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# Rapid Build-up of Fish Biomass in a Caribbean Marine Reserve

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**Abstract:** Marine reserves, where fishing is excluded, have been argued to be an effective means of managing complex reef fisheries and of protecting populations of species vulnerable to overfishing. The argument rests on predictions of increases in abundance and size of fishes after the elimination of fishing mortality, which in turn leads to greater egg production per unit of reef and greater export via pelagic dispersal to fishing grounds. This study reports responses of fish populations to area closure in a small Caribbean marine reserve surrounding the island of Saba in the Netherlands Antilles. Part of the reserve has been closed to fishing since 1987, and the remainder is subject only to light fishing. Fish populations were visually censused and sizes of individuals present estimated from counts in fished and unfished areas of the marine park in 1991 and 1993. For four of five commercially fished families, biomass was greater in the unfished area than in the fished. Predictions of greater abundance and size in the unfished area were upheld for many of the species observed. Between 1991 and 1993 overall biomass of commercially important families increased 60%, based largely on increases in abundance between years. The predatory snappers (Lutjanidae) increased 220%. Fishing pressure in Saba was reduced between censuses due to changing employment opportunities. It was notable that populations increased in both fished and unfished areas of the park, and the latter is probably an effect of this reduced fishing intensity. Reserves have been suggested as refuges for species vulnerable to overexploitation, especially groupers. Despite protection from fishing, the Saba Marine Park has low population densities of such species, perhaps due to a lack of supply of larvae from unprotected source areas. My study shows that target fish populations may respond swiftly to reductions in fishing pressure and that reserves could play an important role in fisheries management. But protection of vulnerable species is only likely to be successful if networks of reserves are established throughout species ranges to link larval supply and settlement areas.

Crecimiento rápido en la biomasa de peces en una reserva marina del Caribe

**Resumen:** Las reservas marinas, donde la pesca está excluida, han sido consideradas como un medio efectivo para manejar las complejas pesquerías de arrecifes y para proteger poblaciones de especies vulnerables a la sobrepesca. El argumento se basa en las predicciones de un incremento en la abundancia y tamaño de los peces luego de la remoción de la mortalidad por pesca, lo que a su vez conduce a una mayor producción de huevos por unidad de arrecife y a una mayor exportación por medio de la dispersión pelágica a las áreas de pesca. Este estudio reporta las respuestas de las poblaciones de peces a la clausura de un área en una pequeña reserva marina del Caribe que rodea la isla de Saba en las Antillas Holandesas. Parte de la reserva ha estado cerrada a la pesca desde 1987 y el resto ha estado sujeto solo a una pesca reducida. Las poblaciones de peces fueron sensadas visualmente y el tamaño de los individuos presentes estimados a partir de conteos en las áreas pescadas y no pescadas del parque marino en 1991 y 1993. La biomasa para cuatro de las cinco familias sujetas a la pesca comercial fue mayor en el área cerrada a la pesca que en aquella sujeta a la misma. Las predicciones de una mayor abundancia y tamaño en el área libre de pesca fue apoyada para muchas de las especies observadas. Entre 1991 y 1993 la biomasa total de las familias comercialmente importantes incrementó un 60%, debido principalmente a aumentos en abundancia entre los distintos años. Los pargos predadores (Lutjanidae) aumentaron un 220%. La presión pesquera en Saba fue reducida entre los censos de

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bido al cambio de oportunidades de empleo. Fue notable que las poblaciones aumentasen tanto en las áreas pescadas como en aquellas no pescadas del parque, el incremento en las áreas sujetas a la pesca es probablemente el efecto de esta reducción de la presión pesquera. Las reservas han sido propuestas como refugios para las especies vulnerables a la sobreexplotación, en especial para las chernas. A pesar de estar protegido de la pesca, el Parque Marino de Saba tiene bajas densidades poblacionales de estas especies, quizás debido a una falta de suministro de larvas de áreas "fuentes" no protegidas. Este estudio demuestra que las poblaciones de peces sujetas a la pesca responderían rápidamente a reducciones en la presión pesquera y que las reservas podrían jugar un papel importante en el manejo pesquero. Sin embargo, la protección de especies vulnerables sólo sería exitosa si se establecen redes de reservas a lo largo de todo el área de distribución de las especies a los efectos de conectar las áreas de provisión de larvas y las áreas de asentamiento.

## Introduction

Marine reserves are becoming widely used to protect and manage marine habitats. Their increasing use stems partly from the growing need to protect the marine environment from human impact and partly from the proposition that they may be an effective means of managing coral reef fisheries (Davis 1989; Plan Development Team 1990; Roberts & Polunin 1991). Reef fisheries are notoriously difficult to manage with traditional methods because of the large numbers of species caught, the kinds of gear used, and the number of places at which catches are landed (Roberts & Polunin 1993a).

Protecting an area from fishing may lead to increases in numbers and sizes of species that are fishing targets (Plan Development Team 1990; Roberts & Polunin 1991). These effects are expected to lead to increased egg production in reserves, which will then, through planktonic dispersal, replenish fishing grounds outside reserves. A number of studies have confirmed predictions of increase in size and number of fishery species following protection (reviews in Roberts & Polunin 1991, 1993a, 1993b; Russ 1991; Dugan & Davis 1993; Polunin & Roberts 1993), although not for all species present in catches. Only a handful of studies have examined rates of build-up of biomass following protection (Alcala 1988; Beinssen 1989; Russ & Alcala 1989; Bohnsack et al. 1992). The second set of studies suggests that biomass may increase rapidly after protection.

In addition to their fishery management function, marine reserves may be one of the only effective ways of conserving species vulnerable to overexploitation. Fishing intensity on tropical coral reefs is rapidly increasing over large regions (McManus 1988), and large, predatory fish species have all but disappeared from heavily fished areas (del Norte et al. 1989; Sadovy 1989). Local extinctions of some species have been widespread, and the possibility of global extinctions is now being considered (American Fisheries Society 1991; Sadovy 1993).

Fishing gear used on reefs is relatively unselective and, due to the multispecies nature of catches, easily-caught species can be eliminated from a site without necessarily reducing overall catch rates (Medley et al. 1993). Spe-

cies most threatened by fishing are large, and they mature at sizes above the size at first capture. Two such species are protected in parts of the U.S. because their numbers have declined from over-fishing, the huge jewfish (*Epinephelus itajara*) and the Nassau grouper (*Epinephelus striatus*).

This study reports on the effects of marine reserve protection on fish populations surrounding the Caribbean island of Saba in the Netherlands Antilles. The results show that populations have responded rapidly to protection with increases in numbers, sizes, and overall biomass of many species. These findings suggest that the predicted fishery management and species conservation functions of reserves may be achieved relatively quickly after reserve establishment.

## Methods

The Saba Marine Park was established in 1987 and surrounds the island (Fig. 1). Since establishment, approximately 15% of the park has been designated as a no-fishing zone, and regulations are enforced by a daily marine park patrol. Compliance with regulations is high.

Fish populations inside and outside the no-fishing zone were censused in 1991, and those findings are presented in Polunin and Roberts (1993). In 1993 the survey was repeated using the same methods and sites as the original census to allow for trends in populations and rates of change in biomass to be established.

Fish populations were quantified using two well-tested methods. Demersal fishes were counted, using SCUBA, with a modification of the stationary point-count method developed by Bohnsack and Bannerot (1986). A tape measure 10 meters long was placed across the reef at the point to be counted; all fishes observed within or passing through a 5-meter radius of the center of the tape, extending upwards in a cylinder above the reef, were counted during a 15-minute period. The lengths of individuals observed were estimated visually to the nearest centimeter. Tests of the method during the first study in Saba have shown that it is feasible to quantify the entire diurnally active, noncryptic fish

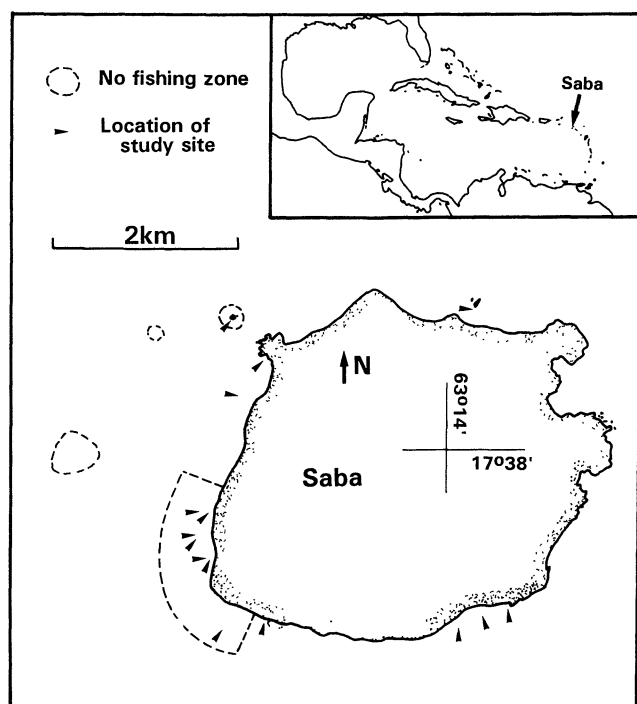


Figure 1. Map of the island of Saba, Netherlands Antilles, showing the locations of the no-fishing zones and the sites at which counts were made.

community using this method (Bohnsack & Bannerot 1986; Polunin & Roberts 1993). Visual estimation of fish lengths was accurate to within 3% of the actual lengths (Polunin & Roberts 1993). For parrotfishes, which are sequential hermaphrodites (Robertson & Warner 1978) and sexually dimorphic, the sexes were recorded separately in counts to determine sex ratios.

Populations of roving pelagic piscivores were quantified using the method of Thresher and Gunn (1986). Abundance and size of pelagic piscivorous species were estimated from the same points as counts of demersal fishes. At approximately 3-minute intervals during the census period, the observer turned 360° and recorded all individuals observed within a radius of 10 meters, extending from the reef to the surface, and estimated their lengths in centimeters. Mean values for each point were calculated from the five replicate counts.

Estimates of fish biomass were calculated from length estimates for species of five families commonly fished commercially: Acanthuridae (surgeonfishes), Scaridae (parrotfishes), Serranidae (groupers), Haemulidae (grunts), and Lutjanidae (snappers). Length-weight relationships were obtained from Bohnsack and Harper (1988), and weights were calculated separately and summed for every individual of a species observed in a count. In the 1991 analysis, biomass per count was calculated using a slightly less accurate method (Polunin & Roberts 1993), so the figures were recalculated for the present study so as to be comparable.

In order to characterize the habitat at each point sampled, visual estimates were made of the dominant components of the benthos, including hard corals, gorgonians, sponges, sand, and bare substrata. The structural complexity of the substratum, which is known to have an important influence on fish community structure (Roberts & Ormond 1987), was estimated on a six-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. This semiquantitative scale has proved effective in previous studies (Polunin & Roberts 1993; Roberts et al. 1992; Roberts & Polunin 1993b).

Fish counts were made at two depths, 5 meters and 15 meters, on the outer slope zone of the reef. Mooring buoys have been set up at sites throughout the marine park, and sampling was centered around them (Fig. 1). At each site during both years, exact points for counts were chosen haphazardly by the observer in order to approximate random sampling. Numbers of counts made were 22 at 5 meters (23 in 1993) in the unfished zone and 22 in the fished zone, and 15 at 15 meters in the unfished zone and 18 in the fished zone. To ensure comparability, sampling took place at approximately the same time of year in both years (March–April in 1991 and April–May in 1993).

Data on fish numbers and biomass were analyzed using three-way repeated measures ANCOVA, with year, fishing level, and depth as factors and structural complexity of the habitat as covariate. Data were tested for normality prior to analysis, and the square-root transform was used for these data to increase approximation to normality. For fish lengths, data from 5 meters and 15 meters were pooled, and a two-way ANOVA was performed with year and fishing level as factors. Data on percentage of cover for habitat characteristics were arcsine square-root transformed before analysis with three-factor repeated measures ANOVA. Parrotfishes are sequential hermaphrodites, changing from female to male with increasing size. The sex ratios of parrotfishes were calculated in fished and unfished zones to determine whether fishing skewed ratios toward greater female bias. Only the four species that are large enough to be caught and common enough to obtain meaningful results were used in the calculations.

## Results

### Habitat Characteristics and Species Diversity

Habitat differences between fished and unfished areas of the Saba Marine Park may affect fish populations independently of fishing regulations. It is important first to establish how comparable the two areas are. In the 1991



Table 1. Habitat characteristics in fished and unfished areas of the Saba Marine Park in 1991 and 1993.

Parameter <sup>a</sup>	Depth/Fishing <sup>b</sup>		1991 <sup>c</sup>	1993	Significance <sup>d</sup> (main effects)	
Structural Complexity	5 m	F	2.8	2.6	year	NS
	5 m	UF	3.4	3.2	fishing	NS
	15 m	F	3.2	3.4	depth	NS
	15 m	UF	2.8	2.8		
Hard Coral Cover	5 m	F	10.7	11.7	year	$p = 0.04$
	5 m	UF	15.3	18.8	fishing	NS
	15 m	F	25.2	34.6	depth	$p < 0.001$
	15 m	UF	23.5	24.1		
Gorgonian Cover	5 m	F	0.9	1.9	year	$p = 0.03$
	5 m	UF	1.4	1.1	fishing	$p < 0.01$
	15 m	F	0.6	0.6	depth	NS
	15 m	UF	5.6	0.7		
Plexaura <sup>e</sup>	5 m	F	10.7	11.9	year	NS
	5 m	UF	6.6	6.0	fishing	NS
	15 m	F	5.9	4.7	depth	NS
	15 m	UF	9.4	8.7		
Sand	5 m	F	16.2	16.3	year	NS
	5 m	UF	11.7	14.3	fishing	NS
	15 m	F	22.5	11.3	depth	NS
	15 m	UF	20.0	11.5		
Bare Substratum	5 m	F	54.7	52.1	year	NS
	5 m	UF	63.2	59.2	fishing	NS
	15 m	F	45.2	46.7	depth	$p < 0.001$
	15 m	UF	31.0	45.9		
Sponges	5 m	F	6.8	3.3	year	NS
	5 m	UF	1.8	0.6	fishing	NS
	15 m	F	0.7	2.1	depth	$p < 0.01$
	15 m	UF	10.8	9.0		

<sup>a</sup> Figures for structural complexity are the average values on the 0–6 scale used. Figures for other components of the substratum are percentage cover values (untransformed).  
<sup>b</sup> F = fished; UF = unfished.  
<sup>c</sup> Data for 1991 are from Polunin & Roberts (1993).  
<sup>d</sup> Significance levels are given for analyses performed on arcsine square-root transformed data for measures of percentage cover.  
<sup>e</sup> Plexaura is a dominant component of the gorgonian cover and has been separated from the other species for the purposes of habitat analysis.

survey, the only significant difference between areas was in the percentage cover of gorgonians in deep water (15 meters; Table 1), but the difference was slight. Cluster analysis revealed that sites within clusters were drawn almost equally from fished and unfished areas, with a division between the two main clusters based on depth (Polunin & Roberts 1993).

Three-way ANOVA confirmed that habitat differences between fished and unfished areas remained minimal in 1993 (Table 1) with percentage cover of gorgonians still the only significant difference. Percentage cover of hard coral had increased significantly between years, but the increase was even between fished and unfished zones (Table 1). Habitat structural complexity, perhaps the habitat characteristic most important to fish populations, did not differ significantly between fished and unfished areas between years or between depths (Table 1). Cluster analysis of the 1993 data showed a pattern of clustering very similar to the 1991 data. Thus, habitat differences should not affect interpretation of fishing effects in this study.

Species richness per count (numbers of species) did not differ significantly between fished and unfished

zones or between depths, but there was a small but significant increase in species richness between years ( $p = 0.002$ ; 1991  $\bar{x} = 25.9$ , 1993  $\bar{x} = 28.1$ ). Structural complexity had a significant influence on species richness (covariate  $p < 0.001$ ). Overall, the total number of species observed in the Saba Marine Park was similar between years: 130 in 1991 versus 126 in 1993.

Status of Fish Stocks

There was a marked increase in fish biomass at the family level between 1991 and 1993 (Figs. 2 and 3). For species from the five families combined, the increase was 60% over the two-year period. Biomass of groupers, grunts, snappers, and parrotfish was significantly higher in the unfished than in the fished zone (Table 2). There was a significantly higher biomass of snappers, surgeonfish, and parrotfishes in 1993 and trends of increase for groupers and grunts. For herbivores—parrotfishes and surgeonfishes combined—there was a strong increase in biomass from 1991 to 1993, although there were no significant differences between fished and unfished zones. In contrast, predators—grunts, snappers, and groupers

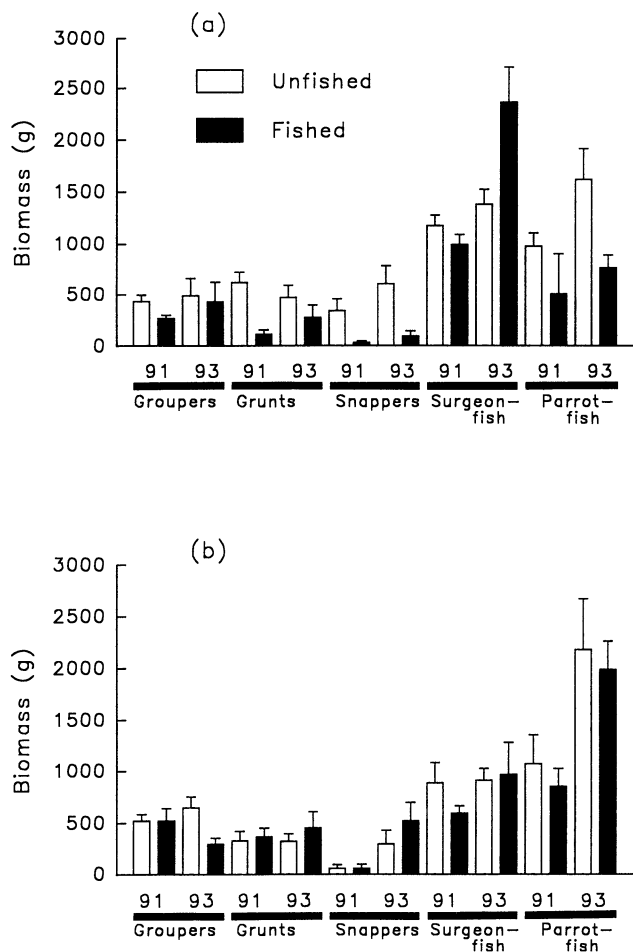


Figure 2. Changes in biomass of the different families of commercially fished species between 1991 and 1993 at 5 meters (a) and 15 meters (b). Error bars show the standard error of the mean.

combined—had a significantly higher biomass in the unfished zone and exhibited a trend of increase between 1991 and 1993.

Table 2 shows differences underlying these trends for species for which there were significant effects of fishing, depth, or year. Three of the six grouper species observed, four of seven grunts, and five of eight parrotfishes showed no significant differences and are not included in the table. There were strong increases between 1991 and 1993 for both species of snapper, one species of surgeonfish, and one species of parrotfish. Among the 21 species that did not show a significant increase in biomass between 1991 and 1993, 13 showed a higher average biomass in 1993. Biomass was significantly higher in the unfished area for all three species that showed a significant effect, all of which were predatory species.

Increases in abundance of fishes contributed considerably to the increases in biomass observed. There were significant increases in abundance between 1991 and

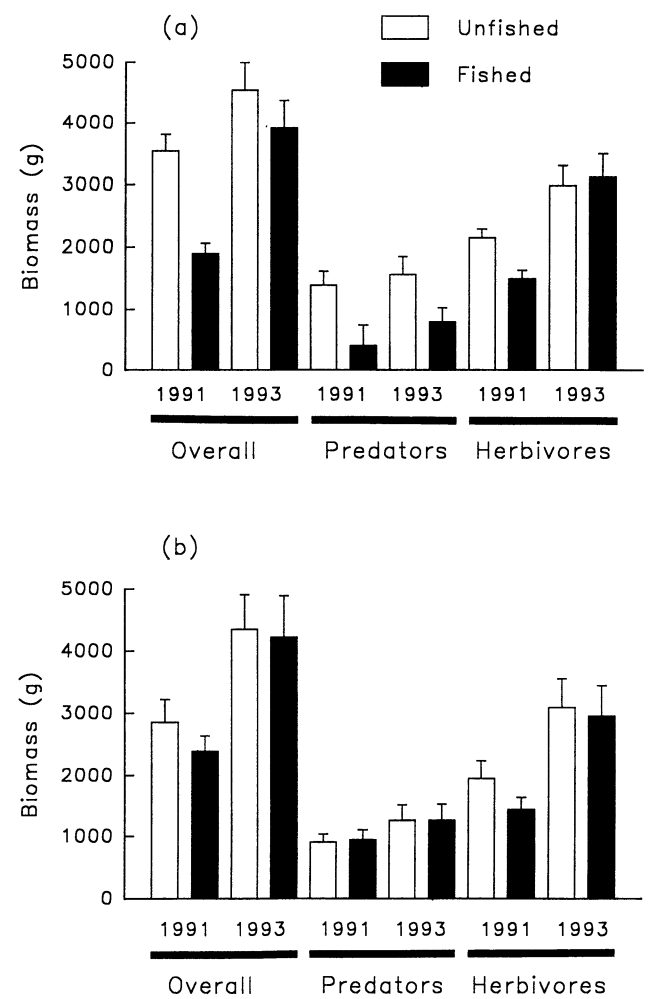


Figure 3. Changes in biomass for predators (groupers, grunts, and snappers), herbivores (parrotfishes and surgeonfishes), and overall (all five families combined) between 1991 and 1993 at 5 meters (a) and 15 meters (b). Error bars show the standard errors of the mean.

1993 for three of five families: snappers, surgeonfish, and parrotfish (Table 3). Although not significant, mean abundance of groupers and grunts was also higher in 1993 than 1991. Abundance of pelagic piscivores decreased significantly from 1991 to 1993, due mainly to a reduction in numbers of the most common species, *Caranx ruber*. Increases in abundance were greater in deeper water (15 m) for parrotfishes and shallow water (5 m) for surgeonfishes. At the species level there were significant increases from 1991 to 1993 for two of eight parrotfish, two species of snapper, and two of three species of surgeonfish. The only significant decrease in abundance between years was for an uncommon species of grouper, *Epinephelus adscensionis*. Significant effects of fishing on abundance were present for only four species, all predators, three of which were more abundant in the unfished zone. The sex ratios of parrotfishes did

Table 2. Significant biomass differences detected for fish species and families in the Saba Marine Park between 1991 and 1993 surveys.

Species/Family	Fishing <sup>a</sup>		Depth (m)		Year		Interaction(s) <sup>b</sup>
	Significance	Status	Significance	Status	Significance	Status	
Groupers							
<i>Epinephelus fulvus</i>	<0.001	UF > F	NS		NS		NS
<i>E. cruentata</i>	<0.01	UF > F	<0.01	15 > 5	NS		NS
<i>E. guttatus</i>	NS		<0.01	15 > 5	=0.02	91 > 93	NS
Grunts							
<i>Haemulon flavolineatum</i>	NS		=0.04	15 > 5	NS		F*D
<i>H. chrysargyreum</i>	NS		<0.001	5 > 15	NS		NS
Snappers							
<i>Lutjanus mahogoni</i>	NS		NS		<0.01	93 > 91	NS
<i>L. apodus</i>	NS		NS		<0.01	93 > 91	NS
Parrotfishes							
<i>Scarus taeniopterus</i>	NS		<0.01	15 > 5	NS		D*Y
<i>Sparisoma rubripinne</i>	NS		<0.03	5 > 15	NS		NS
<i>S. viride</i>	NS		<0.001	15 > 5	<0.001	93 > 91	NS
Surgeonfishes							
<i>Acanthurus coeruleus</i>	NS		<0.001	5 > 15	<0.001	93 > 91	F*Y,D*Y
<i>A. babianus</i>	NS		<0.001	5 > 15	NS		F*D
<i>A. chirurgus</i>	NS		=0.02	5 > 15	NS		NS
Groupers	<0.005	UF > F	=0.03	15 > 5	NS		NS
Grunts	<0.005	UF > F	NS		NS		F*D
Snappers	=0.05	UF > F	NS		<0.001	93 > 91	F*D
Parrotfishes	=0.04	UF > F	<0.01	15 > 5	<0.001	93 > 91	NS
Surgeonfishes	NS		<0.001	5 > 15	<0.001	93 > 91	F*D,F*Y
Predators <sup>c</sup>	<0.001	UF > F	NS		NS		F*D
Herbivores <sup>d</sup>	NS		NS		<0.001	93 > 91	NS
Overall <sup>e</sup>	<0.005	UF > F	NS		<0.001	93 > 91	NS

<sup>a</sup> UF = unfished; F = fished.  
<sup>b</sup> F = fishing; D = depth; Y = year.  
<sup>c</sup> Groupers, snappers and grunts combined.  
<sup>d</sup> Surgeonfishes and parrotfishes.  
<sup>e</sup> The five families combined.  
Data were square-root transformed prior to analyses (NS = not significant).

not suggest that the low fishing intensities present in Saba are causing any skew in sex ratios toward a lower frequency of males in the fished area. Indeed, males were more available in the fished area for three of the four species.

Size was analyzed for only the 15 species that were sufficiently common in both fished and unfished zones to provide reasonable statistical power (Table 4). Of these, only the nine that showed a significant effect are presented in Table 4. Species not showing significant differences were *Epinephelus cruentata*, *Sparisoma rubripinne*, *Acanthurus chirurgus*, *Haemulon carbonarium*, *Lutjanus apodus*, and *Kyphosus sectatrix*. All of the five species for which there was a significant fishing effect were larger in the unfished than the fished zone, which supports the prediction that fish should grow older and therefore larger under reduced fishing mortality. Differences between years were divided between increases (one species) and decreases (four species) from 1991 to 1993. These results indicate that changes in size had a much smaller influence on increases in biomass than did abundance.

Size differences are difficult to analyze because differences between years may be obscured by differences in

the relative abundance of juveniles versus older fishes. Hence, a pulse of new recruits in 1993, which was not present in 1991, might obscure an increase in the size of larger fishes between years. To account for this complication, results of statistical analyses were also compared with size-frequency histograms to check whether any such confounding effects were present. The results confirmed the findings of the statistical analyses.

Large grouper species were uncommon in the sites surveyed and belonged to only two species: *Mycteroperca tigris* and *M. interstitialis*. So few individuals were observed that records for the two species were pooled ( $n = 6$ ) and a chi-squared test performed. No significant difference in sighting frequency was detected (chi-squared = 0.66, 1 df).

Discussion

Trends in Saba Fish Populations

The first survey of fish populations in the Saba Marine Park (Polunin & Roberts 1993) showed that in shallow water (5 m) biomass of fishes was significantly higher for all five commercially fished families in the unfished

Table 3. Significant abundance differences detected for fish species and families within the Saba Marine Park between 1991 and 1993 surveys.

Species/Family	Fishing <sup>a</sup>		Depth (m)		Year		Covariate	Interaction <sup>b</sup>
	Significance	Status	Significance	Status	Significance	Status		
Groupers								
<i>Epinephelus fulvus</i>	<0.001	UF > F	NS		NS		NS	D*Y
<i>E. cruentata</i>	<0.01	UF > F	<0.001	15 > 5	NS		<0.001	F*D
<i>E. guttatus</i>	NS		<0.003	15 > 5	=0.03	91 > 93	NS	NS
Grunts								
<i>Haemulon flavolineatum</i>	<0.02	F > UF	<0.02	15 > 5	NS		<0.005	F*D
<i>H. chrysargyreum</i>	NS		<0.001	5 > 15	NS		<0.001	NS
<i>H. aurolineatum</i>	<0.001	UF > F	<0.001	5 > 15	NS		<0.001	NS
Snappers								
<i>Lutjanus mahogoni</i>	NS		NS		<0.03	93 > 91	NS	NS
<i>L. apodus</i>	NS		NS		<0.005	93 > 91	<0.002	NS
Parrotfishes								
<i>Scarus taeniopterus</i>	NS		<0.001	15 > 5	<0.01	93 > 91	NS	D*Y,F*D*Y
<i>Sparisoma rubripinne</i>	NS		<0.02	5 > 15	NS		NS	NS
<i>S. viride</i>	NS		<0.001	15 > 5	<0.001	93 > 91	<0.005	NS
Surgeonfishes								
<i>Acanthurus coeruleus</i>	NS		<0.001	5 > 15	<0.001	93 > 91	NS	F*D,D*Y
<i>A. babianus</i>	NS		<0.001	5 > 15	<0.005	93 > 91	<0.02	F*D*Y
<i>A. chirurgus</i>	NS		=0.04	5 > 15	NS		NS	F*D
Pelagic piscivores	NS		<0.005	15 > 5	<0.001	91 > 93	NS	NS
Families								
Groupers	<0.001	UF > F	<0.001	15 > 5	NS		NS	NS
Grunts	NS		NS		NS		<0.001	NS
Snappers	NS		NS		<0.001	93 > 91	<0.005	NS
Parrotfishes	NS		<0.001	15 > 5	<0.001	93 > 91	NS	D*Y
Surgeonfishes	NS		<0.001	5 > 15	<0.001	93 > 91	NS	F*D,F*Y*D
Predators <sup>c</sup>	<0.001	UF > F	<0.005	15 > 5	NS		<0.001	NS
Herbivores <sup>d</sup>	NS		<0.003	5 > 15	<0.001	93 > 91	NS	F*D*Y
Overall <sup>e</sup>	NS		NS		<0.001	93 > 91	NS	F*D*Y

<sup>a</sup> UF = unfished; F = fished.  
<sup>b</sup> F = fishing; D = depth; Y = year.  
<sup>c</sup> Groupers, snappers and grunts combined.  
<sup>d</sup> Surgeonfishes and parrotfishes.  
<sup>e</sup> The five families combined.  
Data were square-root transformed prior to analyses (NS = not significant).

zone of the park than in the fished zone (surgeonfishes were reported as not differing significantly in the 1993 paper, but the refined method of biomass calculation used here showed that there was a higher biomass in the unfished zone for them as well). In deeper water (15 m) the differences were not significant (Roberts & Polunin 1993a). The difference in results between depths was attributed to a higher fishing pressure near the shore from line and spear fishing.

The original study was based on a “snapshot” survey four years after fishing regulations had been implemented. It suggested that protection from fishing could produce a rapid build-up in fish numbers and biomass and, to a lesser extent, increases in average size. Due to an absence of baseline data, however, the possibility that differences between fished and unfished areas were present prior to park establishment could not be ruled out.

This study revealed a rapid build-up of overall fish biomass in both fished and unfished zones of the park between 1991 and 1993. It also shows that population sizes of many species have continued to increase since

1991 and that differences between fished and unfished zones detected in the first survey were probably a result of protection from fishing. Intriguingly, while biomass typically remained higher in the unfished area, increases in biomass were generally greater in the fished area. There was a drop in the abundance of pelagic piscivores between years and an increase in the point diversity (numbers of species per count) but not in overall diversity (numbers of species present). Build-up in biomass was greatest for the snappers (220% increase) and parrotfishes (90% increase).

At one time, fishing was an important source of food for Saba’s population. Over the past 30 years, however, fishing has declined to its present low levels. There are fewer than 15 full-time commercial fishers, and they do most of their fishing on the Saba Bank approximately 10 km offshore. Only 50 or so people fish recreationally, mostly by trolling or spearfishing in shallow water close to shore.

Why did fish biomass increase more between years in the fished area than in the unfished area? Changes in



Table 4. Species for which there were significant size differences detected by ANOVA.

Species	Year		Fishing		Year*fishing	df
	Significance	Status	Significance	Status		
Groupers						
<i>Epinephelus fulvus</i>	NS		=0.05	UF > F	NS	377
Grunts						
<i>Haemulon</i>						
<i>chrysargyreum</i>	<0.001	91 > 93	NS			78
<i>H. flavolineatum</i>	<0.001	91 > 93	<0.005	UF > F	=0.02	102
Snappers						
<i>Lutjanus mahogoni</i>	<0.03	93 > 91	NS		NS	35
Parrotfishes						
<i>Scarus taeniopterus</i>	<0.05	91 > 93	NS		<0.02	239
<i>Sparisoma viride</i>	NS		<0.001	UF > F	NS	215
<i>S. aurofrenatum</i>	NS		<0.001	UF > F	<0.01	276
Surgeonfishes						
<i>Acanthurus coeruleus</i>	<0.001	91 > 93	NS		NS	693
<i>A. bahianus</i>	NS		<0.04	UF > F	NS	511

Fifteen species were tested. UF = unfished; F = fished.

fishing intensity over time is the most likely explanation. After 1987, fishing ceased in part of the park. By the time of the survey in 1991, populations had had time to build up in this area. Between 1991 and 1993, fishing pressure in the fished zone decreased in Saba due to shifts in employment of local people away from fishing and toward construction (Susan White, Saba Marine Park Manager, personal communication). Because there were so few fishers, such a shift in employment could have had a large effect on overall fishing activity. At present, populations of fishes in the fished zone have responded strongly to this reduction in fishing, and those in the unfished area have continued to increase at a slower rate.

There are alternatives to this explanation. Differences may be due to observer bias, but this is unlikely. In 1991 the survey was carried out by two of us, but efforts were made to ensure between-observer comparability of data, and tests showed that differences were small (Polunin & Roberts 1993a). Furthermore, sampling effort by each observer was similar between the fished and the unfished zones, so it would be difficult to produce differential results between fished and unfished zones through an observer effect. In addition, because I collected 78% of the 1991 data, the potential for observer bias was small.

There is the possibility that habitat change within the park drove a change in the fish populations. For this to be a viable explanation, changes would have to be different between fished and unfished areas. There was a significant interaction term (fishing level × year) in the results of the ANOVA only for gorgonians, however, which made up a small proportion of cover. Examination of the mean levels for each parameter (Table 1) show changes in coral cover between years that differed between fishing levels, but the changes were in opposite directions and were restricted to deep water. Changes in fish populations were in the same direction (but of different magnitudes) and were evident at both depths.

Thus, there is little evidence to support a habitat-based explanation for differential increases in fish populations.

Recruitment variability between years rather than fishing regulations may have led to the increases in biomass, with a good year or years for recruitment occurring subsequent to the 1991 survey. But the data do not show particularly strong pulses of juvenile fishes for any but a few species, although overall recruitment was good. It is not clear that this source of increase could by itself satisfactorily explain the differences in rates of biomass build-up between fished and unfished zones.

A final possibility is that increases in biomass in the fished area have been supplemented by emigration from the unfished area. An important but as yet little-tested prediction made for marine reserves is that catches surrounding a reserve will increase due to net movement out of the protected area (Ballantine 1989; Alcala & Russ 1990; Roberts & Polunin 1993a). If true, this would compensate fishermen for possible lost production due to closure of an area and make establishment of marine reserves more politically and socially attractive (Fisk 1992). On theoretical grounds, this source of supplementation of biomass in the fished area is plausible (DeMartini 1993) but has probably had less influence on the observed changes than shifts in fishing pressure. Monitoring of fish populations around Saba will be continued annually and should help to identify the ultimate extent of biomass build-up and to determine the reasons for the differences in responses in fished and unfished areas.

Use of Marine Reserves to Protect Species Vulnerable to Overfishing

A number of life-history and behavioral characteristics can make a species especially vulnerable to overfishing, including large size at sexual maturity, long lifespan, low fecundity or recruitment success, low population den-

sity, sequential hermaphroditism, and behaviors that increase ease of capture, such as aggregation at spawning sites. Numerous species of reef fishes possess some or many of these characteristics. Certain species of grouper have all of these traits and are among the species most heavily affected by fishing.

A particular concern of fisheries managers is the prevalence of sequential hermaphroditism, particularly among the groupers (Bannerot et al. 1987), with sex change being partially dependent on size. Intense fishing, such as is becoming typical on reefs throughout the world, could deplete populations of males to the extent that reproductive output of a species is impaired (Bohnsack 1989; Sadovy 1993). The majority of grouper species cannot be sexed visually. Consequently, it was not possible to determine whether fishing in Saba has affected their sex ratios. But data for four species of parrotfishes do not suggest that the low intensities of fishing there have had any impact on sex ratio.

Large species of grouper are very uncommon in Saba. Data from this study did not show any difference in abundance between fishing levels, but so few individuals were observed (six) that statistical power was low. They are more frequent on the deep, unfished pinnacles that lie offshore from the park areas surveyed, but they could not be called common compared, for example, to populations on some Indo-Pacific reefs or reefs of Belize (Polunin & Roberts 1993; Roberts & Polunin 1993b). It is difficult to know whether this is an effect of less-suitable habitat in Saba, where reefs generally consist of a veneer of corals and invertebrates over a volcanic base rock (van't Hof 1991), or whether it is because they have been fished out in the past. Close monitoring of populations within the park, however, may show whether they respond to reduced fishing pressure over the long term.

The arguments for using marine reserves in fishery management rest on the larval dispersal phase allowing the export of benefits (eggs, larvae, and possibly adults). But this dispersal phase also means that populations within reserves will probably rarely be self-sustaining, highlighting one of the problems with marine parks as refuges for vulnerable species. If population sizes have been greatly reduced in the supply areas, then replenishment of reserve populations could be limited by low recruitment. Consequently, successful conservation of such species, and of biodiversity in general, will depend on understanding the interconnections among larval source and settlement areas and on establishing protected areas in networks throughout coral-reef regions.

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Appendix 1

Mean numbers of individuals observed per count of fish species and families in the study areas in Saba, Netherlands Antilles.

Family/Species	5 Meters				15 Meters			
	Unfished		Fished		Unfished		Fished	
	1991	1993	1991	1993	1991	1993	1991	1993
Serranidae								
<i>Epinephelus fulvus</i>	3.1	2.4	2.1	1.6	2.2	3.8	2.4	2.5
<i>E. cruentata</i>	0.3	0.4	0.4	0.3	1.4	1.2	0.5	0.5
<i>E. guttatus</i>	0.0	0.0	0.04	0.0	0.12	0.06	0.3	0.07
<i>E. adscensionis</i>	0.04	0.04	0.0	0.05	0.0	0.0	0.0	0.0
<i>Mycteroperca tigris</i>	0.08	0.04	0.0	0.1	0.07	0.07	0.1	0.05
<i>M. interstitialis</i>	0.0	0.0	0.0	0.05	0.0	0.0	0.05	0.0
Haemulidae								
<i>Haemulon flavolineatum</i>	0.5	0.6	0.2	0.6	0.4	0.4	1.3	1.5
<i>H. crysargyreum</i>	0.5	0.8	0.3	0.3	0.3	0.4	0.3	0.3
<i>H. carbonarium</i>	0.5	0.4	0.1	0.4	0.5	0.4	0.4	0.4
<i>H. macrostomum</i>	0.0	0.05	0.0	0.0	0.07	0.0	0.0	0.0
<i>H. aurolineatum</i>	0.0	0.0	0.0	0.0	0.2	0.4	0.0	0.0
<i>Anisotremus surinamensis</i>	0.3	0.1	0.0	0.1	0.0	0.2	0.05	0.07
Lutjanidae								
<i>Lutjanus mabogoni</i>	0.2	0.5	0.3	0.2	0.1	0.3	0.1	0.3
<i>L. apodus</i>	0.2	0.6	0.1	0.2	0.1	0.2	0.0	0.4
Acanthuridae								
<i>Acanthurus coeruleus</i>	2.8	5.7	3.4	10.8	3.2	3.6	1.7	3.3
<i>A. babianus</i>	4.1	3.7	3.6	5.6	1.4	3.1	1.9	1.9
<i>A. chirurgus</i>	0.6	0.4	0.2	0.3	0.1	0.04	0.2	0.4
Scaridae								
<i>Scarus taeniopterus</i>	1.6	0.9	0.4	0.5	0.9	4.3	1.5	3.2
<i>S. vetula</i>	0.2	0.1	0.0	0.04	0.0	0.1	0.1	0.3
<i>S. coeruleus</i>	0.0	0.05	0.05	0.0	0.0	0.1	0.0	0.0
<i>Sparisoma aurofrenatum</i>	1.8	1.7	1.7	2.0	1.5	2.5	1.5	2.0
<i>S. rubripinne</i>	0.4	0.5	0.1	0.3	0.1	0.0	0.0	0.2
<i>S. viride</i>	0.3	1.8	0.7	0.9	1.4	2.4	1.5	2.9
Total numbers								
Serranidae	3.5	3.0	2.5	2.1	3.7	5.1	3.4	3.0
Haemulidae	1.8	2.0	1.0	2.2	1.5	1.7	1.8	1.9
Lutjanidae	0.4	1.1	0.3	0.4	0.2	0.5	0.1	0.6
Acanthuridae	7.6	9.9	7.2	16.7	4.7	6.8	3.8	5.6
Scaridae	4.2	5.1	2.8	3.7	3.8	9.5	4.7	8.7
Overall <sup>a</sup>	17.6	20.9	13.9	25.1	13.9	23.6	13.7	19.9
Predators <sup>b</sup>	5.8	6.0	3.8	4.7	5.5	7.3	5.3	5.6
Herbivores <sup>c</sup>	11.8	14.9	10.1	20.4	8.5	16.3	8.5	14.3

<sup>a</sup>Serranidae, Haemulidae, Lutjanidae, Acanthuridae and Scaridae combined.

<sup>b</sup>Serranidae, Haemulidae, and Lutjanidae combined.

<sup>c</sup>Acanthuridae and Scaridae combined.

Appendix 2

Mean biomass per count of fish species and families in the study areas in Saba, Netherlands Antilles.

Family/Species	5 Meters				15 Meters			
	Unfished		Fished		Unfished		Fished	
	1991	1993	1991	1993	1991	1993	1991	1993
Serranidae								
<i>Epinephelus fulvus</i>	316	228	202	174	332	414	219	192
<i>E. cruentata</i>	65	61	46	15	107	117	38	46
<i>E. guttatus</i>	0	0	15	0	49	16	87	9
<i>E. adscensionis</i>	40	38	0	35	0	0	0	0
<i>Mycteroperca tigris</i>	10	160	0	195	34	99	75	49
<i>M. interstitialis</i>	0	0	0	11	0	0	101	0
Haemulidae								
<i>Haemulon flavolineatum</i>	94	79	10	52	38	32	171	168
<i>H. corysargyreum</i>	140	142	86	137	20	35	23	22
<i>H. carbonarium</i>	154	107	14	62	159	92	130	109
<i>H. macrostomum</i>	0	65	0	0	78	0	0	0
<i>H. aurolineatum</i>	0	0	0	0	32	42	0	0
<i>H. parrai</i>	0	0	0	0	0	16	0	0
<i>Anisotremus surinamensis</i>	229	74	0	19	0	101	42	151
Lutjanidae								
<i>Lutjanus mahogoni</i>	36	118	30	28	18	54	16	81
<i>L. apodus</i>	303	483	0	64	35	240	39	436
Acanthuridae								
<i>Acanthurus coeruleus</i>	602	941	572	1768	617	576	352	678
<i>A. babianus</i>	363	319	349	479	209	314	186	179
<i>A. cetrurgus</i>	207	114	69	115	59	20	55	110
Scaridae								
<i>Scarus taeniopterus</i>	306	169	87	95	119	463	187	449
<i>S. vetula</i>	85	69	0	13	0	8	24	63
<i>S. iserti</i>	0	0	0	0	0	0	12	0
<i>S. coeruleus</i>	0	24	30	0	0	93	0	0
<i>S. coelestinus</i>	0	0	0	0	0	0	99	0
<i>Sparisoma aurofrenatum</i>	232	237	201	294	247	317	113	227
<i>S. rubripinne</i>	126	210	47	182	75	41	0	77
<i>S. viride</i>	229	907	136	179	628	1255	417	1173
Total biomass								
Serranidae	432	487	262	429	522	646	521	295
Haemulidae	616	467	110	271	328	318	365	450
Lutjanidae	339	601	30	92	53	294	55	516
Acanthuridae	1172	1374	990	2362	884	910	593	967
Scaridae	976	1616	501	762	1069	2177	852	1988
Overall <sup>a</sup>	3534	4545	1894	3916	2856	4345	2385	4217
Predators <sup>b</sup>	1386	1556	403	791	903	1259	940	1261
Herbivores <sup>c</sup>	2148	2989	1491	3125	1953	3087	1444	2955

<sup>a</sup>Serranidae, Haemulidae, Lutjanidae, Acanthuridae and Scaridae combined.

<sup>b</sup>Serranidae, Haemulidae and Lutjanidae combined.

<sup>c</sup>Acanthuridae and Scaridae combined.

