

Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves*

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ABSTRACT: We studied the coral-reef fish communities of Saba Marine Park (Netherlands Antilles) and Hol Chan Marine Reserve (Ambergris Caye, Belize) in the Caribbean to assess differences between them and adjacent ecologically similar sites after 4 yr of protection from fishing. Forty-five percent of target species commonly recorded in visual censuses in Belize (23% of all recorded target species), and 59% at Saba (22%), showed greater abundance, size or biomass in shallow protected sites. These differences are considered primarily to reflect increased survivorship with the cessation of fishing mortality. The greatest estimated biomasses were observed in locally protected snapper (Lutjanidae) in Belize and Saba, and grunt (Haemulidae) at Saba. In both protected areas the local stock of visible demersal target fishes was 1.9 to 2.0 times greater in biomass and 2.2 to 3.5 times greater in commercial value than in fished sites. Larger local stock of many target species is likely to support higher egg output from the protected areas, while larger predator biomass will mean more intense predation at the protected sites.

INTRODUCTION

Marine protected areas have been in existence for several decades (Bjorklund 1974), yet there has been little evaluation of whether they achieve the aims for which they were set up. One objective of marine reserves has been to help conserve fish stocks, but understanding of factors affecting reproduction, recruitment, movement and survivorship of fishes (Roberts & Polunin 1991), and in particular determining the structure of complex communities such as those of coral reefs (Sale 1991), is at a very early stage of development.

In this context, empirical studies of how fish stocks may respond to local protection are urgently needed, yet there have been few studies addressing this issue (Bell 1983, Russ 1985, Alcala 1988, Buxton & Smale 1989, Clark et al. 1989, Russ & Alcala 1989, Alcala &

Russ 1990, Roberts & Polunin 1991, in press). Experience of the North Sea in both world wars has shown that protection over areas sufficiently large to encompass whole stocks is effective and leads to recovery (e.g. Cushing 1981). At lesser spatial scales, however, success of local reserves will be greatly affected by factors such as adult migration (Polacheck 1990, DeMartini in press), and larval supply and settlement (Doherty & Williams 1988), which are little understood. It is also expected that there will be variations among different types of fishes (DeMartini in press), for example in growth rate or stock-recruitment relations. At present there is, however, scarcely any basis for predicting these differences.

Yet, where area closure is to be employed in the maintenance or rehabilitation of local fishery stocks, it is important that its operation mechanisms be understood and ultimate positive effects be predictable. Even where reserves are set up for other purposes, such as tourism, it is very desirable that the measures be acceptable to local fishing communities (Polunin 1990). If mechanisms and rates of fishery recovery can be better understood, area closure stands to be a sim-

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ple but effective device in fisheries management (e.g. Plan Development Team 1990, Appeldoorn et al. 1992).

We therefore investigated effects on local populations of reef fishes of 2 Caribbean marine reserves, one in northern Belize and the other at Saba in the northern Netherlands Antilles, both of which had been in existence for 4 yr. Our first purpose here was to test the prediction that where fishing has been halted in these reserves, fishes will be more numerous and on average larger relative to areas outside which are still exploited. Beyond this, we sought an indication of whether recovery might vary in rate or characteristics among different types of fishes at the same site and among widely separated sites which had been established at the same time.

MATERIALS AND METHODS

Study sites. Waters adjacent to some 25% of the circumference of the island of Saba were declared a no-fishing zone in 1987 (Fig. 1). Restrictions have been enforced by marine park personnel since then, although occasional fishing, for example from newly arrived yachts, does sometimes occur. Around much of Saba, corals, gorgonians and other reef-related organisms merely form a veneer over the volcanic-rock substratum, but around the southwestern corner of the island true reefs with a carbonate framework have developed. These reefs generally slope either gently from the shallows into deep water, or onto a shallow

platform before dropping into deep water. The no-fishing zone occupies part of this reef area.

Saba supports few commercial fishermen and although there is some trap-fishing close to the island, intensive fishing is mostly restricted to the offshore Saba Bank. Regular fishing on Saba's reefs is recreational, and is based on hand-lining and spearing. This fishing is largely confined to areas close inshore. Before the marine park was established, fishing was concentrated on the area which is now protected.

The Hol Chan Marine Reserve lies approximately 4 km south of the town of San Pedro, Ambergris Caye in Belize (Fig. 1). It includes an area of coral reef which has been effectively closed to fishing since 1987. The Reserve centres on a deep channel through the reef called the Hol Chan Cut. Three fished areas chosen for comparison with the Reserve were therefore also reef-channel sites: San Pedro Cut, Mata Cut and Basil Jones Cut.

Subsistence fishing has been conducted for hundreds of years around Ambergris Caye (Woods et al. 1988). Commercial reef-fishing has been conducted for over 30 yr; snapper and grouper are major targets and part of this catch has been, and still is being, exported (Craig 1969). Spawning aggregations are used to target large groupers (Carter 1989) and fears of a decline in this and other reef resources have been expressed for 20 yr or more (Manuel Heredia, Chairman, Caribena Producers Cooperative Society Ltd, San Pedro, pers. comm.). Fishing offshore from San Pedro town has declined by 90% in the last decade, most fishing is

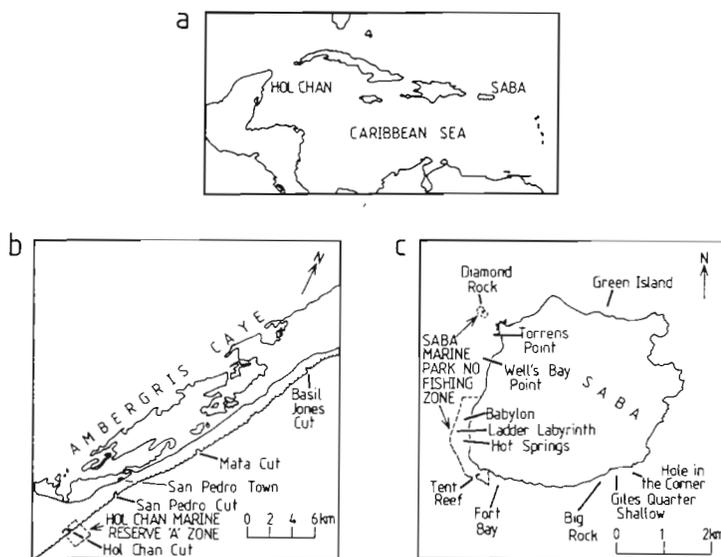


Fig 1. (a) The Caribbean region, (b) the southern end of Ambergris Caye, Belize, showing the area covered by Hol Chan Marine Reserve 'A' Zone and of the other reef cuts investigated, and (c) Saba, Netherlands Antilles, with the 2 no-fishing zones within Saba Marine Park, and other locations where sampling was carried out

now conducted within a 10 n miles radius of the town and this exploitation is considered to be declining due to greater direct involvement of young fishermen in the tourist industry than previously was the case (Ruben Gonzalez, Manager, Caribena Producers Cooperative Society Ltd, San Pedro, pers. comm.). The San Pedro and Mata cuts lie close to the town of San Pedro (Fig. 1) and are subject to a high but unquantified fishing effort, based on hand-lining, spearing and use of Antillean fish-traps. Basil Jones Cut is more distant from San Pedro town and is more lightly fished. Some reef fishes, especially haemulids in all 4 areas, may be subject also to beach traps when they venture outside of the areas where they are observed during the day (Woods et al. 1988, p. 141).

Quantification of fish numbers and sizes.

At Saba, fish counts were made at depths of 5 and 15 m at sites inside and outside the no-fishing zone. In Belize, counts of reef fishes were made at depths of 2 m, in the back-reef zone behind the reef crest, and 15 m, on the

outer slope. Replicate counts were made in areas both to the north and to the south of each cut on the Belize reef. Locations of the cuts are shown in Fig. 1.

Demersal fishes were counted using a modification of the stationary point-count method developed by Bohnsack & Bannerot (1986) in the Caribbean. A tape measure 10 m long was placed across the substratum at the point to be counted and all fishes observed within or passing through a 5 m radius from the centre of the tape, extending in a cylinder to the surface, were counted during a 15 min period. The lengths of all individuals observed were estimated visually to the nearest cm.

Consistency between replicate counts, and between us as individual observers, was estimated by our setting up 2 separate areas, making initial counts in our own areas and then in each others' and second counts in our own areas again and then once more in each others'. This procedure was repeated at a site in Saba and a site in Belize. Estimates of similarity between replicate counts of the same diver, and of different observers, were then calculated using Spearman's Rank Correlation.

Accuracy of length estimation was evaluated using an adaptation of the method of Bell et al. (1985). Fifty random lengths of white electrical cable between 5 and 60 cm long were cut by a third party. At the end of the field study they were placed on the bottom in a line, with individual pieces separated by distances of at least 30 cm. We then estimated the length of each section from a distance of 3 m. This allowed a correction factor to be calculated for each observer, which was then applied to lengths of fishes estimated during the study.

Abundance and size of pelagic piscivorous species were also estimated from the same points as counts of demersal species using a method developed by Thresher & Gunn (1986) specifically for such species. At approximately 3 min intervals during the census period, the diver turned full circle and recorded numbers and lengths of all individuals observed within a radius of 10 m extending from the substratum up to the surface. Mean values were calculated from the 5 replicate counts for each point on the reef.

Quantification of habitat characteristics. In order to control for habitat differences among sites censused, visual estimates were also made of the dominant components of the benthos within each area sampled. The structural complexity of the substratum was also estimated on a 6 point scale: 0, no vertical relief; 1, low and sparse relief; 2, low but widespread relief; 3, moderately complex; 4, very complex with numerous caves and fissures; and 5, exceptionally complex with high coral cover, and numerous caves and overhangs.

Statistical analysis of data. Tests for normality (Kolmogorov-Smirnov 1-sample) and homoscedasticity (Bartlett's) of length and abundance data were conducted. Where it was warranted, square-root or stronger transformation was effected to increase approximation to normality. Habitat percentage-cover data were arcsin-square-root transformed. ANOVA and Student-Neuman-Keuls (SNK) methods were used to evaluate differences among samples. Habitat data were also analysed using cluster analysis (average linkage method), with the Bray-Curtis similarity index calculated from the raw percentage data. Estimates of fish biomass were made from corrected mean length estimates for species of 5 families which are commonly exploited commercially [surgeonfishes (Acanthuridae), parrotfishes (Scaridae), groupers (Serranidae), grunts (Haemulidae) and snappers (Lutjanidae)], followed by multiplication by the number observed during the counts. This procedure will have underestimated biomass because of the power relationship between length and mass. Previously published Caribbean mass-length data (Bohnsack & Harper 1988) were used to calculate fish biomass values on the basis of corrected mean lengths of the fishes involved. Biomass data were then analysed using ANOVA and the SNK test.

RESULTS

Fishes recorded

Information on fishes susceptible to exploitation was derived from discussion with local fishermen, observation of catches and examination of local fishing records. Thirty-eight exploited demersal species were recorded from point counts in Belize, together with a further 7 pelagic species (Table 1). At Saba, 32 exploited demersal species and a further 8 pelagic fishes were recorded. Twenty-five demersal and 6 pelagic exploited species were common to both areas. Among the exploited species, 16 demersal and 1 pelagic fish were recorded only in Belize, and 8 demersal plus 2 pelagic species were encountered only around Saba (Table 1).

Habitat differences and similarities among sites

At Saba, habitats were very similar between fished and unfished sites in both shallow-water (5 m) and deep (15 m) areas. A significant difference by ANOVA between fished and unfished areas in terms of gorgonian (excluding *Plexaura* spp.) cover ($p < 0.002$) was attributable to differences only at 15 m. Structural complexity of the habitat between fished and unfished

Table 1. Reef-associated fish species subject to exploitation which were recorded in underwater censuses in Belize and Saba. Fishes are grouped by family

Belize	Saba
<i>Negaprion brevirostris</i>	<i>Holocentrus ascensionis</i>
<i>Holocentrus ascensionis</i>	<i>Myripristis jacobus</i>
<i>Myripristis jacobus</i>	<i>Heteropriacanthus cruentatus</i>
<i>Mulloidichthys martinicus</i>	<i>Mulloidichthys martinicus</i>
<i>Malacanthus plumieri</i>	<i>Ocyurus chrysurus</i>
<i>Ocyurus chrysurus</i>	<i>Lutjanus apodus</i>
<i>Lutjanus analis</i>	<i>L. mahogoni</i>
<i>L. apodus</i>	<i>Anisotremus surinamensis</i>
<i>L. griseus</i>	<i>Haemulon aurolineatum</i>
<i>L. jocu</i>	<i>H. carbonarium</i>
<i>L. mahogoni</i>	<i>H. flavolineatum</i>
<i>Anisotremus virginicus</i>	<i>H. macrostomum</i>
<i>A. surinamensis</i>	<i>Epinephelus adscensionis</i>
<i>Haemulon album</i>	<i>E. cruentatus</i>
<i>H. carbonarium</i>	<i>E. fulvus</i>
<i>H. flavolineatum</i>	<i>E. guttatus</i>
<i>H. parrai</i>	<i>E. striatus</i>
<i>H. plumieri</i>	<i>Mycteroperca interstitialis</i>
<i>H. sciurus</i>	<i>M. tigris</i>
<i>Epinephelus cruentatus</i>	<i>Scarus coelestinus</i>
<i>E. fulvus</i>	<i>S. coeruleus</i>
<i>E. guttatus</i>	<i>S. iserti</i>
<i>E. striatus</i>	<i>S. taeniopterus</i>
<i>Mycteroperca bonaci</i>	<i>S. vetula</i>
<i>Scarus guacamaia</i>	<i>Sparisoma aurofrenatum</i>
<i>S. iserti</i>	<i>S. rubripinne</i>
<i>S. taeniopterus</i>	<i>S. viride</i>
<i>S. vetula</i>	<i>Halichoeres radiata</i>
<i>Sparisoma aurofrenatum</i>	<i>Acanthurus bahianus</i>
<i>S. chrysopterus</i>	<i>A. chirurgus</i>
<i>S. rubripinne</i>	<i>A. coeruleus</i>
<i>S. viride</i>	<i>Kyphosus sectatrix</i>
<i>Lachnolaimus maximus</i>	<i>Balistes vetula</i>
<i>Acanthurus bahianus</i>	<i>Calamus bajonado</i>
<i>A. chirurgus</i>	<i>Caranx latus</i>
<i>A. coeruleus</i>	<i>C. lugubris</i>
<i>Kyphosus sectatrix</i>	<i>C. ruber</i>
<i>Balistes vetula</i>	<i>Trachinotus falcatus</i>
<i>Calamus bajonado</i>	<i>Tylosurus crocodilus</i>
<i>C. calamus</i>	<i>Sphyraena barracuda</i>
<i>Caranx bartholomei</i>	<i>S. picudilla</i>
<i>C. latus</i>	<i>Scomberomorus regalis</i>
<i>C. ruber</i>	
<i>Trachinotus falcatus</i>	
<i>Tylosurus crocodilus</i>	
<i>Sphyraena barracuda</i>	
<i>Scomberomorus regalis</i>	

areas was indistinguishable by ANOVA. Cluster analysis of habitat data indicated no overall differences between shallow fished and shallow unfished sites (Fig. 2a).

An overall dissimilarity in habitat data was evident among the 15 m deep sites in Belize, but not among shallow-water sites (Fig. 2b). Shallow sites did differ by ANOVA in gorgonian (excluding *Plexaura* spp., $p < 0.001$), rubble ($p < 0.001$) and seagrass ($p < 0.001$),

coverage of the substratum, but none of these specifically separated the unfished or lightly-fished sites from the fished sites. The dissimilarity between 15 m sites was due largely to differences between Hol Chan on the one hand and the other 3 cuts on the other in structural complexity (Hol Chan with a mean index of 3.2 and the other sites together averaging 2.1; $p < 0.0001$), hard-coral cover (Hol Chan with a mean of 45.0% and the other sites averaging 8.6%; $p < 0.0001$) and bare-rock area (Hol Chan with a mean of 1.4% and the other sites averaging 27.6%, $p < 0.0001$).

These data indicate that in deep water at Hol Chan and Saba, habitat differences could confound differences arising from fishing pressure. On both shallow reef areas by contrast, variations in fish abundance and size data are attributable to exploitation and its cessation within the protected area.

Sources of variability in census data

Mean similarity of abundances of all fishes in duplicate areas censused by the same observer was high at 76.6% (± 1 SE 4.2, $n = 8$). Mean similarity of between-observer counts of total fish abundance was 62.8% (± 1 SE 2.6, $n = 16$).

Both of us underestimated lengths under water, but the positive correlations between estimated and actual length were high (r_s 0.987 and 0.992). These indicated a relatively constant underestimation, which averaged 2.9% for one of us and 13.8% for the other.

Variations in species abundance, mean length and biomass between sites

Saba

In shallow water at Saba 7 species showed significantly greater abundances in unfished areas than fished areas (Table 2). A single species, the Bermuda chub *Kyphosus sectatrix*, was more common in fished areas than in the no-fishing zone. Visual-census length-frequency for 2 species in shallow water at Saba are illustrated in Fig. 3a, b.

Twenty-two percent of fished species (29% of demersal and 0% of pelagic) showed greater abundance, size or biomass in the unfished relative to the fished areas in shallow water at Saba. A further 7% of target

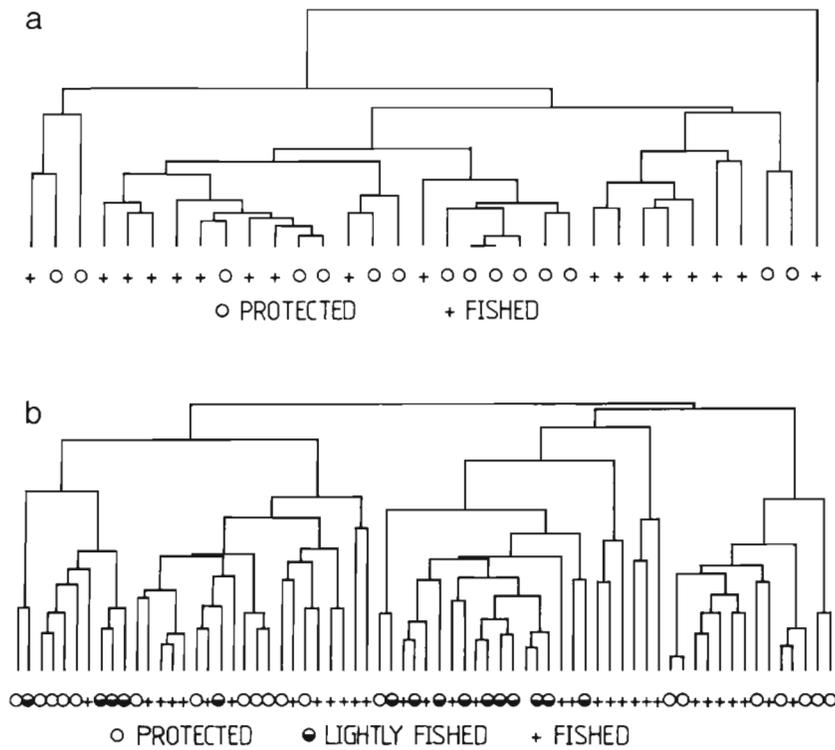


Fig 2. Dendrograms of substratum coverage similarity (average linkage method using Bray-Curtis indices) between protected and fished areas in (a) Saba at 5 m and (b) Belize at 2 m

fishes, namely the Nassau grouper *Epinephelus striatus*, queen triggerfish *Balistes vetula* and jolthead porgy *Calamus bajonado*, were observed only in the no-fishing zone, but their numbers were too low to be included in the statistical analysis.

Belize

Twelve species exhibited significant differences among the 4 localities in Belize for abundance, mean length or both (Table 3). Visual-census length-frequency data for 2 species in shallow water in Belize are illustrated in Fig. 3c, d.

Of 11 species showing abundance differences, 9 had the greatest values at either Hol Chan Cut (no fishing) or Basil Jones Cut (light fishing), with the other cuts similar to each other; for the other 2 species (coney *Epinephelus fulvus* and redband parrotfish *Sparisoma aurofrenatum*), Hol Chan and San Pedro had similar densities, and these were greater than those at the other 2 sites. Of 4 species showing mean length differences, Hol Chan exhibited the greatest sizes in 2 (stoplight parrotfish *S. viride* and blue tang *Acanthurus coeruleus*), and greater sizes together

Table 2. Target species of fishes which exhibited significant differences ($p < 0.05$) between fished and unfished foreereef sites at 5 m depth around Saba

Variable	p	Greater in Reserve or not
Abundance		
<i>Myripristis jacobus</i>	<0.001	Yes
<i>Lutjanus apodus</i>	<0.002	Yes
<i>Anisotremus surinamensis</i>	<0.002	Yes
<i>Haemulon carbonarium</i>	<0.0005	Yes
<i>H. flavolineatum</i>	<0.01	Yes
<i>Scarus taeniopterus</i>	<0.005	Yes
<i>S. vetula</i>	<0.04	Yes
<i>Kyphosus sectatrix</i>	<0.02	No
Mean length		
<i>H. flavolineatum</i>	<0.01	Yes
Biomass		
<i>L. apodus</i>	<0.01	Yes
<i>A. surinamensis</i>	<0.02	Yes
<i>H. carbonarium</i>	<0.006	Yes
<i>H. flavolineatum</i>	<0.0001	Yes
<i>Epinephelus fulvus</i>	<0.02	Yes
<i>S. taeniopterus</i>	<0.002	Yes
<i>S. vetula</i>	<0.05	Yes
<i>Acanthurus bahianus</i>	<0.02	Yes
<i>A. chirurgus</i>	<0.02	Yes

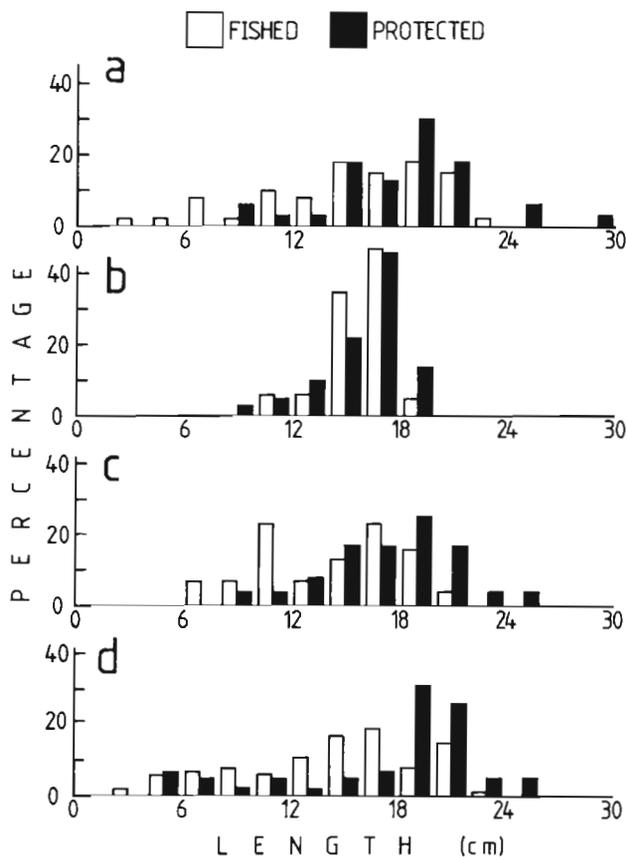


Fig. 3. Percentage-frequency/length-interval data of 4 reef fish species in fished and protected areas at Saba: (a) *Sparisoma aurofrenatum*, (b) *Myripristis jacobus*; and Ambergris Caye, Belize: (c) *Epinephelus fulvus*, and (d) *Acanthurus coeruleus*. For simplicity, data from Basil Jones Cut, the lightly-fished site in Belize, are omitted

with San Pedro for another (striped parrotfish *Scarus iserti*). For the fourth species (doctordfish *A. chirurgus*) Hol Chan tended to have smaller fishes than Mata and Basil Jones Cuts, but San Pedro was similar to all other cuts (Table 3).

Twenty-three percent of fished species in Belize (25% of demersal and 14% of pelagic fishes) showed abundance, size or biomass greater in unfished or lightly fished relative to fished, areas, while a further 4% (2 species) showed limited evidence of this. A further 8% of target fishes, namely gray snapper *Lutjanus griseus*, black margate *Anisotremus surinamensis*, Calamus bajonado and saucereye porgy *C. calamus*, were observed exclusively within the Reserve, but at densities too low to be included in the statistical analysis. Among target species, only *Acanthurus chirurgus* exhibited a contrary trend for mean lengths (relatively small animals in the reserve), but abundances were greater at Hol Chan relative to all the other areas.

Local population biomass and value in reserves

The commercial market for fish is well developed at San Pedro in Belize, much of the catch is exported (to Jamaica) and the price which was paid for exported fish at the Caribena Cooperative varied primarily by family and by size (Table 4). Consequently we combined our data on abundance and biomass by family.

The Saba Marine Park no-fishing zone had greater estimated biomasses of grouper, grunt, snapper, parrotfish and all demersal target families combined (Table 5). There were significant differences between Hol Chan and the other Belize reef cuts in biomass for snapper, parrotfish and all demersal target families combined (Table 6). Biomass was not calculated for pelagic species due to a particularly large error expected in visual length estimation for these roving animals.

In both areas total demersal target-fish biomasses in protected areas were approximately twice as large as those in fished areas outside (Mata and San Pedro Cuts in the case of Belize). Some families showed a greater biomass difference than others (Tables 5 & 6).

We used wholesale prices (Table 4) together with length-frequency information (e.g. Fig. 3), as an indicator of encounter rate by fishermen of demersal target stocks at the 2 m depth sites. The mean for the 2 fished sites (San Pedro and Mata Cuts) was 1.85 Belizean dollars (B\$) count⁻¹, while the mean for the Hol Chan Marine Reserve was B\$4.08 count⁻¹. This difference in value was contributed to especially by the snapper *Ocyurus chrysurus* and the parrotfishes *Sparisoma viride* and *Scarus guacamaia*. Counts in the lightly fished cut, Basil Jones, had an intermediate mean value of B\$2.96 count⁻¹.

There was no developed commercial marketing of reef fish at Saba similar to that in Belize, and therefore Belize prices (Table 4) were also used for valuation of the protected local fish stocks at Saba. The mean value of fish in families showing significant differences at Saba (snapper, grunt, grouper and parrotfish) was B\$1.48 count⁻¹ in fished areas and B\$5.30 count⁻¹ in the no-fishing zone of the Marine Park, a 3.5-fold difference in value of protected target fishes. This difference was contributed to mostly by the snapper *Lutjanus apodus*, the grunts *Anisotremus surinamensis*, *Haemulon flavolineatum* and *H. carbonarium* and the parrotfishes *Scarus vetula* and *Sparisoma viride*.

DISCUSSION

Specific time-series data for protected and control sites are not available for either area investigated here.

We cannot therefore prove conclusively that the differences observed in the fish communities have arisen solely from differences in fishing pressure. The habitat data have indicated, however, that fishing effects are likely to have played a substantial role in generating the differences which we observed. There were very few cases where species departed from the prediction of greater abundance or size expected in protected or lightly fished areas relative to fished sites. Our successful replication of these findings in 2 quite separate areas, together with the evidence from other recent investigations of this type (Bell 1983, Russ 1985, Alcalá 1988, Buxton & Smale 1989, Clark et al. 1989, Russ & Alcalá 1989, Alcalá & Russ 1990, Roberts & Polunin in press), support the conclusion that differences between fished and unfished areas are not simply due to differences other than fishing. We conclude that in protected areas of both Saba and Belize there has been increase in numbers and sizes of target reef-fish species following the prohibition of fishing.

It is worth assessing how extensive numerical and size differences were across all target species observed and what mechanisms may have been involved. The proportion of target species showing differences was similar in both areas, namely 31% of target species in Belize and 29% at Saba. Thus around 70% of target species at both sites apparently showed no significant abundance, size or biomass differences. Either protection has had no effect on these species, or it has, but the response has been undetected by us.

Table 4. Price paid (B\$) in 1991 for whole fish at the Caribena Cooperative in San Pedro, Ambergris Caye (R. Gonzalez pers. comm.) (1 oz = 28 g, 1 lb = 454 g; 1 B\$ = ca 0.5 US\$)

Fish	Whole or fillet	Size	B\$ lb ⁻¹
Snapper	Whole	5–8 oz	1.60
	Whole	8 oz–1 lb	1.80
	Whole	1–3 lb	2.00
	Whole	> 3 lb	2.25
Grouper	Whole	5 oz–1 lb	1.35
	Fillet	> 1 lb	1.50
Grunt	Whole	> 5 oz	1.25
Parrotfish	Whole	5 oz–1 lb	1.25
	Whole	> 1 lb	1.50
Jack	Whole	All	1.35
Barracuda	Whole	All	1.75

Table 3. Target species of fishes exhibiting significant differences ($p < 0.05$) in abundance, mean size or biomass among fished (SP: San Pedro Cut; MC: Mata Cut), lightly fished (BJ: Basil Jones Cut) and unfished (HC: Hol Chan Marine Reserve) areas in Belize

Variable	p	Site order of differences SNK test $p < 0.05$
Abundance		
<i>Ocyurus chrysurus</i>	<0.05	HC > MC = BJ = SP
<i>Lutjanus jocu</i>	<0.0001	HC > SP = MC = BJ
<i>Haemulon plumieri</i>	<0.0001	BJ > MC = SP = HC
<i>Epinephelus fulvus</i>	<0.001	HC = SP > MC = BJ
<i>Scarus guacamaia</i>	<0.001	HC > SP = MC = BJ
<i>S. iserti</i>	<0.04	BJ > HC = SP = MC
<i>S. taeniopterus</i>	<0.003	BJ > SP = MC = HC
<i>Sparisoma aurofrenatum</i>	<0.001	HC = SP > MC = BJ
<i>S. viride</i>	<0.001	BJ > HC = SP = MC
<i>Acanthurus chirurgus</i>	<0.002	HC > MC = SP = BJ
<i>Tylosurus crocodilus</i>	<0.0001	HC > SP = MC = BJ
Mean length		
<i>Scarus iserti</i>	<0.0005	HC = SP > BJ = MC
<i>Sparisoma viride</i>	<0.002	HC > SP = BJ > MC
<i>Acanthurus chirurgus</i>	<0.02	SP = (MC = BJ > HC) ^a
<i>A. coeruleus</i>	<0.003	HC > BJ = SP = MC
Biomass		
<i>O. chrysurus</i>	<0.02	HC > SP = MC = BJ
<i>L. jocu</i>	<0.0005	HC > SP = MC = BJ
<i>H. carbonarium</i>	<0.02	BJ > HC = SP = MC
<i>H. plumieri</i>	<0.0005	BJ > HC = SP = MC
<i>E. fulvus</i>	<0.002	SP = (HC > BJ = MC) ^a
<i>Scarus guacamaia</i>	<0.001	HC > SP = BJ = MC
<i>Sparisoma viride</i>	<0.01	HC = BJ > MC = SP

^aHol Chan significantly different from Basil Jones and Mata Cut, but San Pedro not significantly different from any of these sites

Table 5. Saba target fish by group, showing nonsignificant (ns) and significant differences between fished and protected areas in terms of mean abundance (numbers count⁻¹) and mean overall biomass (g fresh wt count⁻¹)

Fish	p	Group means in:	
		Fished area	Protected area
Abundance			
Snapper	ns		
Grunt	<0.0001	0.6	2.4
Grouper	ns		
Parrotfish	ns		
Surgeonfish	ns		
Overall demersal	<0.0001	13.6	18.6
Overall pelagic	ns		
Biomass			
Snapper	<0.02	29	344
Grunt	<0.0001	109	655
Grouper	<0.02	254	414
Parrotfish	<0.003	476	940
Surgeonfish	ns		
Overall demersal	<0.0001	1843	3525

Table 6. Belize target fish by group, showing nonsignificant (ns) and significant differences between fished and protected areas in terms of mean abundance (numbers count⁻¹) and mean overall biomass (g fresh wt count⁻¹) at 2 m depth. Abbreviations as for Table 3

Fish	ANOVA significance HC and/or BJ > other cuts	Group means at:			
		HC	BJ	SP	MC
Abundance					
Snapper	HC >, p < 0.01	4.4	3.1	2.1	2.2
Grunt	ns				
Grouper	HC >, p < 0.005	1.2	0.4	1.0	0.5
Parrotfish	BJ >, p < 0.0001	6.8	18.9	13.0	10.1
Surgeonfish	ns				
Overall demersal	ns				
Overall pelagic	HC >, p < 0.0001	0.9	0.1	0.1	0
Biomass					
Snapper	HC >, p < 0.0001	1345	679	410	388
Grunt	ns				
Grouper	ns				
Parrotfish	HC & BJ >, p < 0.003	1208	953	808	447
Surgeonfish	ns				
Overall demersal	HC >, p < 0.02	5993	3729	2856	2879

Enforcement is certainly strong in both reserves and its failure cannot explain the lack of detected differences in the majority of species. In addition, very few of the species listed in Table 1 are likely to be so lightly fished as to be little influenced by the effective local protection provided at Saba and in Belize. We conclude that effects may well have occurred which have been hidden by fish movements or which our methodology has been unable to detect. There are several potential explanations for the lack of differences detected for these species. For 21 species (45%) in Belize and 25 species (59%) at Saba, frequencies were very low in counts such that statistical analysis was impossible, or the likelihood of detection of differences was small given the low statistical power available. By increasing the point-count area censused we might have better analysed trends in these rarer species, but water clarity prevented us from routinely sampling larger areas. When the low-frequency species are excluded, a greater proportion of target species show differences. Thus half of the common species showed greater abundance, size or biomass in the Belize reserve and some two-thirds in the Saba no-fishing zone.

Secondly, detectability of fishes also reduced the likelihood of detecting effects of protection. This was bound to be true of nocturnal species, particularly holocentrids. Our detection of these will have been much more variable than of conspicuous diurnally active fishes. A third factor is movement, because increased survivorship in the reserve will be obscured by exchange of animals with fished animals across the protected-area boundaries. Spawning migrations of large grouper are known in Belize and exploited by

fishermen (Carter 1989). The lack of difference in sufficiently abundant pelagic species such as *Caranx ruber* can be explained by their mobility and has been supported by the modelling work of DeMartini (in press). Although unstudied in Belize and Saba, diel migrations of grunt in and out of reef areas are expected (McFarland et al. 1979), particularly where there are extensive seagrass beds in which they can feed. Because patterns and rates of movement are still little studied in reef fishes (Polacheck 1990), it is hard to quantify the role of movement in the different species involved here.

Several mechanisms could contribute to the reserve effects which we have observed. Abundance and size changes could relate to immigration and, or alternatively, greater survivorship of large fishes in protected areas.

Because we have no data on movement of the fishes involved, it is hard to disprove any role for immigration, but we suspect that the increased abundances which we have observed primarily reflect increased survivorship in Saba and Belize protected areas relative to fished sites outside of them. It is impossible to determine from our data whether differences in levels of recruitment or survivorship of young fishes between protected and fished areas have affected the numbers present.

We have not measured the extent to which greater numbers and sizes of fishes in the 2 marine reserves represent actual increases. A more or less constant survivorship in the reserves and falling survivorship in areas outside could have produced the same result. However, given a history of reef fishing which greatly precedes initiation of protection measures, especially in Belize, a substantial increase in numbers and sizes of target species is likely in the reserves. At the same time, survivorship may have continued to decline in fished areas, although we cannot test this because fisheries statistics scarcely differentiate between reef-associated and nonreef species. Any recovery of local fish populations under protection would indicate that fishing mortality is high relative to natural mortality in both areas. The fact that in Saba only 2 species showed effects attributable to fishing in deep water, while many did in shallow water, is consistent with fishing intensity being greatest in the shallows.

If we compare target-species biomasses in the 2 protected areas with those in fished sites (Tables 5 & 6), and divide these biomass differences by the area sampled (78 m²) and time-scale involved (4 yr), then the indica-

tion is that in Belize fresh-weight fish productivity has been $10 \text{ t km}^{-2} \text{ yr}^{-1}$ and at Saba $5 \text{ t km}^{-2} \text{ yr}^{-1}$ between 1987 and 1991. The apparent 2-fold difference between the regions could reflect a difference in productivity of the reef systems, the continental site being the more productive. However, it can equally be explained by recovery from greater growth overfishing along the Ambergris Caye reef than around Saba. Because fishing intensity does appear to be low in Saba, the indication is that many desirable fish species are highly susceptible to local depletion around these reefs.

There appear to be no published data on fishery harvests from small areas of Caribbean coral reef, but our estimates of approximate target-species biomass productivity do compare favourably with data from the Pacific (Munro & Williams 1985, Russ 1991). Our figures for productivity, however, are subject to error. In particular, we cannot extrapolate from the specific zones which we studied to whole reefs without further information. We assume also that our mean biomass data for fished sites are similar to those in protected areas before protection. In addition our sampling will have overestimated numbers of large mobile species because our technique recorded fish presence, regardless of whether the animal involved was in the sample area fleetingly or was a long-term resident.

There are 2 particularly significant implications of the increase in target-fish biomass. Firstly, natural predation will be substantially greater in the protected areas than on fishing grounds and this can be expected to have impacts on local prey survivorship and on interactions, especially competition, between prey species. Predator biomass was 1.8-fold greater in Belize and 3.5-fold greater at Saba in shallow water.

Secondly, because of the power relationship between length and fecundity, it is expected that such reserves must be supporting much greater egg and larval output per unit area than fished sites. Consequently reserves should be enhancing the input of propagules to sites elsewhere. Whether this flux will lead to greater larval supply, settlement and actual recruitment depends on a host of little-studied factors affecting survivorship in the plankton, at metamorphosis and after settlement (Doherty & Williams 1988, Roberts & Polunin 1991).

If stock size is generally below the threshold value indicated by the Beverton-Holt model (Beverton & Holt 1957), then greater recruitment might occur from a protected site with greater local fish biomass. There is no information on what this threshold value might be for any of the stocks in the present paper, and the status of the fishery is in any case unknown.

Although an estimate has been made of the market value of the increased standing stock of target fish in

the reserve, a strategy of rotation to exploit this value does not necessarily follow. The protected areas could be contributing economically more through a recruitment function, as discussed above, than they might do through occasional harvests, which can rapidly deplete stocks following the reopening of fishing. Which of these and other strategies would be most appropriate for the conditions requires better understanding of the local fisheries and population dynamics.

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