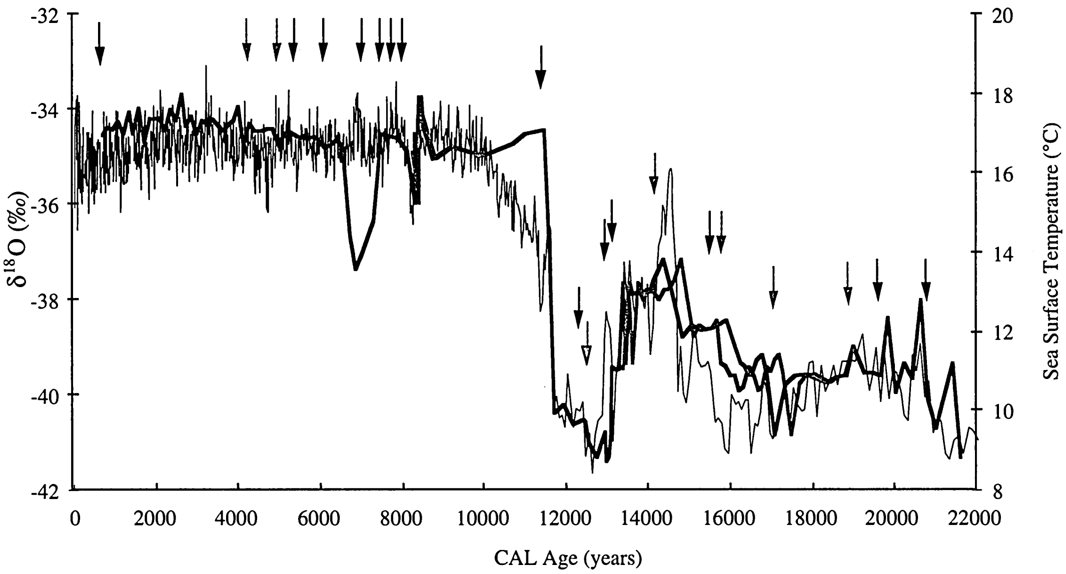


**Fig. 3.** Comparison of paleoclimatic records from GISP2 (*30*) (blue line) and from MD 90-917 versus cal yr B.P. Chronology of the SST record is obtained by linear fits between two successive AMS $^{14}C$ ages on tephra (red arrows) and within peaks of abundance of planktonic foraminifera (black arrows) (*9, 11*). The $^{14}C$ ages were corrected from the varying measured $R_{surf}$ (red line) (*10*) and using a constant $R_{surf}$ of 390 years (*14*) (green line), then converted to calendar ages (*8*). The use of the ~520-year $R_{surf}$ estimate at ~8200 years (*4*), slightly older than the modern one during the sapropel event, permits a better correlation between the two records.

shifts (Fig. 3), a better correlation, particularly in the steepness of the cold-to-warm transition at ~15,600 cal yr B.P., is obtained by using a $R_{surf}$ of ~800 years between 15,000 and 17,000 cal yr B.P. The large $R_{surf}$ values at 17,000 and 15,700 cal yr B.P. could correspond either to a pervasive feature of H1 or to separate short events. Adkins *et al.* (*7*) pointed out that $R_{interm}$ would have changed rapidly in ~160 years from the estimate of the lifetime of modern benthic corals. Hence, the H1 event may have constituted a succession of short surges and therefore a balance of rapid invasion and retreat between the Southern intermediate waters and the GNAIW. Atlantic $R_{surf}$ changes would then be attributable to the rapid resumption and cessation of thermohaline convection (*23*).

### References and Notes


1. M. Stuiver, T. F. Braziunas, B. Becker, B. Kromer, *Quat. Res.* **35**, 1 (1991).
2. E. Bard, *Paleoceanography* **3**, 635 (1988).
3. E. Bard *et al.*, *Earth Planet. Sci. Lett.* **126**, 275 (1994).
4. Y. Facorellis, Y. Maniatis, B. Kromer, *Radiocarbon* **40**, 963 (1998).
5. E. L. Sikes, C. R. Samson, T. P. Guilderson, W. R. Howard, *Nature* **405**, 555 (2000).
6. W. S. Broecker *et al.*, *Paleoceanography* **3**, 659 (1988).
7. J. F. Adkins, H. Cheng, E. A. Boyle, E. R. Druffel, R. L. Edwards, *Science* **280**, 725 (1998).
8. M. Stuiver *et al.*, *Radiocarbon* **40**, 1041 (1998).
9. G. Siani, thesis, Université de Paris-Sud Orsay (1999).
10. See supplementary Web material at *Science* Online (www.sciencemag.org/cgi/content/full/294/5548/1917/DC1).
11. D. Mercone *et al.*, *Paleoceanography* **15**, 336 (2000).
12. The peaks of abundance of glass shards and of foraminifera do not show the distribution tails (*9*), as is characteristic of bioturbation processes. Using sample resolution, sedimentation rate, and the assumption of a content of 100% glass shards before bioturbation (*32*), the aging ranges from 30 years (with a mixing depth of 2 cm) to 80 years (with 4 cm); these values are negligible with respect to $R_{surf}$ age changes and associated uncertainties (*10*).
13. N. Kallel, M. Paterne, L. D. Labeyrie, J. C. Duplessy, M. Arnold, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **135**, 97 (1997).
14. G. Siani *et al.*, *Radiocarbon* **42**, 271 (2000).
15. W. S. Broecker, R. Gerard, *Limnol. Oceanogr.* **14**, 883 (1969).
16. R. Zahn, M. Sarnthein, H. Erlenkeuser, *Paleoceanography* **2**, 543 (1987).
17. M. Sarnthein *et al.*, *Paleoceanography* **9**, 209 (1994).
18. W. F. Ruddiman, A. McIntyre, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **35**, 145 (1981).
19. N. Combourieu-Nebout, M. Paterne, J. L. Turon, G. Siani, *Quat. Sci. Rev.* **17**, 303 (1998).
20. G. Bond *et al.*, *Nature* **360**, 245 (1992).
21. I. Cacho *et al.*, *Paleoceanography* **14**, 698 (1999).
22. T. F. Stocker, D. G. Wright, *Radiocarbon* **40**, 359 (1998).
23. To test the sensitivity of the $R_{surf}$ age to carbon exchange with the atmosphere and the underlying intermediate water, we wrote a simplified equilibrium equation of a surface water $^{14}C/^{12}C$ ratio. The equation and results are discussed in (*10*).
24. W. S. Broecker, T. H. Peng, S. Trumbore, G. Bonani, W. Wolfli, *Global Biogeochem. Cycles* **4**, 103 (1990).
25. L. Vidal *et al.*, *Clim. Dyn.* **15**, 909 (1999).
26. R. Zahn *et al.*, *Paleoceanography* **12**, 696 (1997).
27. H. G. Ostlund, C. Craig, W. S. Broecker, D. Spencer, Eds., *GEOSECS Atlantic, Pacific, and Indian Ocean Expeditions. Shorebased Data and Graphics, GEOSECS Expedition, 7* (U.S. Government Printing Office, Washington, DC, 1987).
28. E. Michel *et al.*, *Paleoceanography* **10**, 927 (1995).
29. K. A. Hughen *et al.*, *Radiocarbon* **40**, 483 (1998).
30. R. B. Alley *et al.*, *Nature* **362**, 527 (1993).
31. U. von Grafenstein *et al.*, *Science* **284**, 1654 (1999).
32. E. Bard *et al.*, *Clim. Dyn.* **1**, 101 (1987).


33. We acknowledge helpful comments from T. Goslar, J. Cochran, D. Paillard, M. Fontugne, P. Jean-Baptiste, and Institut Français de Recherche et Technologie Polaire for Marion Dufresne coring facilities. Supported by Ministero Italiano degli Affari Esteri (G.S.), CNR (R.S.), CNRS and Commissariat à l'Energie Atomique, and the Marine and Science Technology IIIrd program–Clivamp and the Institut National des Sciences de l'Univers: Environment et Climat du Passé: Histoire et Evolution programs of the European Union. This is LSCE Contribution number 685.

20 June 2001; accepted 10 October 2001


# Effects of Marine Reserves on Adjacent Fisheries


**Callum M. Roberts,[1,2]* James A. Bohnsack,[3] Fiona Gell,[2] Julie P. Hawkins,[2] Renata Goodridge[4]**



**Marine reserves have been widely promoted as conservation and fishery management tools. There are robust demonstrations of conservation benefits, but fishery benefits remain controversial. We show that marine reserves in Florida (United States) and St. Lucia have enhanced adjacent fisheries. Within 5 years of creation, a network of five small reserves in St. Lucia increased adjacent catches of artisanal fishers by between 46 and 90%, depending on the type of gear the fishers used. In Florida, reserve zones in the Merritt Island National Wildlife Refuge have supplied increasing numbers of world record–sized fish to adjacent recreational fisheries since the 1970s. Our study confirms theoretical predictions that marine reserves can play a key role in supporting fisheries.**


Marine reserves, areas that are closed to all fishing, have been attracting much attention for their dual potential as conservation and fishery management tools (*1–5*). A synthesis of more than 100 studies of reserves worldwide shows that protection from fishing leads to rapid increases in biomass, abundance, and average size of exploited organisms and to increased species diversity (*6*). Such effects are of great interest to fishery managers, because rebuilding exploited populations in reserves offers prospects of fishery enhancement (3, 7).

Because reserves contain more and larger fish, protected populations can potentially produce many times more offspring than can exploited populations. In some cases, studies have estimated order-of-magnitude differences in egg production (8). Increased egg output is predicted to supply adjacent fisheries through export of offspring on ocean currents (9–11). In addition, as protected stocks build up, reserves are predicted to supply local fisheries through density-dependent spillover of juveniles and adults into fishing grounds (7).

Whereas the effects of reserves within their boundaries have strong empirical support, evidence that they enhance fisheries is sparse (4). Several studies have suggested export by showing higher densities of exploited species or greater catch per unit effort adjacent to reserve borders (12–14). When a reserve in the Philippines was reopened to fishing, catches collapsed in nearby areas, which suggests that the reserve had previously supported fisheries (15). Catches rose again after renewed compliance (16). However, none of these studies showed an increase in total production after reserve creation. We investigated the effects on neighboring fisheries of marine reserves in Florida (United States) and St. Lucia.

The Soufrière Marine Management Area (SMMA) was created in 1995 along the southwest coast of the Caribbean island of St. Lucia (2, 17). It encompasses 11 km of coast and includes a network of five marine reserves that constitute about 35% of coral reef fishing grounds (Fig. 1). This network was designed to rehabilitate the severely overexploited reef fishery (2).

The marine reserves had a rapid impact on reef fish populations. Visual censuses of reserves and adjacent fishing areas (18) revealed that combined biomass of five commercially important fish families tripled in reserves in 3 years (Fig. 2). Biomass doubled in adjacent fishing areas, despite redirection of fishing effort from reserves (Fig. 2). In the last 2 years, biomass held fairly steady, with further increases probably prevented by damage to reefs from Hurricane Lenny in late 1999 (19).

We studied the reef fishery in the SMMA for two 5-month periods (20), in 1995–1996, immediately after reserves were created, and in 2000–2001, after 5 years of protection. We collected data from two trap-fishing methods—large traps soaked overnight and small drop-and-lift traps, baited and soaked for 1 or 2 hours—that account for >70% of fish caught. Catches increased significantly between 1995–1996 and 2000–2001 (Fig. 3). Mean total catch per trip for fishers with large traps increased by 46%, and for fishers with small traps by 90%. Catch per trap increased 36% for big traps and by 80% for small traps (Fig. 3).

Total fishing effort remained stable over the course of the study. There were 22 full-time trap fishers in 1995–1996 and 20 in 2000–2001. There was no significant change in the number of trips per week that fishers made [(4.4 per fisher in 1995–1996 versus 3.9 in 2000–2001, Mann-Whitney $U$ test, not significant (NS)] or in numbers of large or small traps set per fisher (Mann Whitney $U$ tests, NS in both cases). Goodridge (21) reported on the immediate impacts of the SMMA on the reef fishery. Comparing data from 1994 and 1995 (before protection) with data from 1995 and 1996 (after protection), she found that mean catch per unit effort (CPUE) for small traps had decreased by 28%, whereas CPUE for large traps increased by 24%, resulting in little net change in total landings. Seventy-five percent of 12 full-time reef fishers interviewed in the year after reserve creation reported having to increase their fishing effort to catch the same amount of fish as

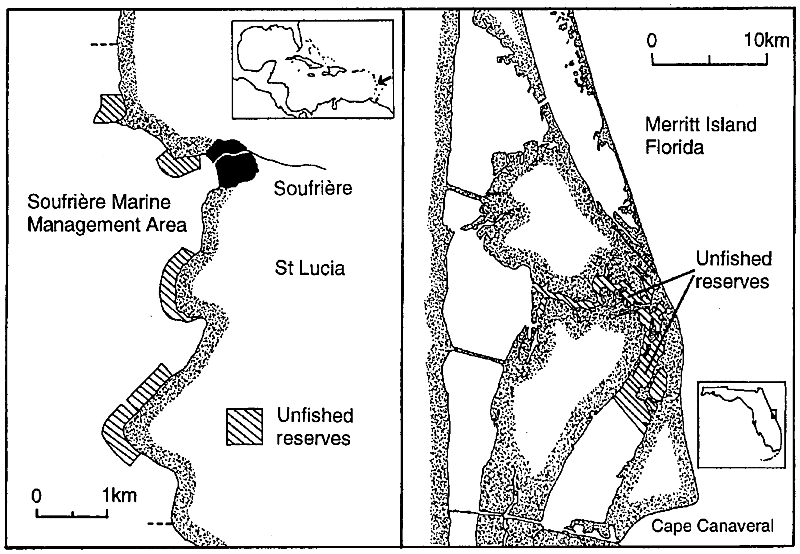


**Fig. 1.** Location of the study sites and marine reserve zones in St. Lucia (left) and Florida (right).

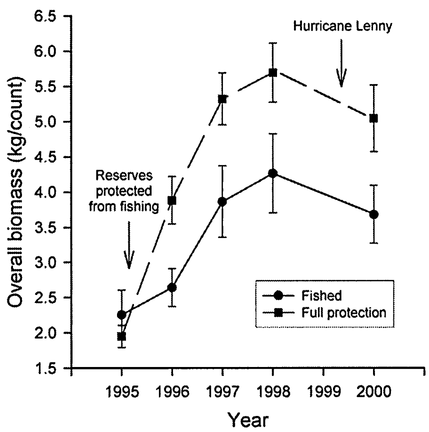


**Fig. 2.** Build-up of commercially important fish biomass in marine reserves and adjacent fishing grounds in St. Lucia (mean ± SE). Two-way analysis of variance: protection from fishing, $P < 0.001$; time, $P < 0.001$; protection from fishing × time, NS).

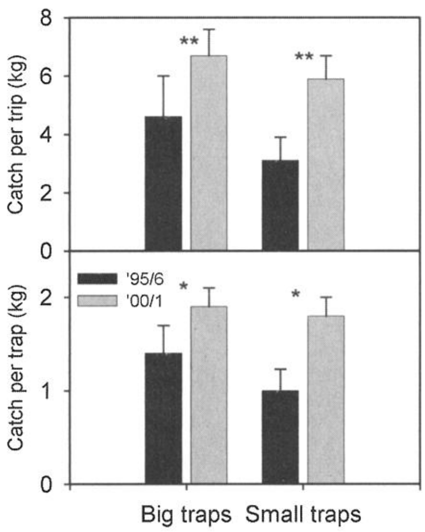


**Fig. 3.** Comparison of fish catches and catch per unit effort between 1995–1996 and 2000–2001 for the two principal forms of fishing gear used in the St. Lucian reef fishery. Differences were tested with the Mann-Whitney $U$ test and were significant at $P < 0.001$ (**) and $P < 0.002$ (*). For sample sizes see (20).

[1]Department of Organismic and Evolutionary Biology, Harvard University, 16 Divinity Avenue, Cambridge, MA 02138, USA. [2]Environment Department, University of York, York, YO10 5DD, UK. [3]Southeast Fisheries Science Center, National Oceanic and Atmospheric Administration Fisheries, 75 Virginia Beach Drive, Miami, FL 33149, USA. [4]Department of Marine Resource and Environmental Management, Faculty of Natural Science, University of the West Indies, Cave Hill, Barbados.

*To whom correspondence should be addressed. E-mail: cr10@york.ac.uk

before. The remaining 25% said they were unable to catch as much.

Our findings indicate that in 5 years, reserves have led to improvement in the SMMA fishery, despite the 35% decrease in area of fishing grounds (*22*). There were more fish in the sea, and evidence for little initial impact of reserves on total catches in the first year of implementation (*21*), together with constant fishing effort since protection began, indicates a greater weight of total landings. Interviews with local fishers (conducted in Creole via an interpreter) showed that most felt better off with reserves than without (Table 1). Younger fishers were especially positive about the benefits.

The Merritt Island National Wildlife Refuge at Cape Canaveral, Florida, has the oldest fully protected marine reserve in the United States. It encompasses two areas of estuarine habitat that

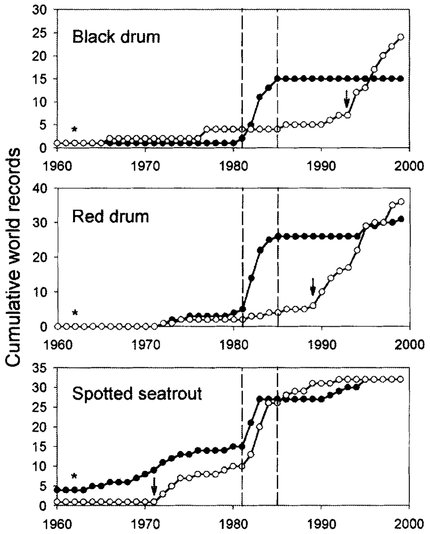


**Fig. 4.** Cumulative world records for game fish in the 200-km coastal section adjoining the Merritt Island refuge (open circles) compared to records from all the rest of Florida (filled circles). Asterisks mark the time of protection from fishing within the refuge. Vertical dashed lines show a period of rapid accumulation of new world records after addition of new line classes by the IGFA. Arrows mark the points at which there was a rapid increase in accumulation of new records for each species from areas around the Merritt Island refuge.

have been closed to public access and fishing since 1962, for security of the Kennedy Space Center (Fig. 1). The Banana Creek reserve covers 16 $km^2$ and is separated by land from the 24-$km^2$ North Banana River reserve.

Johnson *et al.* (*23*) showed that protection from fishing at Merritt Island has benefited several game-fish species. When protected areas were compared with adjacent fishing grounds, relative abundances (standardized catch per unit experimental fishing effort) were 12.8 times greater for black drum (*Pogonias cromis*), 6.3 times greater for red drum (*Sciaenops ocellatus*), 2.3 times greater for spotted sea trout (*Cynoscion nebulosus*), and 5.3 times greater for common snook (*Centropomus undecimalis*). Reserves also had more larger and older fish.

Long-established reserves are predicted to supply trophy-sized fish to recreational fisheries through spillover across boundaries (*9*). The International Game Fish Association (IGFA) registers world-record fish catches according to strict criteria for line-strength classes, rod types, and the gender of fishers (*24, 25*). Examining frequencies of world record–sized catches in relation to proximity to Merritt Island allowed a test of the hypothesis that the refuge exports trophy fish.

For analysis, the area defined as adjacent to the reserves extended 100 km north and 100 km south of the land bridge that separated the reserves (*26*). World-record catches were concentrated in the area adjacent to the Merritt Island refuge for three of the four species. This region encompasses only 13% of the Florida coast, but of world record–size fish caught in Florida between 1939 and 1999, it accounted for 62% of 39 records for black drum, 54% of 67 records for red drum, 50% of 32 records for spotted sea trout, but only 2% of 84 records for common snook. Black drum, red drum, and spotted sea trout are year-round residents of the refuge, although tagging studies show they may travel distances of tens of kilometers (*23, 27–30*). Common snook are at the northern limit of their range at Merritt Island and tend to disappear from the estuary in winter (*23*). Because the refuge does not appear to supply common snook to the fishery, this species was not analyzed further.

Before closure, the area near Merritt Island supported an intensive recreational fishery (*31*). Recovery from this heavily exploited state takes time, particularly for the accumulation of large individuals of long-lived species in reserves (*13, 32, 33*). If the Merritt Island refuge were supplying fish to the adjacent recreational fishery, we would expect frequencies of world-record catches to increase over time. Figure 4 shows cumulative numbers of world record–size fish caught adjacent to the refuge compared with numbers of those caught elsewhere in Florida. For each species, a threshold point was reached at which the reserve began to supply trophy fish. The abrupt nature of these thresholds is easily explained. It is only when fish originating from the reserves have grown larger than existing fish of world-record sizes that new records can accumulate.

The time at which species crossed that threshold was linked to their longevity: after 9 years for spotted sea trout (longevity 15 years) (*28*), 27 years for red drum (longevity 35 years) (*27*), and 31 years for black drum (longevity 70 years) (*29*). Reserves would also have been supplying smaller fish for years before catches of record-sized fish became apparent.

Figure 4 also shows rapid accumulation of new records between 1981 and 1985, when new line classes were introduced (*24*). By 1985, only spotted sea trout had passed the record size threshold at Merritt Island refuge. Black and red drum do not show any comparable burst of new records. By the late 1980s, the shorter-lived spotted sea trout had evidently reached its full growth potential, and the rate of accumulation of new records tailed off. By contrast, black and red drum records are still accumulating rapidly. Since 1985, all the new Florida records for black drum, and most records for red drum, have been won for fish caught adjacent to Merritt Island refuge.

The marine reserves described here differ in many ways. In St. Lucia, reserves were designed to enhance artisanal, subsistence fisheries. They protect coral reef habitats and relatively sedentary fish species. In Florida, reserves were designed to prohibit access to a rocket launch site, and wildlife protection was a subsidiary goal. However, they have protected estuarine habitats and relatively mobile fish species, and they have supplied recreational fisheries with record-size fish. Despite these contrasts, both examples demonstrate that reserve effects extend beyond their boundaries. In these cases, we believe the keys to successful fishery enhancement have been the relatively large fractions of habitat protected and resolute enforcement, and, in Florida, the long period over which protection has extended.

**Table 1.** Results of a survey of Soufrière fishers asked the question: "Has the fishery gotten better, gotten worse, or stayed the same since the Soufrière Marine Management Area was established?" Figures show percentage of interviewees responding in each way.

| Age of interviewees | Number interviewed | Fishery better | Fishery the same | Fishery worse | Don't know or won't say |
|---|---|---|---|---|---|
| 15–30 | 23 | 47.8 | 8.7 | 21.7 | 21.7 |
| 31–45 | 22 | 45.5 | 18.2 | 22.7 | 13.6 |
| 46–60 | 15 | 26.7 | 13.3 | 26.7 | 33.3 |
| 61–85 | 11 | 9.1 | 18.2 | 54.5 | 18.2 |

### References and Notes


1. C. M. Roberts, *Trends Ecol. Evol.* **12**, 35 (1997).
2. ———, J. P. Hawkins. *Fully Protected Marine Reserves: A Guide.* (Endangered Seas Campaign, World Wildlife Fund–United States, Washington, DC, 2000).

3. National Research Council, *Sustaining Marine Fisheries*. (National Academy Press, Washington, DC, 1999).
4. ———, *Marine Protected Areas: Tools for Sustaining Ocean Ecosystems* (National Academy Press, Washington, DC, 2001).
5. Scientific consensus statement on marine reserves (available at www.nceas.ucsb.edu/Consensus).
6. B. Halpern, *Ecol. Appl.*, in press.
7. J. A. Bohnsack, *Aust. J. Ecol.* **23**, 298 (1998).
8. W. A. Palsson, R. E. Pacunski, *The Response of Rocky Reef Fishes to Harvest Refugia in Puget Sound*, vol. 1, *Puget Sound Research '95* (Puget Sound Water Quality Authority, Olympia, WA,1995).
9. J. A. Bohnsack, in *Reef Fisheries*, N. V. C. Polunin, C. M. Roberts, Eds. (Chapman & Hall, London, UK, 1996), pp. 283–313.
10. C. M. Roberts, *Science* **278**, 1454 (1997).
11. S. R. Palumbi, in *Marine Community Ecology*, M. D. Bertness *et al*., Eds. (Sinauer, Sunderland, MA 2001), pp. 509–530.
12. G. R. Russ, A. C. Alcala, *Mar. Ecol. Prog. Ser.* **132**, 1 (1996).
13. T. R. McClanahan, S. Mangi, *Ecol. Appl.* **10**, 1792 (2000).
14. S. A. Murawski, R. Brown, H.–L. Lai, P. J. Rago, L. Hendrickson, *Bull. Mar. Sci.* **66**, 775 (2000).
15. A. C. Alcala, G. R. Russ, *J. Conserv. Int. Explor. Mer* **46**, 40 (1990).
16. G. R. Russ, A. C. Alcala, *Coral Reefs* **18**, 307 (1999).
17. The SMMA was established after 3 years of local negotiations. Strong community involvement has led to good compliance. Since its inception, the SMMA has been patrolled daily by wardens who keep fishers out of reserves. Daily surveys of fishing ($n$ = 138) conducted in 2000 and 2001 showed that illegal trap fishing in reserves was only 19.9% of the fishing effort conducted in adjacent grounds.
18. Annual censuses of demersal fishes were performed with stationary point counts (*34*). A 10-m tape was placed across the reef, and all fish observed within a 5-m radius of the center of the tape were counted for 15 min and their lengths estimated visually to the nearest centimeter. Two hundred and seventy-five counts were made annually by C.M.R. and J.P.H., split approximately equally between 5- and 15-m depths. Data were pooled across depths and observers before analyses. Fish biomass was calculated from length estimates for species from five commercially important families: Acanthuridae (surgeonfishes), Scaridae (parrot fishes), Serranidae (groupers), Haemulidae (grunts), and Lutjanidae (snappers) (*35*).
19. C. M. Roberts, J. P. Hawkins, unpublished data.
20. Goodridge *et al.* (*36*) assessed catches and fishing patterns at Soufrière between October 1995 and February 1996. Our second survey spanned September 2000 to February 2001. Trip catches were weighed and measured when landed. Additional CPUE data were obtained by weighing catches as they were hauled at sea. Sample sizes for trip catches were 59 and 133 for large traps in 1995–1996 and 2000–2001, respectively, and 33 and 53 for small traps. Sample sizes for catch per trap were 59 and 128 for large traps in 1995–1996 and 2000–2001, respectively, and 33 and 51 for small traps.
21. R. Goodridge, thesis, University of the West Indies, Barbados (1996).
22. A plausible alternative to marine reserves increasing fish stocks and catches is an oceanographic regime shift that increased recruitment regionally (*37*). However, we know of no evidence for similar fishery or stock improvements in nearby islands. Furthermore, during interviews in 2000 and 2001, Soufrière fishers complained of growing numbers of fishers visiting the SMMA from villages to the north and south, an impression confirmed by our daily boat surveys. This suggests that the benefits were localized to Soufrière reserves and adjacent fishing grounds.
23. D. R. Johnson, N. A. Funicelli, J. A. Bohnsack, *N. Am. J. Fish. Manage.* **19**, 436 (1999).
24. International Game Fish Association (IGFA). *The IGFA Rule Book for Freshwater, Saltwater, and Fly Fishing* (IGFA Fishing Hall of Fame and Museum, Dania Beach, FL, 2000).
25. Line classes included in this study are 1, 2, 4, 6, 8, 10, 15, 24, and 37 kg for spinning tackle; and 1, 2, 3, 4, 5, 8, and 10 kg for fly tackle.
26. Most record locations were reported as a body of water or a port. Each record was assigned to 1 of 30 50-km coastal segments for spatial analyses.
27. M. D. Murphy, R. G. Taylor, *Fish. Bull.* **88**, 531 (1990).
28. ———, *Trans. Am. Fish. Soc.* **123**, 482 (1994).
29. M. D. Murphy, D. H. Adams, D. M. Tremain, B. L. Winner, *Fish. Bull.* **96**, 382 (1998).
30. M. J. Schirripa, C. P. Goodyear, *Bull. Mar. Sci.* **54**, 1019 (1994).
31. Data from 1959–1962 show that annual landings from the area around Merritt Island averaged 2.7 million kg from an average of 628 commercial fishers, and 1.47 million kg from an average of 764,000 sport fishers (*38*).
32. G. R. Russ, A. C. Alcala, *Ecol. Appl.* **6**, 947 (1996).
33. J. Sladek Nowlis, C. M. Roberts, *Fish. Bull.* **97**, 604 (1999).
34. J. A. Bohnsack, S. P. Bannerot, *NOAA Tech. Rep. No. 41* (National Marine Fisheries Service, FL, 1986).
35. J. A. Bohnsack, D. E. Harper. *NOAA Technical Memorandum NMFS–SEFC–215* (National Marine Fisheries Service, FL, 1988).
36. R. Goodridge, H. A. Oxenford, B. G. Hatcher, F. Narcisse, *Proc. Gulf Caribb. Fish Inst.* **49**, 316 (1997).
37. J. J. Polovina, W. R. Haight, R. B. Moffitt, F. A. Parrish, *Crustaceana* **68**, 203 (1995).
38. W. W. Anderson, J. W. Gehringer, *U.S. Fish and Wildlife Service Special Scientific Report Series No. 514* (U.S. Fish and Wildlife Service, FL, 1965).
39. We thank the St. Lucia Department of Fisheries, SMMA, S. George, P. Hubert, K. Wulf, N. Faustin, R. Nicholas, N. Florent, P. Butcher, I. Pascal, V. Joseph, and A. Joseph. N. Troubetskoy, M. Allard, and K. Allard (Scuba St. Lucia) provided scuba gear and fills and M. Nugues and C. Schelten helped with fieldwork. H. Oxenford and B. Hatcher helped with the first fishery survey. We thank S. Palumbi for hospitality at Harvard. C.M.R. was supported during the writing of this paper by the Hrdy Visiting Professorship in Conservation Biology at Harvard. Work in St. Lucia was supported by grants from the U.K. Darwin Initiative, the Natural Environment Research Council, The Pew Charitable Trusts, and the U.K. Department for International Development. We also thank M. Leech, D. P. Blodgett Jr., and the IGFA for world-record fish data in Florida, and J. S. Ault, B. A. Bohnsack, D. R. Johnson, S. G. Smith, and R. R. Warner for comments.

20 August 2001; accepted 15 October 2001

# Ecological Meltdown in Predator-Free Forest Fragments

**John Terborgh,[1]* Lawrence Lopez,[2] Percy Nuñez V.,[3] Madhu Rao,[4,5] Ghazala Shahabuddin,[6] Gabriela Orihuela,[7] Mailen Riveros,[8] Rafael Ascanio,[9] Greg H. Adler,[11] Thomas D. Lambert,[10] Luis Balbas[12]**

**The manner in which terrestrial ecosystems are regulated is controversial. The "top-down" school holds that predators limit herbivores and thereby prevent them from overexploiting vegetation. "Bottom-up" proponents stress the role of plant chemical defenses in limiting plant depredation by herbivores. A set of predator-free islands created by a hydroelectric impoundment in Venezuela allows a test of these competing world views. Limited area restricts the fauna of small (0.25 to 0.9 hectare) islands to predators of invertebrates (birds, lizards, anurans, and spiders), seed predators (rodents), and herbivores (howler monkeys, iguanas, and leaf-cutter ants). Predators of vertebrates are absent, and densities of rodents, howler monkeys, iguanas, and leaf-cutter ants are 10 to 100 times greater than on the nearby mainland, suggesting that predators normally limit their populations. The densities of seedlings and saplings of canopy trees are severely reduced on herbivore-affected islands, providing evidence of a trophic cascade unleashed in the absence of top-down regulation.**

Ecosystems are structured by the amount of energy flowing through them and by how much primary productivity reaches consumers (primarily herbivores), predators, and decomposers. Plant growth is enhanced through bottom-up effects exerted by light, warmth, and the availability of moisture and nutrients. However, plants are subject to top-down forces when they are eaten by consumers.

The degree to which top-down versus bottom-up forces regulate terrestrial ecosystems has not been resolved (*1, 2*). Proponents of the top-down view argue that the world is green because predators regulate the numbers of herbivores, thereby limiting the damage herbivores do to vegetation (*3, 4*). Advocates of a bottom-up view argue that herbivores are limited by low forage quality and/or by constitutive and inducible plant defenses, which render much foliage unpalatable or indigestible (*5, 6*).

A naïve test of the top-down versus bottom-up models is simple in principle but difficult in practice because vertebrate predators and their prey operate on spatial scales lying beyond the practical reach of direct experimentation (*7*). However, if all relevant predators could be excluded from a sufficiently large experimental area, the top-down model would predict that consumer populations would expand, whereas the bottom-up model would predict little change in consumer numbers. The prediction is naïve, because many ecosystems have both top-