

Coral Reef Habitats as Surrogates of Species, Ecological Functions, and Ecosystem Services

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Abstract: *Habitat maps are often the core spatially consistent data set on which marine reserve networks are designed, but their efficacy as surrogates for species richness and applicability to other conservation measures is poorly understood. Combining an analysis of field survey data, literature review, and expert assessment by a multidisciplinary working group, we examined the degree to which Caribbean coastal habitats provide useful planning information on 4 conservation measures: species richness, the ecological functions of fish species, ecosystem processes, and ecosystem services. Approximately one-quarter to one-third of benthic invertebrate species and fish species (disaggregated by life phase; hereafter fish species) occurred in a single habitat, and Montastraea-dominated forereefs consistently had the highest richness of all species, processes, and services. All 11 habitats were needed to represent all 277 fish species in the seascape, although reducing the conservation target to 95% of species approximately halved the number of habitats required to ensure representation. Species accumulation indices (SAIs) were used to compare the efficacy of surrogates and revealed that fish species were a more appropriate surrogate of benthic species (SAI = 71%) than benthic species were for fishes (SAI = 42%). Species of reef fishes were also distributed more widely across the seascape than invertebrates and therefore their use as a surrogate simultaneously included mangroves, sea grass, and coral reef habitats. Functional classes of fishes served as effective surrogates of fish and benthic species which, given their ease to survey, makes them a particularly useful measure for conservation planning. Ecosystem processes and services exhibited great redundancy among habitats and were ineffective as surrogates of species. Therefore, processes and services in this case were generally unsuitable for a complementarity-based approach to reserve design. In contrast, the representation of species or functional classes ensured inclusion of all processes and services in the reserve network.*

Keywords: biodiversity conservation, complementarity, conservation planning, coral reef, ecosystem services, habitat representation, habitat value, marine reserve, species richness

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Paper submitted June 18, 2007; revised manuscript accepted November 21, 2007.

Hábitats de Arrecifes de Coral como Sustitutos de Especies, Funciones Ecológicas y Servicios de Ecosistemas

Resumen: *Los mapas de hábitat a menudo son el núcleo de datos espacialmente consistentes sobre el cual se diseñan las redes de reservas marinas, pero su eficacia como sustitutos de la riqueza de especies y su aplicabilidad en otras medidas de conservación es poco conocida. Combinando el análisis de datos de campo, revisión de literatura y evaluación de expertos de un grupo de trabajo multidisciplinario, examinamos el grado en que los hábitats Caribeños proporcionan información útil para la planificación sobre 4 medidas de conservación: riqueza de especies, las funciones ecológicas de especies de peces, los procesos del ecosistema y los servicios del ecosistema. Aproximadamente entre una cuarta parte y un tercio de las especies de invertebrados bentónicos y de peces (desagregados por etapa de vida; en lo sucesivo especies de peces) ocurrieron en un solo hábitat, y la parte anterior de los arrecifes dominada por Montastraea consistentemente presentó la mayor riqueza de todas las especies, procesos y servicios. Los 11 hábitats fueron necesarios para representar a las 277 especies de peces en el paisaje marino, aunque al reducir el objetivo de conservación a 95% de las especies se requería aproximadamente la mitad de los hábitats para asegurar la representación. Los índices de acumulación de especies (IAE) fueron utilizados para comparar la eficacia de sustitutos y reveló que las especies de peces eran un sustituto más adecuado de las especies bentónicas (IAE = 71%) que las especies bentónicas fueron para los peces (IAE = 42%). Las especies de peces de arrecifes también se distribuyeron más ampliamente que los invertebrados y, por lo tanto, su uso como sustitutos simultáneamente incluyó hábitats en manglares, pastos marinos y arrecifes de coral. Las clases funcionales de peces sirvieron como sustitutos efectivos de especies de peces y bentónicas, lo cual, por la facilidad con que son muestreadas, las hace una medida particularmente útil para la planificación de la conservación. Los procesos y servicios del ecosistema exhibieron gran redundancia entre hábitats y fueron ineficientes como sustitutos de especies. Por lo tanto, los procesos y servicios en este caso fueron inadecuados para un método de diseño de reservas basado en complementariedad. En contraste, la representación de especies o clases funcionales aseguró la inclusión de todos los procesos y servicios en la red de reservas.*

Palabras Clave: arrecife de coral, complementariedad, conservación de la biodiversidad, planificación de la conservación, representación del hábitat, reserva marina, riqueza de especies, servicios de los ecosistemas, valor del hábitat

Introduction

A central tenet of most conservation planning, whether stated explicitly or not, is the protection—or at least representation—of as many species as possible within a prescribed region (Usher 1986; Margules & Pressey 2000). Given the difficulty in sampling species composition continuously across a region, virtually all planning uses surrogates (Sarkar & Margules 2002). One of the most widely applied methods is the use of vegetation or habitat maps to stratify units of diversity (Noss 1987; McNeill 1994; Margules & Pressey 2000; Oliver et al. 2004). Maps are either used directly as a surrogate for diversity (Fernandes et al. 2005) or combined with environmental data to model species distributions or beta diversity (Faith 2003; DeWoody et al. 2005; Harborne et al. 2006a). Other surrogates include taxonomic proxies in which distribution patterns for readily sampled species are assumed to hold true for distributions of other taxa in the community (Oliver & Beattie 1996; Warman et al. 2004).

The efficacy of habitat-based diversity surrogates has received little quantitative evaluation with notable exceptions, including studies by Ward (1999), Oliver et al. (2004), and Stevens and Connolly (2004). Indeed, the use of surrogates (primarily land-cover classes) for conservation has been strongly criticized (Brooks et al. 2004), and

surrogate efficacy varies as a function of the spatial and temporal scales of observation, accuracy of surrogate classification, and degree to which the processes driving the distribution of the surrogates extend to the conservation features (e.g., species) of interest. Pressey (2004) points out that many studies attempt to mitigate this problem through the use of a range of complementary surrogates (e.g., Noss et al. 2002; Cowling et al. 2003).

Ideally, surrogates span a range of key conservation measures. The potential list of such measures is extensive (Usher 1986; Roberts et al. 2003a). We focused on 4: species representation, functional roles of species in the ecosystem, ecosystem processes, and ecosystem services. Species representation is simply the desire to incorporate all species in the region within a reserve system, which is fundamental to much conservation planning (Margules & Pressey 2000).

The functional role of species is categorized here by their trophic status and habitat use, and the concept recognizes explicitly that ecosystems may contain a degree of ecological redundancy (Peterson et al. 1998). A system with a high degree of interchangeable species for a given function is potentially more resilient to processes that cause species depletion, such as fishing or disease (Bellwood et al. 2004; Hooper et al. 2005; Micheli & Halpern 2005). Conversely, species-poor systems may be

highly vulnerable to the loss of a few key species. A particularly striking example occurred on Caribbean coral reefs during the last 2 decades after disease eradicated a single dominant herbivore, the sea urchin (*Diadema antillarum*) (Lessios 1988). The disease event occurred in 1983 and resulted in widespread algal blooms (Hughes 1994), some of which persist today (Gardner et al. 2003). Although a classification of species functions is itself a proxy for individual trophic processes, the classification method is reasonably simple to implement and allows reserve designers to ensure that all species functions are represented in a reserve system.

Community and ecosystem processes such as secondary consumption and carbon cycling (Hatcher 1997) underpin the dynamics of individual species, productivity of ecosystems, and their vulnerability to and recovery from disturbance. Not surprisingly, the explicit incorporation of processes within reserve design is gaining momentum (Pressey 2004). Lastly, successful reserves support important ecosystem services from which people receive either direct benefits, such as fisheries, or indirect benefits, such as defense from storms. Reserve-selection algorithms are increasingly incorporating socioeconomic data on ecosystem services as costs (Sala et al. 2002; Stewart et al. 2003). By explicitly examining the role of habitats as surrogates for ecosystem services, we hope to facilitate the incorporation of services within future reserve-selection algorithms.

We sought to evaluate the degree to which classes of marine habitat can be used as surrogates for all 4 conservation measures listed earlier. Maps of habitats are the only spatially consistent data source for many ecosystems (Green et al. 1996; Friedlander et al. 2003; Oliver et al. 2004), and this is particularly true of marine ecosystems because an extensive, submerged field survey is expen-

sive and logistically difficult (Mumby et al. 1999). As a result, much conservation planning in marine ecosystems is dominated by habitat representation (Leslie et al. 2003; Roberts et al. 2003b; Stewart et al. 2003; Fernandes et al. 2005). Habitat mapping in marine ecosystems is constrained by the depth and clarity of overlying water. Not surprisingly, some of the most accurate and detailed maps have been created for coral reefs, which typically occur in shallow, clear water (Mumby & Edwards 2002). In this study we had 2 principal aims. First, we sought to determine the degree to which coral reef habitats—some of the most detailed designations possible from remote sensing in marine systems—act as a surrogate for 4 principal conservation measures. To the best of our knowledge, this is the first attempt to test the efficacy of these habitats as effective surrogates for a diverse range of criteria. Second, we sought to provide specific ecosystem-level insight into the relative importance of each habitat for conservation planning.

Methods

The efficacy of reef habitats as surrogates for 4 conservation criteria was assessed through a combination of analysis of field survey data, literature review, and expert assessment by a multidisciplinary working group.

Habitat Classes and Species Composition

The habitat classification was originally created through a hierarchical classification of species-level percent-cover data collected in 1-m² quadrats at 180 sites of the Turks and Caicos islands of the southern Bahamas Archipelago (see Supplementary Material) (Mumby & Harborne 1999). Each habitat category (Table 1) can be mapped routinely

Table 1. Classification of coral reef and lagoonal habitats of the Bahamas (each class also has a Caribbean-wide distribution).

Habitat type	Characteristics
Marine-terrestrial interface fringing mangroves	found on shorelines, tidal creeks and offshore islands and surveys; refers to sites along the outer edge of stands of red mangrove (<i>Rhizophora mangle</i>)
Lagoon	
dense sea grass	dominated by <i>Thalassia</i> but may contain <i>Syringodium</i> ; categories 5 and 6*
medium-density sea grass	dominated by <i>Thalassia</i> but may contain <i>Syringodium</i> and <i>Halodule</i> ; categories 3 and 4*
sparse sea grass	dominated by the genera <i>Syringodium</i> and <i>Halodule</i> ; categories 1 and 2*
sand and sparse algae	sand with a sparse algal community
patch reef	a geomorphological term but is typically dominated by a community of massive corals and dense gorgonians
macroalgal dominated	found in both lagoonal and reef environments; very low-relief hard bottom with mixed macroalgal community and few gorgonians
Outer coral reef	
<i>Acropora palmata</i> dense gorgonians	found in reef-crest environments between approximately 1 and 5m; <i>A. palmata</i> visually dominates often just seaward of the <i>A. palmata</i> zone but also found in shallow, wave-swept areas; extremely high densities of gorgonians (> 10/m ²) and little hard coral cover
sparse gorgonians and algae	also known as a gorgonian plain; sparse gorgonians on hard bottom with some macroalgae
<i>Montastraea</i> reef	<i>Montastraea</i> dominant reef-building coral; typically in relatively sheltered areas; has extremely high structural relief (Geister 1977)

*Categories proposed by Mumby et al. (1997).

from high-resolution (<4 m pixel) satellite and airborne imagery (Mumby & Edwards 2002). The classification can be applied throughout the Caribbean region.

We collected field data in 7 regions of the Bahamas Archipelago between 2002 and 2004. In each region, each habitat type was sampled at a minimum of 3 sites, each separated by approximately 5 km, in each region. Our focus here was species presence or absence at the scale of the Bahamas; therefore, we pooled the data for all regions and sites for each habitat. Analyses of species abundance patterns by region will be reported separately.

Benthos

At each site we quantified the species composition of the benthic community in between 20 and 40 randomly placed 1-m² quadrats. We filmed the content of quadrats in 20-cm swaths with a high-resolution digital video camera. Following completion of all the swaths within a given quadrat, cryptic organisms and areas of high relief (e.g., under ledges and the sides of large mounds) were filmed in more detail. We projected the video recording of each quadrat onto a large monitor for analysis, which consisted of identification (presence or absence) of species of scleractinian corals (minimum diameter 1 cm), macroalgae, macroscopic mobile invertebrates, sponges, and gorgonians to the highest taxonomic resolution possible (for details, see Harborne et al. 2006a).

Fish Species and Life Phase

For all but nocturnal (e.g., Apogonidae) and highly cryptic (Clinidae and Gobiidae) fish species, we used discrete-group visual fish census methods (Green & Alevizon 1989). Species were divided into 3 groups and their density and size estimated along belt transects. Transect size and number were optimized with data from equivalent surveys within the Caribbean (Mumby et al. 2004). The following list of families is indicative rather than exhaustive, but transect dimensions and number of transects at each site (in parentheses) were 30 × 2 m (4) for Pomacentridae, Labridae, Holocentridae, and small Serranidae; 30 × 4 m (10) for Scaridae, Acanthuridae, Pomacanthidae, Chaetodontidae, Diodontidae, and Monacanthidae; and 50 × 4 m (5) for Haemulidae, Lutjanidae, Carangidae, Balistidae, planktivorous Labridae, large Serranidae, and other large predators. All surveys of each fish group were undertaken by the same observer. For fisheries-related analyses (see below), the lengths of individual reef fishes were converted to biomass with the allometric scaling relationships of Bohnsack and Harper (1988). Species were disaggregated into life-phase categories (juvenile, intermediate, and adult) in recognition that many species undertake ontogenetic migrations among habitats (Lindeman et al. 1998). All future references to fish

species or data on fish life phase (e.g., *Sparisoma viride* terminal phase) are referred to as species data.

Functional Attributes of Reef Fishes

We selected 3 functional traits of species to reflect the functional role of fishes in reef ecosystems (Micheli & Halpern 2005): (1) trophic group, (2) adult size, and (3) adult mobility and habitat use. A species' trophic group, in combination with its size, is a determinant of that species' role in energy transfer within a food web and in controlling other species within the assemblage. A species' mobility and habitat use is likely correlated with the species' responses to disturbances affecting benthic habitat, such as impacts from storms, bleaching, or destructive fishing practices. Functional classification schemes based on continuous traits, instead of the categories used here (e.g., Petchey et al. 2004), were not applicable because detailed natural-history and ecological information were not available for a large number of species in the data set. Similarly, we could not disaggregate the function of individual species by size because of a lack of diet data by size (most diet data are reported for adult fishes only). Each species was assigned to 1 of 9 trophic groups (herbivore-algal turf, herbivore-algal turf and macroalgae, omnivore, planktivore, small-invertebrate feeder, large-sessile-invertebrate feeder, large-mobile-invertebrate feeder, joint invertivore and piscivore, and piscivore); 1 of 5 size classes (fork length ≤10 cm, 11–25 cm, 26–50 cm, 51–100 cm, and >100 cm); and 1 of 3 mobility and habitat-use categories (sedentary or territorial closely associated with the seafloor, roving demersal species, and mobile pelagic species). Information about the diets, trophic levels, and habitat use and mobility of individual species were obtained from FishBase (Randall 1967; Claro et al. 2001; Froese & Pauly 2003). Assignment of the 260 fish species in the data set to combinations of these 3 functional traits resulted in 77 functional groups.

Ecosystem Processes and Services

We recently undertook an extensive review of ecosystem processes in Caribbean coral reef, sea-grass bed, and mangrove systems (Harborne et al. 2006b). Published measurements of each ecosystem process (e.g., primary production, calcification, bioerosion) were categorized into 3 classes (high, medium, and low) in which the range of process values were of approximately equal width. Data were then disaggregated into habitat classes, which yielded an overall ordinal score (3, high; 2, medium; 1, low; and 0, absent) for each process in each habitat. Sixteen process variables were included (Table 2). Our use of the term *ecosystem process* is consistent with its use in much of the ecological literature (e.g., Hooper et al. 2005), and this term is equivalent to the term *supporting services*, which is used within the wider category of

Table 2. Relative magnitude (0, absent; 3, highest) of ecosystem processes and services of each coral reef, sea grass, and mangrove habitat.

Category and class	Subclass	Mangroves	Dense sea grass	Medium density sea grass	Sparse sea grass	Sand	Patch reef	Acropora palmata	Macroalgal dominated	Dense gorgonians	Sparse gorgonians	Montastraea reef
Process												
biogeochemical	gross community calcification	1	1	1	1	0	2	3	1	1	1	3
biogeochemical	nitrogen fixation	1	3	2	1	2	1	3	3	1	1	3
grazing	density of Acanthuridae	1	1	0	0	0	3	3	1	2	2	2
grazing	density of <i>Diadema antillarum</i>	1	2	1	1	1	3	3	0	2	2	2
grazing	density of <i>Sparisoma viride</i>	0	1	0	0	0	3	3	1	2	1	3
grazing	density of <i>Stegastes planifrons</i>	0	0	0	0	0	3	0	0	1	1	3
habitat quality	vulnerability to mass coral bleaching	0	0	0	0	0	3	3	1	1	1	3
habitat quality	community bioerosion	0	0	0	0	0	3	3	0	1	1	3
habitat quality	coral recruitment	0	0	0	0	0	3	2	0	1	1	3
habitat quality	vulnerability to diseases	0	1	1	1	0	3	3	2	3	3	3
habitat quality	vulnerability to hurricane damage	3	1	1	1	2	3	3	1	1	1	2
invertivory	density of common invertivores	3	3	1	0	0	3	2	0	2	1	3
physical	wave energy dissipation	3	0	0	0	0	0	3	0	2	2	2
planktivory	density of planktivores	0	0	0	0	0	1	1	0	1	1	3
predation	density of <i>Epinephelus striatus</i>	3	1	1	0	0	0	0	3	2	3	3
primary production	gross community primary productivity	2	2	2	1	1	2	3	3	2	1	2
Service												
building resources	generation of sand	0	0	0	0	0	1	3	2	1	1	3
building resources	mangrove wood	3	0	0	0	0	0	0	0	0	0	0
fisheries	density of <i>Panulirus argus</i>	3	3	2	0	0	3	1	3	1	1	3
fisheries	density of <i>Strombus gigas</i>	0	3	3	3	3	1	1	1	0	1	0
fisheries	<i>Euchema</i> sp. seaweed	0	2	3	3	1	1	0	0	0	0	0
fisheries	value of finfish (US 200/m ²)	0.05	0.23	0.23	1.94	0.26	0.38	3.06	1.88	0.54	0.34	4.16
fisheries	value of finfish	1	1	1	2	1	1	3	2	1	1	3
fisheries & tourism	density of <i>Epinephelus striatus</i>	3	1	1	0	0	0	0	3	2	3	3
pharmaceutical products	sponge diversity and abundance	3	1	1	0	0	1	1	1	1	1	3
tourism & cultural	curio and jewelry	0	2	3	2	0	3	1	1	1	1	3
tourism, education, cultural	ease of access for education	3	3	3	1	1	3	2	1	1	1	1
tourism, education, cultural	bonefishing, snorkeling, swimming	0	0	0	1	3	3	2	1	1	1	3

ecosystem services by the Millennium Ecosystem Assessment (2005). *Supporting services* implies people do not place a direct value on these processes even though they are essential for the functioning of the ecosystem.

Ecosystem services of coral reefs were reviewed by Moberg and Folke (1999) but not disaggregated by habitat. As a multidisciplinary working group, we convened a meeting to quantify ecosystem services by habitat and to assign an ordinal score to each service (Table 2). Working group members were from the fields of reef ecology, theoretical ecology, fisheries, ecological and fisheries economics, and social anthropology, all within a Bahamian context. Habitat-level categories for 11 processes were defined. Fisheries-related services were quantified from the benthic and fish community data described earlier for

each habitat. Three equally spaced categories of finfish value were derived from a habitat-level analysis of the mean total dollar value of reef fishes per unit area of reef surveyed. The observed biomass of harvestable fishes was converted to dollars with the 2006 value of reef fishes at Bahamian fish markets. Data on the density of fisheries invertebrates were also extracted from Bahamian field survey as was sponge diversity and abundance. Other services were determined by expert opinion.

Analyses

We subjected lists of species and species functions for each habitat to 3 descriptive statistics and analyses: (1) number of species and functional classes per habitat, (2)

number of unique species and functional classes in each habitat, and (3) complementarity of species and functional classes among habitats. For 95% and 100% of all elements (i.e., species, functional classes) in the ecosystem, an algorithm identified the minimal set of habitats required and their ordering from first (the habitat with most elements) to last. The algorithm used was an exhaustive, “brute force” approach that compared every possible combination of habitats and selected the combination that encompassed the greatest total number of elements for each level of habitat richness (from one habitat to all habitats). Results are reported separately for the fish and benthic taxa and for all species combined.

Data on ecosystem processes and services (ordinal scores of 0–3 per habitat for each process or service) were subject to 4 descriptive statistics and analyses: (1) number of processes or services per habitat, (2) total process or services score per habitat (e.g., each high value = 3), (3) mean dollar value (US\$) of harvestable reef fishes per 200 m² of habitat, which was then converted to a 3-point score consistent with number 2, and (4) complementarity of processes or services such that 95% or 100% of all processes or services would be represented in their highest state. The algorithm mirrored that described earlier, but the elements used were the high category of each process or service rather than simply presence or absence.

To compare the efficacy of different surrogates, we used the “species accumulation index of surrogacy value” (SAI) approach of Ferrier and Watson (1997) and Ferrier (2002). The method is best illustrated with an example. We first identified the ideal complement of habitats to represent 95% of fish species by deploying algorithm 3 for fish species (see above). Then we asked whether this habitat selection (derived from representation of fish species) would also prove to be a useful surrogate for representing benthic species. Specifically, we asked to what extent the use of the habitat complement from fish species would provide a better means of representing benthic species than simply choosing an equivalent number of habitats by chance. The SAI method has 4 steps. First, a “random” benthic species accumulation curve was derived from the mean number of benthic species selected in a random set of n habitats (see Supplementary Material), where n varied between 1 and 11. Second, an “optimal” accumulation curve was derived directly from the benthic data that always added the habitat offering greatest complementarity among benthic species. This is directly analogous to the complementarity analysis (3) described earlier for species. Third, an alternative benthic species accumulation curve was generated in which the selection of habitats was derived from the surrogate (i.e., those habitats offering greatest complementarity for fish species) (Supplementary Material). In other words, the surrogate curve used the sequence of habitats that would have been chosen when representing the full comple-

ment of fish species. Lastly, the SAI, or efficacy of the surrogate, was expressed on a percentage scale in which 0% indicated that the surrogate performed no better than a random selection of habitats and 100% indicated that the surrogate was perfect and selected an equivalent representation of benthic species. The SAI was calculated as the area between the surrogate and random curve divided by the area between the optimal and random curve (Supplementary Material). It was then expressed as a percentage, and in this example yielded a value of 71%, which implies that selecting habitats on the basis of fish species was not only much better than making a random habitat selection but a moderately good approximation to the use of benthic data directly.

Results

Species-Based Metrics

A total of 260 benthic species and 277 fish species were found in the 11 habitats studied. In general, reef habitats had the highest scores for species-based metrics, followed by mangroves and lastly by lagoonal sea-grass habitats. *Montastraea* reef was consistently the highest-ranking habitat in terms of number of species, number of unique species, number of species functions, and ranking for complementarity (Table 3). This habitat alone accounted for 66% of all fish species and 76% of all benthic taxa in the seascape. Nearly one-third (29%) of fish species were associated with a single habitat (Table 3). Of these, relatively few were found in lagoon habitats, and these were typically either juvenile phases (e.g., of *Lutjanus griseus* in mangrove fringe) or small cryptic species, such as those in the genus *Xyrichtys* (razorfish) found in sea-grass beds and *Sphoeroides* (puffers) found in mangroves and sea grass. The outer *Montastraea* reef contained both planktonic-feeding fishes (e.g., *Clepticus parrae*) and fishes associated with deep, cryptic habitats, such as *Gramma melacara*. A similar proportion of benthic invertebrate species (27%) were also associated with a single habitat. Nevertheless, the distribution of benthic species was even more heavily skewed toward forereef habitats, with *Montastraea* reef containing 66% of all unique species (vs. only 35% for reef fish). Almost all of the unique benthic species in this habitat were Porifera (sponge). Most of the unique lagoonal species were either algae (e.g., *Caulerpa sertularoides* in mangroves) or mobile invertebrates such as gastropods.

To represent 95% of benthic species in a reserve, only 4 of the 11 habitats needed to be included (Table 3): 2 reef and 2 sea-grass habitats. To move from representing 95% of species to all species required a near doubling of the number of habitats (from 4 to 7), which left 4 habitats redundant (sparse sea grass, sand, algal hard bottom,

Table 3. Importance of habitats in contributing to species richness and representation of unique species and achieving either 95% or 100% complementarity of all species in the seascape.

Habitat	No. fish spp.		No. unique fish spp.		No. fish functions		No. unique fish functions		No. benthic spp.		No. unique benthic spp.		Compl.* fish spp.		Compl.* fish functions		Compl.* benthic spp.		Compl.* all spp.	
	No. fish spp.	No. unique fish spp.	No. fish functions	Unique fish functions	No. benthic spp.	No. unique benthic spp.	95%	100%	95%	100%	95%	100%	95%	100%	95%	100%	95%	100%	95%	100%
Fringing mangroves	67	6	40	1	50	5	3	3	3	3	3	3	3	3	3	3	5	6	6	6
Sparse sea grass	32	3	26	0	24	0	8	0	24	0	8	0	8	0	8	0	3	3	9	9
Medium-dense sea grass	31	1	26	0	52	6	9	0	52	6	9	0	9	0	9	0	3	3	7	7
Dense sea grass	48	5	39	1	44	5	6	1	44	5	6	1	6	1	6	1	6	6	4	4
Sand and sparse algae	4	1	3	0	2	0	10	0	2	0	10	0	10	0	10	0	1	1	11	11
Macroalgal dominated	148	10	49	1	171	0	4	1	171	0	4	1	4	1	4	1	5	5	2	2
Patch reef	148	6	59	1	148	2	5	1	148	2	5	1	5	1	5	1	7	7	8	8
<i>A. palmata</i>	104	5	56	0	115	4	7	0	115	4	7	0	7	0	7	0	4	4	5	5
Dense gorgonians	78	1	45	1	105	2	11	1	105	2	11	1	11	1	11	1	2	2	10	10
Sparse gorgonians	172	14	62	0	182	0	2	0	182	0	2	0	2	0	2	0	2	2	3	3
<i>Montastraea</i> reef	184	28	65	3	198	47	1	3	198	47	1	3	1	3	1	1	1	1	1	1

*Complementarity and order of habitats needed, optimal first choice; 2, next-greatest complementarity; etc.

and sparse gorgonians). Mangroves were only required to represent all benthic species.

The representation of fish species required a greater number and diversity of habitats. Six habitats, including reef, sea grass, and mangrove systems, were required to represent 95% of species. All habitats had to be included for all fish species to be represented, which suggests that none of the habitats are redundant for species of reef fishes.

Only 10% of fish species functions were unique to a habitat, indicating reasonably high levels of functional redundancy. A combination of 2 reef habitats and mangrove was needed to represent 95% of functions, although twice as many habitats (including sea-grass beds) were required to represent all functions. In general, twice as many habitats were required to represent fish species than their ecological functions.

Ecosystem Processes and Services

Montastraea reef was again the greatest contributor to ecosystem processes and services, with the greatest overall scores and first selection for complementarity analysis (Table 4). In contrast to species-level indices, however, high levels of redundancy were found with only 2 and 3 habitats required to represent all ecosystem processes and services, respectively, at their highest levels. Ecosystem processes were apparently adequately represented by *Montastraea* reef and the reef crest, *Acropora palmata*. High levels of ecosystem services were distributed more evenly across the seascape and included sea grass, mangrove, and one reef habitat (Table 4).

Efficacy of Surrogates

The efficacy of surrogates (or SAI) generally fell into 2 groups: those with low utility, where SAI was <50% and those with high utility where SAI was >70% (Table 5). With only one equivocal exception (where SAI was 60.1%), ecosystem processes and services proved to be ineffective surrogates of species-level information. In contrast, habitat selections designed to represent benthic species, fish species, or fish functional classes all proved to be highly effective at representing ecosystem processes (Table 5). Benthic species were also an effective surrogate of ecosystem services, but fish-based surrogates were only moderately effective (SAI = 48.8% and 67.4% for the surrogates fish species and functions, respectively).

Functional classes of reef fishes represented complements of fish species reasonably well (SAI = 71.6%), but, surprisingly, the fit was no better than the use of fish species as a surrogate for entirely different taxa (i.e., benthic invertebrate species). Indeed, fish species- and functional classes in particular—were good surrogates for benthic species, whereas the converse was not true; habitats selected to represent benthic species were

Table 4. Importance of habitats in representing ecosystem processes and services and achieving either 95% or 100% complementarity of all high values of each process or service in the seascape.

Habitat	No. processes	Process score	Compl.* processes		No. services	Services score	Compl.* services	
			95%	100%			95%	100%
Fringing mangroves	4	18			5	16	3	3
Sparse sea grass	0	6			2	12		
Medium-dense sea grass	0	10			4	17	2	2
Dense sea grass	2	16			3	16		
Sand and sparse algae	0	6			2	9		
Macroalgal dominated	3	16			2	15		
Patch reef	10	36			4	17		
<i>Acropora palmata</i>	11	38	2	2	2	14		
Dense gorgonians	1	25			0	9		
Sparse gorgonians	2	23			1	11		
<i>Montastraea</i> reef	11	43	1	1	7	22	1	1

*Complementarity and order of habitats needed; 1, optimal first choice; 2, next greatest complementarity; etc.

ineffective at representing species of reef fishes (SAI = 41.7%).

Discussion

Few researchers, if any, have simultaneously evaluated the adequacy of a widely used surrogate for a diverse range of conservation criteria. Although we do not suggest that a single surrogate is preferable to a suite of complementary measures, it is important to assess the full utility of available surrogates. Here, we evaluated whether tropical coastal habitats offered useful information at the scale of species and ecosystems and for both diversity and socioeconomic criteria.

Several recent comparable studies used a combination of taxonomic surrogates and reserve-selection algorithms (e.g., diversity hotspots or complementarity) to simulate a suite of reserves (Ward et al. 1999; Gladstone 2002; Beger et al. 2003). The adequacy of the resulting reserve network in representing additional taxa was then evaluated and used to measure the combined efficacy of the surrogate and algorithm. We asked the question differently because we did not wish to address the spatial variability of habitat distribution at this stage, which undoubtedly influences such analyses. Rather, we asked, How would

the use of a common surrogate (marine habitat maps) influence a planner's ability to realize putative diversity and socioeconomic objectives for a marine reserve or reserve network? First, the representation of all species in the seascape requires inclusion of all habitats. This conclusion was largely driven by the need to represent all life phases of fish species and is somewhat surprising given that such taxa are generally far more mobile than benthic invertebrate species, most of which are sessile. The greater mobility of fishes may be expected to increase their distribution among habitats, thereby increasing the scope for redundancy of life phases among habitats. Although inclusion of all habitats was needed to represent all life phases, interhabitat redundancy was considerable because only one-quarter to one-third of species exhibited unique habitat fidelity. Relaxing the species-representation criterion from 100% to 95% nearly halved the number of habitats required to achieve the target. Thus, a small reduction in diversity targets offered a flexible range of habitat composition within reserves, thereby improving the likelihood that diversity targets would be compatible with other conservation criteria.

Fish species were more appropriate taxonomic surrogates than benthic invertebrates. This now appears to be a generic conclusion for coral reefs because Beger et al. (2003) arrived at a similar conclusion in the Pacific.

Table 5. Efficacy of different surrogates (%) in predicting a complementary set of species from an equivalent number of habitats.*

Surrogate	Data set to be represented				
	benthic spp.	fish spp.	fish function	processes	services
Benthic	-	41.7	65.5	71.0	76.7
Fish	71.4	-	86.0	71.0	48.8
Fish function	82.7	71.6	-	88.8	67.4
Processes	56.1	33.7	60.1	-	48.2
Services	23.4	6.7	35.4	38.7	-

*Values represent the species accumulation index (SAI) (100% indicates the habitat surrogate perfectly selected an equivalent representation of benthic species).

Table 6. Conclusions regarding the use of 4 conservation metrics for managing coral reefs.

<i>Metric</i>	<i>Benefits</i>	<i>Limitations</i>	<i>Suggested use</i>
Species composition (further disaggregated by life phase for fishes)	transparent link to many conservation aims (e.g., protection of $x\%$ of species within reserves)	expensive to acquire at adequate scales and may require high levels of expertise	good metric for habitat complementarity; fish species are better able to be surrogates for benthic species than vice versa and are easier to identify
Functional classification of fish species	easy to survey because limited taxonomic expertise required; provide focus on ecological processes pertaining to fish	reasonable surrogate for fish species	identifying habitats that underpin key trophic pathways (e.g., with high levels of tertiary production); prioritizing the importance of habitats for conservation
Ecosystem processes	can be assigned directly to habitat maps without requiring further field survey; provide insight into spatial distribution of ecological processes	unsuitable surrogate for species	prioritizing the importance of habitats for conservation; secondary, modifying criteria to a reserve design primarily founded on biodiversity metrics
Ecosystem services	provide transparent link between habitat maps and many coastal management goals (e.g., fisheries, coastal defense)	unsuitable surrogate for species	prioritizing the importance of habitats for conservation; proxy for reserve cost

Moreover, fish species are arguably a more tractable surrogate for reef diversity surveys because reef-fish identification is generally much easier than that of many benthic taxa, as the latter can exhibit marked phenotypic variation (Veron 1995) and their taxonomy frequently requires revision (Fukami et al. 2004). A number of large-scale volunteer-based organizations engage recreational scuba divers in fish surveys, which provides a wealth of data (Pattengill-Semmens & Semmens 2003).

The representation of reef fishes exhibited a strikingly different complement of habitats than that of benthic species. A likely cause of this divergence in pattern is the complex spatial nature of fishes' ontogeny. Many reef fishes use sea-grass beds, mangroves, and coral reefs at different stages of ontogeny (Nagelkerken et al. 2001; Mumby et al. 2004). Therefore, broad corridors of habitat are required to represent all stages of their populations. Methods to incorporate such ontogenetic habitat connectivity in conservation metrics are under development (Mumby 2006) and will be necessary to manage the fisheries of species concerned (e.g., *L. apodus*) and to realize diversity goals.

It is possible that sampling biases contributed to the observed divergence of habitat requirements needed to represent fish and benthic taxa. Although the total number of fish species and benthic "species" sampled were similar and every effort was made to resolve species-level identification, we could not sample every benthic species in the seascape for 2 reasons. First, infaunal communities were not sampled because it was logistically infeasible to collect and process an adequate number of samples across the Bahamas. Second, some species require microscopic identification (e.g., components of "algal turf" and

some encrusting red coralline algae), and this was not carried out for similar reasons. The effects of such sampling biases on our conclusions are not clear because ignoring infauna underestimates the richness of lagoonal habitats (Schlacher et al. 1998), whereas the grouping of some algal species underestimates the richness of reef habitats. Although these limitations temper the clarity of our conclusions, they do not, in our opinion, detract from the importance of our results because the data presented were generated systematically and consistently among habitats and have much greater taxonomic resolution than data from earlier studies (e.g., Mumby & Harborne 1999).

Fish species functions showed greater habitat redundancy than fish species. Conceivably, field data on fish functional categories might be easier to acquire than species-level data because of the reduced taxonomic expertise required. Indeed, functional-based taxonomic surrogates have been advocated in other systems and found to be useful (Steneck & Dethier 1994; Zalvaleta & Hulvey 2004). Although functional classes of reef fishes were reasonably good surrogates of fish species, their use as a surrogate is best carried out with caution. The increased habitat redundancy in functional classes could lead to important habitat classes for fish species being omitted. For example, the inclusion of all fish-species functions did not require the habitat "sparse gorgonians," yet this habitat harbored 14 unique life phases of fish species.

A metrics-orientated approach to designing marine reserves with a focus on ecosystem processes or services is unlikely to suit diversity goals. Even though metrics were constrained only to include a process or service if the value was *high*, we found high levels of redundancy such that typically only 2 or 3 habitats were required. A

reserve system derived from such priorities could miss between 18% and 25% of all surveyed marine species in the seascape. In contrast, a reserve system designed on the basis of fish species would represent at least 90% of all ecosystem processes and services.

We suggest that the high level of apparent redundancy in metrics of functional categories, processes, and services renders them generally unsuitable for a complementarity-based approach to reserve design. Rather, assuming that the aim is to achieve both diversity conservation and ensure high levels and representation of ecosystem services, reserve design might be better served through the use of process or service metrics as secondary modifying criteria to a diversity-based approach (Table 6).

Some minimal representation of all habitats is required to achieve representation of all species. Nevertheless, because habitats exhibit marked variability in their score for many conservation metrics—with *Montastraea* reefs dominating all targets—the relative weighting of habitat importance needs to be prioritized accordingly (i.e., there is no reason to assign equal importance to each habitat as is often the case in marine conservation initiatives). Indeed, a substantial literature exists on quantifying habitat value for conservation (Usher 1986; Rossi & Kuitunen 1996), although its application in some ecosystems (including marine) is often severely constrained by a lack of data or appropriate analyses. Although we recognize that species lists and metrics have their limitations and that representation of elements in reserves does not imply persistence (Gaston et al. 2002), we hope the metrics presented here for species, species functions, ecosystem processes, and services help practitioners weight the importance of habitats for their particular priorities. Future analyses will seek to examine how surrogacy value varies across a wide range of spatial and temporal scales (sensu Ferrier 2002). With increasing levels of climate-driven disturbance in the Caribbean (Gardener et al. 2003), it will become increasingly important to consider how subtle declines in habitat quality influence the composition of species and their associated contributions to ecosystem processes and services.

Acknowledgments

This work was supported by grants from the National Science Foundation's Biocomplexity in the Environment Program (OCE-0119976); the National Oceanic and Atmospheric Administration's National Undersea Research Program, administered by the Caribbean Marine Research Center (CMRC-03-NRDH-01-04A, under awards NA06RU0228 and NA16RU1496); the U.S. Environmental Protection Agency (R832223); and the Royal Society. We thank the Bahamas Department of Marine Resources.

Supplementary Material

A map of the study area (Appendix S1) and the effects of the number of habitats on the accumulation of fish species (Appendix S2) are available as part of the on-line article from <http://www.blackwell-synergy.com/>. The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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