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Development of a systematic classification scheme of marine habitats to facilitate regional management and mapping of Caribbean coral reefs

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Abstract

Most coastal habitat mapping is conducted on an *ad hoc* basis with little consistency in terminology and ambiguous documentation. These limitations obstruct interpretation and integration of maps for coral reef science and management, particularly at regional (international) scales where standardisation is urgently required. This paper advocates an objective, systematic approach to habitat classification which couples coastal geomorphology and benthic cover. Benthic classes are derived and described objectively using agglomerative hierarchical classification of field data and Similarity Percentage analysis of resulting clusters. The scheme has a hierarchical structure to accommodate various user requirements, variable availability of data, and the spatial scales of most remote sensing methods. We illustrate our approach with a scheme based on extensive field data from the Turks and Caicos Islands and Belize. While the scheme will not represent all habitats of the Caribbean, it provides a useful basis for a regional classification and illustrates the systematic approach. Standardised regional maps of coastal habitats will help development of predictive models of coral metapopulation dynamics, aid the identification of larval source and sink areas, and facilitate strategic transboundary planning of protected areas to maximise species, habitat, and ecosystem conservation. Habitats might also be interpreted to reflect ecosystem processes such as productivity and trophic guild structure, thereby allowing the ecosystem function to be examined at larger scales.

1. Introduction

Coastal habitat maps are a fundamental requirement in establishing coastal management plans (Cendrero, 1989). In the context of conserving reef diversity, habitat maps provide an inventory of habitat types and their statistics (Luczkovich et al., 1993; Mumby et al., 1995a; Spalding and Grenfell, 1997), the location of environmentally sensitive areas (Biña, 1982), allow representative networks of habitats to be identified (McNeill, 1994), identify hot spots of habitat diversity, permit changes in habitat cover to be detected (Loubersac et al., 1989), and allow boundary demarcation of multiple-use zoning schemes (Kenchington and Claasen, 1988). Further, the conservation of marine habitats may serve as a practicable surrogate for conserving other scales of diversity including species and ecosystems (Gray, 1997). In essence, coastal habitats are manageable units and large-scale maps allow managers to visualise the spatial distribution of habitats, thus aiding the planning of networks of marine protected areas and allowing the degree of habitat fragmentation to be monitored. As Gray (1997) states, a mosaic of marine habitats must be protected if complete protection of biodiversity is to be achieved.

Although habitat maps have obvious uses in coastal management, the term *habitat* is rarely defined explicitly. The terminology employed in habitat maps often mixes geomorphology (e.g. spur and groove zone), physiognomy (e.g. coral reef), ecology (e.g. turf algae), and geological history (e.g. relict reef). This is because the majority of habitat mapping is carried out non-systematically on an *ad hoc* basis where the definition of classes is subjective and usually based upon very limited field data (see Sheppard et al., 1995 for an exception). Field survey is expensive and *ad hoc* approaches to habitat mapping are favoured because of their relatively

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low cost. However, due to the absence of field data, the definition of classes may be incorrect and not applicable to the area concerned. Further, the description of habitat classes often lacks quantitative descriptors even when field data are used (e.g. <2% of coral reef habitat maps reviewed by Green et al. (1996) have quantitative descriptors).

Non-systematic classification of habitats and ambiguous documentation create problems at several scales. First, meaningful interpretation of the habitat classification scheme may be difficult on the scale of individual habitat maps. This difficulty applies to managers using the scheme for planning and field surveyors attempting to adopt it *in situ*. Second, integrating several habitat maps on say, a national scale is difficult because there is little or no standardisation in terms. Thus, not only is it difficult to decide when two terms are synonymous but the lack of quantitative detail also obscures actual differences in habitat types thereby decreasing the probability that habitats will be distinguished correctly. These integration problems may be ameliorated if a national organisation coordinates or undertakes the mapping (Mumby et al., 1995a), but the problems tend to be exacerbated at international scales. Large disparities in terminology exist at this latter scale because most habitat mapping is funded by governments or country-specific aid projects whose scope rarely exceeds national boundaries. Unfortunately, because coral reefs are transboundary resources, it is at these larger regional scales that integration and standardisation are most needed in conjunction with regional management initiatives (Done et al., 1996).

Regional management of coral reefs is vital since empirical evidence and theoretical advances are unequivocal in highlighting the importance of large-scale processes on coral reef ecosystem sustainability and function (Caselle and Warner, 1996; Cornell and Karlson, 1996; Hatcher, 1997). At large scales, organisms with a pelagic phase during their life history (e.g. sessile invertebrates, fish) form metapopulations whose dynamics are open at the local scale (Warner and Hughes, 1989; Gaines and Lafferty, 1995; Alexander and Roughgarden, 1996) and therefore the processes required to maintain the structure of local populations (e.g. recruitment) may be strongly influenced by events occurring elsewhere. For example, some reefs may be net sources of larvae to reefs downstream, whereas other reefs may be net larval sinks, reliant on sites upstream for their larval supply (Roberts, 1997). The hydrological connectivity between coral reefs and other systems also modifies the local environment through the transfer of pathogens, pollutants, nutrients and sediments. Thus, poor agricultural practices can affect coral reefs downstream (e.g. Nowlis et al., 1997) and possibly beyond international boundaries. A standardised international habitat classification would provide a common dialogue with which to address resource conflicts and clarify the function and status of reefs at large scales.

The need for a regional approach to coastal zone monitoring was realised through the CARICOMP (Caribbean Coastal Marine Productivity) network in which 25 sites from 16 countries cooperate in the monitoring of coastal systems using standardised methods (Ogden et al., 1997). Unfortunately, there is no parallel precedent for regional standardisation in terms of coastal habitat mapping even though funding agencies are encouraging international projects (e.g. World Bank, 1995). To the best of our knowledge, the only structured marine habitat classification scheme available for the Caribbean is in an unpublished report by Sullivan et al., (1994). The scheme has been used successfully by the authors and has influenced development of the scheme outlined here. However, in our opinion, it has limitations for habitat mapping including: (i) its inconsistent use of biological, substratum, historical and geomorphological terms for separating different habitats, and (ii) the inflexibility of some terms for describing habitats. For example, the habitat "forereef-terrace" does not describe the benthic communities associated with forereefs yet several species assemblages can be mapped within this zone using high resolution remote sensing (Mumby et al., 1998).

This paper aims to describe a systematic and objective approach to coastal habitat classification and discuss the use of such schemes in science and management. Our goal is to outline methods and highlight practical considerations rather than provide a description of the scheme. A fully illustrated scheme is available from the authors.

2. Rationale and development of the scheme

2.1. Criteria and intended spatial scales

Most coral reef habitat mapping is achieved using optical remote sensing (Green et al., 1996) and the spectral and spatial resolutions of a sensor determine which aspects of the benthos are mappable, and therefore the appropriate definition of habitat. Green et al. (1996) defined the term, "descriptive resolution" to identify the level of habitat detail to which a remote sensing method describes the benthos. A coarse descriptive resolution would differentiate coral reefs from seagrass beds whereas a finer resolution would differentiate different coral species assemblages and seagrass standing crops, for example. Descriptive resolution is hierarchical and the concept of habitat embodied here follows this theme.

Habitats are defined in this paper using two attributes: geomorphological structure and benthic cover. These attributes were chosen because they exert a combined influence on the spectra recorded by a remote sensing sensor (Sheppard et al., 1995), and can be interpreted realistically within a remotely sensed image. The hierarchical structure of the scheme is designed to accommodate different user needs, technical expertise, and remote sensing data sources. Mumby et al. (1997b, 1998) compared the descriptive resolutions of various remote sensing methods for mapping coral reef habitats of the Turks and Caicos Islands. They concluded that general benthic cover classes were distinguishable from lower resolution data from the satellite sensors Landsat MSS (Multispectral Scanner), Landsat TM (Thematic Mapper), SPOT (Système Probatoire de l'Observation de la Terre) XS (Multispectral), and SPOT Pan (Panchromatic) whereas detailed benthic cover classes (high descriptive resolution) were mappable using colour aerial photography and high resolution digital airborne multispectral imaging. Geomorphological structure can be inferred from either types of data although higher resolution data are preferable (Bainbridge and Reichelt, 1989).

Given ideal conditions, geomorphological classes are generally easy to map using remotely sensed data for three reasons. First, labelling such classes is relatively straightforward because several geomorphological classification schemes exist (Hopley, 1982; Kuchler, 1986; Holthus and Maragos, 1995). Assemblages of benthic organisms and associated substrata are less amenable to standard classifications because they exhibit great variation even within geomorphological zones (Fagerstrom, 1987). Second, geomorphological zones have more distinct boundaries than benthic assemblages which tend to exhibit change along gradients such as depth (Huston, 1994). Assemblages, can therefore be viewed as convenient groupings of species/substrata which merge gradually into other groupings unless there are sharp boundaries in environmental conditions (Gray, 1997). Such gradients make the classification of ecological habitats somewhat inexact and the placement of boundaries rather arbitrary. Third, geomorphology can usually be interpreted from remotely sensed imagery in the absence of field survey. To infer the nature of ecological assemblages without field survey is potentially foolhardy.

The hierarchical structure of the classification scheme described here generally reflects the capability of remote sensing sensors. Most of the fine levels of the hierarchy can be mapped at high spatial resolutions (metre) using digital airborne multispectral imagery (e.g. CASI - Compact Airborne Spectrographic Imager) and to some extent using colour stereo aerial photography (Sheppard et al., 1995). The coarse levels are more suited to satellite imagery with a spatial scale of tens to hundreds of metres.

2.2. Derivation of geomorphological categories

Geomorphological categories (Table 1) were extracted from the excellent classification of Holthus and Maragos (1995). Categories were included on a functional basis to avoid redundancy of terms. For example, the term escarpment is used where the angle of incline exceeds 45° irrespective of position within the seascape. In this example, other users of the scheme may wish to add extra hierarchies to reflect whether the escarpment occurs on the barrier reef or a rhomboid reef.

2.3. Derivation of benthic classes

An important aspect of the classification scheme described here is the quantitative ecological approach to

Table 1
The hierarchy of classes contained within the geomorphological component of the classification scheme. Quantitative diagnostic features are given where appropriate. Further documentation is contained in an unpublished report available from the authors

First tier			Second tier		
Code	Label	Characteristics	Code	Label	Characteristics
1.	Backreef				
2.	Reef crest				
3.	Spur and groove		3.1	Low relief spurs and grooves	Spurs <5m in height
			3.2	High relief spurs and grooves	Spurs >5m in height
4.	Forereef	Reef with <45° slope			
5.	Escarpment	Either reef or lagoon with >45° slope			
6.	Patch reef		6.1	Dense patch reef	Aggregated coral colonies (living or dead) where colonies cover >70% of the benthos
			6.2	Diffuse patch reef	Dispersed coral colonies (living or dead) where colonies cover *ca* < 30% of the benthos
7.	Lagoon floor	Lagoon floor with <45° slope	7.1	Shallow lagoon floor	Depth <12 m
			7.2	Deep lagoon floor	Depth >12 m

defining the benthic classes. Percent cover data were collected using replicate 1 m^2 quadrats at 200 sites in the Turks and Caicos Islands (see Mumby et al., 1997b) and semi-quantitative data were obtained from >1500 plotless transects in Belize (for methods see Mumby et al., 1995b). Hard corals and macroalgae were identified to species level, sponges were identified to taxa or lifeform, and gorgonians were recorded in units of density (No. m^{-2}). Derivation of classes using detailed data from two widely separated areas of the Caribbean provides a moderate level of robustness and an explicit link between the final habitat map and benthic assemblages on the reef.

Similarity in benthic assemblages between sites was measured objectively using the Bray–Curtis Similarity coefficient (Eq. (1); Bray and Curtis, 1957) because it has a number of biologically desirable properties and has been shown to be a particularly robust measure of ecological distance (Faith et al., 1987). Agglomerative hierarchical classification with group-average sorting was used to classify field data because it is one of the most popular and widely available algorithms which, to paraphrase Clarke (1993), allow data to "tell their own story". Because the algorithm sorts sites into a hierarchy of similarity (Fig. 1), natural hierarchical structure in the data was reflected in the classification scheme. Percent cover data were not transformed so that dominant cover features were allowed to exert an appropriately large influence on the classification. This was because it was deemed more likely that remote sensing would discriminate habitats on the basis of dominant benthic features rather than more cryptic species or substrata. There is nothing novel in this approach to classification; ecologists have classified species assemblages for many years (see Ott and Auclair, 1977; Done, 1982; Greig-Smith, 1983). However, most coral reef habitat classification schemes do not have such an objective basis. The Bray–Curtis similarity is given as:

$$S_{jk} = \left[1 - \frac{\sum_{i=1}^{p} |x_{ij} - x_{ik}|}{\sum_{i=1}^{P} \left(x_{ij} + x_{ik} \right)} \right], \tag{1}$$

where x_{ij} is the abundance of the ith species in the jth sample and where there are p species overall.

Characteristic and discriminating species or substrata of each class were determined using Similarity Percentage (SIMPER) analysis (Clarke, 1993) in the software PRIMER (Plymouth Routines in Multivariate Ecological Research). To identify characteristic features, SIMPER calculates the average Bray–Curtis similarity between all pairs of intra-group samples (e.g. between all sites of the first cluster). Because the Bray–Curtis similarity is the algebraic sum of contributions from each species (Eq. (1)), the average similarity between sites of the first cluster can be expressed in terms of the average contribution from each species. The standard deviation provides a measure of how consistently a given species contributes to the similarity between sites. A good characteristic species contributes heavily to intra-habitat similarity and has a small standard deviation. To identify discriminating features, SIMPER calculates the average Bray–Curtis dissimilarity (the complement of similarity) between all pairs of intergroup samples (e.g. all sites of the first cluster against all sites of the second cluster). Again, because the Bray–Curtis dissimilarity is the algebraic sum of contributions from each species, the average dissimilarity between sites of the first two clusters can be expressed in terms of the average contribution from each species. A good discriminating species contributes heavily to inter-habitat dissimilarity (see Table 2 for an example).

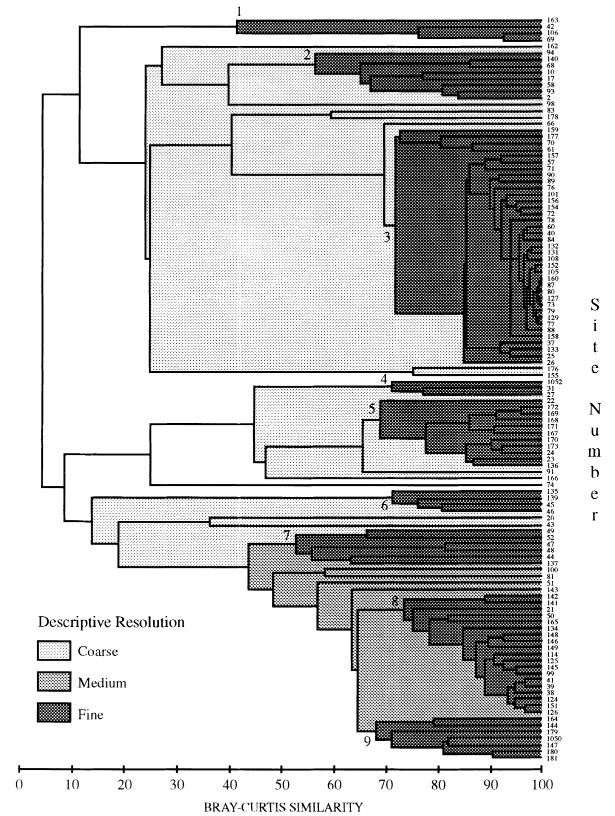

Fig. 1. Hierarchical classification of coral reef survey data from the Turks and Caicos Islands showing three levels of descriptive resolution. Smaller clusters were excluded from the classification and absolved higher up the hierarchy. Benthic classes described in Table 3 (parentheses) include clusters 2 (class 2.4), 3 (3.4), 5 (2.3), 6 (2.1), 7 (2.2), 8 (1.4.1), and 9 (1.4.2).

Habitat classes derived from the Turks and Caicos Islands and Belize were subsumed into a single scheme and SIMPER analysis clarified which classes were synonymous. Although the data collected to generate the scheme were species-specific and at least semi-quantitative, the description of each class has been simplified to lifeform level where possible and classes are recognisable *in situ* using rapid visual assessment methods such

Table 2
SIMPER analysis of dissimilarity between clusters 8 and 9 of Fig. 1 and classes 1.4.1 and 1.4.2 of Table 3. The term "average abundance" represents the average abundance, biomass, density (etc.) of each feature. "Average contribution" represents the average contribution of feature *i* to the average dissimilarity between habitats (overall average = 36%). Ratio = contribution average/standard deviation. Percent contribution = average contribution/average dissimilarity between habitats (36%). The list of features is not complete so percent values do not sum to 100%. The major discriminating features are the percent cover of bare substratum, *Lobophora variegata* and *Montastraea annularis* and the collective difference in coral cover between classes

Feature	Average abundance		Average contribution	Ratio	Percent contribution
	Cluster 9	Cluster 8			
Bare substratum	61.9	87.5	11.5	2.5	32
Lobophora variegata	13.1	0.8	5.7	1.5	16
Montastraea annularis	8.1	0.7	3.5	1.3	10
Sand	4.0	2.5	2.4	0.8	7
Gorgonians	8.6	4.9	2.3	1.3	7
Madracis mirabilis	3.4	0	1.5	0.7	4
Sponges	3.8	2.4	1.3	1.4	4
Agaricia agaricites	1.7	0.2	0.7	1.4	2

as a glass-bottomed bucket. An outline of the scheme with quantitative descriptors is given in Table 3 but we emphasise that its inclusion is for illustrative purposes only. Space limitations preclude full explanation.

Hierarchical multivariate analyses and SIMPER are powerful tools for describing benthic classes but the definition and labelling of classes must consider the users' perception and intuitive expectation of the scheme. In this case, no class was quantitatively dominated by hard corals (i.e. using percent cover) reflecting the overall dominance of macroalgae on Caribbean reefs (Hughes, 1994). However, to describe reefs with the highest coral cover as *algal-dominated* may be politically unacceptable and confuse interpretation (*pers. obs.*). Thus, we have sacrificed systematic accuracy to aid intuitive acceptance of the scheme, adding the caveat that algal-dominated and bare substratum dominated reefs must have $<1\%$ coral cover.

2.4. Merging geomorphological and benthic classes to describe habitats

Habitats are described by assigning a geomorphological and benthic class to each polygon on a habitat map (e.g. use of "low relief spur and groove + branching corals" in the legend). This structure is systematic in that geomorphological and benthic classes are not mixed or used interchangeably, and it also provides flexibility. For example, "low relief spur and groove" might also be coupled with "ribbon and fire corals with green calcified algae".

Providing that supporting documentation is clear, use of a hierarchical classification scheme allows some areas to be mapped in greater detail than others without confusing interpretation. Where assignment of a label is uncertain, the designation should reflect this. For example, if the depth of the lagoon is unknown, the geomorphological component should be labelled at a coarser level of the hierarchy (i.e., lagoon). Similarly, the benthic class "sparse massive and encrusting corals" may be used in areas which are data rich but "massive and encrusting corals" might be more appropriate elsewhere.

In practice, a coastal mapping strategy is envisaged which uses Landsat TM data to make a regional marine habitat map of coarse descriptive resolution, and that this would be augmented using CASI or possibly colour aerial photography, with finer descriptive resolution, at specific sites of interest. The hierarchical classification scheme outlined here integrates these mapping activities.

2.5. Limitations of the classification scheme

While the hierarchical structure of the classification scheme can accommodate the descriptive resolution of most widely used remote sensing methods, the limitations of remote sensing will affect uptake of the scheme by a wide range of researchers. First, optical remote sensing methods only penetrate the clearest waters (horizontal Secchi distance 30–50 m) to a depth of *ca* 25 m, and therefore, the scheme cannot easily be extended beyond this threshold. Acoustic remote sensing methods using sonar (Sotheran et al., 1997) avoid the depth limitation (although they are limited in shallow water <0.5 m) so future research should examine the integration of these approaches for coral reef mapping.

The second major limitation of remote sensing is its poor descriptive resolution despite the incorporation of field data to aid multispectral classification (Mumby et al., 1997b). Although satellite imagery can discriminate habitats at the coarsest level of the hierarchy, expensive airborne methods are needed to resolve the detailed habitats outlined here. However, even digital airborne methods require additional interpretation. For example, the spectral signature of a habitat dominated by "*Lobophora*" (Table 3, class 2.3) is unlikely to be distinguish-

Table 3
The hierarchy of classes contained within the benthic component of the classification scheme. Quantitative diagnostic features are given where appropriate. Quantitative estimates based on ⩾ six 1 m^2 quadrats. Further documentation contained in an unpublished report available from the authors

First tier		Second tier		Third tier	
Code and label	Characteristics	Code and label	Characteristics	Code and label	Characteristics
1. Coral classes	>1% hard coral cover	1.1. Branching corals	*Acropora* spp. visually dominate		
		1.2. Sheet corals	*Agaricia* spp. visually dominate		
		1.3. Ribbon and fire corals with green calcified algae	*Agaricia tenuifolia* visually dominant		
		1.4. Massive and encrusting corals		1.4.1. Sparse massive and encrusting corals	1–5% hard coral cover
				1.4.2. Dense massive and encrusting corals	>5% hard coral cover
2. Algal dominated	>50% algal cover; <1% hard coral cover	2.1. Green algae			
		2.2. Fleshy brown algae and sparse gorgonians	=3 gorgonians m^{-2}		
		2.3. *Lobophora*	Monospecific *Lobophora* beds		
		2.4. *Euchema* and *Amphiroa*	Rare assemblage dominated by red algae with encrusting sponges		
3. Bare substratum dominated	Dominated by bare substratum; <1% hard coral	3.1. Bedrock/rubble and dense gorgonians	>3 gorgonians m^{-2} (usually >8 m^{-2}) and *ca* 30% algal cover		
		3.2. Bedrock/rubble and sparse gorgonians	=3 gorgonians m^{-2} and little algal cover		
		3.3. Rubble and sparse algae	No gorgonians		
		3.4. Sand with sparse algae	>90% sand		
		3.5. Mud			
		3.6. Bedrock	No gorgonians		
4. Seagrass dominated	>10% seagrass cover	4.1. Sparse seagrass	Standing crop 1–10 $g.m^{-2}$; cover <30%		
		4.2. Medium density seagrass	Standing crop 11–80 $g.m^{-2}$; cover 30–70%		
		4.3. Dense seagrass	Standing crop >80 $g.m^{-2}$; cover >70%		
		4.4. Seagrass with distinct coral patches	Seagrass visually dominant, coral cover may reach 3%, gorgonians may be present		

able from "fleshy brown algae with sparse gorgonians" (Table 3, class 2.2). An image interpreter may, however, distinguish these classes on the basis of their context within the reef system (see Mumby et al., 1997a). In this example, class 2.3 would be expected in sheltered lagoonal environments whereas class 2.2 is more commonly associated with hard bottoms nearer the reef where fish grazing intensity is higher (Lewis et al., 1987). Where airborne remote sensing is not affordable or is inadequate, recreational diving programmes or volunteer organisations may be able to provide data at low cost (Wells, 1995). For example, the data set reported here for Belize was obtained by volunteers at no cost to the host Government. A multivariate discriminant function (Hand, 1981) might then be used to assign diver records to the appropriate benthic class, possibly over the internet (PJM unpublished results).

At the intended spatial scales of remote sensing, the classification scheme outlined here represents almost all habitats found throughout the Turks and Caicos Islands and Belize. We do not suggest, however, that the scheme represents the Caribbean or all user requirements. For example, relatively marginal reefs such as those in Florida may have additional benthic classes (e.g. Oculinid reefs) and geomorphological terms (e.g. transitional reefs, Sullivan et al., 1994), and other users may wish to place greater emphasis on other aspects of the benthos. For example, distinguishing seagrass on muddy substrata from seagrass on limestone substrata (Lidz et al., 1997) or adding more detailed levels to the hierarchy such as distinct species assemblages within, say, the class "dense massive and encrusting corals" or indictating whether stands of the reef building branching coral, *Acropora palmata*, are living or dead since its populations have declined in much of the Caribbean region (see Sheppard et al., 1995 and references therein). Our aim is to advocate a systematic and objective approach to habitat classification and present the template of a regional scheme, rather than provide the definitive solution.

2.6. Future extensions of habitat classifications for analysis of reef processes and function

Management applications of habitat maps were stated in the introduction but as ecology embraces larger scales (Levin, 1992), habitat maps will become instrumental in bridging the gap in scale between field studies and regional or global processes. For example, future spatially-realistic metapopulation models (Hanski and Simperloff, 1997) for corals of the Caribbean will probably need estimates of local spatial heterogeneity (Preece and Johnson, 1993). Habitat maps might also be translated into new data layers reflecting important processes such as primary productivity (Hatcher, 1988) or functional guild structure (Fagerstrom, 1991). For example, Hatcher (1988) provides a schematic summary of diel gross and net community primary productivity and production-to-respiration ratios for similar geomorphological and benthic classes to those described here. Areas of back reef are documented as having a gross community primary productivity of between 2.6 and 40.0 g C m^{-2} d^{-1} but if the benthic class is also known, the accuracy of the estimate could be increased to 0.8–2.8 g C m^{-2} d^{-1} for a coralline algal assemblage or 0.9–12.1 g C m^{-2} d^{-1} for a turf algal assemblage. Geographical information systems (GIS) and spatial statistics allow such patterns to be examined at large spatial scales (Farina, 1998).

3. Conclusions

Habitat classification schemes should be determined objectively and have a systematic but intuitively understandable structure. Quantitative descriptors and photographic keys will ease adoption of the scheme by others and facilitate data integration.

Coral reef diversity must be conserved if we are to ensure a sustainable benefit from reef functions in terms of protein and carbohydrate resources, building materials, coastal defence, and tourism (Done et al., 1996). Given the connectivity of coral reefs in the Caribbean, reef science and management must have regional as well as national foci (Done et al., 1996; Gray, 1997; Roberts, 1997) and a standardised approach to habitat mapping is essential. A common currency in habitat maps is helpful for understanding large-scale ecological issues of ecosystem function, coral population dynamics, and the conservation of diversity at multiple scales.

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