 4.9; Letourneur 1996), than on very diverse Pacific reefs such as in Papua New Guinea, where the ratio has been recorded as >25 species per family (Jones et al. 2004). Furthermore, whether the relationship between species, genera, or family richness and intra-habitat variability in community structure is also seen in other reef taxa (e.g., corals), or indeed other ecosystems, remains to be tested.

High intra-habitat variability at island scales in the community structure of fishes on *Montastraea* reefs reflected differences in a number of fish families, and again highlights the need to include species-rich habitats in multiple marine reserves separated by hundreds of kilometers to capture the full biodiversity of these habitats. The greatest variation was in those families that are generally small, demersal, and have particular benthic requirements for turf and filamentous algae (acanthurids, e.g., Robertson 1991) and territories (pomacentrids, e.g., Itzkowitz 1977). Similarly, labrids from the genera *Halichoeres* and *Thalassoma* have high site fidelity (Jones 2005), and the biomasses of small serranids are affected by coral and algal cover (Sluka et al. 1996). Microhabitats used by these families may vary significantly among islands, but not affect the biomasses of larger species such as lutjanids and haemulids as strongly. Families that exhibit the highest inter-island variation are not highly valued by fisherfolk in the Bahamas. Fishing pressure on more commercially important species such as large serranids has reduced their populations dramatically (e.g., Dahlgren 1999); reduction in fishing pressure benefits these species, as well as by-catch species such as scarids (Mumby et al. 2006).



PLATE 1. The abundance of large, commercially important grouper, such as this Nassau grouper (*Epinephelus striatus*), appears to have limited intra-habitat variation, but this is likely to be because of over-exploitation rather than a naturally homogenous distribution. Photo credit: C. Dahlgren.

Exploitation of targeted species has probably reduced their natural intra-habitat variation (Newman et al. 2006) so that inter-island differences in families such as serranids and lutjanids are unlikely to be currently detectable. Most of these commercially important species are piscivores or invertivore/piscivores, and over-fishing around all islands also appears to have reduced intra-habitat variation in these functional groups. However, we suggest that inter-island differences would exist in more lightly fished populations, and marine reserves should be replicated at scales that capture both observable and *potential* differences in community structure (see Plate 1).

Significant variation in the functional group “grazers of turf algae” reflected family patterns for acanthurids and pomacentrids. Similar variables that affect these families (e.g., differences in microhabitats among islands) probably also affect invertivores of small, mobile prey that includes some labrids, chaetodontids, and grammids. The biomass of planktivores exhibited the greatest variation of any functional group at the inter-island scale. This may be explained by *Montastraea* reefs being surveyed at different distances from the escarpment, a habitat that attracts planktivores such as *Chromis cyanea* because of the availability of prey items (de Boer 1978). Planktivores represent an important trophic link between reef and open-water communities through predation and coprophagy (reviewed by Hobson 1991), and *Montastraea* reefs on different islands may have food webs that function differently. The causes of inter-island variation in the grazers of turf and macroalgae functional group (mainly scarids) are currently unclear, but may involve variation in primary production, recruitment, habitat quality, and fishing intensity (van Rooij et al. 1996, Russ 2003, Mumby et al. 2006).

There was less evidence of intra-habitat variation at the inter-reef scale on *Montastraea* reefs, which is consistent with the suggestion that the use of habitats as surrogates of biodiversity is best applied over scales of tens of square kilometers (Nagendra 2001). Few analyses among patches separated by tens of kilometers were significant with the Bonferroni correction, but without it there was evidence of variability in the structure of the entire fish community and families such as Lutjanidae and Scaridae. For analyses of functional groups, clear intra-habitat variation at the reef scale was seen in the invertivores of large, mobile prey. This variation may reflect factors such as intra-island differences in the availability of mangrove nursery habitat that enriches populations of species such as haemulids that are in this functional group (Mumby et al. 2004a). It also seems that factors that are likely causes of inter-island variation in grazers of turf algae, such as differences in microhabitat quality and primary production, also lead to significant variation of this functional group within islands. While there is some evidence of reef-scale variation of fish families and functional groups, and greater survey effort than was possible in this study may have revealed it to be more extensive, it is clearly less significant than inter-island variation. Consequently, the implication for conservation planning is, from a biodiversity and ecological function perspective, that a further reserve on a different island is a greater priority than one that contains a different reef on the same island.

The grazing intensity of parrotfishes varied dramatically among islands, and to a lesser extent within islands. Grazing is a key process on reefs, because of its role in regulating macroalgae that can detrimentally affect coral population dynamics (McCook et al. 2001,

Mumby 2006). Such intra-habitat variation may, therefore, have considerable ecological importance. For example, grazing intensity is positively correlated with natural rates of coral recruitment (Mumby et al. 2007a), and suggests that intra-habitat variation in grazing may influence the potential recovery rates of corals from disturbance, such as hurricanes. The implication for marine reserve planning is that some areas of *Montastraea* reef may be much more able to recover from disturbances than others, and could be prioritized within reserve selection algorithms. Ignoring intra-habitat variation may lead to reserves being sited on reefs with low grazing intensity that have a greater probability of becoming dominated by macroalgae (Mumby et al. 2007b). The ecosystem service of fisheries value did not vary significantly among islands. This was expected, given the results for highly exploited families and functional groups, but we again suggest that there is the potential for significant intra-habitat variability under lower exploitation conditions. This suggestion is supported by the large coefficients of variation and maximum differences between pairs of islands, which indicate that the power of the nested ANOVA may have been limited by insufficient sampling effort.

CONCLUSIONS

The use of maps to maximize habitat heterogeneity, and hence biodiversity, in marine reserves is a powerful tool for conservation planners. However, while the data support this general principle for reef fishes, there is a caveat: Habitat labels on maps mask important variations in fish community structure and functioning and a key ecosystem process. Furthermore, intra-habitat variation varies among habitats, is highest for those habitats with high numbers of species, and is greater at scales of hundreds of kilometers than scales of tens of kilometers. Therefore, the use of habitat maps as surrogates of biodiversity during tropical conservation planning on Caribbean reefs has at least two aims: to maximize both habitat heterogeneity and the inclusion of a larger proportion of the most species-rich habitats in marine reserves. The latter principle is rarely included in reserve selection algorithms but, if combined with replication of reserves at scales of hundreds of kilometers, is critical to effectively capture variation in important components of community biodiversity and function. Although the focus was on a tropical coastal ecosystem, our approach and conclusions are intended to be applicable and comparable with a range of other ecosystems, because the general need to document within-habitat heterogeneity and incorporate it into conservation planning has been clearly articulated (Ferrier 2002).

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APPENDIX A

List of the 153 species recorded during this study plus the functional group to which they were assigned and their mean biomass in each of the eight habitat types (*Ecological Archives* A018-058-A1).

APPENDIX B

Results of univariate and multivariate analyses of fish community structure and functional groups with density data (*Ecological Archives* A018-058-A2).