
Designing Effective Marine Protected Areas in Seaflower Biosphere Reserve, Colombia, Based on Biological and Sociological Information

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Abstract: *Ecologists have paid increasing attention to the design of marine protected areas (MPAs), and their design advice consistently recommends representing all habitat types within MPAs or MPA networks as a means to provide protection to all parts of the natural ocean system. Recent developments of new habitat-mapping techniques make this advice more achievable, but the success of such an approach depends largely on our ability to define habitat types in a way that is ecologically relevant. We devised and tested the ecological relevance of a set of habitat-type definitions through our participation in a stakeholder-driven process to design a network of MPAs, focusing on no-take marine reserves in the Seaflower Biosphere Reserve, San Andrés Archipelago, Colombia. A priori definitions of habitat types were ecologically relevant, in that our habitat-type definitions corresponded to identifiable and unique characteristics in the ecological communities found there. The identification of ecological pathways and connectivity among habitats also helped in designing ecologically relevant reserve boundaries. Our findings contributed to the overall design process, along with our summary of other general principles of marine reserve design. Extensive stakeholder input provided information concerning the resources and their patterns of use. These inputs also contributed to the reserve design process. We anticipate success for the Seaflower Biosphere Reserve at achieving conservation and social goals because its zoning process includes detailed yet flexible scientific advice and the participation of stakeholders at every step.*

Diseño de Áreas Marinas Protegidas Efectivas en la Reserva de la Biosfera Seaflower, Colombia, en Base a Información Biológica y Sociológica

Resumen: *Los ecólogos han puesto mayor atención en el diseño de áreas marinas protegidas (AMP), y sus sugerencias de diseño recomiendan consistentemente la representación de todos los tipos de hábitat en los AMP o en las redes de AMP como una forma de proporcionar protección a todas las partes del sistema oceánico natural. Desarrollos recientes de técnicas de mapeo de hábitat nuevas hacen que estas recomendaciones sean*

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más realizables, pero el éxito de esta metodología depende, en buena medida, de nuestra capacidad de definir tipos de hábitat de manera ecológicamente relevante. Participando en un proceso conducido por grupos de interés para diseñar una red de AMPs, concentrada en reservas marinas sin extracción en la Reserva de la Biosfera Seaflower, Archipiélago San Andrés, Colombia, diseñamos y probamos la relevancia ecológica de un conjunto de definiciones de tipos de hábitat. Las definiciones a priori de tipos de hábitat fueron ecológicamente relevantes porque nuestras definiciones de tipos de hábitat correspondieron a características únicas e identificables de las comunidades ecológicas encontradas ahí. La identificación de trayectorias ecológicas y la conectividad entre hábitats también ayudaron al diseño de límites de reserva ecológicamente relevantes. Nuestros hallazgos contribuyeron al proceso de diseño en su conjunto, junto con nuestra recopilación de otros principios generales para el diseño de reservas marinas. La participación de los grupos de interés proporcionó información concerniente a los recursos y sus patrones de uso. Esta participación también contribuyó al proceso de diseño de la reserva. Anticipamos el éxito para la Reserva de la Biosfera Seaflower en el cumplimiento de sus metas sociales y de conservación porque en su proceso de zonificación se incluyen recomendaciones científicas detalladas pero flexibles y la participación de grupos de interés en cada etapa.

Introduction

In response to worldwide declines in marine resources, a paradigm shift has occurred toward better and more precautionary conservation and management of marine resources (Ludwig et al. 1993; Dayton 1998). Scientists and ocean managers have shown growing interest in marine reserves—areas that are closed to fishing and protected from other major human impacts. Leaving a certain fraction of all populations off-limits to extraction provides substantially greater long-term stability of marine resources than other management strategies (Sladek Nowlis & Bollermann 2002). Marine reserves can also halt the loss of biodiversity and changes in species interaction too commonly seen under current management strategies by conserving habitats and biological communities (Dayton et al. 1995; Boehlert 1996). Marine reserves are a precautionary approach to management that reduces the risks of overexploitation (Sladek Nowlis & Friedlander 2004) and represents ecosystem-based management by allowing ecosystems to function naturally within their borders (Buck 1993). They may also provide catch enhancements, particularly if local fisheries are overfished (Sladek Nowlis & Roberts 1999). At the very least, marine reserves create a buffer that protects vulnerable exploited species with relatively little opportunity cost to the fishing industry.

Despite their gaining popularity, there is still widespread confusion as to how to effectively design marine reserves and the more general marine protected areas (MPAs)—areas with site-specific regulations but not necessarily comprehensive protection. To be effective, it is generally accepted that MPA networks should be distributed along environmental gradients and should protect representative species and habitat types (Ballantine 1997; Murray et al. 1999), although rare and vulnerable habitat types should be represented more fully (Sladek Nowlis & Friedlander 2004). Because coral reef ecosystems will function properly only when a mosaic of habitat

types is connected biologically (Ogden 1988; Appeldoorn et al. 2003), marine protected-area networks should strive to include a range of interconnected habitat types. Arbitrary declaration of areas as MPAs based on poor ecological knowledge can prevent biodiversity objectives from being met (Vanderkluft & Ward 2000).

Our objective was to develop and test the effectiveness of a set of ecologically relevant definitions of habitat type in the context of design of an MPA network and to incorporate this information into a stakeholder-driven process. Numerous studies have identified the value of stakeholder involvement in achieving successful marine policy, from increasing compliance to shaping more culturally sensitive regulations (e.g., Fiske 1992; Pollnac et al. 2001; Appeldoorn & Lindeman 2003). We developed a set of habitat-type definitions based on knowledge and experience, tested their ecological relevance, and worked with stakeholders and resource managers to apply these and other general ecological design criteria to the development of a network of marine reserves within a larger MPA system. Our project uniquely incorporated biological and sociological information prior to the establishment of protected areas.

Methods

The Archipelago

The Archipelago of San Andrés, Old Providence, and Santa Catalina is a Colombian protectorate located in the southwestern Caribbean, approximately 700 km northwest of mainland Colombia, and includes two barrier reefs surrounding the main populated islands of San Andrés and Old Providence, five large atolls, and other less defined coral banks that extend for more than 500 km along the Nicaraguan Rise (Geister & Díaz 1997). The archipelago possesses some of the highest marine biodiversity and endemism in the Caribbean (Garzon-Ferreira & Acero

1992; Acero & Garzon-Ferreira 1994; Roberts et al. 2002) and was declared an international biosphere reserve (The Seaflower Biosphere Reserve) by the United Nations Educational, Scientific, and Cultural Organization (UNESCO) in 2000.

The native islander population of the archipelago is distinct within Colombia for characteristics that include an Anglo-Puritan and African heritage, Protestant religious tradition, and English native language. The Colombian Constitution grants special status to archipelago natives as an ethnic minority group and encourages programs to protect the archipelago's environment and culture, including traditional marine tenure rights.

The Corporation for the Sustainable Development of the Archipelago of San Andrés, Old Providence, and Santa Catalina (CORALINA), the environmental management agency for the archipelago, is currently developing a regional system of multiple-use, zoned MPAs (CORALINA 2000). The MPAs will be zoned for various uses and will include no-take reserves designated as "no-fishing" and "no-entry" zones. An initial phase of the project focused on Old Providence and Santa Catalina Islands (OPSC) through collaboration among CORALINA, The Ocean Conservancy, and visiting scientists. The small islands of OPSC are among the least environmentally and culturally degraded locations in the Caribbean region. These islands reach a height of 350 m, with a land area of 18 km² and a population of 4140. Full and part-time fishing are important economic activities in OPSC, although the recreational dive and snorkel business has expanded in recent years. The OPSC barrier reef is 32 km long and covers an area of 255 km², making it one of the largest reefs in the Americas (Geister & Díaz 1997). The OPSC reef complex is unique because it surrounds the only high-elevation volcanic island found in the region (Geister 1992). McBean Lagoon National Park, the only national park in the archipelago, encompasses 995 ha of mangroves, barrier reef, lagoon, seagrass beds, and four small cays.

Ecological Assessments

Sampling was conducted during August 2000. Ideally, we might have sampled throughout the year to identify seasonal patterns known to affect commercially exploited species. However, we were able to learn about this seasonality through interviews of fishers. Moreover, our assessments focused on nearshore reef-associated species, which do not exhibit a great deal of seasonal variation.

SAMPLING STRATEGY

We identified coral reef habitat types from existing habitat maps (Díaz et al. 1996). Habitat types were pooled a priori based on information from local authorities and our ex-

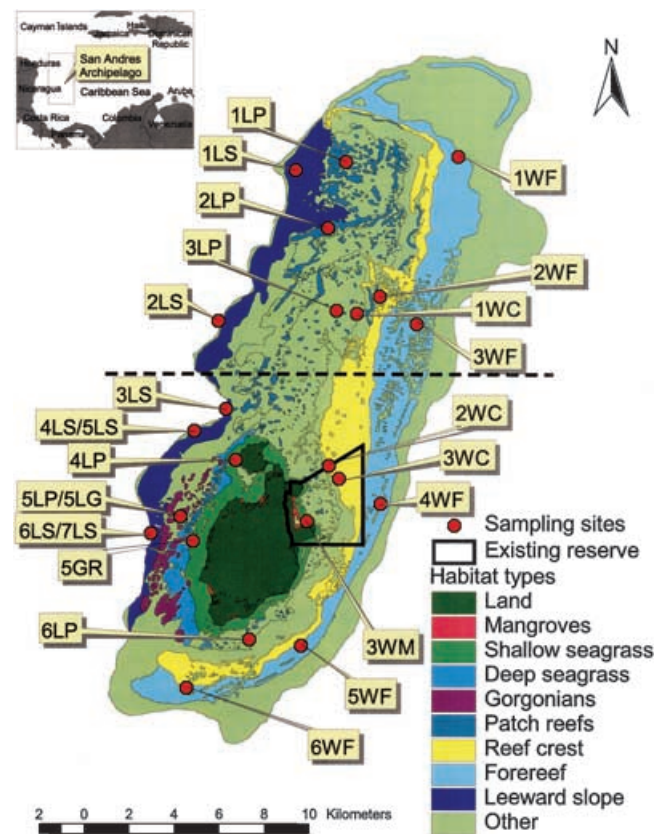


Figure 1. The Old Providence and Santa Catalina reef complex showing major habitat types encountered during the study, an existing no-take marine reserve, and the sampling site locations. The study area was separated into an island subarea (south of the dotted line, sites near land) and a bank subarea (north of the dotted line, sites away from land) (LP, lagoonal patch reefs; LS, leeward slope; WF, windward forereef; WC, windward crest; LG, lagoonal gorgonian; GR, seagrass beds; WM, windward mangroves).

periences with the ecological function of various habitat types elsewhere in the Caribbean. When pooled, habitat types included forereef, reef crest, lagoon patch reefs, gorgonian-dominated areas, leeward slope reefs, seagrass beds, mangrove lagoons, and other basin formations (e.g., sand, rubble).

We designed the sampling strategy to test for differences in coral community composition and fish assemblage structure among habitat types, by depth, by degree of wave exposure, and between bank and island sites (Díaz et al. 1996; Sánchez et al. 1998). We sampled habitat types around the islands and on the northern bank if they occurred in both places. These habitats included forereef, crest, patch-reef, and leeward slopes (Fig. 1). Gorgonian, seagrass, and mangrove habitats were sampled only around the island locations owing to their absence on the northern bank.

BENTHIC COMMUNITY ASSESSMENT

Within sites, we sampled benthic communities randomly along haphazardly placed transect lines within the appropriate habitat type. Where the habitat was continuous over a large area, we placed the transect line along an isobathymetric contour. When patchy habitat precluded this type of sampling, the transect line was positioned to maximize the inclusion of the appropriate habitat type within each sample. We sampled 1-m² quadrats along at least one 30-m transect line at each site. Where time permitted, a second transect line was surveyed.

Within each transect, we sampled 6–10 quadrats, depending on scuba time constraints. We used randomly generated numbers to position quadrats along the transect line. Within each quadrat, observers identified corals, gorgonians, algae, and macroinvertebrates to the lowest possible taxa and estimated the percent cover (for encrusting forms) or counted the numbers (for upright or mobile forms) of each of these taxa (for discussion of quadrat sampling techniques, see Rogers et al. 1994). To measure reef complexity or rugosity, we draped a small-link chain along the full length of the centerline of each quadrat (Risk 1972). A ratio of distance along the reef surface contour to linear horizontal distance gave an index of spatial relief or rugosity.

Where observed in these surveys, we enumerated conch and lobster. However, our technique failed to assess the status of these species well because conch do not prefer the reef habitats on which we focused and lobsters are inactive during the day. Instead, we relied on feedback from fishing communities as to the history, status, and location of these species. Studies have demonstrated the value and accuracy of such information (Valdés Pizzini et al. 1997).

FISH ASSEMBLAGE CHARACTERIZATION

We characterized the fish fauna based on visual censuses. Three divers swam as many 25-m-long transects as conditions allowed per site, separating each by at least 5 m. Two of the divers identified all fishes 2 m on either side of the transect, for a total of 100 m² surveyed per transect. The third diver sampled a similar transect but only enumerated snappers, groupers, and grunts, three important fish families for fisheries. Each fish observed within the transect boundaries was identified to the lowest possible taxa and enumerated, and its total length was classified into 5-cm length bins.

Data Analyses

We used detrended correspondence analysis (DCA) to identify clusters of similar sampling sites in ordination space based on benthic habitat characteristics (Gauch 1982). We log_e(x)-transformed values, and taxa that oc-

curred in <20% of the number of stations than the most common taxon were downweighted. The amount that each species was downweighted was inversely related to its frequency of occurrence and was useful as a means for primarily comparing differences among the most common species while not ignoring or giving undue weight to rare taxa. We compared the resulting clusters to our a priori definitions of habitat types as a test of their ecological relevance.

We converted length estimates of fishes from visual censuses to weight using the allometric length-weight conversion, $W = aSL^b$, where parameters a and b are constants (fitting parameters obtained from FishBase, www.fishbase.org), SL is standard length in millimeters, and W is weight in grams. In cases where length and weight information did not exist for a given species, we used the parameters from similar-bodied congeners. Species diversity was calculated from the Shannon-Weaver diversity index (Ludwig & Reynolds 1988), $H' = -\sum (p_i \ln p_i)$, where p_i is the proportion of all individuals counted that were of species i . The evenness component of diversity was expressed as: $J = H' / \ln(S)$, where S is the total number of species present (Pielou 1977).

We used DCA to examine the fish assemblage associations among sampling sites. The clustering was based on characteristics of the fish assemblage alone. We compared the resulting patterns to our a priori habitat-type definitions as another test of their ecological relevance.

We used nested analyses of variance to examine differences in the fish assemblage characteristics (number of species, number of individuals, and biomass) among habitats and sampling strata, with habitat type nested within bank or island strata. Number of individuals and biomass were log_e(x + 1)-transformed to conform to the parametric assumptions of the analysis of variance and back-transformed for purposes of data presentation. We conducted unplanned multiple comparisons using the Tukey-Kramer HSD (honestly significant difference) test.

Community Information Collection

CORALINA organized meetings with fishers to discuss the current status of fisheries, knowledge of local fishes, and potential zoning options for MPAs. Initial meetings concentrated on traditional resource knowledge and education relevant to marine reserves. In addition, meetings were held with dive and snorkel tour operators to obtain their opinions on where to locate reserves. Maps were used as a focus for discussion and allowed local fishers to illustrate traditional knowledge and identify locations of resources and resource-use patterns. Later meetings focused on identifying a variety of potential MPA zoning options and produced some areas of consensus among stakeholder preferences.

Results

Benthic Habitat Characteristics

The 24 sampling sites possessed three exposure regimes (windward, leeward, and lagoon) and seven major habitat types (patch-reef, reef slope, reef crest, forereef, mangrove, seagrass, and gorgonian). Live coral cover ranged from <1% at the South Bank forereef to >38% along the Cathedral leeward slope and Manta City lagoonal patch reefs (Table 1). Coral cover and coral species richness were typically highest on the patch reefs and along the leeward slope, with the lowest values recorded on the forereef.

Based on data from 68 benthic taxa, including 34 scleractinian coral species, the DCA showed distinct clusters of sampling locations within defined habitat types (Fig. 2). The windward habitats (reef crest and forereef) presented separate, discrete groups, whereas leeward habitats (lagoon patch reef and slope) overlapped to a small extent (Fig. 2a). The first axis of the DCA was significantly linearly correlated with rugosity ($r^2 = 41\%$, $df = 1$, $F = 13.21$, $p = 0.0017$). Plotting rugosity values on the ordination biplots showed that high rugosity values occurred more often in leeward habitats (Fig. 2b). Leeward habitats also possessed higher coral (Fig. 2c) and sponge cover, more coral species, and a higher density of gorgonian corals. The highest values for all of these variables occurred at stations along the leeward slope. Windward habitats had the highest algae cover (Fig. 2d) and lowest coral abundance and coral diversity.

Fish Assemblage Structure

There were large variations in fish assemblage characteristics among locations, with distinct characteristics in each habitat type (Table 2). The DCA of the fish data identified seven groups that corresponded to major habitat types (Fig. 3). There was a clean separation in fish assemblage structure among the habitat types identified a priori, and there was good concordance among locations within each habitat type. Seagrass habitats were not replicated owing to the low densities of observable fish within them during daylight hours, whereas mangrove habitats were not replicated because of their rarity.

The fish assemblage structure gradually shifted across the platform from windward to leeward (Fig. 3). In addition to the change in assemblage structure, species richness and diversity increased overall from windward to leeward. The gorgonian site was near reef habitat, whereas mangrove and seagrass sites were widely separated from reef sites.

Fish Assemblage Characteristics

Fish assemblage characteristics differed between bank and island sites and among habitats. The number of

species observed differed significantly between the bank and island sites and among habitats (overall: $F_{10,15} = 13.5$, $p < 0.001$; bank and island: $F_{1,15} = 6.9$, $p = 0.019$; habitat[bank and island]: $F_{9,15} = 15.03$, $p < 0.001$). Although the greatest numbers of species were recorded on the island patch-reef, gorgonian, and slope habitats, respectively, the low number of species observed in the seagrass beds and mangroves resulted in the overall species richness being higher at bank sites. Patch reef was the only habitat that differed significantly in species number between bank and island locations ($p < 0.05$), with species number being higher at island sites.

The number of individuals observed differed significantly among habitats but did not differ between bank and island sites, despite an average of 26% more individuals at island sites (overall: $F_{10,15} = 9.25$, $p < 0.001$; bank and island: $F_{1,15} = 0.21$, $p = 0.650$; habitat[bank and island]: $F_{9,15} = 9.93$, $p < 0.001$). The greatest number of individuals was observed at island slope, island patch-reef, and mangrove sites, respectively, with seagrass having the lowest observed number of individuals. The number of individuals observed on island slope transects was significantly greater than on bank slope transects ($p < 0.05$). No other habitat comparisons between bank and island sites differed significantly ($p > 0.05$).

Fish biomass differed significantly among habitat types but not between bank and island sites, although biomass was on average 44% higher at island sites (overall: $F_{10,15} = 3.71$, $p = 0.011$; bank and island: $F_{1,15} = 0.001$, $p = 0.968$; habitat[bank and island]: $F_{9,15} = 4.063$, $p = 0.008$). Biomass was highest in the mangroves, followed by island slope and island patch-reef habitats. Fish biomass on the island slope and crest habitats was 351% and 150% higher, respectively, than on similar bank habitat types.

Fish assemblage structure differed greatly among habitat types and locations (Table 2), often reflecting ecological links between the fish and habitat. Piscivores and mixed piscivores and invertivores were most common in habitats that exhibited high structural complexity, including complex reef and mangrove environments. The complexity likely attracts increased settlement of fish and thus a food supply. Herbivores were most abundant in windward crest and lagoonal patch-reef environments, both characterized by abundant algae. Although windward forereef habitats had even more algae, these environments lacked any real structure to provide shelter. Planktivorous fishes were most abundant along leeward slopes, where upwelling provides abundant plankton. Thus, fish assemblages seemed to be shaped by habitat characteristics through ecological processes and connectivity among habitat types.

Morgan's Head is an important transition habitat that harbors a large number of juvenile grunts, snappers, and surgeonfishes. Lazy Hill Bar (SLP) was a large shoal with high scleractinian coral cover surrounded by an extensive gorgonian bed and sand. This shoal was also located in

Table 1. Habitat characteristics for locations sampled around Old Providence and Santa Catalina Islands.

Location	Map code	Depth (m)	Exposure	Habitat	Rugosity	Coral cover (%)	Coral species (n)	Gorgonian density (m ⁻²)	Gorgonian species (n)	Algal cover (%)	Sediment cover (%)	Sponge cover (%)
North bank patch reefs	1LP	9.9	lagoon	patch reefs	1.98	37.74	21	9.29	4	17.46	7.93	2.29
North bank leeward slope	1LS	17.4	lagoon	slope	1.63	22.77	15	6.25	8	40.10	4.90	6.50
South Bank crest	1WC	1.8	leeward	reef crest	1.55	10.51	15	5.76	10	44.49	24.82	0.59
North bank windward forereef	1WF	18.6	windward	forereef	1.02	1.55	7	1.00	3	41.10	29.80	3.95
North bank leeward patches	2LP	6.7	lagoon	patch reefs	2.10	31.50	12	17.15	9	41.55	3.90	0.40
North bank leeward slope	2LS	15.8	leeward	slope	1.58	30.68	19	5.90	7	41.45	6.40	4.70
Inactive pinnacles	2WC	4.6	lagoon	reef crest	1.15	5.02	8	0.30	1	54.96	15.40	0.50
South bank <i>Acropora</i> forereef	2WF	8.2	windward	forereef	1.33	4.21	5	0.00	0	60.71	15.18	0.79
South bank lagoon patches	3LP	8.4	lagoon	patch reefs	2.09	24.07	18	1.39	7	52.24	2.73	0.63
Blue Hole	3LS	20.7	leeward	slope	1.42	19.72	14	8.00	3	26.25	11.70	12.10
Active pinnacles	3WC	5.5	windward	reef crest	1.86	14.43	10	0.00	0	56.44	12.22	4.00
South bank forereef	3WF	17.7	windward	forereef	1.06	0.14	1	1.18	2	68.36	3.73	1.95
McBean Lagoon	3WM	1.2	lagoon	mangrove	—	—	—	—	—	—	—	—
Morgan's Head*	4LP	5.9	lagoon	patch reefs	1.66	17.85	15	7.53	8	48.95	22.50	1.30
Felipe's Place	4LS	18.3	leeward	slope	1.39	42.88	17	1.50	2	30.15	0.50	3.15
Crab Cay forereef	4WF	20.7	windward	forereef	1.06	0.70	3	0.50	3	37.50	17.60	1.67
Freshwater Bay seagrass	5GR	4.6	leeward	seagrass	1.00	0.00	0	0.00	0	4.98	0.00	0.00
Lazy Hill bar	5LG	4.6	lagoon	gorgonian	1.28	1.90	6	7.80	9	29.15	31.00	1.50
Lazy Hill bar*	5LP	6.7	lagoon	patch reefs	1.66	29.69	23	9.70	11	31.69	13.04	3.59
Felipe's Place Shelf	5LS	9.9	leeward	slope	1.46	15.17	20	7.57	12	45.37	2.60	0.53
Manchineel Bay forereef	5WF	18.9	windward	forereef	1.01	7.06	7	1.13	4	27.88	40.25	1.19
Manta City	6LP	6.9	lagoon	patch reefs	1.60	38.07	11	0.30	1	17.86	19.60	1.02
Cathedral*	6LS, 7LS	18.7	leeward	slope	1.49	38.13	21	3.03	4	29.74	4.00	6.32
South forereef	6WF	13.4	windward	forereef	1.12	1.47	7	2.80	6	64.83	10.20	0.50

* Mean of two surveys.

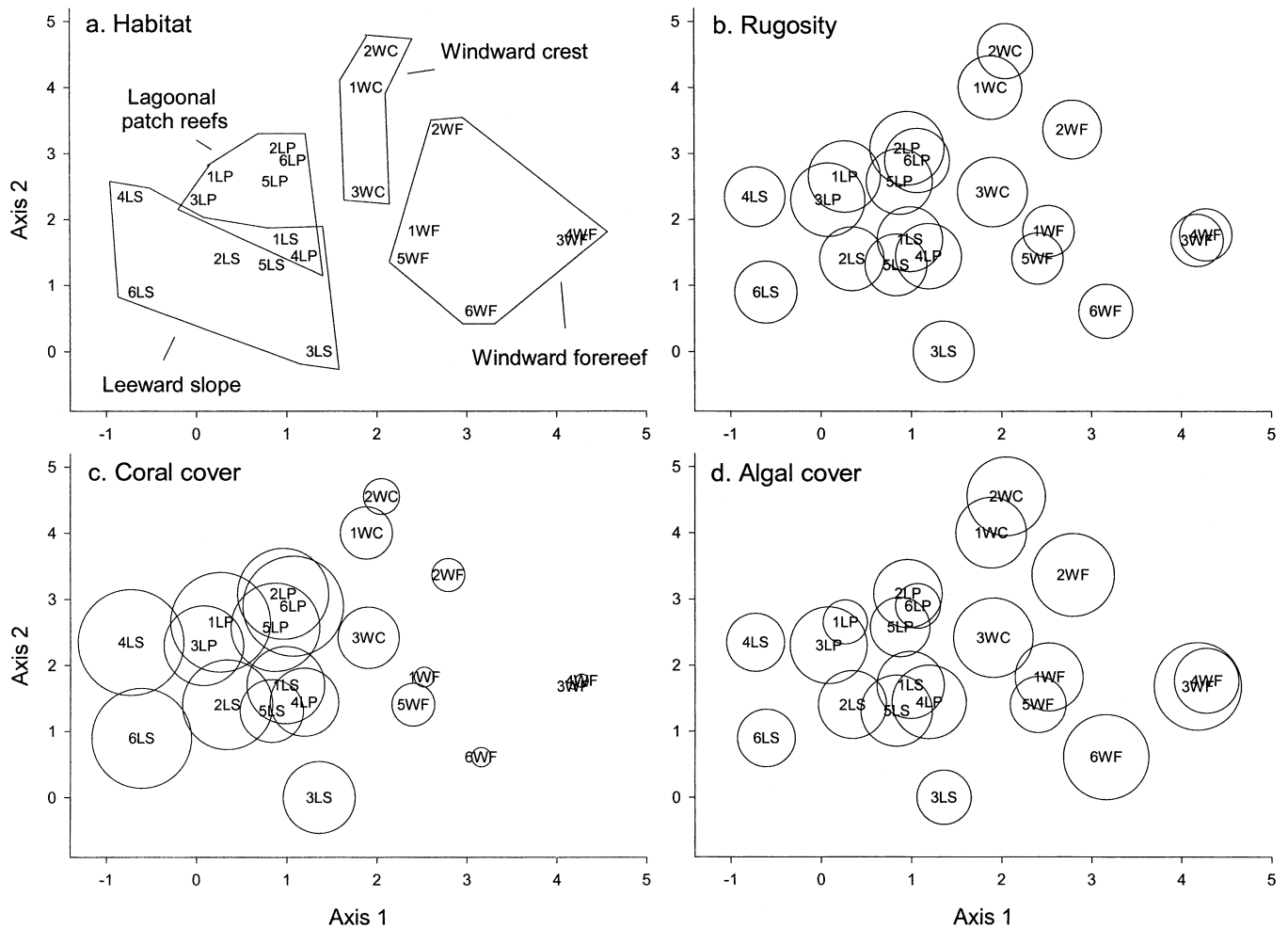


Figure 2. Detrended correspondence analysis of Old Providence and Santa Catalina benthic community (68 spp.): (a) major hard-bottom habitat types (LS, leeward slope; LP, lagoonal patch reefs; WC, windward crest; WF, windward forereef) and (b-d) physical and biological variables (circles are proportional to the value of each variable at each station). Location codes defined in Table 1.

fairly close proximity to seagrass beds and deep-water slope habitat. The connectivity of these habitats provided a rich fish assemblage that was dominated by snappers, grunts, and goatfishes.

Local Resource Knowledge

Meetings conducted with fishers revealed their extensive current and historical knowledge about the distribution and life-history traits of important fisheries species (Fig. 4). Fishers also provided information on the status of these fisheries, including gear used, locations of fishing activity, trends in landings, and resource-allocation conflicts (Table 3).

BAITFISH

Fishers rely on baitfish for chum or as bait for traps, handlines, and trolling. Target species around OPSC consist

mainly of sprat (*Harengula* spp.) and fry (*Jenkinsia lamprotaenia*). Baitfish are typically taken with cast nets, scoop nets, or screens. The major locations for catching baitfish are McBean Lagoon (nearly a no-take reserve, this seasonal traditional use is the only extractive activity allowed) and the mangrove area near the footbridge between the two islands, but most shallow embayments yielded baitfish at one time or another. No information was given on spawning, although elsewhere in the Caribbean fry are known to aggregate and spawn monthly (Friedlander & Beets 1997). According to fishers, the current status of these stocks appears to be healthy.

CONCH

Fishers consider the queen conch (*Strombus gigas*) the most overfished resource in the archipelago and rated their status around OPSC as poor (1 on a scale of 1 to 10). Juveniles were previously abundant in the grass, sand, and

Table 2. Fish assemblage characteristics from 25 x 4 m belt transects at sampling locations around Old Providence and Santa Catalina Islands.^a

Location	Map code	No. species	No. individuals	Biomass (g)	Diversity	Evenness	Percentage of total biomass by trophic guild ^b					
							berbtv	mobile invert	mi/p	pisc	sessile invert	plank
North bank patch reefs	1LP	21.50	110.63	2912.75	2.40	0.79	53.88	19.44	3.70	3.88	13.76	5.34
North bank leeward slope	1LS	22.00	140.83	1723.04	2.28	0.75	51.52	22.22	3.77	1.33	11.15	10.02
South bank crest	1WC	19.00	112.50	2415.88	2.33	0.79	66.94	18.09	9.17	0.06	3.60	2.13
North bank windward forereef	1WF	15.83	112.33	7987.94	1.91	0.70	13.46	70.91	2.18	6.22	0.57	6.66
North bank leeward patches	2LP	21.75	131.38	5140.55	2.42	0.79	73.70	17.35	4.51	0.57	2.43	1.44
South bank leeward slope	2LS	18.17	126.50	1917.01	2.10	0.73	35.22	18.52	9.25	3.97	10.87	22.16
Inactive pinnacles	2WC	18.71	80.43	2605.31	2.47	0.85	67.99	26.26	4.55	0.00	0.13	1.07
South bank <i>Acropora</i> forereef	2WF	16.88	89.63	2937.63	2.19	0.78	67.99	12.62	0.76	2.64	2.38	13.61
South bank lagoon patches	3LP	21.88	93.38	9323.90	2.47	0.80	11.79	14.95	70.75	0.22	1.49	0.79
Blue Hole	3LS	22.20	469.60	16547.41	1.56	0.50	6.39	12.94	9.18	53.14	1.39	16.96
Active pinnacles	3WC	15.88	132.63	9482.27	2.12	0.77	91.82	5.06	0.59	1.86	0.44	0.23
South bank forereef	3WF	15.17	101.83	1663.52	1.98	0.73	36.17	40.47	2.72	0.00	7.82	12.81
McBean Lagoon	3WM	8.14	190.43	8326.80	1.33	0.65	0.43	19.59	79.32	0.37	0.06	0.22
Morgan's Head ^c	4LP	20.57	189.29	10099.51	2.19	0.73	29.95	45.02	23.94	0.04	1.00	0.06
Felipe's Place	4LS	23.78	256.78	8571.68	1.89	0.60	15.53	46.35	12.02	4.39	1.44	20.28
Crab Cay forereef	4WF	10.25	65.25	629.89	1.58	0.68	29.08	35.96	3.56	0.00	22.11	9.29
Freshwater Bay seagrass	5GR	3.50	12.50	123.74	0.83	0.72	18.96	81.04	0.00	0.00	0.00	0.00
Lazy Hill bar	5LG	22.75	150.50	3795.68	2.25	0.72	45.90	48.70	2.15	0.82	2.12	0.31
Lazy Hill bar ^c	5LP	26.91	161.55	4795.90	2.67	0.81	22.39	24.38	31.94	8.39	4.20	8.69
Felipe's Place Shelf	5LS	22.00	259.20	7245.01	1.81	0.58	13.00	2.64	2.23	3.21	0.48	78.44
Manchineel Bay forereef	5WF	14.00	83.75	3611.24	1.94	0.74	26.52	44.30	0.10	0.04	1.95	27.08
Manta City	6LP	30.14	219.57	4409.54	2.68	0.79	13.97	53.85	9.60	0.00	4.66	17.92
Cathedral ^c	6LS, 7LS	23.00	172.67	4339.03	2.12	0.68	29.04	10.80	7.82	12.19	14.41	25.74
South forereef	6WF	14.38	151.75	4881.75	1.80	0.68	18.38	50.42	0.88	0.28	2.10	27.93

^aValues are means of two to four transects per location.^bAbbreviations: berbtv, herbivores; mobile invert, mobile invertebrate feeders; mi/p, mobile invertebrate and piscivore feeders; pisc, piscivores; sessile invert, sessile invertebrate feeders; plank, planktivores.^cMean of two surveys.

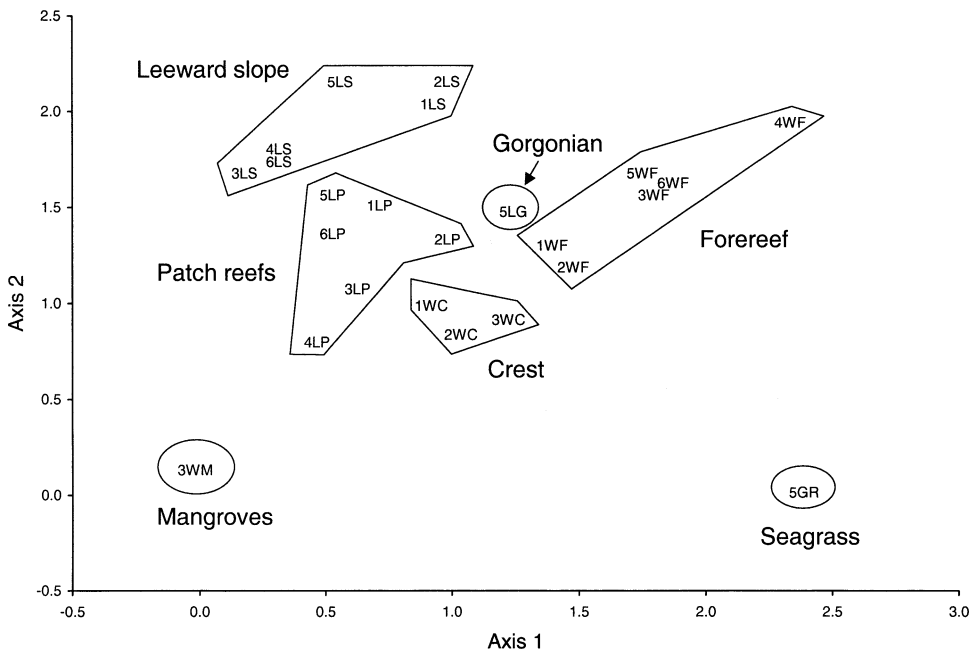


Figure 3. Detrended correspondence analysis of Old Providence and Santa Catalina fish assemblage. Location codes defined in Table 1.

rubble habitats around OPSC and in the shallow bank area to the north. Adult conchs were previously common toward the northern tip of the barrier reef and along the grass and rubble areas leeward of the islands. Deeper conch populations (42–44 m) occur along the northeast shelf, and these deeper areas may act as a refuge from fishing pressure because hand-collection of conchs is constrained by depth. Conchs are reported to spawn in the summer, but some fishers observed spawning in December. Fishers believed that a lack of understanding and education has led to overfishing of juvenile conchs.

LOBSTER

The most important areas for lobster (*Panulirus argus*) harvest are along the northwest tip of the barrier reef and an area approximately 6 km northeast of the islands along the windward barrier reef. Other important adult lobster habitats include the entire barrier reef and leeward patch reefs near the shelf break. Juvenile lobsters are common in McBean Lagoon and along the mangrove habitats near the footbridge connecting OPSC. Year-round spawning has been observed around OPSC. Fishers rate the status of lobsters as moderately overfished (4 of 10).

REEF FISH

A variety of reef fish are caught with traps, handlines, and spears. Most trap fishing is for personal consumption, and there is only one full-time commercial trap fisher on the island. Common trap-caught species include margates (*Haemulon album*), goatfishes (Mullidae), surgeonfishes (Acanthuridae), and small groupers, mainly coney (*Cephalopholis fulvus*) and graysby (*Cephalopho-*

lis cruentatus). Handlining is often conducted for snappers, groupers, grunts, and jacks. Yellowtail snappers (*Ocyurus chrysurus*) are often caught with handlines in 33–40 m of water. Spearfishers target many of the same species sought by handliners but also seek blue (*Scarus coeruleus*), midnight (*Scarus coelestinus*), and rainbow parrotfishes (*Scarus guacamaia*), queen (*Balistes vetula*) and gray triggerfishes (*Balistes capriscus*), and chubs (*Kyphosus sectatrix* and *K. insisor*). Spearfishing is normally conducted in shallower water than handlining and is preferred by younger fishers. Fishers expressed concern over the absence of large parrotfishes in the lagoon in recent years as a result of overfishing.

Several grouper spawning aggregations are known and targeted by fishers. Nassau grouper (*Epinephelus striatus*) form spawning aggregations in January and February near the northern tip of the barrier reef and at the northeast bank in approximately 40 m of water. Black (*Mycteroperca bonaci*) and yellowfin (*M. venenosa*) groupers are reported to spawn at similar times of year along the northwest tip of the barrier reef. These aggregations have been fished for many years, and fishers reported that the abundance and size of these species has declined over time.

BOTTOM FISH

Deep-dwelling species such as snappers (*Lutjanus vivanus*, *L. bucanella*, *Etelis oculatus*, *Pristipomoides macrophtalmus*) and jacks (*Seriola rivoliana*, *S. durmerili*) are the main target of deep-water fishing. Other species include the redeye or vermilion snapper (*Rhomboplites aurorubens*), Nassau grouper, Warsaw grouper (*Epinephelus nigritus*), and snowy

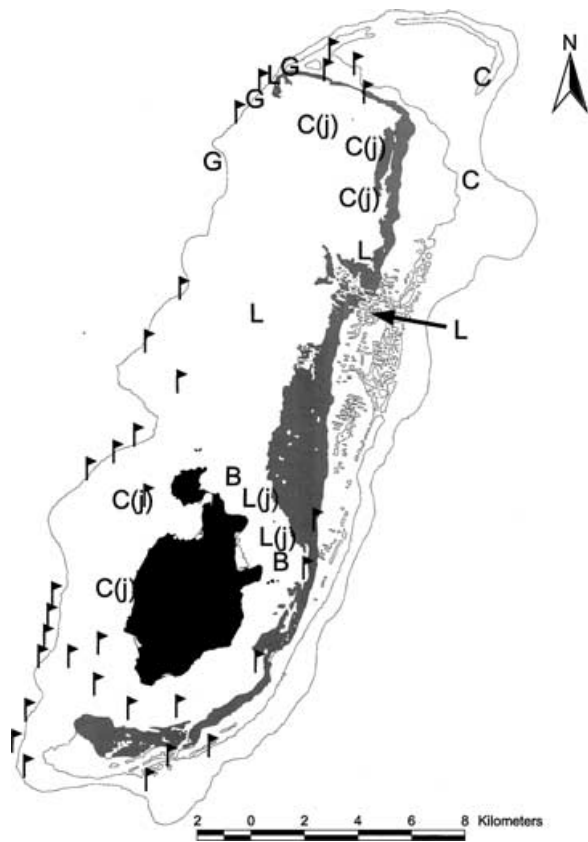


Figure 4. Important locations for major fisheries species and for snorkeling and diving. Information collected through consultations with local fishers and dive and snorkel operators (C, conch; C(j), juvenile conch; L, lobster; L(j), juvenile lobster; G, grouper spawning sites; B, baitfish). Flags indicate important sites for snorkeling and diving.

grouper (*Epinephelus niveatus*). Fishing for these species typically occurs in depths ranging from 80 to 200 m, and fishers use handlines, electric reels, and bottom long-lines. Localized overfishing has occurred for some target species.

PELAGICS

Pelagic species are taken almost exclusively by trolling with artificial lure or bait. Sargassum drifts into the area in the late summer and early fall and is followed by a variety of pelagic species. Major target species include wahoo (*Acanthocybium solandri*) (June-January), rainbow runner (*Elagatis bipinnulata*) (August-December), amberjack (*Seriola rivoliana*, *S. dumerili*) (September), tunas (September-January), dolphinfish (*Coryphaena* spp.) (September-November), and bonito (*Katsuwonus pelamis*) (year-round). These resources are seasonally abundant and currently healthy.

With its small population and limited tourism, the most frequent user conflict within OPSC is among artisanal fishers over the use of illegal gear or nontraditional methods. The major conflict at the present time, however, centers on industrial fishing by outsiders that takes place primarily in the area of the northern cays but occasionally affects the reefs around OPSC as well. Major issues that have resulted from this situation are the increasing difficulty of access to collective fishing grounds by artisanal fishers, failure to respect or acknowledge traditional fishing rights and sea tenure, demands for local autonomy in licensing and management, lack of benefit to the island community, severe overfishing of some species including exploitation of threatened and endangered species, and neglecting to enforce existing fisheries regulations that include gear restrictions and closed seasons (Howard et al. 2003).

Community-Based MPA Zoning Options

Fishers considered a range of zoning options, including an MPA around the entire island for artisanal fishing only (restricting both fishing with scuba and catching turtles) and a no-take zone around OPSC if traditional zones on banks to the north were reserved for artisanal fishing. The majority of the dive sites are located along the leeward reef break between 12 and 36 m of water. Popular snorkel locations include Morgan's Head (4LP), Manta City (6LP), and several reef passes along the southeast windward barrier reef. A modest amount of diving and snorkeling also occurs to the far north near the tip of the barrier reef. In later meetings stakeholders identified some consensus areas of closure, primarily reef crest habitat and areas directly adjacent to the islands (Fig. 5a & 5b).

Discussion

Habitat-Driven Marine Zoning

Both benthic characteristics and fish assemblages were closely linked to the habitat types in which they were found. Consequently, our definitions of habitat type can serve as a focus of marine reserve design for reefs in the Seaflower Biosphere Reserve and other areas with similar ecologies because inclusion of all these habitat types is likely to ensure the inclusion of most species in the management area throughout their life cycles.

A number of additional ecological considerations should shape sound marine zoning processes. These considerations include the total coverage of each zone type, size and shape of individual zones, and actual selection of areas for specific zoning designations. A comprehensive zoning process, as is being implemented in the Seaflower MPAs, may be preferable to designating marine reserves solely because additional zone types can reduce a

Table 3. Summary of major fisheries resources, habitats, gear used, spawning seasons, and current status based on information from Old Providence and Santa Catalina Islands fishing communities.

Fishery	Major species	Habitat	Gear	Spawning season		Status
				year round	year round	
Bait	sprats (<i>Harengula</i> spp.) fry (<i>Jenkinsia lamprotaenia</i>)	mangroves	cast nets, small mesh seines		good	
Bottom fish	snappers (Lutjanidae)	deep slopes	handlines, electric reels			fair, some localized depletion
Reef fish	groupers (Serranidae)	patch reefs, reef crests, slopes	spear, traps, handlines	varies among species	overall good	
	parrotfishes (Scaridae)					
Conch	surgeonfishes (Acanthuridae)					
	snappers (Lutjanidae)					large parrotfish overfished in lagoon
	grunts (Haemulidae)					
	chubs (Kyphosidae)					
	triggerfishes (Balistidae)					
Lobster	groupers			Jan. -Feb.		grouper spawning aggregations overfished
	black (<i>Epinephelus bonaci</i>) Nassau (<i>E. straitus</i>) queen conch (<i>Strombus gigas</i>)	seagrass beds, other (sand, rubble)	by hand, scuba and snorkeling	Jan. -Feb. Summer		poor, severely overfished
Pelagics	spiny lobsters (<i>Panulirus argus</i>)	patch reefs	by hand, scuba and snorkeling	year round		fair, some localized depletion
	bonito (<i>Katsuwonus pelamis</i>)	reef crests forereefs open ocean, most abundant during summer and fall	traps trolling, artificial lures and natural bait	varies among species		good
Pelagics	wahoo (<i>Acanthocybium solandri</i>)					
	rainbow runner (<i>Elagatis bipinnulata</i>)					
	amberjack (<i>Seriola rivoliana</i> , <i>S. dumerili</i>)					
	tuna (Scombridae)					
	dolphinfish (<i>Coryphaena</i> spp.)					

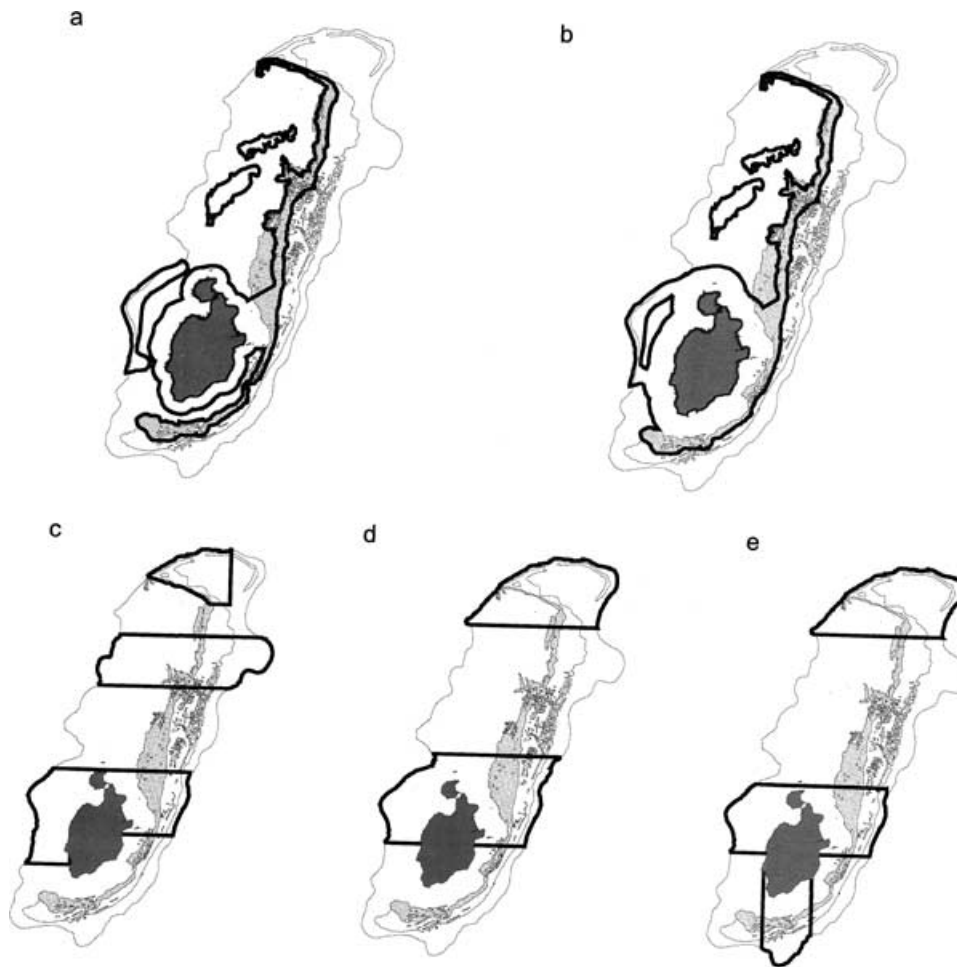


Figure 5. Proposed no-take marine reserve areas of the Old Providence and Santa Catalina reef complex: (a) stakeholder half-mile-wide band, (b) stakeholder mile-wide band; (c-e) three examples of scientific recommendations for a network of no-take marine reserves. Heavy lines demarcate boundaries.

number of user conflicts and provide buffers to protect marine reserves from inevitable edge effects.

TOTAL COVERAGE OF RESERVE NETWORKS

Total coverage plays a central role in the design and implementation of a marine reserve network (Sladek Nowlis & Friedlander 2004). Coverage influences the biological outcomes and largely determines the socioeconomic impacts of reserve creation (Sladek Nowlis & Roberts 1997; Sladek Nowlis 2000). Consequently, stakeholder input is vital to the development of goals for the reserve network.

Reserve networks need to protect a population consisting of 30% to 50% of its unfished size to ensure against collapses in the face of large uncertainties (Lauck et al. 1997; Mangel 2000; Sladek Nowlis & Bollermann 2002). Coverage needs to account for movement rates and the extent of ecological disasters. Highly mobile fish require greater coverage, but fortunately most of the species of concern within the archipelago probably move long distances infrequently (Appeldoorn 1997; Appeldoorn et al. 2003). Natural and human-caused ecological disasters disrupt equilibrium processes inside reserves and

make them less effective at meeting management goals. Thus, reserve coverage needs to be scaled up to account for ecological disasters (Allison et al. 2003). Larger reserve networks provide additional insurance against fishery collapses and ecological disasters, so our recommendation (38–41%) should be taken as a minimum, with coverage as high as 60% potentially appropriate (Table 4).

SIZE AND SHAPE OF INDIVIDUAL RESERVES

The size and shape of a reserve can have important biological effects on its performance. If individual reserves are too few and large, export of production from reserves to fishing grounds may be limited. If reserves are small they may provide only limited protection for many species.

Generally, individual marine reserves within the Seaflower Biosphere Reserve should cover at least 10 km² to contain viable populations of a wide range of species. To ensure that reserves are not too large, individual reserves should be established on every coastal shelf within the biosphere reserve. Larger or more complex shelves should be considered collections of ecologically distinct subshelves, each of which should have a representative

Table 4. Stakeholder and scientific proposals for no-take zoning of marine protected areas around Old Providence and Santa Catalina Islands.*

Habitat type	Total area	Stakeholder 1 proposal		Stakeholder 2 proposal		Scientific 1 proposal		Scientific 2 proposal		Scientific 3 proposal	
		ha	%*	ha	%*	ha	%*	ha	%*	ha	%*
Mangroves	43.7	43.7	100	43.7	100	38.2	87	36.1	83	43.7	100
Gorgonians	396.8	107.1	27	242.1	61	303.3	76	178.4	45	178.6	45
Deep seagrass	474.1	290.8	61	290.8	61	320.3	68	155.1	33	163.6	35
Patch reefs	1089.6	281.2	26	323.3	30	437.6	40	390.8	36	337.8	31
Shallow seagrass	1128.4	1093.6	97	1093.6	97	824.2	73	681.3	60	886.0	79
Leeward slope	1992.2	447.4	22	470.1	24	1010.7	51	834.9	42	750.3	38
Crest	2638.1	1941.7	74	2052.8	78	886.2	34	1110.8	42	1002.8	38
Forereef	3792.8	314.1	8	325.3	9	1533.9	40	1400.2	37	1354.6	36
Other	15860.7	2761.0	17	4047.0	26	5981.0	38	5762.5	36	6131.6	39
Total	27416.4	7280.6	27	8888.7	32	11335.4	41	10550.1	38	10849.0	40

*Percentage indicates amount of each habitat type included in the proposal.

portion set aside as a no-fishing or no-entry area. For example, we identified differences between bank and island sites of the same habitat types on OPSC, indicating the need to designate reserves on both bank and island subshelves. Representative portions of each habitat type within each subshelf should be included within the marine reserve network.

Enforcement and compliance will be greatly aided if reserve borders are straight lines running north-south and east-west or utilizing other obvious navigational reference points. Beyond these general criteria, the size and shape of individual marine reserves should be determined largely by stakeholder input. Adoption of a stakeholder proposal is an ideal outcome as long as the proposal meets scientific and enforcement criteria.

AREA SELECTION

Marine reserve networks have the greatest chance of including all species, life stages, and ecological linkages if they encompass representative portions of all ecologically relevant habitat types (Ballantine 1997; Friedlander & Parrish 1998; Murray et al. 1999). Our survey identified ecologically relevant habitat types. Moreover, we showed that proximity to land makes reef habitats in the south ecologically distinct from those in the north (Appeldoorn et al. 2003), a finding that confirmed the importance of links between coral reefs and other nearshore habitats (Ogden 1988). Based on these findings, ecologically relevant habitat types include leeward forereef (associated with banks and islands), patch reefs (banks and islands), gorgonian beds (banks and islands), shallow sea grass (<3 m depth, separated due to its potential importance as a nursery area; Lindeman et al. 1998; Nagelkerken et al. 2000), deep sea grass, mangroves, reef crest (banks and islands), windward forereef (banks and islands), and other lagoonal basin formations (banks and islands).

It would be beneficial to more substantially represent several ecologically critical areas in a marine re-

serve network. Many species of reef fish aggregate in large numbers at specific times and locations to spawn (Johannes 1978; Domeier & Colin 1997). Throughout the Caribbean, a number of grouper species have declined in abundance owing to the extirpation of spawning aggregations through overfishing (Domeier & Colin 1997; Beets & Friedlander 1999). Closure of spawning grounds is a highly successful management strategy for groupers in the Caribbean (Beets & Friedlander 1999). We identified several spawning-aggregation sites of groupers at the northern end of the barrier reef; protecting them should be a high priority for the MPA zoning plan.

Other rare and ecologically significant habitats should be represented more fully in conservation areas of any MPA zoning plan. The only large stand of mangroves on the islands is within the McBean Lagoon National Park. This habitat was probably much more common in the past and likely serves as important nursery habitat for a number of abundant species. There were notable aggregations of grunts at three windward forereef sites. Based on the frequency and extent of these aggregations, we believe these were small-scale localized phenomena. Therefore, inclusion of a representative proportion of windward forereef habitat in reserve zones should adequately protect some grunt spawning sites.

The extensive seagrass around OPSC represents an important habitat for juvenile fishes, lobsters, and conchs and an important foraging habitat for reef-related predators (Parrish 1989). It may be important to distinguish shallow (<3 m in depth) from deep seagrass beds because the shallower areas may be more likely to serve as nursery areas (Lindeman et al. 1998; Nagelkerken et al. 2000).

In addition to focusing on inclusion of habitats, it is also valuable to examine ecological connections among habitats. Coral reef ecosystems consist of linked coral reef, mangrove, and seagrass habitats (Ogden & Gladfelter 1983). The higher biomass associated with the island habitats is likely a result of their proximity to

productive nursery areas such as seagrass beds and mangroves (Appeldoorn et al. 2003). In particular, Morgan's Head contained shoreline boulders, structurally complex patch reefs, and soft-bottom habitat, and it was closely linked to seagrass beds and mangrove habitat between Old Providence and Santa Catalina (Appeldoorn et al. 2003), making it one of the most productive, diverse, and ecologically important locations around OPSC. Size-frequency distributions and abundances of grunts and snappers indicated ontogenetic migrations from shallow seagrass and mangrove habitats through patch-reef and gorgonian habitats to deeper sites. Thus, it is imperative that complete habitat linkages be protected. The most obvious such corridor is from the seagrass and mangrove habitats between Old Providence and Santa Catalina, westward along the patch-reef habitat of Morgan's Head, through the gorgonian habitat of Lazy Hill Bar, to the slope environment of Felipe's Place. Similarly, McBean Lagoon represents a relatively large mangrove stand surrounded by seagrass beds and diverse coral habitats. If placed in these two areas with high habitat connectivity, reserves are more likely to maintain productive populations within their borders.

Incorporating the knowledge, concerns, and interests of stakeholder groups into the management process will increase the perceived legitimacy of decisions and make compliance with regulations easier (Bunce et al. 2000). By airing concerns and priorities, stakeholders develop a sense of ownership and a better understanding of the management process. We therefore recommend that biological and enforcement criteria be conveyed to stakeholders and that support be provided to stakeholder groups to create and collaborate on proposals that meet these criteria in the most desirable way possible.

Based on the areas stakeholders identified as preferable, we developed some examples of how our recommendations might look in map form (Fig. 5c-e). These maps differ from stakeholder proposals primarily in the straight-line boundaries of proposed areas and the inclusion of a more balanced proportion of habitat types. These areas ranged from 38% to 41% coverage of the entire shelf around OPSC, with over 30% coverage of each habitat type (Table 4). The maps also provide substantially greater coverage ($\geq 60\%$) for important sites of mangroves, shallow seagrass beds, and spawning aggregations.

Ecological Examination of Community-Based MPA Zoning Recommendations

Stakeholder input is a means to consider invaluable information about the biology and socioeconomic properties of ocean use (Johannes 1997). Stakeholders should be exposed to the development of scientific and enforcement criteria and then encouraged to develop reserve designs that meet these criteria for consideration.

Stakeholder involvement has played an important role in moving these processes forward, including identification of some priority areas for inclusion in the no-take and no-entry zones around OPSC (Fig. 5a & 5b). Both stakeholder proposals included all mangrove lagoons and most of the seagrass beds around each island (Table 4), thus incorporating maximum amounts of nearshore settlement and nursery habitat for fish. In overall size, both proposals were close to what we recommended, although both should be increased somewhat in total size. The shortcomings include a lack of representation of deep-water habitats (forereef and leeward slope). These constitute major adult habitats and spawning areas—the places most threatened by fishing. Their proximity to land makes the proposed near-shore areas poor choices for overrepresentation unless land-based impacts are controlled. The necessary inclusion of critical nearshore habitats should act as a strong incentive to address land-based conservation issues, but these efforts should be given spatial priority based on proximity to such critical habitats, given the unlikely possibility that all land-based stresses could be controlled. Of even greater concern, the boundaries in the stakeholder proposals are not straight lines and will complicate compliance.

Next Steps

Our objective was to facilitate effective MPA zoning of OPSC by providing biological and sociological information about placement of reserve zones to stakeholder groups and the management agency (CORALINA). The next step is for the community and CORALINA to continue to work together to use these data to help develop final MPA zoning plans for the area. Our recommendations will only be successful if local citizens incorporate them into their own preferences for zoning. Continued discussions between technical experts and community members are essential for effectively meshing these two perspectives.

Once zones are established, it is imperative that long-term monitoring be established to determine the effectiveness of the zoning plan and to guide future modifications. Monitoring should include ecological measures, but social criteria such as acceptability and patterns of fish catches are equally important. Incorporating sound science with community knowledge is imperative for developing highly effective marine protected areas and for assuring the long-term viability of the coastal marine ecosystem and vitality of the island community and lifestyle.

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