



Cascading effects of fishing on Galapagos rocky reef communities

Jorge I. Sonnenholzner¹, Lydia B. Ladah^{1,3,*}, Kevin D. Lafferty²

¹CICESE, Department of Biological Oceanography, Apartado Postal # 2732, CP 22800, Ensenada, Baja California, Mexico

²Western Ecological Research Center, US Geological Survey, Marine Science Institute, University of California, Santa Barbara, California 93106, USA

³Correspondence address: CICESE, Department of Biological Oceanography, PO Box 434844, San Diego, California 92143-4844, USA

ABSTRACT: A replicated comparison of heavily and lightly fished areas in the Galapagos suggested that fishing predators led to an increase in herbivores and a dramatic shift in the algal community toward crustose barrens. We sampled 10 highly fished and 10 lightly fished shallow rocky reefs in the southeastern area of the Galapagos Marine Reserve, Ecuador. Negative associations between consumers and resources suggested top-down control. At cold sites, there was a negative association between slate-pencil urchins *Eucidaris galapagensis* and non-coralline algae. In addition, at cold sites, pencil urchins were less abundant where there were many predators. An indirect positive association between predators and non-coralline algae occurred at warm and cold sites. Fishing appeared to affect this trophic cascade. The spiny lobster *Panulirus penicillatus*, the slipper lobster *Scyllarides astori*, and the Mexican hogfish *Bodianus diplotaenia* were significantly less abundant at highly fished sites. Urchin density was higher at highly fished sites. Non-coralline algae were nearly absent from highly fished sites where a continuous carpet of the anemone *Aiptasia* sp. was recorded and the algal assemblage was mainly structured by encrusting coralline and articulated calcareous algae.

KEY WORDS: Trophic cascade · Fishing · Predation · Population structure · *Eucidaris galapagensis* · Galapagos Marine Reserve · Ecuador

—Resale or republication not permitted without written consent of the publisher—

INTRODUCTION

How might overfishing affect marine ecosystems in the Galapagos? While fishing can greatly reduce fished stocks, it can also have dramatic indirect effects, particularly through trophic cascades (Sala et al. 1998a, Pinnegar et al. 2000, Jackson et al. 2001, Bascompte et al. 2005). Sea urchins are often identified as important grazers in such trophic cascades. For instance, because sea urchins can structure reef communities (Schiel & Foster 1986, Hughes et al. 1987, Pearse & Hines 1987), the fishing of urchin predators can indirectly increase the abundance of urchins, which can then over-graze algae (Tegner & Dayton 1981, Tegner & Levin 1983). Evidence for this effect comes from comparisons of fished areas with marine

reserves, which can restore food webs (Sala et al. 1998b, Shears & Babcock 2002, Behrens & Lafferty 2004, Lafferty 2004, Guidetti 2006).

Fishing has strongly altered the biomass and size distribution of fisheries species in parts of the Galapagos Marine Reserve (GMR) (Ruttenberg 2001, Branch et al. 2002, Bustamante et al. 2002, Okey et al. 2004). Some fishery species are top predators, and their removal might explain the high abundance of urchins and other grazers on Galapagos reefs (Bustamante et al. 2007). If so, overfishing could indirectly lead to overgrazing. To investigate the direct and indirect effects of fishing in the GMR, we compared communities on fished and protected rocky reefs.

In the GMR, the slate-pencil sea urchin *Eucidaris galapagensis* (sometimes *E. thouarsii*) (Doderlein) is

the most common species of urchin (Danulat & Edgar 2002). It is not a fishery species. An omnivore, it often grazes in open shallow reef habitats (Glynn et al. 1979). Three conspicuously prevalent predators of urchins, lobsters (spiny and slipper) (Martinez 2000, authors' pers. obs.) and hogfish (Wellington 1975, authors' pers. obs.), support commercial fisheries in the GMR (Danulat & Edgar 2002, Edgar et al. 2004, Hearn 2006). Spiny lobsters (locally called the red and green lobsters *Panulirus penicillatus* and *P. gracilis*, respectively) have been an important part of the GMR fishing economy since the 1960s, but yield has steadily declined since the 1980s (Reck 1983, Murillo et al. 2002, Hearn 2004). The slipper lobster *Scyllarides astori* is currently exploited at a local scale (Hearn 2006), and is caught incidentally in the spiny lobster fishery (2 to 3% of the total lobster catch) (Bustamante et al. 2000, Hearn 2004). Incidental catch also occurs for certain species of fish (e.g. *Bodianus diplotaenia*, *Arothron meleagris*) (Ruttenberg 2001, Murillo et al.

2002, 2003, Molina et al. 2004), and fishermen have reported a decline in *B. diplotaenia* abundance in fished areas (pers. comm.). This wrasse has a large head and mouth, with robust jaw teeth well suited for its diet of large, heavily shelled invertebrates (Hobson & Chess 2001).

MATERIALS AND METHODS

Study sites. The GMR lies in the eastern Pacific Ocean, 1000 km off the coast of Ecuador. It includes 18 major islands and over 100 islets (Snell et al. 1995). We studied 20 shallow rocky reefs in the southeastern bio-geographic area of the GMR (Danulat & Edgar 2002) off Santiago, Santa Cruz, Baltra, and Seymour Islands (Fig. 1). The site selection maximized dispersion and minimized variance in bottom topography and depth. Ten sites were open to fishing and 10 sites were within fishing exclusion zones established in 1992. Because

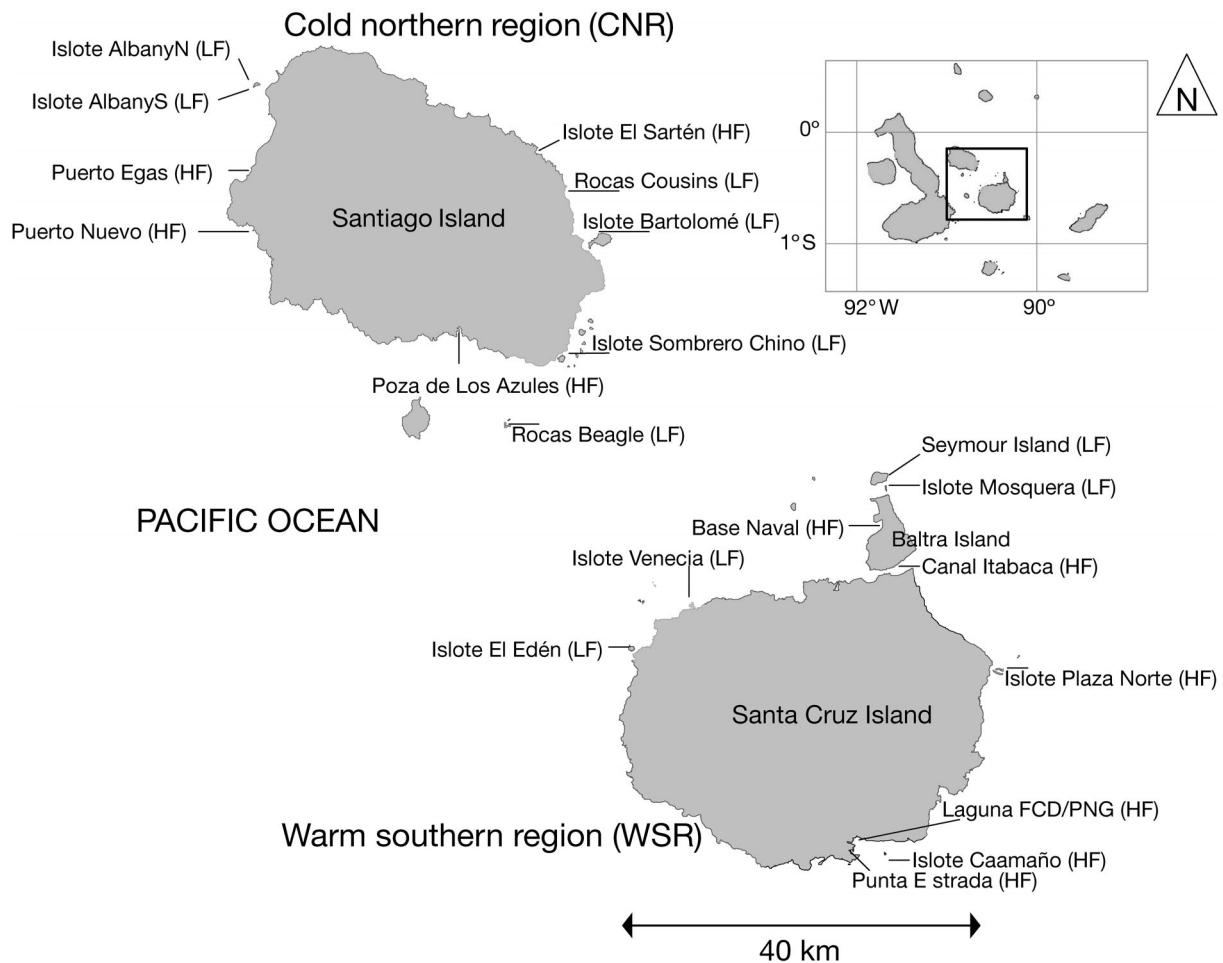


Fig. 1. Southeastern area of the Galapagos Marine Reserve, Ecuador. Data on lobsters, fish, urchins and algae were field collected at 20 sites with different levels of protection from fishing. HF: highly fished sites; LF: lightly fished sites

compliance with exclusion zones was low before 1998, we selected sites that, for various reasons (special tourism sites, sites easily observed by the national park, personal knowledge of fishing effort, etc.), had experienced a relatively long-term reduction in fishing effort. Nonetheless, due to uneven compliance with fishing regulations that continues until the present, and lack of quantitative information on fishing effort, we chose to categorically designate the no-fishing sites as lightly fished (LF) and the sites open to fishing as heavily fished (HF).

A map of seafloor substratum types and habitat features (charts 1:10 000 and 1:25 000 scale) was produced from a side-scan sonar survey conducted from 2000 to 2001 (Briones et al. 2002). Each chart was categorized into areas likely and not likely to contain reef habitats for urchin, lobsters, and fish at depths from 0 to 20 m below mean lower low water. SCUBA divers pre-surveyed all sites that were safely accessible by boat. Of these, 36 sites had appropriate habitat. Due to limitations in resources, we randomly selected 20 sites stratified by geographic position and fishing category, resulting in 5 NW lightly fished, 5 NW heavily fished, 5 SE lightly fished, and 5 SE heavily fished sites (see Appendix 1 for additional site information; available at: www.int-res.com/articles/suppl/m343p077_app.xls).

Lobster and fish density estimates. From April 2000 to August 2002 (multiple visits per site), diver pairs surveyed lobsters (red spiny lobster *Panulirus penicillatus* and slipper lobster *Scyllarides astori*) during 2 transects of 20 min duration (after 19:00 h) at 2 depth strata (2 to 5 and 8 to 10 m, $n = 2$ transects per depth stratum per site, total area surveyed per site = 400 m²). This resulted in an index of lobster population density expressed as the mean number of individuals seen per diver per hour for each sampling site (individuals diver⁻¹ h⁻¹) (Hearn 2006): abundance = $N / \Sigma (T_1 \times B_1 + \dots T_n \times B_n)$, where N is the total number of individuals counted in all dives per site, T_1 is the duration (time spent in hours) of the first dive, B_1 is the number of divers on the first dive, and T_n and B_n are the duration of and number of divers on the last dive. Unfortunately, we did not collect data on lobster size from all of our sites. However, a concurrent lobster tagging study (done over a broader region at 27 sites, including 8 of our sites, and similarly categorized as HF or LF) provided a similar dataset on average lobster total lengths (TL) for each species (J. I. Sonnenholzner unpubl. data).

Diver pairs surveyed the Mexican hogfish *Bodianus diplotaenia* (Labridae) once per site from May to November 2001 using randomly placed, non-overlapping video transects (VT, 25 × 4 m, total area surveyed 200 m²). Divers with a Hi-8 mm videocassette recorder swam slowly back and forth on either side of the tran-

sect line (swath 2 m wide and 5 m above the bottom) during a standard 40 min observation period. Transect width was only 4 m, permitting comparable assessments in water of variable visibility (which generally exceeded 30 m). Subsequent review of the video allowed quantification of adult fish (>20 cm size class).

Predation. Divers collected all the whole test remains of the sea urchin *Eucidaris galapagensis* within the 10 × 2 m transects at all sampling sites. Our index of predation was the number of dead tests seen per live urchin (Sala et al. 1998a). This measure is imperfect; predation events do not always leave remains, and test remains do not indicate a particular predator with absolute certainty (Sala 1997).

Urchin and algal density. At each site, divers estimated urchin density in 3 replicate 10 × 2 m retractable transect lines deployed between 2 and 8 m depth in October and November 2003. Surveying after 09:00 h optimized underwater visibility. Divers measured non-coraline algal abundance (foliose species like *Ulva lactuca*, *Padina durvillaei*, and *Dictyota* sp. with flattened or membranous blades, but also including more filamentous species, such as *Gracillaria* spp.) as percentage cover by using 7 quadrants of 0.5 × 0.5 m (0.25 m²) placed during the urchin transects. On each visit, divers took an average temperature from 12 stations at sample depth to the nearest 0.1°C. We then calculated the mean temperature of each site across the course of the study (an average of 16 visits between April 2000 and November 2003).

Statistical analysis. To determine whether communities differed between HF and LF sites, we conducted a MANOVA with algae, sea urchins, lobsters, and hogfish as dependent variables. We also conducted 2 main types of analyses using general linear models. The first assessed associations between trophic levels. The second compared communities at LF and HF sites. Temperature (continuous), habitat (rock or rock and sand), and the spatial position of each site (distance along a NW to SE axis) were possible factors in the MANOVA and GLMs. We initially entered all second-order interactions into a model, but, to preserve degrees of freedom, discarded them if they were non-significant. Similarly, the final model contained only significant main effects (unless a main effect had a significant interaction). For each analysis, we inspected residuals for normality (and the data were transformed if significantly non-normal). We confirmed homogeneity of variances with the Cochran test. Transformation of predator abundances to Z-scores all weighted equally (Z-scores are standardized to a mean of 0 and a standard deviation of 1). We considered that urchin mortality could result from the entire predator community. While the predator species are unlikely to have equivalent per capita effects as predators, we approximated the

potential effects of the predator guild by summing the Z-scores of each predator density (we also looked at each predator species separately). We report F -statistics, R^2 values, means, and standard errors, unless otherwise indicated. For illustrative purposes, we provide Pearson correlation coefficients between species to indicate direct negative and indirect positive associations in a food web diagram. The electronic appendix reports information on sample dates, sample sizes, means, standard deviations, etc.

RESULTS

Physical factors

A plot of the distribution of temperature (mean dive temperature at survey depth from all site visits) among sites was bimodal (a group of 12 cold sites at 21 to 23°C and a group of 8 warm sites at 24 to 26°C). Differences in temperature between HF (60% warm) and LF (20% warm) sites were marginally significant ($\chi^2 = 3.4$, $p = 0.06$), making statistical control of temperature potentially important for isolating fishing effects. There were no significant differences in the distribution of habitat types between HF (40% with sand) and LF (60% with sand) sites ($\chi^2 = 0.79$, $p = 0.37$). HF and LF sites were sufficiently interspersed that their average position

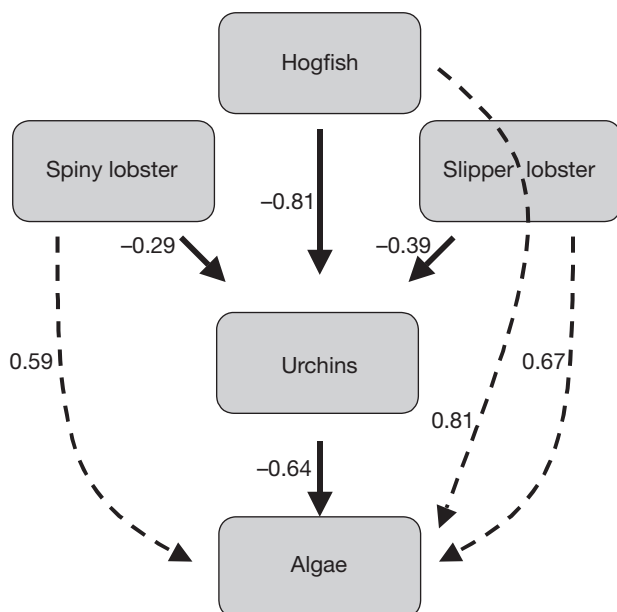


Fig. 2. Simplified Galapagos rocky-reef food web. Solid arrows between boxes represent feeding links. Dashed arrows between boxes suggest indirect effects (trophic cascades). Correlation coefficients (for cold sites) listed to the left of each line. Hogfish: *Bodianus diplotaenia*; spiny lobster: *Panulirus penicillatus*; slipper lobster: *Scyllarides astori*; urchins: *Eucidaris galapagensis*

along the main spatial gradient (NW to SE) did not differ statistically ($F_{1,18} = 1.59$, $p = 0.22$).

Evidence for consumer-resource effects

Direct consumer effects

Where urchin predators were abundant, pencil urchins *Eucidaris galapagensis* were uncommon and the index of predation on urchins was high, at least at cold sites (Fig. 2). The index of predation increased with the summed abundance of predators, but this effect was only seen at colder sites, where the index of predation was higher (Table 1). Urchin density declined strongly with the index of predation, particularly at cold sites (ratio of the count of urchin tests preyed on to live urchins; Table 2). Urchin density was not associated with summed predator density (ANOVA, $F_{1,18} = 2.45$, $p = 0.13$). The association between predators and urchins was only statistically significant for fish predators, particularly at cold sites (Table 3).

Non-coralline algae were not associated with urchin abundance, but there was a marginally significant interaction between urchin abundance and temperature (Table 4a). For this reason, we analyzed the association between non-coralline algae and urchins separately at warm and cold sites. Non-coralline algae were not associated with urchin density at warm sites (Table 4b), but declined significantly with urchin density at cold sites (Table 4c).

Table 1. Predation on urchins and predators, $R^2 = 0.73$, $F_{3,16} = 14.7$, $p < 0.0001$. Non-significant factors removed to increase power: habitat, location. Interaction coefficients standardized to the mean here and in Tables 3, 4, 6 & 7

Term	Estimate	SE	t -ratio	Prob > t
Intercept	1.244	0.314	3.96	0.0011
Pred-Z	0.030	0.010	3.19	0.0057
Temp	-0.049	0.013	-3.69	0.0020
Pred-Z × (Temp-23.4)	-0.023	0.007	-3.45	0.0033

Table 2. Urchins and predation on urchins, $R^2 = 0.62$, $F_{3,16} = 8.8$, $p = 0.0011$. Non-significant factors removed to increase power: habitat, location

Term	Estimate	SE	t -ratio	Prob > t
Intercept	100.786	40.714	2.48	0.0249
Test/Urchin	-102.650	26.485	-3.88	0.0013
Temp	-3.471	1.686	-2.06	0.0562
(Test/Urchin-0.11) × (Temp-23.4)	-33.567	13.380	-2.51	0.0233

Table 3. Urchins and predators, $R^2 = 0.48$, $F_{3,16} = 5.0$, $p = 0.012$. Non-significant factors removed to increase power: habitat, location

Term	Estimate	SE	t-ratio	Prob > t
Intercept	-20.361	25.760	-0.79	0.4409
Fish-Z	-3.329	1.538	-2.16	0.0459
Temp	1.457	1.099	1.33	0.2034
Fish-Z × (Temp-23.4)	2.755	1.023	2.69	0.0160

Table 4. Algae and urchins. (a) $R^2 = 0.35$, $F_{3,16} = 2.9$, $p = 0.05$. Non-significant factors removed to increase power: habitat, location. (b) Warm sites, $R^2 = 0.36$, $F_{1,6} = 3.5$, $p = 0.113$. (c) Cold sites, $R^2 = 0.41$, $F_{1,10} = 6.9$, $p = 0.026$

Term	Estimate	SE	t-ratio	Prob > t
(a)				
Intercept	237.899	119.424	1.99	0.0637
Urchin	-0.349	0.926	-0.38	0.7110
Temp	-8.955	5.303	-1.69	0.1107
(Urchin-12.554) × (Temp-23.36)	1.493	0.721	2.07	0.0549
(b)				
Intercept	-36.417	31.482	-1.16	0.2914
Urchin density	3.528	1.896	1.86	0.1121
(c)				
Intercept	62.216	11.435	5.44	0.0003
Urchin density	-2.243	0.856	-2.62	0.0255

Indirect consumer effects

Non-coraline algae were more abundant where predators were common (Fig. 2, Table 5a). When we entered all 3 predators as independent effects, slipper lobsters and hogfish *Bodianus diplotaenia* remained positively associated with non-coraline algal cover, but there was a significant interaction such that the effect of 1 species on algae diminished when the other predator was abundant (Table 5b). Not surprisingly, non-coraline algae increased with the summed abundance of these 2 predators (Table 5c).

Evidence for fishing effects

Direct fishing effects

In the MANOVA, fishing was the only significant independent factor ($F_{5,14} = 54.4$, $p < 0.0001$), and a centroid plot revealed that the dependent variables were sorted from algae, slipper lobsters, spiny lobsters, hogfish, and urchins (log) along the axis of lightly fished to heavily fished.

Table 5. Algae and predators. (a) Sum of predators, $R^2 = 0.72$, ANOVA $F_{1,18} = 47.7$, $p < 0.0001$. Non-significant factors removed to increase power: habitat, location, temperature. (b) Predators separate, $R^2 = 0.72$, ANOVA $F_{3,16} = 41.8$, $p < 0.0001$. Non-significant factors removed to increase power: spiny lobster. (c) Hogfish *Bodianus diplotaenia* plus slipper lobster *Scyllarides astori*, $R^2 = 0.82$, $F_{1,18} = 80.5$, $p < 0.0001$

Term	Estimate	SE	t-ratio	Prob > t
(a)				
Intercept	30.700	3.951	7.77	<0.0001
Pred-Z	14.072	2.037	6.91	<0.0001
(b)				
Intercept	37.159	3.396	10.94	<0.0001
Slipper-Z	39.214	9.742	4.03	0.0010
Fish-Z	20.473	3.486	5.87	<0.0001
Slipper-Z × Fish-Z	-28.910	9.264	-3.12	0.0066
(c)				
Intercept	30.700	3.227	9.51	<0.0001
Fish-Z + Slipper-Z	23.100	2.574	8.97	<0.0001

Predators were less abundant at HF sites than at LF sites (Fig. 3, Table 6a). In particular, hogfish were significantly less abundant at HF than LF sites (1.5 ± 0.61 vs. 4.6 ± 1.47 fish h^{-1} ; Table 6b). Spiny lobsters were also less abundant at HF sites (0.15 ± 0.24) than at LF sites (0.37 ± 0.32 lobsters per diver hour), an effect that was strongest in the north west (Table 6b). Spiny lobsters were smaller at HF sites (22.0 ± 1.0 cm total length [TL]) than at LF sites (25.6 ± 0.9 cm TL)

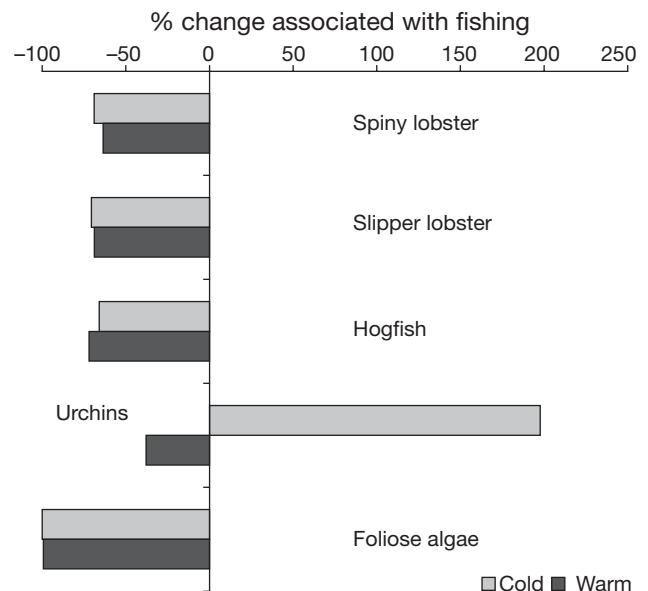


Fig. 3. Fisheries effects at 2 temperatures. Horizontal axis represents a percentage increase or decrease in untransformed mean abundance (or percent composition) for each taxon. Percentage is calculated as $(HF - LF) / LF$

Table 6. Fishing and predators. (a) Sum of predator z-scores, $R^2 = 0.57$, $F_{1,18} = 23.4$, $p < 0.0001$. Non-significant factors removed to increase power: habitat, location, temperature. (b) Hogfish *Bodianus diploaenia* Z-scores, $R^2 = 0.67$, $F_{1,18} = 36.7$, $p < 0.0267$. Non-significant factors removed to increase power: habitat, location, temperature. (c) Spiny lobster *Panulirus penicillatus* Z-scores, $R^2 = 0.56$, $F_{5,14} = 3.59$, $p < 0.0001$. Non-significant factors removed to increase power: habitat. (d) Slipper lobster *Scyllarides astori* Z-scores, $R^2 = 0.48$, $F_{1,18} = 16.8$, $p < 0.0007$. Non-significant factors removed to increase power: habitat, location, temperature

Term	Estimate	SE	t-ratio	Prob > t
(a)				
Intercept	0.000	0.301	-0.00	1.0000
Fishing[high]	-1.459	0.301	-4.84	0.0001
(b)				
Intercept	0.000	0.132	-0.00	1.0000
Fishing[high]	-0.798	0.132	-6.06	<.0001
(c)				
Intercept	-14.001	4.738	-2.96	0.0104
Fishing[high]	-0.808	0.237	-3.40	0.0043
Location	-0.011	0.004	-2.99	0.0098
Temp	0.654	0.212	3.09	0.0080
Fishing[high]	0.013	0.005	2.57	0.0221
× (Location-107.6)				
(Location-107.6)	-0.011	0.004	-2.92	0.0112
× (Temp-23.36)				
(d)				
Intercept	0.000	0.071	-0.00	1.0000
Fishing[high]	-0.290	0.071	-4.10	0.0007

Table 7. Fishing and urchins. (a) $R^2 = 0.42$, $F_{3,16} = 3.8$, $p < 0.0313$. Non-significant factors removed to increase power: habitat, location. (b) Cold sites, $R^2 = 0.51$, $F_{1,10} = 10.3$, $p < 0.0093$. Non-significant factors removed to increase power: habitat, location. (c) Warm sites, $R^2 = 0.41$, $F_{1,6} = 4.2$, $p < 0.086$. Non-significant factors removed to increase power: habitat, location

Term	Estimate	SE	t-ratio	Prob > t
(a)				
Intercept	-20.604	30.289	-0.68	0.5061
Fishing[high]	2.064	1.733	1.19	0.2510
Temp	1.510	1.293	1.17	0.2602
Fishing[high]	-3.011	1.293	-2.33	0.0333
× (Temp-23.36)				
(b)				
Intercept	12.584	1.945	6.47	<0.0001
Fishing[high]	6.254	1.945	3.21	0.0093
(c)				
Intercept	17.706	2.016	8.78	0.0001
Fishing[high]	-4.139	2.016	-2.05	0.0859

($F_{1,27} = 8.1$, $p < 0.001$). Slipper lobsters were significantly less abundant at HF sites (0.059 ± 0.03 vs. 0.23 ± 0.12 lobsters h^{-1} , $R^2 = 0.48$; Table 6d), but the size of slipper lobsters did not differ between HF and LF sites.

Indirect fishing effects

For the comparison of urchin density, there was a significant interaction between fishing and temperature (Table 7a), so we analyzed the 2 temperature groups separately. For cold sites, urchins were significantly more abundant at HF sites ($18.8 \pm 3.1 m^{-2}$) than at LF sites ($6.3 \pm 2.2 m^{-2}$) (Table 7b). There was no significant association between fishing and urchin densities at warm sites (Table 7c).

While the cover of non-coralline algae was substantially lower at HF sites (0.3 ± 3.4) than at LF sites (61.1 ± 3.4) ($R^2 = 0.90$, $F_{1,18} = 163$, $p < 0.0001$), the residuals of this model were not normally distributed, nor could they be transformed. The lack of normality resulted from the presence of 2 distinct algal communities: 100 to 90% non-coralline algae (algal beds/turf) and 0 to 11% non-coralline algae (crustose barrens). Non-coralline algal beds dominated all LF sites. In contrast, all HF sites were barrens of (90%) encrusting coralline and articulated calcareous algae (e.g. *Amphiroa* spp., *Corallina* spp.). This difference in algal communities between HF and LF sites was highly significant (Fisher's exact test, $p < 0.0001$). Divers observed (but did not quantify) that HF sites often had high cover of the anemone *Aiptasia* sp., suggesting that these anemones are resistant to grazing by urchins. In some cases, anemones covered the remaining patches of the algae *Ulva lactuca* and *Padina durvillaei*.

DISCUSSION

Our results are consistent with the hypothesis of top-down control in the GMR and the related expectation that a decrease in predators associated with fishing increases herbivores and reduces algae (Fig. 2). These findings suggest the following scenario. Historically, lobsters *Panulirus penicillatus* and *Scyllarides astori* and, particularly, hogfish *Bodianus diploaenia* kept herbivore populations at low levels, and non-coralline algal communities developed because of a community-level trophic cascade. Where the main predators were fished, herbivores overgrazed edible algae, promoting herbivore-resistant crustose coralline algae (Harrold & Reed 1985). At colder sites, slate-pencil urchins *Eucidaris galapagensis* appear to play a role in this cascade. Slate-pencil urchins also graze on corals (Reaka-Kuda et al. 1996), suggesting they might have broader effects than we mention. It is possible that other grazers we did not measure play an important role at warm sites.

Our results build on a growing number of studies that indicate the importance of top-down effects in

marine systems (Sala et al. 1998a). Trophic cascades can result when predators reduce the abundance of their prey to the extent that the prey's food source (plants or other prey) indirectly increases in abundance. Fishing the predators of herbivores adds a fourth level, fishers, to the top of the trophic cascade. Fishing, therefore, can affect ecosystem processes and the structure of entire communities (Sala 1997).

Like many papers on marine reserves, our study suffers from a lack of before–after comparisons, making it difficult to be certain that differences between HF and LF sites are fishing effects, not persistent site effects. For instance, reserves intentionally chosen for their high resource value might differ from fished areas independent of the effects of fishing. In addition, because it was not practical to take all measures at the same time at the same site, temporal variability could have reduced our power to detect spatial patterns. While we found significant associations between fishing and algae, other factors may contribute to spatial and temporal heterogeneity in the rocky reef community. For instance, localized upwelling will favor algal growth, wave energy may limit urchins to deeper areas, and heterogeneity in substrate type can alter access to shelters and habitat (Wellington 1975). Finally, our measures of urchin predation from found tests were indirect and imperfect, and the mobility and the cryptic nature of lobsters may have hindered accurate estimates of predator density at a particular site.

Our comparisons were spatial, but one might expect temporal patterns as well. Past studies indicate that urchin densities around the Archipelago fluctuate between 2 to 8 and 34 to 50 m² (Glynn et al. 1979, Glynn 1990). For instance, in 1954, *Eucidaris galapagensis* were found to occur at a median density of 19 individuals m⁻² in the western GMR (Malmquist 1991). These would be relatively high densities in our plots, and we cannot, therefore, confirm from our data the hypothesis that urchin density has increased over time as a result of increased fishing (Ruttenberg 2001, Okey et al. 2004). Paired comparisons of the same sites with the same methods would be needed to properly test whether urchin abundance has increased over time, but our results suggest this would only be expected at cold sites.

At other temperate rocky reefs, non-coralline algae provide important food and habitat for a range of species (Lilley & Shiel 2006), suggesting that fishing predators can have additional indirect effects on the community. However, from our results, it is not clear whether changes in algal communities associated with fishing would have significant ecological or economic consequences. Algal abundance strongly affects the growth and mortality rates of marine iguanas (Wikelski

et al. 1997). Iguanas may, therefore, compete with other herbivores for food (Shepherd & Hawkes 2005). Understanding the value of non-coralline algae to the GMR ecosystem would provide the information necessary to weigh indirect effects of fishing against economic benefits.

The patterns seen here would not have been apparent if there were no areas where fishing was restricted, underscoring the value of protected areas, both for preserving historical conditions for future generations and for permitting a better understanding of ecological dynamics. Nonetheless, had restrictions on fishing been better enforced and implemented for a longer period of time, effects of fishing might have been easier to detect.

Future work is desirable. Manipulative experiments would help better understand the causal basis for the patterns we report. Additional replication, particularly an extension to other biogeographic regions, and studies on temporal scales that include ENSO (El Niño Southern Oscillation), would help determine the generality of our results. Consideration of potentially important physical factors such as temperature, currents, wave action, and nutrients, as well as other biological factors (disease and parasitism, other predators and competitors) might help account for the considerable amount of unexplained variance in our results. Furthermore, the GMR food web is much more complex than the elements we have studied (Okey et al. 2004). In particular, we regret not collecting data on other herbivores that might play a role in trophic cascades at warm sites. Finally, consideration of fishing impacts on other top predators (the existing illegal fishery for sharks, and the proposed long-line fishery on pelagic fishes) and less well understood consumers (the intense fishery for sea cucumbers) would be necessary for a full evaluation of the direct and indirect effects of fishing in the Galápagos.

Acknowledgements. We gratefully acknowledge the staff and scientists of the Charles Darwin Research Station for their assistance and the Galápagos National Park Service (GNPS) for granting the research permits and logistic support. This study was partly funded by the OEA/LASPAU and AMELIS CONACYT J37689-V grants and a loan from the Inter-American Development Bank through GNPS. Mike Behrens and Nick Shears provided comments on an earlier draft.

LITERATURE CITED

- Bascompte J, Melian CJ, Sala E (2005) Interaction strength combinations and the overfishing of a marine food web. *Proc Natl Acad Sci USA* 102:5443–5447
- Behrens MD, Lafferty KD (2004) Effects of marine reserves and urchin disease on southern California rocky reef communities. *Mar Ecol Prog Ser* 279:129–139

- Branch GM, Witman JD, Bensted-Smith R, Bustamante RH, Wellington GM, Smith F, Edgar GJ (2002) Criterios de conservación para el bioma marino. In: Bensted-Smith R (ed) *Visión para la biodiversidad*. Fundación Charles Darwin para las Islas Galápagos y Fondo Mundial para la Naturaleza, Puerto Ayora, p 76–86
- Briones EE, Sonnenholzner J, Ortiz E (2002) Caracterización de los humedales marino costeros de las Islas Galápagos: tipos de fondo costero entre profundidades de 0 y 30 metros. Fundación Ecuatoriana de estudios Ecológicos (Eco-Ciencia), Banco Mundial y Servicio Parque Nacional Galápagos, Quito
- Bustamante RH, Reck G, Ruttenberg B, Polovina J (2000) Spiny lobster fishing in the Galapagos Islands: historical trends and current levels of exploitation, management and conservation. In: Phillips BF, Kittaka J (eds) *Spiny lobsters: fisheries and culture*, 2nd edn. Fishing News Books, Oxford, p 210–220
- Bustamante RH, Branch GM, Bensted-Smith R, Edgar GJ (2002) Estado y amenazas para la biodiversidad marina de Galápagos. In: Bensted-Smith R (ed) *Visión para la biodiversidad*. Fundación Charles Darwin para las Islas Galápagos y Fondo Mundial para la Naturaleza, Puerto Ayora, p 84–101
- Bustamante RH, Okey TA, Banks S (2007) Biodiversity and food-web structure of a Galapagos shallow rocky reef ecosystem. In: McClanahan TR, Branch GM (eds) *Food webs and the dynamics of marine benthic ecosystems: a global overview*. Oxford University Press (in press)
- Danulat E, Edgar GJ (2002) Reserva Marina de Galápagos. Línea base de la biodiversidad, Galápagos, Ecuador. Charles Darwin Foundation and the Galápagos National Park Service, Santa Cruz
- Edgar GJ, Bustamante RH, Farina JM, Calvopina M, Martínez C, Toral-Granda MV (2004) Bias in evaluating the effects of marine protected areas: the importance of baseline data for the Galapagos Marine Reserve. *Environ Conserv* 31:212–218
- Glynn PW (1990) Coral mortality and disturbances to coral reefs in the tropical eastern Pacific. In: Glynn PW (ed) *Global ecological consequences of the 1982–83 El Niño Southern Oscillation*. Elsevier Oceanogr Ser 52:55–126
- Glynn PW, Wellington GM, Birkeland C (1979) Coral reef growth in Galapagos: limitation by sea urchins. *Science* 203:47–49
- Guidetti P (2006) Marine reserves reestablish lost predatory interactions and cause community changes in rocky reefs. *Ecol Appl* 16:963–976
- Harrold C, Reed DC (1985) Food availability, sea urchin grazing, and kelp forest community structure. *Ecology* 66:1160–1169
- Hearn A (2004) Evaluación de las poblaciones de langostas en la Reserva Marina de Galápagos (Informe Final 2002–2004). Fundación Charles Darwin and Servicio Parque Nacional Galápagos, Santa Cruz
- Hearn A (2006) Life history of the slipper lobster *Scyllarides astori* Holthuis, 1960, in the Galapagos Islands, Ecuador. *J Exp Mar Biol Ecol* 328:87–97
- Hobson ES, Chess JR (2001) Influence of trophic relations on form and behavior among fishes and benthic invertebrates in some California marine communities. *Environ Biol Fish* 60:411–457
- Hughes TP, Reed DC, Boyle MJ (1987) Herbivory on coral reefs: community structure following mass mortalities of sea urchins. *J Exp Mar Biol Ecol* 113:39–59
- Jackson JBC, Kirby MX, Berger WH, Bjorndal KA and 15 others (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638
- Lafferty KD (2004) Fishing for lobsters indirectly increases epidemics in sea urchins. *Ecol Appl* 14:1566–1573
- Lilley S, Shiel D (2006) Community effects following the deletion of a habitat-forming alga from rocky marine shores. *Oecologia* 148:1432–1939
- Malmquist DL (1991) The past as the key to the present: taphonomy and paleoecology of the Urquina Bay Uplift. In: James MJ (ed) *Galapagos marine invertebrates: taxonomy, biogeography and evolution in Darwin's islands*. Plenum Press, New York, p 393–411
- Martínez C (2000) Ecología trófica de *Panulirus gracilis*, *P. penicillatus* y *Scyllarides astori* (Decapoda, Palinura) en sitios de pesca de langosta de las Islas Galápagos. Tesis de Licenciatura, Universidad del Azuay, Cuenca
- Molina L, Chasiluisa C, Murillo JC, Moreno J, Nicolaides F, Barreno JC, Vera M, Bautil B (2004) Pesca blanca y pesquerías que duran todo el año, 2003. In: *Evaluación de las pesquerías en la Reserva Marina de Galápagos, Informe Compendio 2003*. Fundación Charles Darwin and Servicio Parque Nacional Galápagos, Santa Cruz, p 103–139
- Murillo JC, Espinoza E, Edgar GJ, Nicolaides F and 9 others (2002) La pesca artesanal en Galápagos: comparación de indicadores entre 1997–2001. Informe Galápagos 2001/2002. Fundación Natura and WWF, Quito
- Murillo JC, Chasiluisa C, Molina L, Moreno J and 6 others (2003) Pesca blanca y pesquerías que duran todo el año en Galápagos, 2002. In: *Evaluación de las pesquerías en la Reserva Marina de Galápagos, Informe Compendio 2002*. Fundación Charles Darwin and Servicio Parque Nacional Galápagos, Santa Cruz, p 97–124
- Okey TA, Banks S, Born AR, Bustamante RH and 10 others (2004) A trophic model of a Galapagos subtidal rocky reef for evaluating fisheries and conservation strategies. *Ecol Model* 172:383–401
- Pearse JS, Hines AH (1987) Long-term population dynamics of sea urchins in a central California kelp forest: rare recruitment and rapid decline. *Mar Ecol Prog Ser* 39:275–283
- Pinnegar JK, Polunin NVC, Francour P, Badalamenti F and 7 others (2000) Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. *Environ Conserv* 27:179–200
- Reaka-Kuda ML, Feingold JS, Glynn PW (1996) Experimental studies of rapid bioerosion of coral reefs in the Galapagos Islands. *Coral Reefs* 15:101–107
- Reck GK (1983) The coastal fisheries in the Galapagos Islands, Ecuador. Description and consequences for management in the context of marine environmental protection and regional development. Dissertation, Christian-Albrechts-Universität, Kiel
- Ruttenberg BI (2001) Effects of artisanal fishing on marine communities in the Galapagos Islands. *Conserv Biol* 15:1691–1699
- Sala E (1997) Fish predators and scavengers of the sea urchin *Paracentrotus lividus* in protected areas of the north-west Mediterranean Sea. *Mar Biol* 129:531–539
- Sala E, Boudouresque CF, Harmelin-Vivien M (1998a) Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. *Oikos* 82:425–439
- Sala E, Ribes M, Hereu B, Zabala M, Alva V, Coma R, Garrabou J (1998b) Temporal variability in abundance of the sea urchins *Paracentrotus lividus* and *Arbacia lixula* in the northwestern Mediterranean: comparison between a marine reserve and an unprotected area. *Mar Ecol Prog Ser* 168:135–145
- Schiel DR, Foster MS (1986) The structure of subtidal algal

- stands in temperate waters. *Oceanogr Mar Biol Annu Rev* 24:265–307
- Shears NT, Babcock RC (2002) Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia* 132:131–142
- Shepherd SA, Hawkes MW (2005) Algal food preferences and seasonal foraging strategy of the marine iguana, *Amblyrhynchus cristatus*, on Santa Cruz, Galapagos. *Bull Mar Sci* 77:51–72
- Snell HM, Stone PA, Snell HL (1995) Geographical characteristics of the Galápagos Islands. *Not Galapagos* 55:18–24
- Tegner MJ, Dayton PK (1981) Population structure, recruitment and mortality of two sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in a kelp forest. *Mar Ecol Prog Ser* 5:255–268
- Tegner MJ, Levin LA (1983) Spiny lobsters and sea urchins: analysis of a predator–prey interaction. *J Exp Mar Biol Ecol* 73:125–150
- Wellington GM (1975) The Galapagos coastal and marine environments. Department of National Parks and Wildlife, Quito
- Wikelski M, Carrillo V, Trillmich F (1997) Energy limits to body size in a grazing reptile, the Galapagos marine iguana. *Ecology* 78:2204–2217

Editorial responsibility: Otto Kinne (Editor-in-Chief), Oldendorf/Luhe, Germany

*Submitted: August 30, 2006; Accepted: February 12, 2007
Proofs received from author(s): July 20, 2007*