

Gulf and Caribbean Research

Volume 14 | Issue 2

January 2003

A Caribbean-Wide Survey of Marine Reserves: Spatial Coverage and Attributes of Effectiveness

Richard S. Appeldoorn
University of Puerto Rico

Kenyon C. Lindeman
Environmental Defense, Miami, Florida

Follow this and additional works at: <https://aquila.usm.edu/gcr>



Part of the [Marine Biology Commons](#)

Recommended Citation

Appeldoorn, R. S. and K. C. Lindeman. 2003. A Caribbean-Wide Survey of Marine Reserves: Spatial Coverage and Attributes of Effectiveness. *Gulf and Caribbean Research* 14 (2): 139-154.
Retrieved from <https://aquila.usm.edu/gcr/vol14/iss2/11>
DOI: <https://doi.org/10.18785/gcr.1402.11>

This Article is brought to you for free and open access by The Aquila Digital Community. It has been accepted for inclusion in *Gulf and Caribbean Research* by an authorized editor of The Aquila Digital Community. For more information, please contact aquilastaff@usm.edu.

A CARIBBEAN-WIDE SURVEY OF MARINE RESERVES: SPATIAL COVERAGE AND ATTRIBUTES OF EFFECTIVENESS

Richard S. Appeldoorn¹ and Kenyon C. Lindeman²

¹*Department of Marine Sciences, University of Puerto Rico, Mayagüez, Puerto Rico 00681-9013*

²*Environmental Defense, Caribbean Field Office, 14630 Southwest 144 Terr., Miami, Florida 33186-5617 USA*

ABSTRACT Fully-protected marine reserves can function at several spatial scales, from a single area encompassing few habitats, to local networks of many habitats, to large-scale networks connected by larval dispersal. However, the amount, spatial distribution, and associated administrative attributes of Caribbean marine reserves are collectively unknown. We compiled information on reserves from 21 countries in order to 1) assemble a spatial framework to aid development of networks of reserves at the most effective spatial scales, and 2) aid policy makers in establishing reserves that are science-based and possess optimal management attributes. Since 1961 there have been over 50 reserves established in the Caribbean (an additional 30 in Bermuda) with the rate of implementation increasing since the mid 1980's. Most reserves are small (< 1,200 ha) and few contain the range of habitats necessary for protecting species through their ontogeny. Habitats are often not fully characterized, and the role of reserves in protecting and networking different habitats cannot be ascertained. Reserves are distributed throughout the region, with the highest density in Mesoamerica; but significant geographic gaps exist. It is unlikely that reserve-enhanced larval production significantly networks populations on a regional basis, although this may occur subregionally (e.g., Mesoamerica). Less than 20% of the reserves were scored as fully compliant, but half offer potentially significant levels of protection.

INTRODUCTION

Marine reserves, also known as 'no-take areas', are defined as "...areas of the sea completely protected from all extractive activities. Within a reserve, all biological resources are protected through prohibitions on fishing and the removal or disturbance of any living or non-living marine resource, except as necessary for monitoring or research to evaluate reserve effectiveness." (NCEAS, 2001). Marine reserves often occur as a smaller zoning category within larger marine protected areas (MPAs) that may have a number of differently zoned areas within. Due to an accumulation of empirical and theoretical information over the past decade, marine reserves are now considered one of several critical tools for fisheries management and conservation (e.g., PDT 1990, Roberts 1997, Allison et al. 1998, Hastings and Botsford 1999, Murray et al. 1999, NCEAS 2001). Because marine reserves are areas closed to all forms of extraction, they protect a spatially explicit portion of the ecosystem (assuming that the area is protected from other stresses, such as water quality or benthic habitat degradation). There are unique management capabilities offered by marine reserves, not feasible using other forms of regulation, which are derived from this spatially explicit nature. These include, but are not limited to maintaining system biodiversity, productivity and integrity, enhancing spawning stocks, conserving genetic diversity, serving as biological reference points (i.e., control areas) for assessing the impacts of fishing, and providing

a buffer against management failure (Bohnsack 1999).

Several basic design principles for marine reserves were specified by Ballantine (1997a,b): 1) representation—all marine habitats (as a proxy for their associated biotic assemblages) in each biological region should be represented; 2) replication—all habitats must be replicated; and 3) self sustaining. The latter requires that the system include all structural (habitats and species) and functional (e.g., nursery, feeding and spawning grounds, and cross-habitat transfers of organic matter; see Salm and Clark 1989) components necessary to maintain itself. That is, habitats and areas should be linked in a network fashion. The requirement for connectivity among reserve areas must be viewed on a variety of spatial scales. At one scale, the principal mechanism for genetic exchange and population dispersal in marine organisms is the planktonic egg and larval stage. Temporal scales for this range from a few days (e.g., top shell) to six months (e.g., spiny lobster), but for the majority of species larval periods range from 2–8 weeks (Leis, 1991). Effective distances traveled during this time depend on the poorly understood interaction of current patterns and larval behavior, but recent studies within different areas of the Caribbean indicate that recruitment of reef fish larvae can occur on a local scale (10–100 km) (Swearer et al. 1999, Cowen et al. 2000, Ramirez Mella 2000, Lindeman et al. 2001).

More locally, connectivity may be viewed at the scale of individual organisms that utilize a range of bottom habitats during demersal life stages, either through

ontogeny (e.g., Eggleston 1995, Appeldoorn et al. 1997), through daily feeding migrations (e.g., Stark and Davis 1966, Ogden and Quinn 1984, Tulevich and Recksiek 1994) or for spawning (e.g., Colin et al. 1987, Shapiro 1987, PDT 1990). Scales of movement may range from < 1 km for feeding migrations or individual ontogenetic habitat shifts to > 10 km for spawning migrations and complete ontogenetic migrations. Maintaining habitat connectivity at these smaller scales can be achieved by either creating large, all encompassing reserves or by networking a series of smaller reserves covering specific habitats. The latter may be more socially acceptable, at least initially, but assumes some knowledge of the movements of individuals and their habitat requirements, and the scale of functional processes critical to maintaining habitat integrity.

Typical of world fisheries in general, most resources in the Caribbean are thought to be fully or overexploited, particularly in coastal and coral reef environments (FAO 1993), perhaps for a century or more for some species (Jackson 1997, Jackson et al. 2001). Limitations to assessing these fisheries in a timely and accurate manner include the wide diversity of gear used, multispecies diversity of the catch, the large number and diversity of landing sites, and the limited resources available for collecting and analyzing the necessary information (Mahon 1997, McConney 1998), as well as just the sheer complexity of threats facing shallow-water environments in the Caribbean (e.g., Spalding et al. 2001). Thus, the importance of marine reserves as a management tool within the region is emphasized by the stressed stocks and the need for effective management, the limited options for management using data intensive methods, and the fact that the coastal resources are those most in need of management. Fishery resources generally have a strong association with the bottom and limited means of post-larval dispersal, particularly those associated with coral reefs. These are characteristics in which use of marine reserves should have the greatest impact (PDT 1990, Sladek Nowlis and Roberts, 1997, Chapman and Kramer 1999).

To fully implement marine reserves as an integral component of biodiversity and fisheries management, the challenge of developing functional networks through the principles of connectivity must be met at both local and regional levels. Within the Caribbean, there are over 38 countries and over 50 international organizations with responsibility for fisheries, plus numerous nongovernmental organizations (NGOs). Effective reserve networking will thus entail both national programs and international cooperation. Regional planning must oc-

cur on both an intergovernmental basis and among NGOs to target priority areas. These efforts must address not only scientific issues concerning ecological connectivity at these various scales, but they must also address the legal and social factors (e.g., Kelleher and Kenchington 1991, Bunce et al. 2000) that affect marine reserve implementation and success. This is especially important for decisions affecting the location and size of proposed reserves and their ultimate effectiveness, e.g. public acceptance and compliance.

While the need for management and the role of marine reserves within the Caribbean are clear, progress within the region toward this end is not. We have undertaken a Caribbean-wide survey of existing marine reserves to determine their current status relative to their potential effectiveness to achieve management goals. Although our study builds on past compilations of Caribbean MPAs (e.g., Kelleher et al. 1995, Spalding et al. 2001, Woodley et al. 2000), it differs in its exclusive focus on marine reserves and their status with respect to biological design criteria and compliance. In particular, our objectives were 1) to determine the number, location and size of these reserves, and the coarse habitat types they protect, 2) to identify how long reserves have existed in the region and temporal trends in their establishment, and 3) to assess the level of compliance and the factors potentially affecting their success. We examine patterns among these parameters with a particular emphasis on reserve design principles and connectivity at differing spatial scales. In doing so, we recognize that marine reserves within the region have been designed to serve a variety of goals that may or may not be related to fisheries management, or may be related to only a single species and so designed in consideration of its particular ecology. These differences often make comparisons among reserves difficult in terms of both their structure and administration. However, our purpose is to determine overall patterns within the region as an assessment of the current status of marine reserves, regardless of origin or rationale, as these form a potential basis from which to establish functional networks on the local, subregional, and regional level.

METHODS

This survey was limited to marine reserves (= no take areas), often smaller parts of larger multi-use zoned MPAs, that were designated by the end of 2000. The geographic scope included the Caribbean basin, the Bahamian Archipelago, and Bermuda. The Florida Keys have been summarized in other studies and were not

TABLE 1

Ranks of effective enforcement/compliance of no-take areas.

Rank	Description	Criteria
1	No effective enforcement/compliance.	No difference in fishing intensity within and outside the no-take area.
2	Some effective enforcement/compliance.	Fishing intensity within the no-take area is reduced by 30% relative to outside.
3	Moderately effective enforcement/compliance.	Fishing intensity within the no-take area is reduced by 70% relative to outside.
4	Very effective enforcement/compliance.	Fishing intensity within the no-take area is reduced by 95% relative to outside.

included. This survey was based on an extensive literature review, including a wide array of gray-literature, a search of Web-based information, and interviews and correspondence with many colleagues and local and regional fisheries officers, and MPA managers. We developed a survey instrument that was used to direct our inquiries and compile the information received. Many administrative variations occur and we additionally noted areas that restricted all extraction of at least some key species or that were planned but not yet designated. Parameters sought for each reserve included size, location, habitats encompassed, year established and closure enacted, the responsible management agency and whether anchoring or scuba diving were allowed.

We also scored, based on knowledgeable local reserve experts, the current degree of compliance with the closure. Scores were ranked on a scale of 1–4 according to Table 1. A 4-point scale was chosen to avoid the bias associated with respondents choosing a middle value. The criteria were based on perceived changes in fishing intensity, which was one of the most parsimonious measures, as opposed to some measure of absolute degree of fishing mortality (typically unavailable). Actual estimated impacts of closure will also depend on degree of fishing prior to closure. The lowest rank corresponded to no compliance and the highest rank corresponded to complete enforcement. As no system is perfect, for the latter we accepted a level of 95% reduction in fishing effort. Although somewhat arbitrary, this level is logical if all proposed benefits of marine reserves were to accrue given sufficient size and time, and considering the small size of many current reserves. This level was also based on observations that even low levels of fishing will have some impact (Beets 1997, Coblenz 1997). The middle two ranks were designed to split the remaining range, each being 30% from either extreme. A 30% reduction

should show some impact, perhaps in larger sizes of exploited species (i.e., greater yield per recruit inside reserve), and a 70% reduction was needed to observe some of the desired impacts that would come from full protection (e.g., some degree of protected spawning stock, some changes in community composition).

The issue of compliance is potentially a politically sensitive issue that could lead to an overestimation of reserve effectiveness. Although we relied on knowledgeable local experts, in many cases these were not agency representatives or at least not of the agency responsible for the reserve, and they were persons with whom we had sufficient experience to trust that their assessments would be free of political bias. In addition, our direct experience with specific reserves and published accounts were used to review assessments. In only one case was a local assessment of compliance found to be questionable, and this was clarified and modified in follow-up communications.

Lastly we considered five administrative attributes associated with reserve management and their relationship to reserve success (Pollnac et al. in press). These specific conditions could be ascertained without extensive on-site data collection and included: the designation of a reserve manager/coordinator, whether a specific management plan had been written and whether the plan had been implemented, whether a specifically designated advisory committee existed, and whether this committee met regularly. Responses for these attributes were ranked on a three-point scale. In all cases the extreme ranks referred to full “yes” or “no” responses. The middle rank was given when the situation was not clearly one or the other. The logic behind these rankings was to distinguish between on-site activities that directly incorporate community stakeholders from those related to government or agency function, but that could still signifi-

cantly contribute to successful on-site management. Explicitly, a middle rank was applied when a specific person was identified as having responsibility for a reserve, but that this person was located within a central government agency and could not be considered as being “on site”. Considering management plans, middle ranks were given for those reserves identified as actively developing a management plan, and also to those identified that had only some aspects of an existing plan implemented. With respect to advisory committees, a middle rank was given for advisory committees that were formed from representatives of central government agencies with responsibilities for other areas or functions as well. This ranking was also given to committees that met regularly, but at intervals of at least once per year or longer.

RESULTS

Geographic patterns

A total of 55 no-take marine reserves in 21 countries were identified to date within the wider Caribbean (= Caribbean Basin and Bahamian Archipelago). As complete information from some areas has not yet been obtained, the actual number should be somewhat larger. Another 30 reserves are located on the Bermuda Platform, of which 19 represent wreck sites. In some cases it is difficult to classify protected areas using a simple “no-take”

definition. This occurs when fishing is allowed, but the spatial scope is limited to an extent that there still remain broad areas protected. For example, line fishing from the shoreline is allowed in the Princes Alexandra Nature Reserve, Turks and Caicos Islands (i.e., a perimeter effect only), and in Cayo Doce Leguas, southeast Cuba, lobster fishing and limited catch and release fishing on three species are allowed (i.e., only a negligible impact to fish communities given the large size of reserve). Because of their regional importance, these areas were included in the analyses.

Further analyses will be limited to the wider Caribbean, except when specifically noted. Not all information desired was available for all reserves, and analyses are based on the number of responses obtained. Figure 1 shows the timeline for the establishment of marine reserves in the Caribbean. The first reserves were two small areas within the US Virgin Islands, Buck Island on St. Croix (1961) and Trunk Bay on St. John (1962). Since that time there has been sporadic development of reserves, with the rate of implementation increasing in the mid 1980’s and again in the late 1990’s (Figure 1).

Existing marine reserves are distributed throughout the wider Caribbean (Table 2, Figure 2). Even on this large scale, obvious gaps can be observed, such as the entire island of Hispaniola, the continental coasts of Nicaragua and Honduras, the north coast of Cuba (soon to change) and portions along the southern margin of the

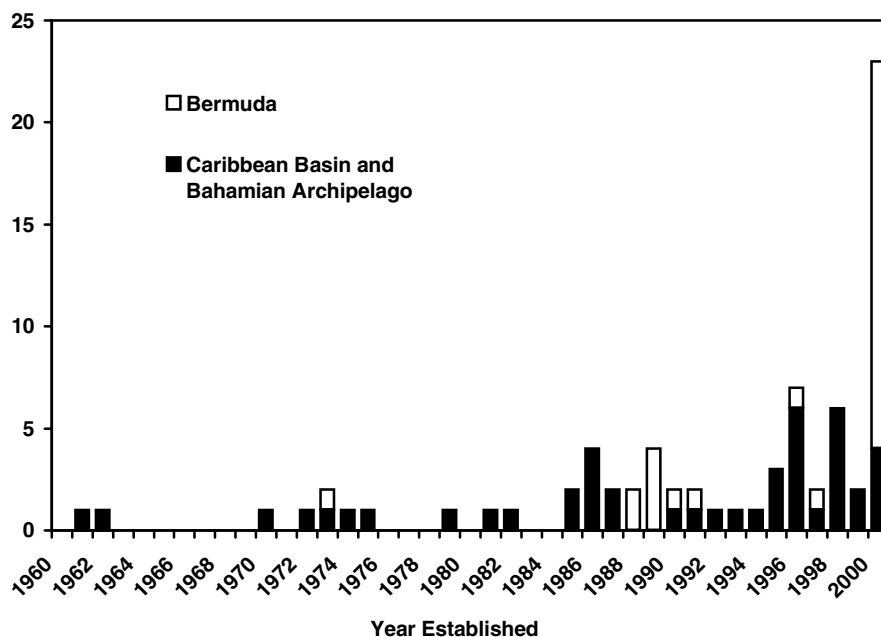


Figure 1. Frequency distribution of Caribbean and Bermudan marine reserves by initial year of full protection. Solid bars are for the Caribbean Basin and Bahamian Archipelago. Open bars are for Bermuda.

CARIBBEAN MARINE RESERVES

TABLE 2

Summary of marine reserve attributes by region and country. Blanks indicate no available information. +: total area for all reserves is unknown but greater than indicated.

Region and Country	Number of Marine Reserves	Total Area (Ha)	Number with Management Plans	Mean Rank Compliance	Earliest Year of Full Protection
MesoAmerica					
Mexico	5	28,870+	4	2.3	1986
Belize	12	19,040+	9	2.8	1982
Honduras	1				
Region Total	18	47,910+			
SW Caribbean					
Costa Rica	5	12,930	2	1	1970
Southern Caribbean					
Colombia	2	20,995	0	3	1995
Venezuela	3	52,380	3	3.3	1972
Region Total	5	73,375			
Lesser Antilles					
Barbados	1	21,000	1	3	1981
Trinidad and Tobago	1	700	1	1	1970
St. Vincent/the Grenadines	1				1984
St. Lucia	1		1	3	1995
St. Eustatius	1		1	2	1996
Saba	1	350	1	4	1987
Region Total	6	22,050+			
Greater Antilles					
Cuba	4	180,000+	0	2.5	1996
Jamaica	3	208+	2	1.5	1992
Cayman Islands	1	1,687	0	2	1986
Puerto Rico	2	916	0	2	1999
US Virgin Islands	3	5,730	3	3.3	1961
British Virgin Islands	2		0	1	1980
Region Total	15	188,541+			
Bahamian Archipelago					
Bahamas	2	46,434	0	3	1986
Turks and Caicos	4	2,454+	1	3	1985
Region Total	6	48,888+			
Bermuda					
	30	1,395	0		1973

basin (Panama, Columbia and Venezuela). The highest density of reserves is in Mesoamerica with 18 (Figure 3), particularly in Belize and Quintana Roo, Mexico. Reporting from Honduras is incomplete and several reserves may subsequently be identified, particularly among the Bay Islands just off the northern Honduran coast. The Greater Antilles region has at least 15 reserves. Region-

ally, lower numbers of reserves are present in the Lesser Antilles (6), Bahamian Archipelago (6), Southwest Caribbean (5), and Southern Caribbean (5) (Table 2).

Areas and habitats

Figure 4 gives the frequency distribution of the area protected by each reserve. Data were available for 75% of

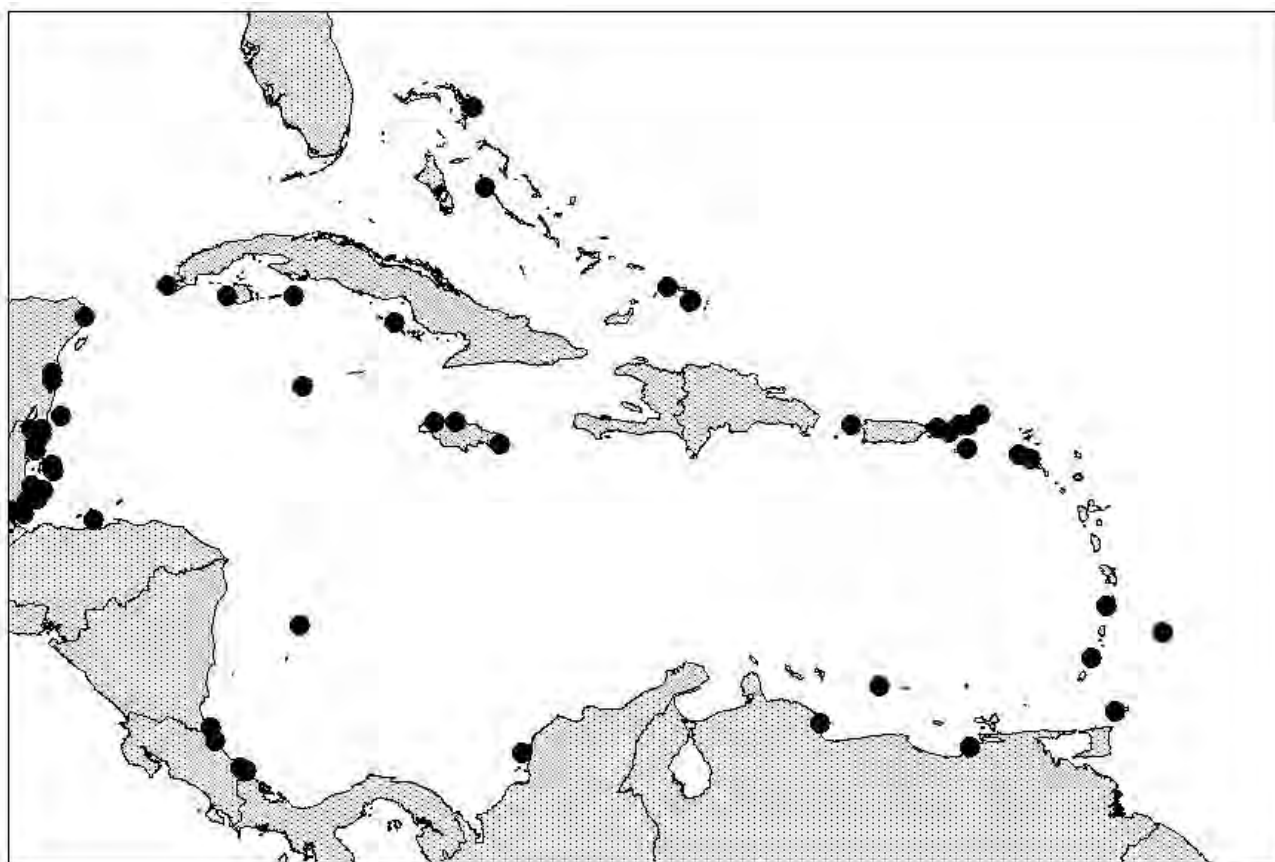


Figure 2. Geographic distribution of Caribbean marine reserves.

the Caribbean sites. Of these, the median area is 1,141 ha and the mean area is 9,840 ha. The smallest reserves are Tortuguero National Park, Costa Rica and Trunk Bay, St. John, USVI, with 19 and 20 ha, respectively. The largest reserve is Cayo Doce Leguas, southeast Cuba at ca. 140,000 ha, while the next largest and fully-protected reserve (Exuma Cays Land and Sea Park, Bahamas) is one-third that size, at 45,584 ha.

Specific information on the habitats protected within each reserve was the most difficult to obtain. At present, no information was given for almost 60% of the identified reserves, and in some other cases only vague descriptions were offered, e.g., “reef”. The majority of reserves are oriented toward the protection of coral reefs, with most also protecting associated habitats where present, such as seagrass beds, sand/algal plains and mangroves. Some reserves, such as those in northern Costa Rica, encompass softbottom areas devoid of reef environments, while several others primarily target large extents of seagrass and or/mangrove, such as McBean Lagoon National Park, Old Providence in Colombia, Corozal Bay

Wildlife Sanctuary in Belize (motivated by manatee protection) and Bell Sound Nature Reserve in the Turks and Caicos Islands (designed to protect bonefish).

With respect to potential damages from anchoring and diving activities, the degree of protection was variable among reserves. Based on a 77% response rate for these questions, 47% of the reserves prohibited anchoring, although this may be actively discouraged at other sites, and 23% prohibited scuba diving activities. A growing number of sites are providing mooring buoys to prohibit anchoring but allow controlled diving activities.

Administrative attributes and compliance

Rates of compliance/enforcement for 88% of the sites are shown in Figure 5. No or marginal compliance (Ranks 1 and 2) were reported for 45% of the reserves, indicating a significant proportion of the reserves are ineffective. Of the remaining, 39% reported some effective compliance and only 16% reported the highest level of compliance.

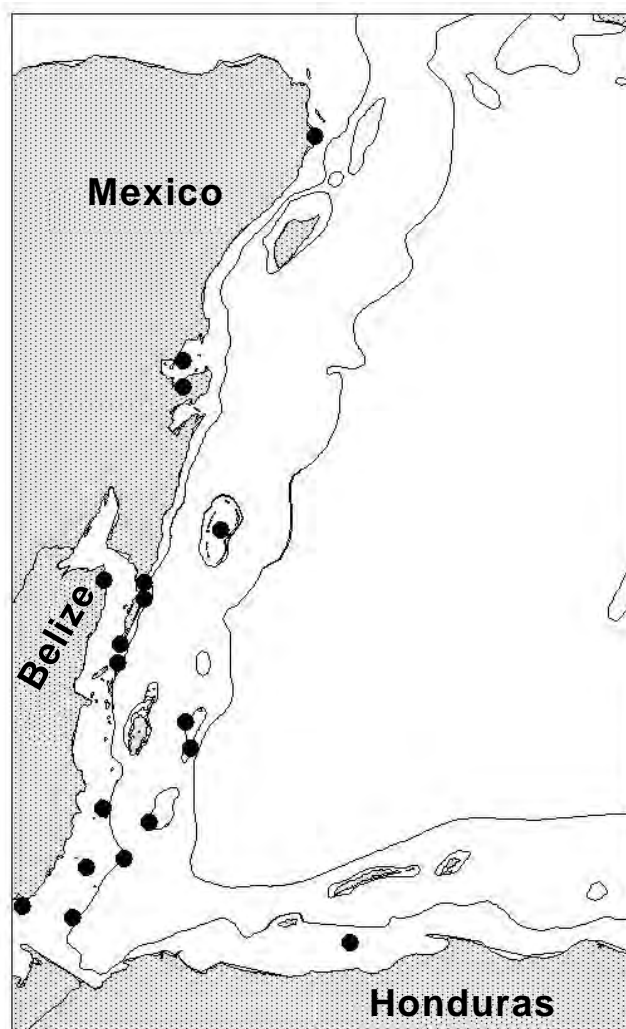


Figure 3. Geographic distribution of marine reserves in Mesoamerica. Depth contour lines are for 200 and 2,000 meters.

The relationships between the rank of reserve compliance and the five administrative attributes (Figures 6–10) show that in all cases a higher enforcement rank is associated with a higher probability of occurrence of attributes expected to contribute to reserve success. Of particular note is the difference between having a written management plan (Figure 7) and whether the management plan had been implemented (Figure 8). In the former, all but one of the reserves showing the highest rank of compliance had a written management plan, but there was no difference among the other compliance ranks in the percentage having a written plan. A more obvious trend was evident when those reserves actively developing a management plan were considered (a further indication of current activity). In contrast (Figure 8), the percentage of reserves having the management plan

fully implemented correlated well with rank of compliance. Further consideration of reserves showing only partial implementation of the management plan (an indication of problems) weakened, but did not eliminate the correlation.

DISCUSSION

The 55 no-take Caribbean reserves identified in this study are substantially more than commonly perceived for the region, and much greater than what is represented in the literature. On a regional level, it is clear that the existing reserves fall far short of fulfilling basic design principles for marine reserves. Reserves are designated for a variety of reasons, and the patterns observed may reflect funding and tourism opportunities rather than a specific concern for fisheries management. While marine reserves can be necessary components of fishery management systems, reserves should be established to serve a variety of needs related to coastal management, conservation, research, education, etc. (see Bohnsack 1998). With this view, the increasing rate at which reserves are being designated and their wide distribution, representing the majority of countries across the region, and a slow, but increasing focus on outreach to fishers and real compliance, are points to build from.

One implication from this study is the difficulty in compiling such information on a region-wide basis. Much of this results from communication problems within and across certain areas. Many of the agencies are understaffed and overburdened, such that personnel cannot easily allocate priority to addressing outside requests for information, especially if the information is not readily at hand. In this sense, the survey was facilitated by prior professional relationships with knowledgeable in-country experts who were willing to respond on the basis of personal interest. A third factor constraining assembly of this information, is that such information may simply not be known. For example, detailed habitat assessments require either a systematic habitat map or considerable *in-situ* experience at the reserve site. Estimation of the effectiveness of a reserve ideally requires surveys of managers, law enforcement personnel, and fishermen, or direct examination of the status of supposedly protected resources. All of these needs are typically underfunded and not subjected to detailed evaluation.

These points can constrain analyses, despite efforts to eliminate biases and obtain information from multiple sources. However, our analyses are based on regional trends, which are not generally subject to the specifics of one particular reserve. Furthermore, the administrative

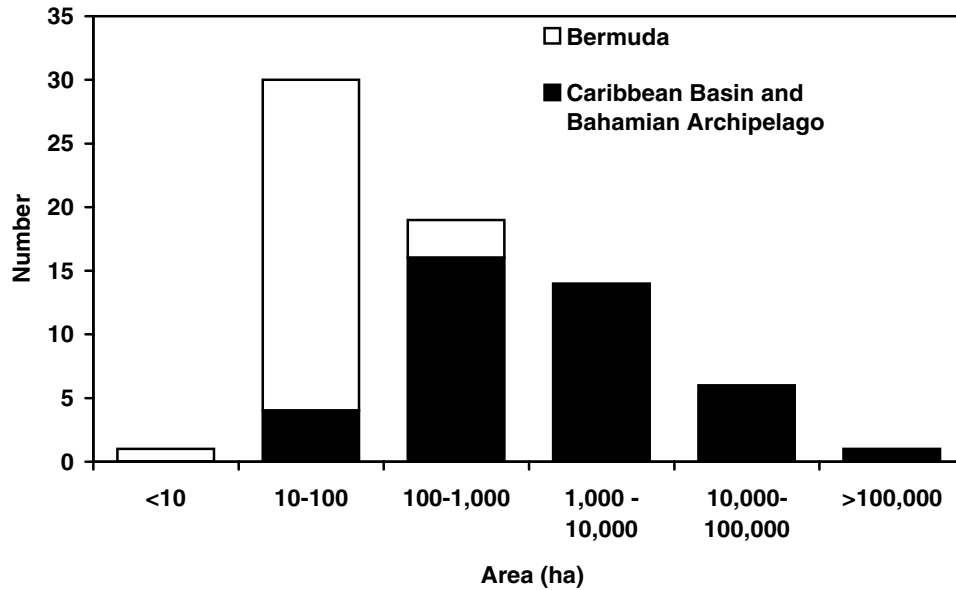


Figure 4. Frequency distribution of Caribbean and Bermudan marine reserves by area protected. Solid bars are for the Caribbean Basin and Bahamian Archipelago (N=41). Open bars are for Bermuda (N= 30).

landscape for MPAs in general, including marine reserves, is extremely dynamic, and reasons for designating reserves are diverse. New reserves are constantly being added, and others modified (Mahon and Mascia, 2003). A reserve with a weak legal basis can be effective given strong leadership (e.g., Woodley et al. 2003), while one with a strong basis can be undercut by weak administration or enforcement (e.g., Beets and Rogers in press). These impede attempts at comparing marine reserves

using standardized criteria. Greater access to and confirmation of available information is possible, but at substantial cost, and would also include examining original documentation and legislation, analysis of funding sources and independent verification using on-site inspection and interviews. However, the extra time and cost of such an endeavor would most likely reduce the analysis to a small subset of sites (e.g., Mascia 2000).

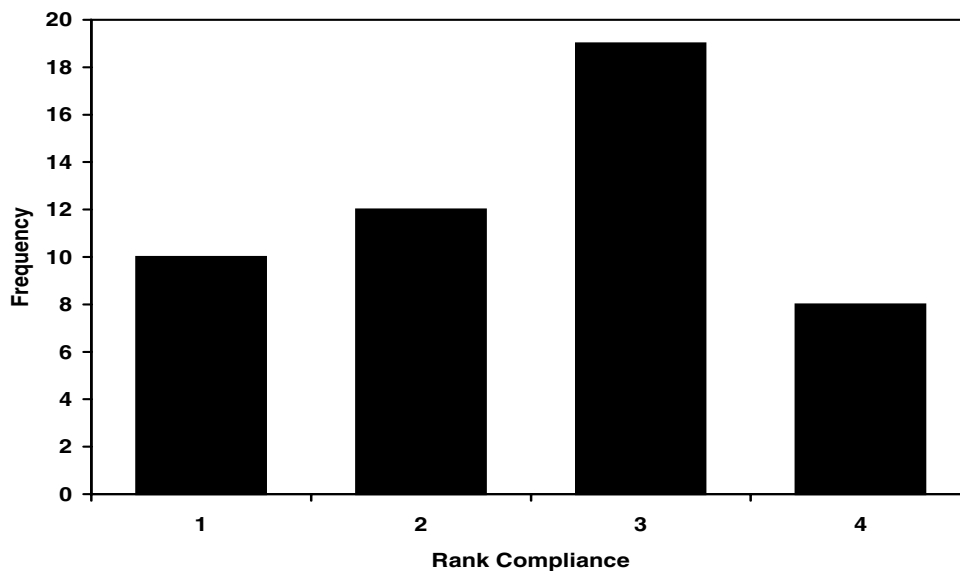


Figure 5. Frequency distribution of Caribbean marine reserves (N=49) by rank level of compliance as defined in Table 1,

CARIBBEAN MARINE RESERVES

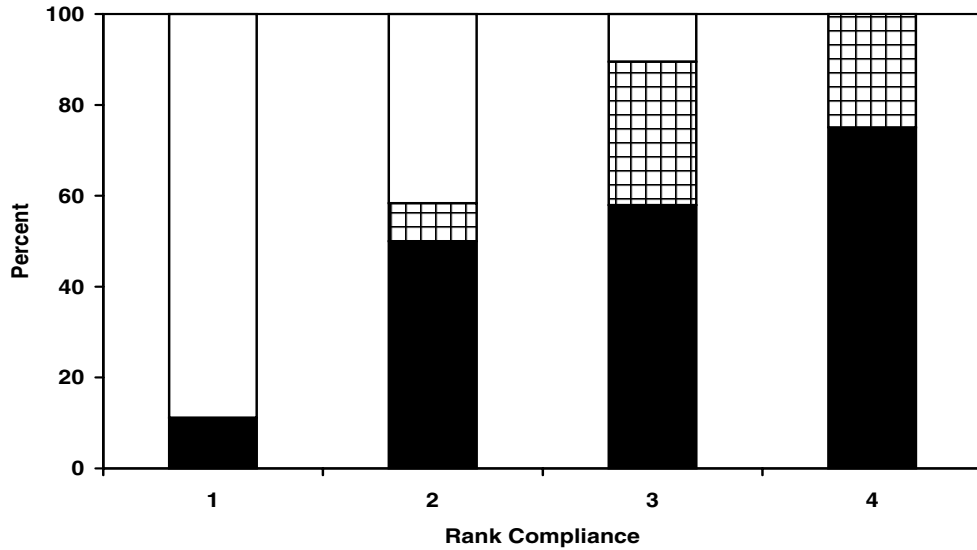


Figure 6. Percent of Caribbean marine reserves with a designated manager (black = on-site; hatched = other) grouped by rank level of compliance as defined in Table 1, where 1 = low and 4 = high.

Representation and replication

The existing reserves are spaced throughout many areas of the region, so they represent species and populations associated with both continental and island environments, which can vary physiographically in manners that influence species distributions (Robins 1971, 1991). In general, however, these reserves overwhelmingly represent coral reefs and associated habitats. In the short-term, this emphasis is understandable given the anthropogenic stress currently placed on reefs within the

region and the charisma and economic importance of reef resources. However, efforts toward the full spectrum of biodiversity conservation and fisheries management must eventually target a broader array of habitats. Distinctly missing in many areas are protected habitats associated with important deep-slope snapper-grouper resources, open shelf areas of soft or hard bottom, as well as dense mangrove or seagrass areas not immediately adjacent to reefs.

The question of replicating representative habitats can be viewed at various spatial scales. One reason this

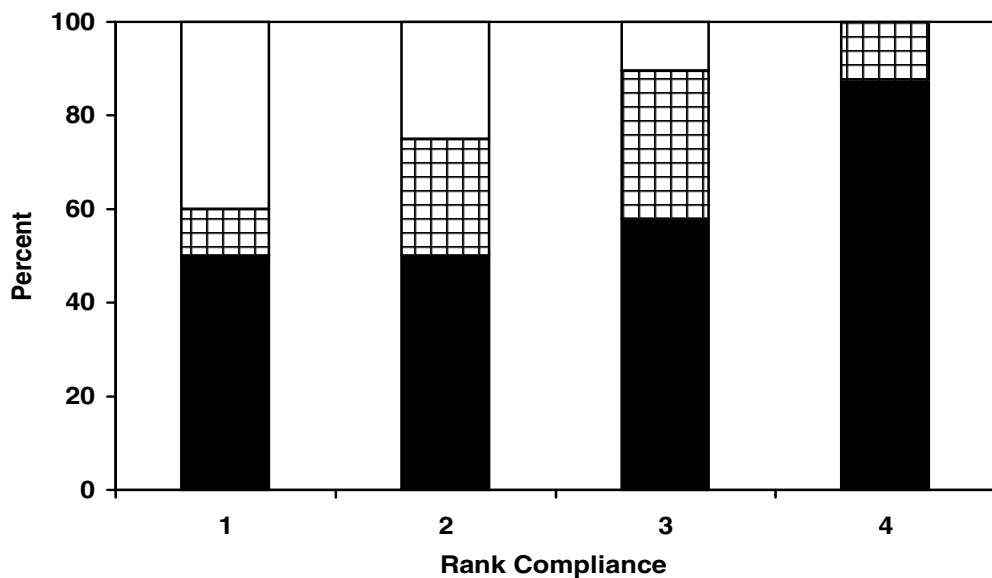


Figure 7. Percent of Caribbean marine reserves with a written management plan (black = fully written; hatched = actively

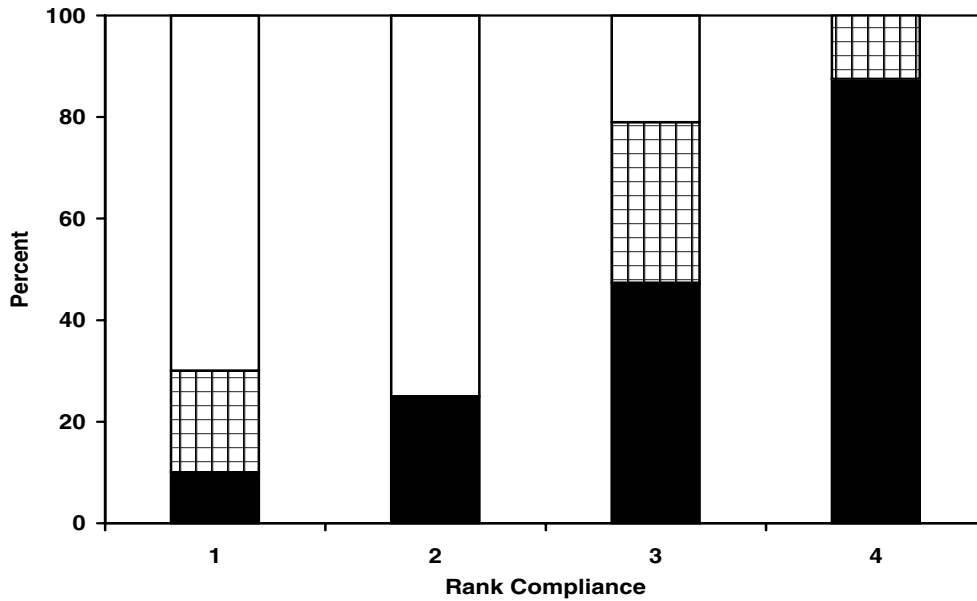


Figure 8. Percent of Caribbean marine reserves with an implemented management plan (black = fully implemented; hatched = partially implemented) grouped by rank level of compliance as defined in Table 1, where 1 = low and 4 = high.

is a design criterion is to ensure that representatives of threatened biota remain intact should something happen to a subset of reserve areas. This could occur in the form of increased anthropogenic pressures coupled with management breakdown or catastrophic natural disturbances such as hurricane damage. In this context, the number of replicates needed is not large and could be based on a statistical probability of reserve collapse. A bet-hedging

strategy would ensure that replicate reserves are spread throughout the region to reduce the probability of more than one or two reserves being lost from any single event. Within this context, the current marine reserves may provide some preliminary degree of replication, at least among the reef associated habitats that are most prevalent within Caribbean reserves.

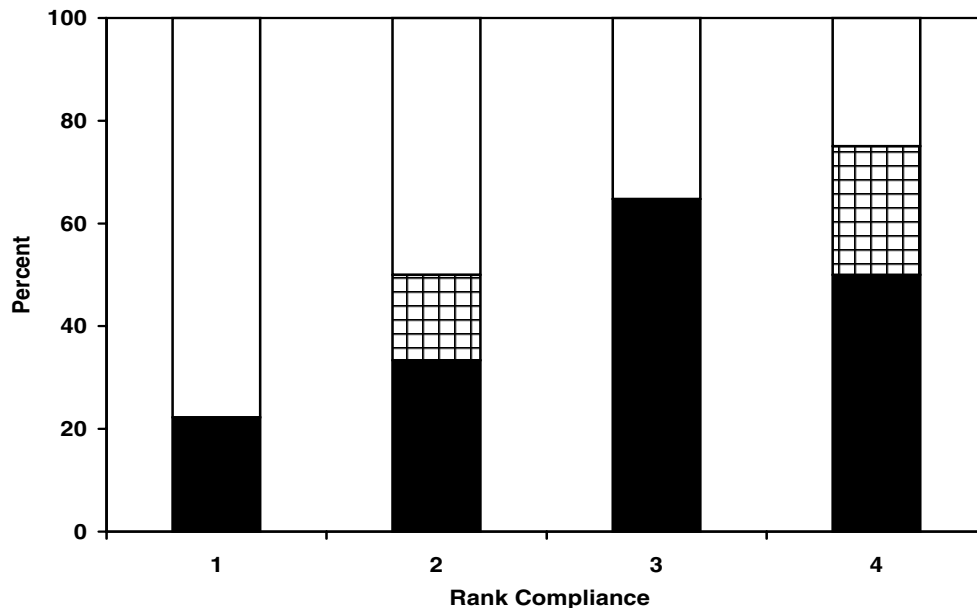


Figure 9. Percent of Caribbean marine reserves with an advisory committee (black = with public stakeholders; hatched = without public stakeholders) grouped by rank level of compliance as defined in Table 1, where 1 = low and 4 = high.

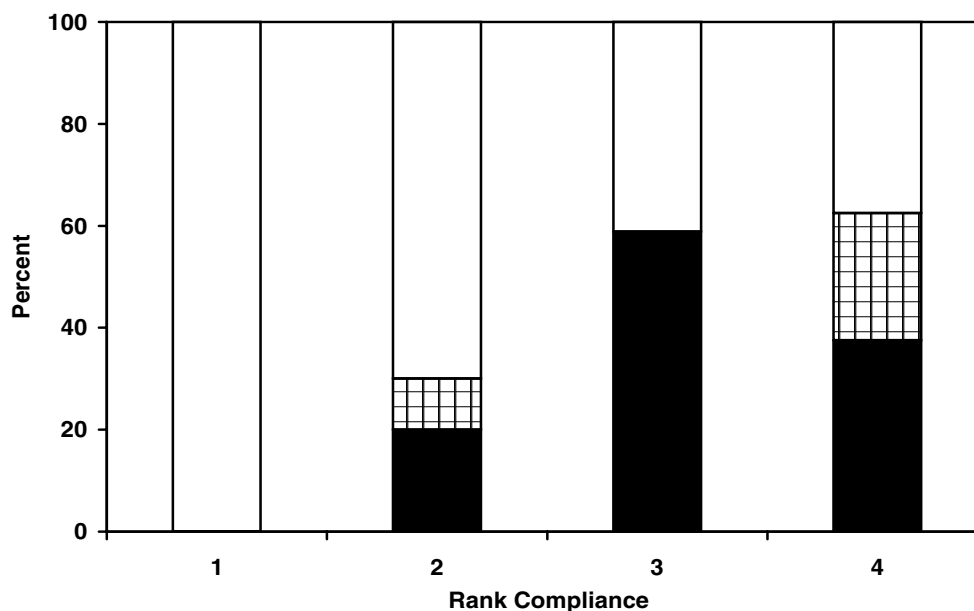


Figure 10. Percent of Caribbean marine reserves with an active advisory committee (black =<1 year interval between meetings; hatched =>1 year between meetings) grouped by rank level of compliance as defined in Table 1, where 1 = low and 4 = high.

On a local scale, however, the requirement for habitat replication becomes greater. Replication is considered one important mechanism to overcome chance errors in reserve location (Appeldoorn 2001), such as being sited in an area acting as a population sink (Crowder et al. 2000). Furthermore, principles of connectivity (see below) require that the spacing between habitat replicates be small enough that replicates do not become ecologically disjunct, so that a damaged reserve could be reseeded from species in a nearby reserve. Given that political jurisdictions tend to be rather absolute, bet-hedging would suggest that each country have several replicates within its own jurisdiction, such that it is not wholly dependent on the effectiveness of neighboring marine reserve policies, especially considering the potential for local larval retention (Kingsford et al. 2002, Sponaugle et al. 2002). The large percentage of current reserves showing poor compliance illustrates this point. Nevertheless, transboundary arrangements for reserve networks are often preferred. At this scale, significant replication is only being approached in Mesoamerica, particularly in Belize and Quintana Roo, Mexico.

Area

An important design principal concerns the total area to be protected. However, there is no established consensus on the total percentage of area that should be closed. A total of 20% (PDT 1990) was recommended based on consideration of spawning potential ratio (SPR),

i.e., the ratio of the reproductive output of an exploited stock relative to that calculated for the same stock under unexploited conditions. Both theoretical arguments and empirical observations suggest that stocks with a SPR below 20–30% are threatened with collapse (Goodyear 1989). More recent studies (see Appeldoorn 1996) suggest that even these levels may not be sufficient, especially for large species. Simple modeling based on larval dispersal alone showed that in overfished stocks, the optimum percent area closed (in terms of fishery yield) increased up to 50% as the intensity of fishing increased (Sladek Nowlis and Roberts 1997). However, blanket use of such percentages may not conform to the specific physiographic or fishery realities of individual areas, may incite unnecessary initial antagonism in regulated interests, and should be used with care. In some instances, protection of substantially lesser percentages of area may protect significant spawning production in the form of key aggregation sites (e.g., Beets and Friedlander 1999), or may be the only politically feasible options. For example, with 25 no-take areas developed over ten years of consensus building and research, and supported by substantial resources (financing, infrastructure, capacity), the Florida Keys National Marine Sanctuary includes only 5% of its area in no-take reserves.

While estimates of the area covered are not available for all Caribbean reserves, just 7,900 km² are nominally protected within the 75% of the reserves for which measures of spatial extent are available. To put this in

perspective, this is only 62% of the total shelf area of Puerto Rico alone. Total area protected within each region is given in Table 2. In terms of total shelf area of the Caribbean, the current reserves protect only a small fraction. If attention is restricted to the nearshore reefs on islands with narrow shelves and to Mesoamerica, the situation is only marginally better on a regional basis. For example, the 30 marine reserves in Bermuda protect less than 2% of the platform. Only in Belize is the extent of protected area approaching suggested levels. Grimshaw and Wade (2001) reported that 28% of the mud benthos in Belize (Corozal Bay) is protected, while 9 and 7% of the coral spur and groove and reef crest habitats, respectively, are protected. For patch reefs and seagrass habitats, however, protected coverage runs less than 3%. While there are social, economic and biological impediments to establishing marine reserves, the extremely small area currently under nominal protection in the region cannot be explained solely by these terms, but rather reflects the low priority allotted to marine and coastal resources in proportion to their local and regional economic importance.

Connectivity and network design

Cross-shelf. On the local scale, many reserves include not only reef environments, but also associated seagrass, patch reef and mangrove environments. On narrow shelves, such as in St. Lucia or St. Eustatius, reserves are typically designated from the shoreline out to unspecified depths; thus all habitats are included, but the area and range of different habitat types may be quite small. This suggests that efforts are being made to include supporting habitats to enhance local habitat connectivity. Nevertheless, the small size of most reserves (Figure 4) suggests that they are of insufficient size to protect all life stages and, in fact, the majority of reserves primarily protect only a part of a reef system, often offshore. In contrast, many reef fishes and invertebrates primarily utilize shallow, vegetated habitats during their early ontogeny. Available information for over twenty-five grunt and snapper species in the Caribbean indicates that successful settlement on deeper shelf reefs does not commonly occur in approximately two-thirds of these species (Lindeman et al. 1998). In terms of trophic relationships, recent studies linking the distribution of grunts and snappers to the extent of available feeding habitat (Kendall et al., in press, Appeldoorn et al. 2003) suggest that populations on a single patch reef forage out to at least 500 m and maximally to 1,000 m, representing areas of 78 and 314 ha, respectively. Over 25% of the Caribbean reserves for which areas are known, and all of the

Bermuda reserves, are less than 350 ha. This suggests that large numbers of reserves may not even encompass the daily foraging range of common reef fish species.

Connectivity requirements based on consideration of ontogenetic migrations argue that local reserves be larger still, or that several small reserves within an area be linked. Such demersal migrations may be on the order of 1 to 10 km depending upon the distribution of habitat (Appeldoorn et al. 1997, Appeldoorn et al. 2003), translating to areas greater than 1,000 ha, again depending on the distribution of habitat. For those reserves for which data are available, fully 50% are greater than this, and 41% are greater than 2,000 ha. While this is encouraging, size alone is insufficient to ensure local habitat connectivity. For example, the Marine Conservation District off St. Thomas, USVI, although the largest reserve in the US Caribbean (5,488 ha), is restricted to deep shelf and shelf-edge habitats. The latter are particularly critical spawning habitat for aggregating fishes, which have increased dramatically since afforded areal protection (Beets and Friedlander 1999). However, full habitat connectivity is not guaranteed because none of the shallow reef, seagrass or mangrove habitats along the southern coast of St. Thomas that serve as settlement, nursery and foraging areas are fully protected.

Regional. Connectivity on the regional scale depends on the ecologically effective range of larval transport, and this will vary among species and according to many other temporal variables. That marine reserves are spread throughout the region is encouraging, as this helps minimize the distance between any two reserves. If larval retention can occur on the scale of 100 km (Jones et al. 1999, Swearer et al. 1999, Cowen et al. 2000, Ramirez Mella 2000), then the spatial distribution of current reserves is still insufficient to guarantee connectivity, except perhaps in Mesoamerica. Further evidence supporting larval retention at this scale comes not only from new information on the physical dynamics of current flow (e.g., Lee and Williams 1999) but also from new information and reviews of larval behavior (Kingsford et al. 2002). On the expected scale of larval retention, geographic gaps in the distribution of reserves around the Caribbean basin shown in Figure 2 may act as replenishment barriers, especially for depleted commercial fish populations. The map also suggests that some island or bank locations could function as critical stepping stones if adequately protected. Examples include Aves Island in the mid-eastern basin, Swan Island between Mesoamerica and Cuba, and the Colombia reefs and Jamaican banks in the western basin.

For larval connectivity to be maintained, significant adult spawning stocks must be protected. Based on genetic arguments, a minimum effective breeding population size has been estimated at about 500 individuals (Franklin 1980, Lande and Barrowclough 1987). Thus, one can then extrapolate, for example using data for coral trout (a medium-sized Indo-Pacific grouper), a minimum reserve size of 10 km² of appropriate habitat, based on an average home range of 20,000 m²/fish (Zeller 1997) with little overlap among individuals. However, half the Caribbean reserves were smaller than 10 km², and with little local replication of reserves it is impossible to protect a sufficient spawning stock for many species. Furthermore, reserve sites have not generally been chosen with larval connectivity or self-sustaining capabilities in mind. Spawning aggregation sites for large groupers and snappers are obvious source locations for larval connectivity and the vulnerability of such species argues further for their protection. Despite this, only four Caribbean reserves (Gladden Spit and Half Moon Cay in Belize, Chinchorro Bank in Mexico, Marine Conservation District in St. Thomas) were specifically designed, among other goals, to encompass spawning aggregation sites. Until recently, inter-regional scales of connectivity have infrequently been a primary criterion in final reserve decision-making although an associated factor, presence of spawning aggregations, has influenced final decisions in Florida (Lindeman et al. 2000). In many current marine reserve design processes, large-scale connectivity issues are now being discussed among scientists, but inter-reserve connectivity is still too infrequently used by managers as a key criterion. Such criteria are needed as it is increasingly plausible that individual reserves can function in a “win-win” manner, in which increased larval production may enhance both local and distant stocks (i.e., significant amounts of larvae may be both advected and retained). At present, larval connectivity criteria must be based on the general patterns available from a few detailed studies. The understanding of site-specific larval dispersal and connectivity patterns will only occur over long time frames as the processes involved are variable over time and must be studied over large spatial and temporal scales.

Administrative attributes and compliance

Effective compliance of marine reserves is a significant problem, with the highest level of compliance being reported for only 16% of the reserves. In a previous survey of Caribbean MPAs, Kelleher et al. (1995) reported that two-thirds were “not achieving full management capacity”. Thus, the rate of full compliance found

may be substantially lower than previously reported. However, sufficient compliance (Levels 3 and 4) at which some tangible benefits may be expected was reported for slightly over half the reserves (55%) in our study, and this is greater than previous estimates, where “some enforcement” was reported for 31% of MPAs (Van't Hof 1988). Funding agencies often require the establishment of reserve areas within larger MPAs and mandate the development of management plans and advisory committees. Unless such mandates are taken seriously at the local level, there is no guarantee they will be successful and may promote overly optimistic reports of progress and effectiveness. The low rate of full compliance found in our study, and the nature of the correlations found between compliance and administrative attributes (i.e., the effect of partial scores for management plans and advisory committees), suggest that our efforts to control for such biases were effective, at least in terms of overall trends.

The relationships between compliance and the administrative attributes quantified here do indicate that these attributes can be important. Orstrom (1990) outlined institutional design principles that can be applied to marine reserves if their social and biological goals are to be achieved (see Mascia 2000). Our list of administrative attributes is not intended to provide a comprehensive measure of the degree to which these principles have been applied or met with respect to individual reserves or collectively. However, each of the attributes are related to design principles in that they indicate if administrative structures or functions exist that would allow these design principles to be met. For example, one of the design principles is that there should be well-defined boundaries on both the resources (area, species) to be managed and the participants to be included in consultative processes. A written management plan should be the instrument that defines these boundaries. A second principle is that there should be specific mechanisms for conflict resolution. An advisory committee and an on-site manager could obviously aid in this function on the long and short time scales, respectively, although in our study there is no guarantee that these were established to serve in this capacity. One simple interpretation of our results is that the probability of effective compliance is enhanced if there is some administrative structure to the reserve and, more importantly, that there is some perception that this structure is playing an active role, even at a reduced level. Nevertheless, we recognize that compliance and associated enforcement issues involve several possible parameters not measured here and encourage more detailed examination of this issue.

Future trends

The rate at which marine reserves will be established in the near future is expected to continue at current or even greater rates. There are several new initiatives within the region that should contribute substantially to the number of reserves and the amount of area protected, as well as fill in some key geographic gaps. For example, in the Sea Flower Biosphere Reserve in the San Andres Archipelago a series of fully-protected areas are being planned for seven platforms within the reserve. These will include representatives of all habitats found, and the complete set may act as important stepping-stones for larval connectivity within the western Caribbean basin. A significant increase in protection will also occur in the eastern Greater Antilles. Two large reserves (St. John, St. Croix) have recently been mandated for the U.S. Virgin Islands under a Presidential Order, while in Puerto Rico, 3% of the shelf is mandated for reserve-based protection. In the northeast Caribbean, an additional five reserves have been announced for the Bahamas with the specific goal of protecting spawning sites of Nassau grouper, and in Cuba, the Caribbean's largest island, a substantial new MPA initiative is underway.

Furthermore, there were several areas identified during the survey that offer protection to a subset of species. For example, while no full reserves were located in the Dominican Republic, there are two nominally protected areas for queen conch, one in Parque del Este on the southeast end and the other in Parque Nacional Jargua on the southern tip. Partial reserves such as these, within larger established MPAs, indicate both a willingness and legislative capability to protect resources on an areal basis. Such areas are potentially important seeds for future reserve development.

Despite the above trends, progress in establishing marine reserves within the region has been slow, and many reserves are still being designated for specific, narrowly defined purposes (Van't Hof 1988) and not in full consideration of their potential role within a local or regional network that would enhance overall benefits. Recent studies indicate that Caribbean marine communities have been substantially altered by overharvesting (Jackson 1997, Jackson et al. 2001), while threats to coastal habitats and water quality are increasing, thus compounding the urgency to best conserve and manage the region's marine resources. Also, low compliance, perhaps being driven by top-down pressures from central governments or funding agencies is a problem that must be overcome. Our results suggest that properly planned and implemented administration can significantly enhance the probability of reserve success. Funding agen-

cies need to specifically address the problem of compliance/enforcement from the onset, and build into the process appropriate education and outreach processes that foster local involvement, acceptance, and compliance.

ACKNOWLEDGMENTS

We wish to thank the over 60 managers, scientists or agency experts who responded to this survey or provided us with additional information. Logistical support for the senior author was provided by the University of Puerto Rico and the University of Rhode Island (while on sabbatical leave) and was aided by funds from Environmental Defense. We also acknowledge the generous support of the J.M. Kaplan Fund. Comments by Tom Van't Hof and two anonymous reviewers, one of whom provided extremely detailed and constructive criticisms, helped improve the manuscript.

LITERATURE CITED

- Allison, G.W., J. Lubchenco, and M.H. Carr. 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications* 8(1) Supplement: S79–S92.
- Appeldoorn, R.S. 1996. Model and method in reef fishery assessment. In: N.V.C. Polunin and C.M. Roberts, eds. *Reef Fisheries*. Chapman & Hall, London, p. 219–248.
- Appeldoorn, R.S. 2001. "Do no harm" versus "Stop the bleeding" in the establishment of marine reserves for fisheries management. *Proceedings of the Gulf and Caribbean Fisheries Institute* 52:667–673.
- Appeldoorn, R.S., A. Friedlander, J. Sladek Nowlis, P. Usseglio, and A. Mitchell-Chui. 2003. Habitat connectivity in reef fish communities and marine reserve design in Old Providence—Santa Catalina, Colombia. *Gulf and Caribbean Research* 14(2):61–77.
- Appeldoorn, R.S., C.W. Recksiek, R.L. Hill, F.E. Pagan, and G.D. Dennis. 1997. Marine protected areas and reef fish movements: the role of habitat in controlling ontogenetic migration. *Proceedings of the 8th International Coral Reef Symposium* 2:1917–1922.
- Ballantine, W.J. 1997a. 'No-take' marine reserve networks support fisheries. In: D.A. Hancock, D.C. Smith, A. Grant, and J.P. Beumer, eds. *Developing and Sustaining World Fisheries Resources: The State of Science and Management* (2nd World Fisheries Congress). CSIRO Publishing, Australia, p. 702–206.
- Ballantine, W.J. 1997b. Design principles for systems of 'no-take' marine reserves. (Abstract). In: T.J. Pitcher, ed. *The design and monitoring of marine reserves*. University of British Columbia, Fisheries Centre Research Report 5(1):4–5.
- Beets, J. 1997. Can coral reef fish assemblages be sustained as fishing intensity increases? *Proceedings of the 8th International Coral Reef Symposium* 2:2009–2014.

- Beets, J. and A. Friedlander. 1999. Evaluation of a conservation strategy: a spawning aggregation closure for red hind, *Epinephelus guttatus*, in the Virgin Islands. *Environmental Biology of Fishes* 55:91–98.
- Beets, J. and C. Rogers. In press. Decline of fishery resources in marine protected areas in the US Virgin Islands: the need for marine reserves. *Proceedings of the 9th International Coral Reef Symposium*.
- Bohnsack, J.A. 1998. Application of marine reserves to reef fisheries management. *Australian Journal of Ecology* 23: 298–304.
- Bohnsack, J.A. 1999. Incorporating no-take marine reserves into precautionary management and stock assessment. In: V.R. Restrepo, ed. *Providing Scientific Advice to Implement the Precautionary Approach Under the Magnuson-Stevens Fishery Conservation Act*. NOAA Technical Memorandum NMFS-F/SPO-40. p. 9–16.
- Bunce, L., P. Ownsley, R. Pomeroy, and R. Pollnac. 2000. *Socio-economic Manual for Coral Reef Management*. Australian Institute of Marine Science, Townsville, Australia, 251 p.
- Chapman, M.R. and D.L. Kramer. 1999. Gradients in coral reef fish density and size across the Barbados Marine Reserve boundary: effects of reserve protection and habitat characteristics. *Marine Ecology Progress Series* 181:81–96.
- Coblentz, B.E. 1997. Subsistence consumption of coral reef fish suggests non-sustainable extraction. *Conservation Biology* 11:559–561.
- Colin, P.L., D.Y. Shapiro, and D. Weiler. 1987. Aspects of the reproduction of two groupers, *Epinephelus guttatus* and *E. striatus*, in the West Indies. *Bulletin of Marine Science* 40:220–230.
- Cowen, R.K., K.M.M. Lwiza, S. Sponaugle, C.B. Limouzy-Paris, and D.B. Olson. 2000. Connectivity of marine populations: open or closed? *Science* 287:857–859.
- Crowder, L.B., S.J. Lyman, W.F. Figueira, and J. Priddy. 2000. Source-sink population dynamics and the problem of siting marine reserves. *Bulletin of Marine Science* 66:799–820.
- Eggleston, D.B. 1995. Recruitment in Nassau grouper *Epinephelus striatus*: post-settlement abundance, micro-habitat features, and ontogenetic habitat shifts. *Marine Ecology Progress Series* 124:9–22.
- FAO. 1993. *Marine fishery resources of the Antilles: Lesser Antilles, Puerto Rico and Hispaniola, Jamaica, Cuba*. FAO Fisheries Technical Paper 326, 235 p.
- Franklin, I.R. 1980. Evolutionary changes in small populations. In: M. Soulé and B.A. Wilcox, eds. *Conservation Biology. An Evolutionary-Ecological Perspective*. Sinauer Associates, Sunderland, MA, USA, p. 135–149.
- Goodyear, C.P. 1989. Spawning stock biomass per recruit: the biological basis for a fisheries management tool. ICCAR Working Document SCRS/89/82, 10 p.
- Grimshaw, T. and D. Wade. 2001. A national environmental quality monitoring plan for the coastal zone of Belize. Consulting Report. ix + 239 p + 26 addenda.
- Hastings, A. and L.W. Botsford. 1999. Equivalence in yield from marine reserves and fisheries management. *Science* 284:1537–1538.
- Jackson, J.B.C. 1997. Reefs since Columbus. *Coral Reefs* 16(Supplement): S23–S32.
- Jackson, J.B.C., M.X. Kirby, W.H. Berger, K.A. Bjorndal, L.W. Botsford, B.J. Bourque, R.H. Bradbury, R. Cooke, J. Erlandson, J.A. Estes, T.P. Hughes, S. Kidwell, C.B. Lange, H.S. Lenihan, J.M. Pandolfi, C. H. Peterson, R.S. Steneck, M.J. Tegner, and R.R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638.
- Jones, G.P., M.J. Milicich, M.J. Emslie, and C. Lunow. 1999. Self-recruitment in a coral reef fish population. *Nature* 402: 802–804.
- Kelleher, G., C. Bleakley, and S. Wells. 1995. *A Global Representative System of Marine Protected Areas, Volume II, Wider Caribbean, West Africa and South Africa*. World Bank, Washington, DC, USA, 93 p.
- Kelleher, G. and R. Kenchington. 1991. *Guidelines for Establishing Marine Protected Areas*. IUCN, Gland, Switzerland, 79 p.
- Kendall, M.S., J.D. Christensen, and Z. Hillis-Starr. In press. Multiscale data used to analyze the spatial distribution of French grunts, *Haemulon flavolineatum*, relative to hard and soft bottom in a benthic landscape. *Environmental Biology of Fishes*.
- Kingsford, M.J., J.M. Leis, A. Shanks, K.C. Lindeman, S.G. Morgan, and J. Pineda. 2002. Sensory environments, larval abilities and local self-recruitment. *Bulletin of Marine Science* 70:309–340.
- Lande, R. and G.F. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management. In: M.E. Soulé, ed. *Viable Populations for Management*. Cambridge University Press, Cambridge, England, p.87–124.
- Lee, T. N. and E. Williams. 1999. Mean distributions and seasonal variability of coastal currents and temperature in the Florida Keys with implications for larval recruitment. *Bulletin of Marine Science* 64:35–56.
- Leis, J. M. 1991. The pelagic stage of reef fishes: the larval biology of coral reef fishes. In: P. F. Sale, ed. *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego, CA, USA, p. 183–230.
- Lindeman, K.C., G.A. Diaz, J.E. Serafy, and J.S. Ault. 1998. A spatial framework for assessing cross-shelf habitat use among newly settled grunts and snappers. *Proceedings of the Gulf and Caribbean Fisheries Institute* 50:385–416.
- Lindeman, K.C., R. Pugliese, G.T. Waugh, and J.S. Ault. 2000. Developmental patterns within a multispecies reef fishery: management applications for essential fish habitats and protected areas. *Bulletin of Marine Science* 66:929–956.
- Lindeman, K.C., T.N. Lee, W.D. Wilson, R. Claro, and J.S. Ault. 2001. Transport of larvae originating in southwest Cuba and the Dry Tortugas: evidence for partial retention in grunts and snappers. *Proceedings of the Gulf and Caribbean Fisheries Institute* 52:732–747.
- Mahon, R. 1997. Does fisheries science serve the needs of managers of small stocks in developing countries? *Canadian Journal of Fisheries and Aquatic Science* 54:2207–2213.
- Mahon, R. and M.B. Mascia. 2003. The Barbados (alias Folkestone) Marine Reserve, Barbados: a late bloomer? *Gulf and Caribbean Research* 14(2):171–180.

- Mascia, M.B. 2000. Institutional emergence, evolution, and performance in complex common pool resource systems: marine protected areas in the wider Caribbean. Ph.D. Thesis, Duke University, North Carolina, USA 388 p.
- McConney, P. 1998. Using "common sense" in co-management. Proceedings of the Gulf and Caribbean Fisheries Institute 50:1115–1121.
- Murray, S.N., R.F. Ambrose, J.A. Bohnsack, L.W. Botsford, M.H. Carr, G.E. Davis, P.K. Dayton, D. Gotshall, D.R. Gunderson, M.A. Hixon, J. Lubchenco, M. Mangel, A. MacCall, D.A. McArdle, J.C. Ogden, J. Roughgarden, R.M. Starr, M.J. Tegner, and M.M. Yoklavich. 1999. No-take reserve networks: sustaining fishery populations and marine ecosystems. *Fisheries* 24(11):1–25.
- National Center for Ecological Analysis and Synthesis (NCEAS). 2001. Scientific Consensus Statement on Marine Reserves and Marine Protected Areas. <http://www.nceas.ucsb.edu/Consensus/consensus.pdf>
- Ogden, J.C. and T.P. Quinn. 1984. Migration in coral reef fishes: ecological significance and orientation mechanisms. In: J.D. McLeavey, G.P. Arnold, J.J. Dodson, and W.H. Neill, eds. *Mechanisms of Migration in Fishes*. Plenum, NY, USA, p. 293–308.
- Orstrom, E. 1990. *Governing the Commons: The Evolution of Institutions for Collective Action*. Cambridge University Press, Cambridge, MA, USA.
- Plan Development Team (PDT). 1990. The potential of marine fishery reserves for reef fish management in the U.S. Southern Atlantic. NOAA Technical Memorandum NMFS-SEFC-261. 40 p.
- Pollnac, R.B., B.C Crawford, and M.L.G. In press. Gorospe. Assessment of socioeconomic factors influencing the success of marine sanctuaries in the Philippines. Proceedings of the 9th International Coral Reef Symposium.
- Ramirez Mella, J.T. 2000. Cross-shelf patterns of ichthyoplankton in La Parguera Bay and adjacent oceanic waters, southwest coast of Puerto Rico. Ph.D. Dissertation. University of Puerto Rico, Mayagüez, PR, USA, 103 p.
- Roberts, C.M. 1997. Ecological advice for the global fisheries crisis. *Trends in Ecology and Evolution* 12:35–38.
- Robins, C.R. 1971. Distributional patterns of fishes from coastal and shelf waters of the tropical Western Atlantic. In: *Symposium on Investigations and Resources of the Caribbean and Adjacent Regions*. FAO, Fisheries Reports 71.2, p. 249–256.
- Robins, C.R. 1991. Regional diversity among Caribbean fish species. *Bioscience* 41:458–459.
- Salm, R.V. and J.R. Clark. 1984. *Marine and Coastal Protected Areas: A Guide for Planners and Managers*. IUCN, Gland, Switzerland, 302 p.
- Shapiro, D.Y. 1987. Reproduction in groupers. In: J.J. Polovina and S. Ralston, eds. *Tropical Snappers and Groupers. Biology and Fisheries Management*. Westview Press, Boulder, CO, USA, p. 295–327.
- Sladek Nowlis, J. and C.M. Roberts. 1997. You can have your fish and eat it, too: Theoretical approaches to marine reserve design. *Proceedings of the 8th International Coral Reef Symposium* 2:1907–1910.
- Spalding, M.D., C. Ravilious, and E.P. Green. 2001. *World Atlas of Coral Reefs*. University of California Press, Berkeley, CA, USA.
- Sponaugle, S., R.K. Cowen, A. Shanks, S.G. Morgan, J.M. Leis, J. Pineda, G.W. Boehlert, M.J. Kingsford, K.C. Lindeman, C. Grimes, and J.L. Munro. 2002. Predicting self-recruitment in marine populations: biophysical correlates. *Bulletin of Marine Science* 70:341–376
- Stark, W.A. and W.P. Davis. 1966. Night habits of fishes of Alligator Reef, Florida. *Ichthyologica* 38:313–356.
- Swearer, S.E., J.E. Caselle, D.W. Lea, and R.R. Warner. 1999. Larval retention and recruitment in an island population of a coral reef fish. *Nature* 402:799–802.
- Tulevech, S.M. and C.W. Recksiek. 1994. Acoustic tracking of adult white grunt, *Haemulon plumieri*, in Puerto Rico and Florida. *Fisheries Research* 19:301–319.
- Van't Hof, T. 1988. Management of coral reefs and associated systems and resources in the Western Atlantic: A status review. *Proceedings of the 6th International Coral Reef Symposium* 1:89–95.
- Woodley, J., P. Acolado, T. Austin, J. Barnes, R. Claro-Madruga, G. Ebanks-Petrie, R. Estrada, F. Geraldles, A. Glasspool, F. Homer, B. Luckhurst, E. Phillips, D. Shim, R. Smith, K. Sullivan Sealey, M. Vega, J. Ward, and J. Wiener. 2000. Status of coral reefs in the Northern Caribbean and Western Atlantic. In: C. Wilkinson, ed. *Status of Coral Reefs of the World: 2000*. Australian Institute of Marine Science, Townsville, Australia, p. 261–285.
- Woodley, J., Z. Sary, and P. Gayle. Fishery management measures instituted at Discovery Bay, Jamaica, with special reference to establishment of the fisheries reserve. *Gulf and Caribbean Research* 14(2):181–193.
- Zeller, D.C. 1997. Home range and activity patterns of the coral trout *Plectropomus leopardus* (Serranidae) *Marine Ecology Progress Series* 154:65–77.