
Effects of Artisanal Fishing on Caribbean Coral Reefs

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Abstract: *Although the impacts of industrial fishing are widely recognized, marine ecosystems are generally considered less threatened by artisanal fisheries. To determine how coral reef fish assemblages and benthic communities are affected by artisanal fishing, we studied six Caribbean islands on which fishing pressure ranged from virtually none in Bonaire, increasing through Saba, Puerto Rico, St Lucia, and Dominica, and reaching very high intensities in Jamaica. Using stationary-point fish counts at 5 m and 15 m depth, we counted and estimated the lengths of all noncryptic, diurnal fish species within replicate 10-m-diameter areas. We estimated percent cover of coral and algae and determined reef structural complexity. From fish numbers and lengths we calculated mean fish biomass per count for the five most commercially important families. Groupers (Serranidae), snappers (Lutjanidae), parrotfish (Scaridae), and surgeonfish (Acanthuridae) showed order-of-magnitude differences in biomass among islands. Biomass fell as fishing pressure increased. Only grunts (Haemulidae) did not follow this pattern. Within families, larger-bodied species decreased as fishing intensified. Coral cover and structural complexity were highest on little-fished islands and lowest on those most fished. By contrast, algal cover was an order of magnitude higher in Jamaica than in Bonaire. These results suggest that following the Caribbean-wide mass mortality of herbivorous sea urchins in 1983–1984 and consequent declines in grazing pressure on reefs, herbivorous fishes have not controlled algae overgrowing corals in heavily fished areas but have restricted growth in lightly fished areas. In summary, differences among islands in the structure of fish and benthic assemblages suggest that intensive artisanal fishing has transformed Caribbean reefs.*

Efectos de la Pesca Artesanal sobre Arrecifes de Coral en el Caribe

Resumen: *Aunque se reconocen ampliamente los impactos de la pesca industrial, los ecosistemas marinos generalmente son considerados menos amenazados por las pesquerías artesanales. Para determinar de que manera la pesca artesanal afecta a los ensambles de peces de arrecifes coralinos y a las comunidades bénticas, estudiamos seis islas Caribeñas en las que la pesca artesanal varió a lo largo de una gradiente desde una intensidad de pesca casi inexistente en Donaire, una mayor intensidad de pesca en Saba, Puerto Rico, St. Lucía y Dominica, e intensidades de pesca muy altas en Jamaica. Utilizando conteos de peces en puntos estacionarios a 5m y 15m de profundidad, cuantificamos y estimamos las longitudes de todas las especies de peces diurnos, no crípticos en áreas réplica de 10 m de diámetro. Estimamos el porcentaje de cobertura de coral y algas y determinamos la complejidad estructural del arrecife. A partir de números y longitudes de peces calculamos la biomasa promedio de peces por conteo para las cinco familias de mayor importancia comercial. Serranidae, Lutjanidae, Scaridae, Acanthuridae mostraron diferencias de orden-de-magnitud en biomasa entre las islas. La biomasa disminuyó a medida que incrementó la presión de pesca. Solo Haemulidae no siguió este patrón. Dentro de las familias, las especies de talla grande disminuyeron a medida que se intensificó la pesca. La cobertura de coral y complejidad estructural fueron mayores en las islas poco pescadas y menores en las más pescadas. En contraste, la cobertura de algas fue un orden de magnitud mayor en Jamaica que en Donaire. Estos resultados sugieren que, después de la mortalidad masiva de erizos herbívoros en el Caribe en 1983/1984 y las consiguientes declinaciones en la presión de pastoreo en los arrecifes, los peces herbívoros no han controlado el crecimiento de algas en áreas intensamente pescadas pero han restringido el crecimiento*

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en áreas ligeramente pescadas. En resumen, las diferencias entre islas en la estructura de ensambles de peces y ensambles bénticos sugieren que la pesca artesanal intensiva ha transformado los arrecifes del Caribe.

Introduction

Fishing is widely recognized as having a major influence on marine ecosystems throughout the world. Spectacular stock collapses of exploited species (Idyll 1973; Myers et al. 1997) and extreme habitat degradation caused by dredging and trawling (Messieh et al. 1991; Collie et al. 1997; Watling & Norse 1998) are just two examples of the impact of industrial fishing. Compared with such activities, artisanal fisheries—those pursued by small-scale fishers using traditional methods—are often viewed as more environmentally benign. From archaeological records, Dalzell (1998) concluded that subsistence fishing on coral reefs in the Pacific has had no impact on coral reef fish communities over the last thousand years. In Hawaii, reef fisheries supported a much larger human population in pre-European times than they do today, and there is no evidence of those fisheries having had adverse impacts (Birkeland & Friedlander 2001). While a number of studies from around the world have demonstrated significant impacts from artisanal fishing (Adam et al. 1997; Coblentz 1997), there is still a widespread perception that artisanal fishing has little impact. For example, the Virgin Islands National Park and the Bonaire marine park in the Caribbean, together with many others like them, continue to allow fishing with artisanal methods (Hawkins et al. 1999; Rogers & Beets 2001).

Artisanal fisheries are especially important in developing countries (Allison & Ellis 2001). Throughout the tropics, coral reefs support artisanal fisheries with an estimated annual yield of approximately 6 million tonnes per year (Munro 1996). In Southeast Asia alone these fisheries are worth approximately US \$2.4 billion (Burke et al. 2002). Apart from the use of motorized boats and modern materials, many artisanal fishing practices have changed little over centuries (Johannes 1997). What has changed is fishing intensity, with many fisheries now supporting greater numbers of people (Polunin & Roberts 1996).

There is growing concern that increased artisanal fishing poses a threat to coral reefs (Russ 2002). Jennings and Polunin (1996) concluded that removing just 5% of fish biomass could significantly alter the structure of reef fish communities because predatory species are preferentially targeted and depleted. Particularly vulnerable species may be threatened with local or even global extinction (Roberts & Hawkins 1999). For example, the giant clam (*Tridacna gigas*) has been eliminated from large areas of the Pacific by artisanal fishers (Wells 1997). Koslow et al. (1994) concluded that intensive fishing depleted a wide range of Jamaican fish groups over a period

of 10 years. Other research from this island reveals that fishing pressure has so reduced fish life expectancies that few are surviving to spawn (Munro 1983).

Fishing can also lead to indirect effects on coral reef habitats. In East Africa, for example, it depleted trigger fish populations to such an extent that their herbivorous sea urchin prey increased in abundance (McClanahan & Shafir 1990). This in turn resulted in less algae and more bioerosion, which decreased coral cover (McClanahan et al. 1996). By contrast, sea urchins virtually disappeared from the Caribbean in 1983 and 1984, when disease killed around 99% of them (Lessios et al. 1984). Recovery from this die-off has been slow (Solandt & Cambell 2001) and has meant that herbivorous fishes have been the major reef grazers in the Caribbean for nearly 20 years. Under these circumstances, fishing could affect the composition of benthic communities by reducing populations of herbivores and thus grazing pressure.

We examined four predictions about how artisanal fisheries may affect fish assemblages and benthic habitats and tested them by comparing coral reefs among six Caribbean Islands subject to different levels of fishing pressure. Our predictions were that (1) fishing will reduce the abundance and biomass of target families and species in proportion to its intensity; (2) the most vulnerable families and species will be affected at lower fishing intensities than the more resilient; (3) within families, larger bodied species will be more vulnerable than smaller ones, and the most vulnerable species may be extirpated from the most intensively fished places; (4) abundance of nontarget species will rise as fishing pressure increases due to removal of predators; and (5) fishing will have cascading effects on benthic communities because depletion of herbivores will reduce grazing pressure and thereby increase algal growth (Hughes 1994). Algae can then begin to overgrow corals. Because corals also provide structure to the reef, structural complexity will fall with increased fishing, assuming that other herbivores, such as urchins, do not compensate. This is unlikely because urchins are still scarce following the 1983–1984 disease outbreak (Lessios et al. 1984).

Methods

We examined reef fish assemblages and habitats in the Caribbean islands of Bonaire, Saba, Puerto Rico, St. Lucia, Dominica, and Jamaica. We were unable to calculate absolute levels of fishing pressure among islands because of differences in the quality of available fisheries data and the

Table 1. Characteristics of fisheries and relative fishing intensities at each of the six study locations.

<i>Location</i>	<i>No. active fishers^a</i>	<i>Length of reef fished (km)</i>	<i>Gears used</i>	<i>Species targeted</i>	<i>Fishing intensity (fishers/km reef)</i>	<i>Reference</i>
Bonaire, leeward coast from Klein Bonaire north to Slagbaai	4 full-time	61.8	hook and line	near-reef pelagics (e.g., jacks, rainbow runners)	0.06	K. De Meyer, Bonaire Marine Park, personal communication and personal observations
Saba, leeward coast from southeast to north of island	10 part-time = 0.83 f.t.e.	6.9	spear	mainly predatory fish such as large snappers and groupers	0.12	D. Kooistra, Saba Marine Park, personal communication and personal observations
Puerto Rico, reefs around La Parguera southwest of island	64 full-time + 2 part-time = 65 f.t.e.	78.3	lines, trap, nets, spear	predominantly snappers, but grunts and near-reef pelagics important; wide variety of reef associated species also targeted	0.83	Matos-Caraballo 1997; Morelock et al. 1994
St. Lucia, reefs of the southwest coast around Soufrière	25 full-time + 4 part-time = 27 f.t.e.	8.4	traps, hook and line, limited spearing, few gill nets	wide range of species including many small-bodied planktivores, invertivores, omnivores and herbivores; predators highly desirable but limited numbers caught; inedible species used for bait	3.23 ^b	Goodridge 1996; Gell et al. 2001
Dominica, reefs of the northwest coast around Portsmouth	32 full-time + 47 part-time = 56 f.t.e.	18.5	traps, hook and line, extensive spear and nets	wide range of species including many small-bodied planktivores, invertivores, omnivores and herbivores; predators highly desirable but limited numbers caught; inedible species used for bait	3.03 ^b	H. Guiste, Chief Fisheries Officer, Dominica, personal communication; Roberts & Hawkins 1996
Jamaica, reefs of the north coast around Discovery Bay	58 full-time + 24 part-time = 70 f.t.e.	9.9	traps, hook and line, extensive spear and nets	virtually everything larger than 10 cm targeted; majority of catch small-bodied; large predators desirable but extremely uncommon	7.14	Allison 1992; Sandeman & Woodley 1994; Sary 1995

^aAbbreviation: f.t.e., full-time equivalent. In Saba we assumed each fisher fished for 1 day every 2 weeks (assuming a 6-day working week) because all fishing on this island is recreational. Hence, each fisher is considered one-twelfth of a full-time equivalent. In all other countries, where fishing is done on a commercial or subsistence basis, we assumed part-time fishers fished for half of their time.

^bAmount of reef available to fishers in St. Lucia and Dominica is virtually identical, but, because the range of gears used in St. Lucia was more limited (i.e., less spear and net fishing), we considered this island slightly less heavily fished than Dominica.

difficulty of standardizing measures of fishing across the different gear types in use. However, using a mixture of published information, personal observations, and communication with fisheries officials and marine park staff, we were able to rank fishing pressure among the islands as shown in Table 1.

The island of Bonaire received virtually no fishing, and reefs in Saba were lightly fished. Levels of fishing were moderately high in Puerto Rico and higher still in St. Lucia. In Dominica, fishing pressure was greater than in St. Lucia, and Jamaican reefs were the most heavily fished. Moving from the least to the most heavily ex-

ploited islands, the range of fishing gears employed expanded. We also calculated a measure of fishing pressure based on the number of kilometers of reef available per fisher within each area (Table 1). We calculated the extent of reef available to fishers in Bonaire, Saba, St. Lucia, and Dominica from published data and personal observations (van't Hof 1983, 1991; Roberts & Hawkins 1996; Gell et al. 2001). For Bonaire and Saba, the least exploited islands, little fishing is done on exposed windward reefs, which were excluded from calculations. For Puerto Rico we calculated reef area by the method of Morelock et al. (1994) and for Jamaica we used

information from Allison (1992) and Sandeman and Woodley (1994).

Using an adaptation of the stationary-point fish count technique of Bohnsack and Bannerot (1986), we surveyed Bonaire in 1994, Puerto Rico, St. Lucia, and Jamaica in 1995, Dominica in 1996, and Saba in 1998. On each count a 10-m tape was laid over the reef and used to indicate the diameter of a cylinder extending 5 m above the reef. For 15 minutes we counted the number and estimated the size in centimeters (based on total body length) of all groupers (Serranidae), snappers (Lutjanidae), parrotfish (Scaridae), surgeonfish (Acanthuridae), and grunts (Haemulidae) present within or passing through the cylinder. We also estimated the number of each species of wrasse (Labridae) and damselfish (Pomacentridae) present and listed all other noncryptic, diurnal species. We made approximately equal numbers of counts at depths of 5 and 15 m (Bonaire, 36 at 5 m, 36 at 10 m; Saba, 44 at 5 m, 33 at 15 m; Puerto Rico, 56 at 5 m, 42 at 15 m; St. Lucia, 138 at 5 m, 137 at 15 m; Dominica, 32 at 5 m, 32 at 15 m; and Jamaica, 64 at 5 m, 48 at 15 m) and pooled the counts at 5 and 15 m in analyses. We separated counts by at least 10 m and did the first at our point of entry into the water. Subsequent counts on a dive were made at the same depth.

Within each census area, after we had completed the fish count, we estimated the percent cover of hard coral and of fleshy and macroalgae combined (erect, foliose algae > 1 cm tall). We also estimated reef structural complexity on a scale of 0–5, progressing by increments of half a unit from 0, representing somewhere totally flat and featureless, to 5, representing extreme complexity. Although semiquantitative, this scale provides a rapid means of assessing complexity and has been used successfully in previous studies (e.g., Polunin & Roberts 1993; Hawkins et al. 1999).

To investigate how fishing pressure affected commercially important families, we calculated biomass by using length-weight relationships (Bohnsack & Harper 1988) of predatory groupers and snappers, invertivorous grunts, and herbivorous parrotfish and surgeonfish. We also looked at the abundance of individual species within these families and the total abundances of wrasses (Labridae) and damselfish (Pomacentridae). In general, the latter two families are of little or no commercial importance. Wrasses are a diverse group of fishes that mainly prey on invertebrates. Only the largest species, *Bodianus rufus*, *Halichoeres radiatus*, *Lachnolaimus maximus*, and *Clepticus parrae*, are targeted by fishers and retained in traps. In our analysis we excluded these species because we wanted to determine whether nontarget species are indirectly affected by fishing.

The Pomacentridae consists of small herbivores, planktivores, and omnivores. In Jamaica they are boiled into "fish tea" (as are many other undersized fish that are caught), but generally the family is of no commercial importance.

Only the largest individuals of the largest species get trapped, although planktivorous species can be caught in gill nets. Jamaican fishers sometimes spear damselfish, but we saw no evidence of this on other islands.

Finally, we compared the total number of noncryptic diurnal species among islands. For all analyses we compared differences among islands with one-way analysis of variance (ANOVA). Data were tested for homogeneity of variance prior to analysis. Because fish-count data contain many zeros, they are usually non-normal and cannot be effectively transformed. However, the results of ANOVA are generally robust to departures from normality (C. Dytham, personal communication).

Results

The four commercially important families—groupers, snappers, parrotfish, and surgeonfish—showed order-of-magnitude differences in biomass among islands (one-way ANOVA: $F_{5,693} = 38.1, p < 0.001$ [groupers]; $F_{5,693} = 21.7, p < 0.001$ [snappers]; $F_{5,693} = 87.2, p < 0.001$ [parrotfish]; $F_{5,693} = 8.0, p < 0.001$ [surgeonfish], with biomass declining as fishing intensity increased (Fig. 1). Groupers, snappers, and surgeonfish declined very abruptly and parrotfish declined steeply. Only grunts showed no clear pattern related to fishing pressure, although their biomass differed significantly among islands (one-way ANOVA: $F_{5,693} = 2.81, p < 0.05$).

The biomass of 7 species of groupers, 6 snappers, 7 parrotfish, 3 surgeonfish, and 11 grunts was considered individually. In all families except grunts, biomass of the largest species declined more steeply with increasing fishing pressure than that of smaller species (see Figs. 2–6 for patterns of decline; two-way ANOVA: $F_{5,4851} = 34.9, p < 0.001$ [island effect], $F_{6,4851} = 13.8, p < 0.001$ [species effect], $F_{30,4851} = 12.7, p < 0.001$ [species × island], groupers [Fig. 2]; $F_{5,4158} = 24.5, p < 0.001$ [island effect], $F_{5,4158} = 23.2, p < 0.001$ [species effect], $F_{25,4158} = 13.1, p < 0.001$ [species × island], snappers [Fig. 3]; $F_{5,4158} = 121.3, p < 0.001$ [island effect], $F_{5,4158} = 127.9, p < 0.001$ [species effect], $F_{25,4158} = 33.4, p < 0.001$ [species × island], parrotfish [Fig. 4]; $F_{5,2079} = 9, p < 0.001$ [island effect], $F_{2,2079} = 19.5, p < 0.001$ [species effect], $F_{10,2079} = 6.6, p < 0.001$ [species × island], surgeonfish [Fig. 5]; $F_{5,7623} = 3.2, p < 0.01$ [island effect], $F_{10,7623} = 11.2, p < 0.001$ [species effect], $F_{50,7623} = 2.7, p < 0.001$ [species × island], grunts [Fig. 6]).

The most lightly fished islands supported a broad range of grouper species, whereas the most heavily fished supported only the two smallest species in any abundance. Species of *Mycteroperca*, the genus that contains the largest groupers, were only present in counts in the least fished islands, Bonaire and Saba (Fig. 2). Trends were similar for snappers, with two of the four largest species found

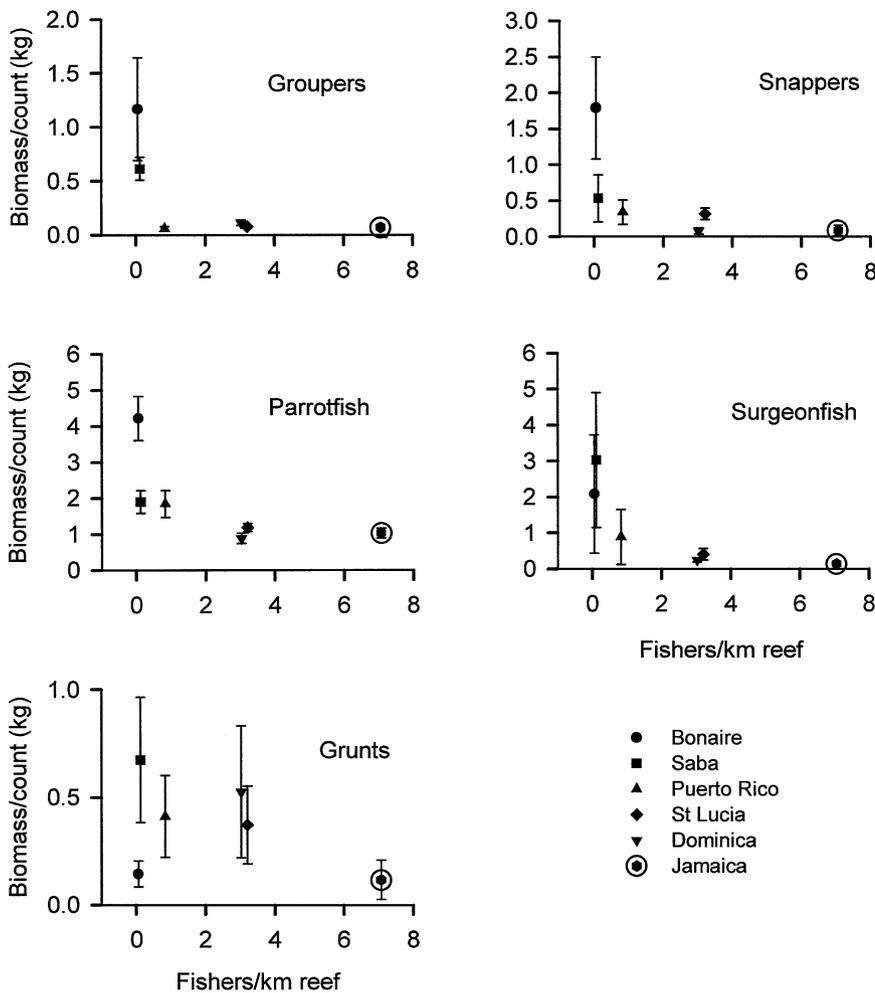


Figure 1. Mean biomass per fish count ($\pm 95\%$ confidence interval) versus fishing intensity (kilometers of reef available per fisher) for groupers (*Serranidae*), snappers (*Lutjanidae*), parrotfish (*Scaridae*), surgeonfish (*Acanthuridae*), and grunts (*Haemulidae*) among islands.

principally in the islands of Bonaire through St. Lucia and biomass declining steeply from levels in Bonaire (Fig. 3). Among the parrotfish, the two largest species present in counts, *Sparisoma viride* and *Scarus vetula*, were, in terms of biomass, both most common in Bonaire and least common in Jamaica, whereas the biomass of the three smallest species, *Scarus taeniopterus/iserti*, and *Sparisoma aurofrenatum*, was similar across islands (Fig. 4). With the decline of larger species as fishing pressure increased, these latter small species made up an increasing fraction of the parrotfish assemblage (Fig. 4). Patterns were less clear for surgeonfish (Fig. 5), and the largest species of grunts were consistently present only in the three least fished islands (Fig. 6).

Mean abundances across the fishing gradient for the nontarget wrasse and damselfish (biomasses were not calculated for these species because of lack of a length-weight relationships) and for total species richness all differed significantly among islands (Fig. 7; one-way ANOVA: $F_{5,381} = 14.7, p < 0.001$ [nontarget wrasse]; $F_{5,401} = 22.7, p < 0.001$ [damselfish]; $F_{5,691} = 104.2, p < 0.001$ [total species richness]), but none showed clear patterns consistent with differences in fishing pressure (Fig. 7).

Patterns of difference in benthic composition existed among islands that were consistent with differences in fishing intensity (Fig. 8). Hard coral cover and structural complexity declined significantly as fishing pressure increased (one-way ANOVA: $F_{5,693} = 106.1, p < 0.001$, for hard coral cover; $F_{5,693} = 38.1, p < 0.001$, for structural complexity), whereas the percent cover of algae increased dramatically as fishing intensities rose (one-way ANOVA: $F_{5,451} = 221.0, p < 0.001$). Levels of algal cover in Jamaica were an order of magnitude greater than in the four least fished islands, and cover was also high in Dominica.

Discussion

Most researchers investigating the effects of fishing contrast sites within countries that are subject to different fishing intensities (e.g., Jennings & Polunin 1995, 1996), often comparing protected marine reserves and nearby fishing grounds (e.g., Polunin & Roberts 1993; Watson & Ormond 1994; Roberts et al. 2001). Our approach of comparing widely separated islands over a gradient of

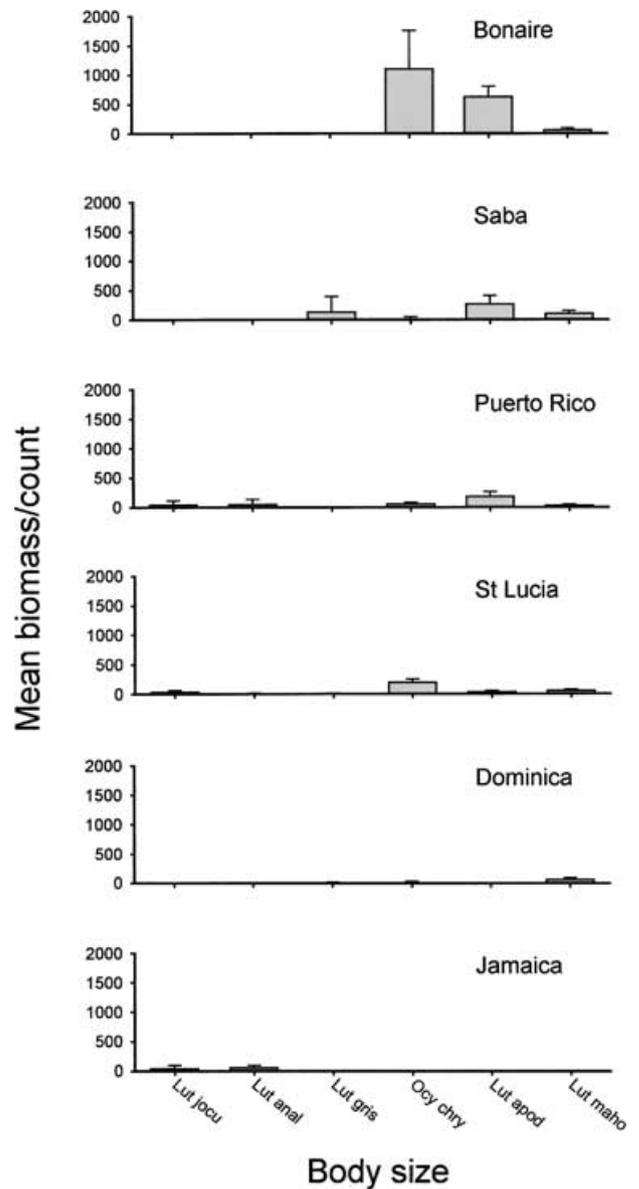
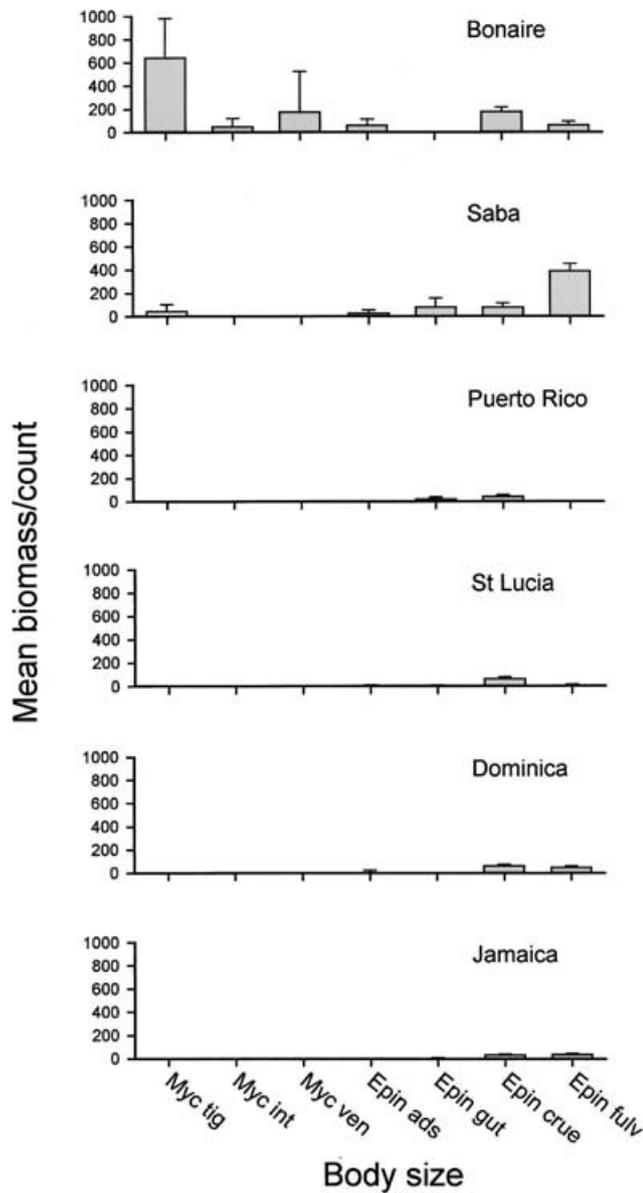


Figure 2. Mean biomass per fish count (±95% confidence interval) for groupers (Serranidae), where species are arranged along the x-axis in order of decreasing body size. Graphs are stacked in order of decreasing fishing pressure (top, least; bottom, most fished). Fishing intensity is measured by kilometers of reef available per fisher (Myc tig, Mycteroperca tigris; Myc int, Mycteroperca interstitialis; Myc ven, Mycteroperca venenosa; Epin ads, Epinephelus adscensionis; Epin gut, Epinephelus guttatus; Epin crue, Epinephelus cruentatus; Epin fulv, Epinephelus fulvus).

Figure 3. Mean biomass per fish count (±95% confidence interval) for snappers (Lutjanidae), where species are arranged along the x-axis in order of decreasing body size. Graphs are stacked in order of decreasing fishing pressure (top, least; bottom, most fished). Fishing intensity is measured by kilometer of reef available per fisher (Lut jocu, Lutjanus jocu; Lut anal, Lutjanus analis; Lut gris, Lutjanus griseus; Ocy chry, Ocyurus chrysurus; Lut apod, Lutjanus apodus; Lut mabo, Lutjanus mahogoni). Lutjanus jocu to Ocyurus chrysurus are all similarly sized, large-bodied species, whereas Lutjanus apodus and Lutjanus mahogoni are small bodied.

fishing pressure has two key advantages. First, it makes it possible to include sites spanning a greater range of fishing pressure than do more local-scale studies. Second, in the case of studies involving marine reserves, it overcomes the problem that fishing may have altered the pool

of species available to colonize and repopulate protected areas. If such alteration has occurred, the response of fish assemblages to protection will be constrained by prior effects of fishing, including possible habitat modification.

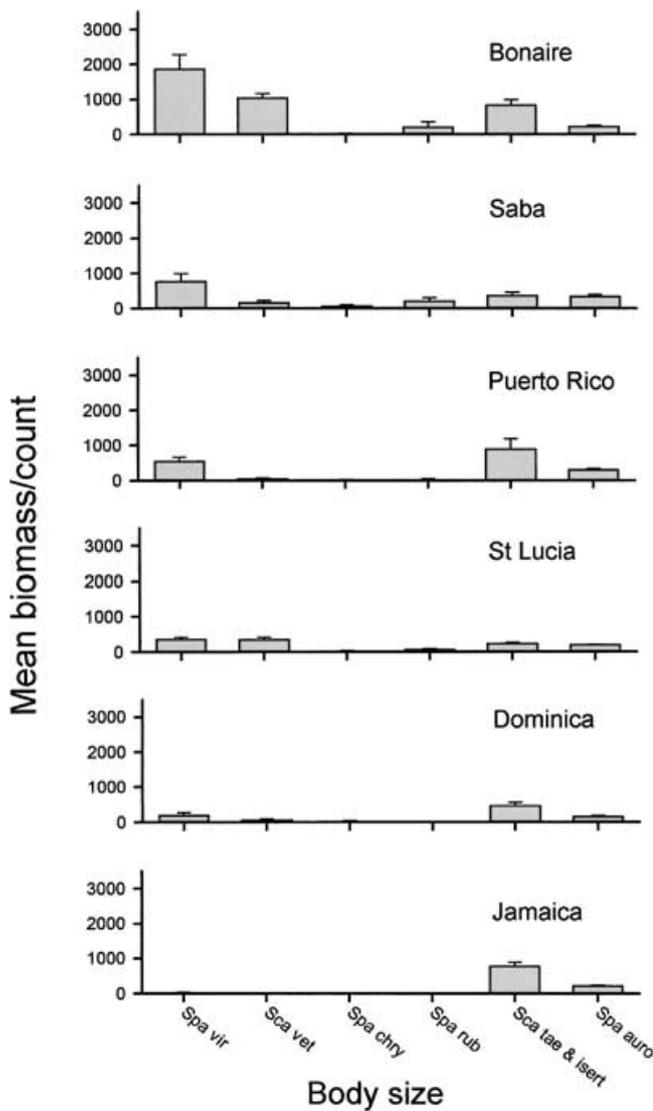


Figure 4. Mean biomass per fish count ($\pm 95\%$ confidence interval) for parrotfish (Scaridae), where species are arranged along the x-axis in order of decreasing body size. Graphs are stacked in order of decreasing fishing pressure (top, least; bottom, most fished). Fishing intensity is measured by kilometer of reef available per fisher (Spa vir, Sparisoma viride; Sca vet, Scarus vetula; Spa chry, Sparisoma chrysopterus; Spa rub, Sparisoma rubripinne; Sca tae & isert, Scarus taeniopterus and Scarus iserti; Spa auro, Sparisoma aurofrenatum). The biomass for Scarus taeniopterus and Scarus iserti was combined because in the field it was impossible to distinguish the young fish of these species.

Contrasting locations spanning a gradient in which fishing intensities have differed for a long time can potentially offer new insights into the effects of fishing. The drawback of our approach is that islands may differ in respects other than fishing pressure. Caution is therefore neces-

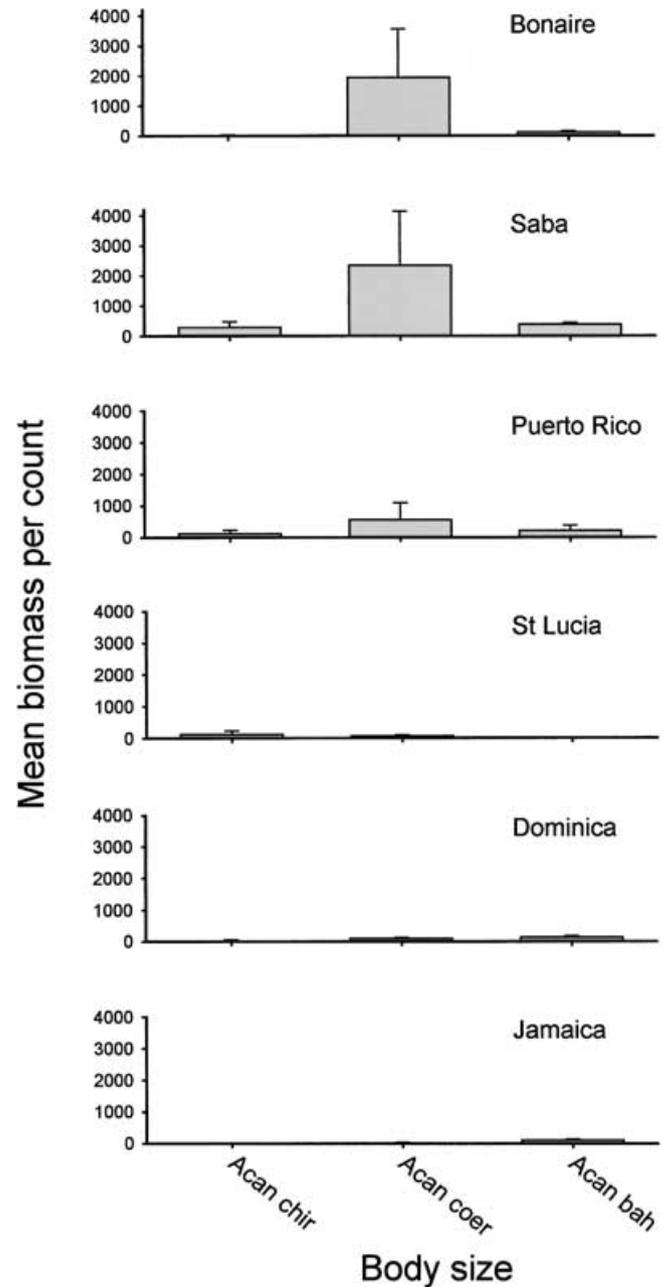


Figure 5. Mean biomass per fish count ($\pm 95\%$ confidence interval) for surgeonfish (Acanthuridae), where species are arranged along the x-axis in order of decreasing body size. Graphs are stacked in order of decreasing fishing pressure (top, least; bottom, most fished). Fishing intensity is measured by kilometer of reef available per fisher (Acan chir, Acanthurus chirurgus; Acan coer, Acanthurus coeruleus; Acan bah, Acanthurus bahianus).

sary in ascribing differences in fish assemblages and benthic communities to exploitation. Keeping this in mind, we examined our results in the light of our predictions about the effects of fishing. We conclude that fishing provides the most parsimonious explanation for many of the

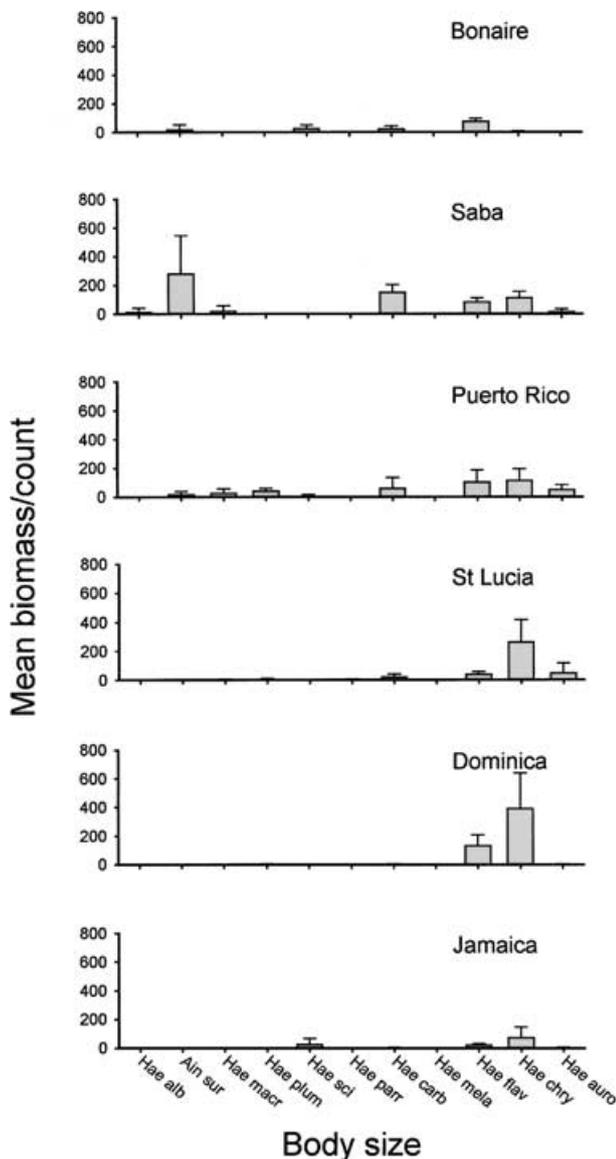


Figure 6. Mean biomass per fish count ($\pm 95\%$ confidence interval) for grunts (*Haemulidae*), where species are arranged along the x-axis in order of decreasing size. Graphs are stacked in order of decreasing fishing pressure (top, least; bottom, most fished). Fishing intensity is measured by kilometer of reef available per fisher (*Hae alb*, *Haemulon album*; *Ain sur*, *Anisotremus surinamensis*; *Hae macr*, *Haemulon macrostomum*; *Hae plum*, *Haemulon plumieri*; *Hae sci*, *Haemulon sciurus*; *Hae parr*, *Haemulon parraii*; *Hae carb*, *Haemulon carbonarium*; *Hae mela*, *Haemulon melanurum*; *Hae flav*, *Haemulon flavolineatum*; *Hae chry*, *Haemulon chrysargyreum*; *Hae auro*, *Haemulon aurolineatum*).

interisland differences in fish populations and benthic communities that we studied.

The first prediction was that fishing would reduce the biomass of commercially important fish families. The

order-of-magnitude declines in biomass seen for four of five families as fishing intensified support this prediction. Such effects have been described from elsewhere. Work in the Philippines by Russ and Alcala (1996) showed that fishing could reduce fish biomass very quickly. It took only 1.5 years of fishing in the newly re-opened Sumilon Reserve to deplete fish stocks that had accumulated during 9 years of protection. In Hawaii the average biomass of fish stocks was 260% greater in the little-fished northwestern islands than in the heavily fished main islands (Friedlander & DeMartini 2002). Other findings from Hawaii also support our second prediction that the most vulnerable families and species will be affected at lower fishing intensities than the more resilient. At little-fished islands, apex predators accounted for 54% of the total fish biomass, whereas they accounted for only 3% in those that were heavily fished (Friedlander & DeMartini 2002). At the family level, our findings illustrate that predatory groupers and snappers undergo dramatic declines in biomass with increased fishing pressure, as did surgeonfish.

Contemporary examples are not the first to illustrate overfishing by artisanal methods in the Caribbean. Fish bones from archaeological middens in St. Thomas and Nevis show that the mean trophic level of catches and the size of groupers, snappers, parrotfish, and surgeonfish were declining as long as 1900 years ago (Wing & Wing 2001). Jackson (1997) argued that Jamaican reef fisheries were probably overexploited by the early 1800s, although Koslow et al. (1994) refer to historical records from the mid-nineteenth century showing that groupers and snappers were still plentiful. By 1881, however, only 15% of the fish consumed in Jamaica could be caught locally (Jackson 1997).

Groupers and parrotfish provided good support for our third prediction, that within families larger-bodied species would be more vulnerable to fishing than small-bodied ones. In these families some of the largest species appeared to have been extirpated by fishing, as has happened in heavily fished islands in Hawaii (Friedlander & DeMartini 2002). For example, species from *Mycteroperca*, the largest-bodied grouper genus, appear to be absent from everywhere except lightly fished Bonaire and Saba. It could be argued that such missing species were never present on the reefs we studied, but all have been previously recorded from the islands, and these locations lie well within their geographic ranges (Humann 1996; Roberts et al. 2002). In 10 months diving in St. Lucia over 8 years, following implementation of a series of marine reserves, we saw a few juveniles but no adults of two *Mycteroperca* species.

In all families, smaller-bodied species dominated fish assemblages in the most heavily fished islands. This was also the case in Friedlander and DeMartini's (2002) Hawaiian study, where small-bodied species comprised 93% of the biomass of carnivores on heavily fished islands,

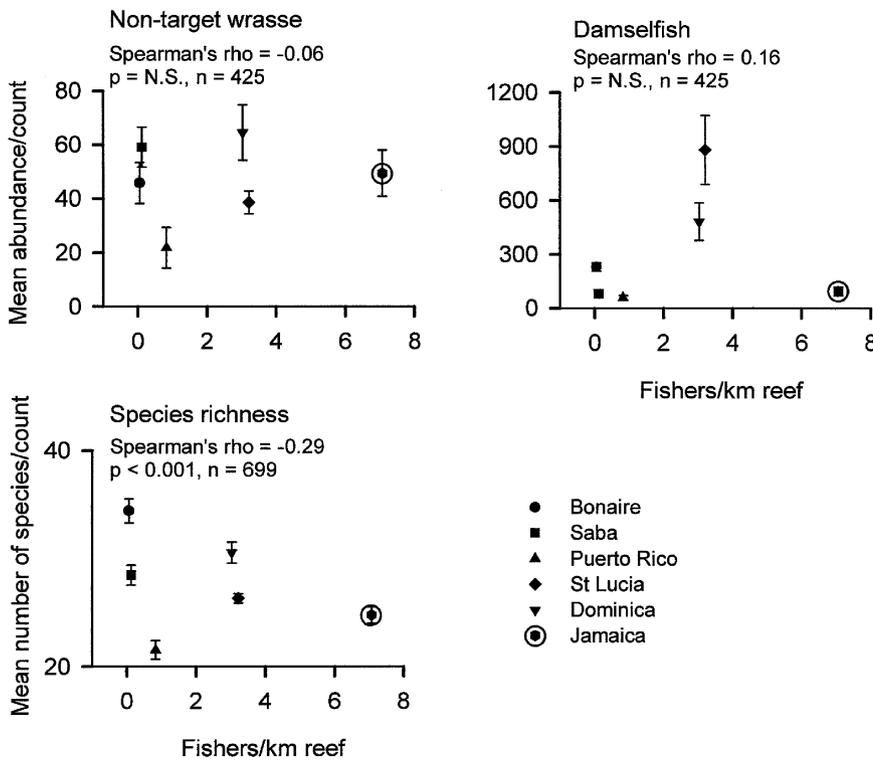


Figure 7. Mean abundance per fish count for species of wrasse (*Labridae*) and damselfish (*Pomacentridae*) not targeted by fishers, and mean species richness of all diurnal fish observed ($\pm 95\%$ confidence interval) in relation to fishing intensity (N.S., not significant).

as opposed to 25% on little-fished islands. High rates of growth, early maturity, and high fecundity probably help small-bodied species withstand higher fishing pressures than larger species (Roberts 1997). In a meta-analysis of 12 studies of marine reserves, Mosquera et al. (2000) found that large-bodied species showed the best response to protection, and densities of the largest species could be up to 33 times higher in protected areas than in fishing

grounds. This greater response is probably due to the fact that large species had been more heavily depleted by fishing than small.

An alternative explanation for the declines in fish biomass could be the fact that the islands' reefs differed in structural complexity. Indeed, this is an important factor because less complex reefs generally support fewer fishes (Roberts & Ormond 1987; Sano 2000; Syms & Jones

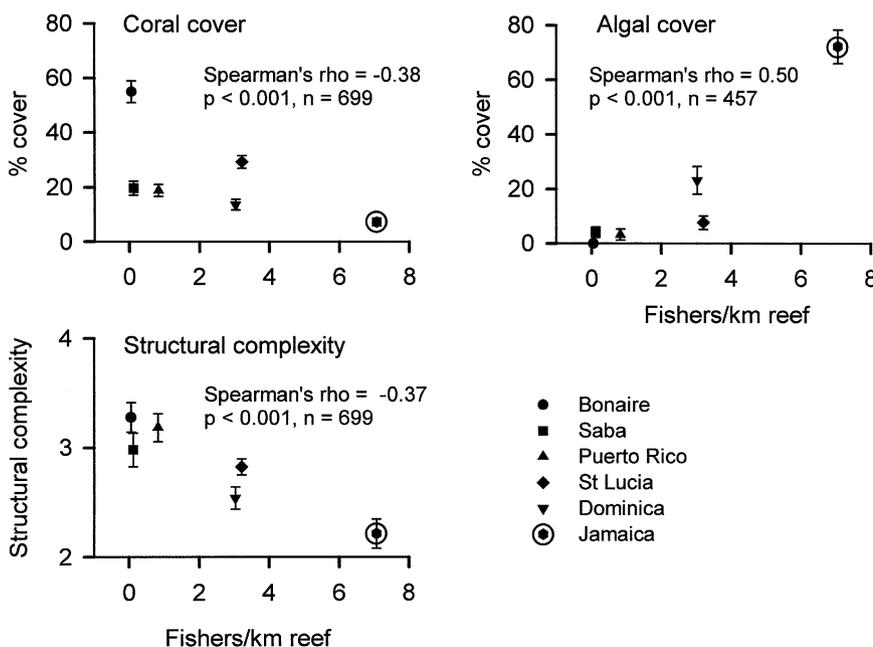


Figure 8. Mean percent cover of hard coral and algae and mean structural complexity per count ($\pm 95\%$ confidence interval). Bonaire is represented as having no algal cover because, at the scale of resolution used in the survey, the substrate was grazed too closely to reveal whether algae were present. Correlation coefficients were calculated based on all the point-count estimates made in each country.

2000). Decreasing structural complexity probably does contribute to the declines in biomass we have shown, although our fifth prediction states that this in itself could be an effect of fishing. This prospect is worrying because it implies a positive feedback loop in which lost structural complexity further compounds the direct impacts of fishing.

We found little evidence to support our fourth prediction that fishing would increase the abundance of nontarget species through depletion of their predators. The data for damselfish show that numbers are highest at intermediate levels of fishing. This may be because predators are reducing their abundance when fishing pressure is low, whereas poor habitat quality could affect populations when fishing pressure is greatest. However, there is no support for this explanation from nontarget wrasses. In their meta-analysis Mosquera et al. (2000) found that nontarget species were just as abundant in marine reserves as in fished areas. When they considered patterns for nontarget species at the family level, this finding held true for wrasses but damselfish were significantly more abundant inside reserves. Moore and Jennings (2000) concluded that although fishing can have indirect effects on nontarget species, these may be clear only for the most vulnerable species.

Our fifth prediction was that by reducing fish herbivore abundance, fishing could have indirect impacts on habitat, increasing algal growth and reducing hard coral cover and thereby structural complexity. In New Zealand and Tasmania, kelp forests have recovered in marine reserves following buildup of lobster populations, which are predators of grazing sea urchins (Babcock et al. 1999; Edgar & Barrett 1999). Parrotfish and surgeonfish are the major fish grazers on Caribbean reefs (Bruggemann 1994). As fishing pressure increased, both families showed order-of-magnitude declines, suggesting that artisanal fishing is seriously reducing levels of herbivory among these islands. Patterns of decline in coral cover and structural complexity, together with increased algal cover, follow our prediction, suggesting that fishing does cause cascading effects on the reef.

An alternative explanation for differences in benthic communities among islands is that patterns of algal growth are related to nutrient input from terrestrial runoff. Watersheds with greater agricultural development and land clearance will release more nutrients through runoff and sedimentation than will less-disturbed watersheds (Sladek Nowlis et al. 1997). Sedimentation can kill corals directly through smothering (Rogers 1990), and higher nutrient levels can promote algal growth at the expense of slower-growing corals (Bell & Tomascik 1993). Because islands have different levels of development, it could be argued that those with less intact watersheds should have more algae on their reefs, less coral, and lower structural complexity. In reality, patterns of land use among islands do not support this reasoning. For ex-

ample, Dominica was the least developed island with the most intact forest (Island Resources Foundation 1991). During our study, underwater visibility there did not fall below 20 m despite 10 days of torrential rain. By comparison, less rainfall in St. Lucia reduces underwater visibility to 5–10 m because of sediment input via rivers (personal observation). Hence, Dominica's intact watersheds appear to help prevent sedimentation and keep nutrient input low. Despite this, the reefs had more than twice as much algae as St. Lucia's. Similarly, St. Lucian watersheds upstream of our study sites had greater forest cover than those on Saba and Puerto Rico, yet algal cover on St. Lucia's reefs was nearly twice as high as in these islands. Reduction of herbivore populations by fishing provides a more consistent explanation than development for differences in algal and coral cover among these islands.

In 1983 and 1984 disease virtually eliminated herbivorous sea urchins (*Diadema antillarum*) in the Caribbean (Lessios et al. 1984). Throughout the region, loss of this important herbivore led to rapid algal increases on many reefs (Carpenter 1990). Our data suggest that the degree to which algal cover has expanded is closely related to the biomass of herbivorous fishes present in an area.

In Jamaica, where fishing pressure is among the highest in the Caribbean (Sary 1995), algae have expanded to dominate the reef (Hughes 1994), whereas in Bonaire, where fishing pressure is at its lowest, herbivorous fishes appear to have held back algal growth even in the absence of urchins. Countries falling between the two extremes of fishing pressure also follow the pattern in which higher biomass of grazing herbivores means lower algal cover. This suggests that fishing has played a key role in determining how the sea urchin die-off, which occurred more than a decade earlier, has ultimately affected Caribbean reefs.

Herbivory is not the only factor involved in transforming reefs from coral to algal dominance. Two devastating storms, Hurricane Allen in 1980 and Hurricane Gilbert in 1988, also facilitated the shift toward algal dominance in Jamaica by destroying coral (Hughes 1994). The case from Jamaica suggests that in the absence of sea urchins, overfished reefs in other Caribbean countries may be threatened by massive algal overgrowth if coral cover is greatly reduced by a storm or some other disturbance.

This possibility is cause for serious concern beyond the fisheries effects. Coral reefs play a vital role in protecting coastal communities and nearshore marine habitats such as seagrass beds from damage by storms and wave action (Bryant et al. 1998). Coral growth helps ensure that reef growth is maintained; otherwise physical forces and bioerosion will degrade the reefs' structural framework, causing their protective function to decline (Glynn 1997). Attractive coral reefs are also extremely important for tourism, which is the mainstay of many Caribbean economies (Jameson et al. 1995). In a study of diver preferences, Williams and Polunin (2000) found that

reefs covered in algae caused the most disappointment to tourists, whereas high coral cover and variety were among tourists' favorite characteristics. A report by Cesar (1996) estimated that a kilometer of coral reef could be worth up to \$1.2 million for all its services and provisions.

Comparative data of the kind we have collected cannot conclusively prove that fishing has produced the differences in fish assemblages and benthic habitats we observed. However, fishing pressure does provide a single coherent explanation for a suite of observations, which other interisland differences do not. Our findings suggest that artisanal fisheries have transformed coral reefs in ways that seriously compromise their ecological and economic value. They underpin arguments for creating marine reserves, where species and habitats can exist undisturbed by fishing (Bohnsack 1998; Murray et al. 1999). Marine reserves can rapidly increase the richness, density, and biomass of exploited species (Roberts 1995; Wantiez et al. 1997), support nearby fisheries (Roberts et al. 2001; Galal et al. 2002; Maypa et al. 2002), and restore habitats (Roberts & Hawkins 2000).

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