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Hurricanes Frances and Jeanne Remove Blooms of the Invasive Green Alga *Caulerpa brachypus* forma *parvifolia* (Harvey) Cribb From Coral Reefs Off Northern Palm Beach County, Florida

BRIAN E. LAPOINTE*, BRADLEY J. BEDFORD, and REX BAUMBERGER

Center for Coastal Research, Harbor Branch Oceanographic Institution, Inc., 5600 U.S. 1 North, Ft. Pierce, Florida 34946

ABSTRACT: Coral reefs worldwide are under stress from a variety of anthropogenic activities that can alter or inhibit recovery from catastrophic physical disturbances such as hurricanes. On coral reefs off southeast Florida, land-based nutrient pollution contributed to a successful invasion of *Caulerpa brachypus* forma *parvifolia* that dominated (up to 90% cover) reefs between January 2003 and August 2004. In September 2004, physical effects from Hurricanes Frances and Jeanne removed virtually all of the *C. brachypus* from the affected reefs. In July 2005, small patches of *C. brachypus* began to re-emerge and the area was affected again by Hurricane Wilma in October 2005. Although these hurricanes provided temporary relief from the *C. brachypus* invasion, the future of these reefs is uncertain because of competition with other opportunistic macroalgae and biota that may respond to the combination of newly created space and continued nutrient stress.

Introduction

Coral reefs are under stress worldwide from a variety of natural and anthropogenic factors, including hurricanes (Gardner et al. 2005), nutrient pollution (Johannes 1975; Bell and Elmetri 1995; Lapointe 1997; NRC 2000), sedimentation (Rogers and Beets 2001), overfishing (Hughes 1994), and climate change (Goreau and Hayes 1994; Hoegh-Guldberg 1999). Catastrophic physical disturbance associated with hurricanes can have dramatic effects on the structure (Geister 1977) and function (Connell 1978) of coral reefs and have generally been considered a routine process vital to the long-term growth and diversity of these shallow water, tropical ecosystems.

In recent decades, escalating anthropogenic stressors have reduced the functional diversity of many coral reef ecosystems, altering their capacity to cope with disturbance (Nystrom et al. 2000). On coral reefs experiencing nutrient pollution, hurricanes can trigger phase shifts away from dominance by hard corals and towards macroalgae, inhibiting recovery of reef coral communities (Kinsey 1988). Following Hurricane Allen in 1980, the previously coral-dominated fore reef at Discovery Bay on Jamaica's north coast was replaced by high biomass populations of the phaeophytes *Sargassum polyceratium*, *Sargassum hystrix*, and *Lobophora variegata* (Lapointe 1997). While this phase shift was attributed by some to overfishing and decreased herbivory (Hughes 1994; Jackson et al. 2001), these reefs experienced simultaneous low-level nutrient enrichment from land-based sources (Lapointe 1997, 1999). At Low Isles in the Great Barrier Reef lagoon, Australia, hard coral communities recovered from cyclones in 1905, 1911, and 1934; but little or no recovery has occurred on these shallow-water reefs since the 1950 cyclone, following increased agricultural runoff, turbidity, and coastal eutrophication that developed in the mid 1900s (Bell and Elmetri 1995).

Coral reefs off southeastern Florida have also experienced increasing anthropogenic nutrient enrichment and macroalgal blooms in recent decades. In 1990, a succession of harmful algal blooms (HAB) and invasions began in Palm Beach County, Florida, with the development of unusually high biomass of the siphonous chlorophyte *Codium isthmocladum* (Lapointe et al. 2005a). These initial HABs were followed by expansive blooms of the rhizomatous chlorophytes *Caulerpa verticillata*, *Caulerpa racemosa*, and, most recently, the Pacific invader *Caulerpa brachypus* forma *parvifolia* (Harvey) Cribb (Cribb 1958). A comprehensive survey in Palm Beach and northern Broward counties in 2001, involving collection and analysis of these HAB species for $\delta^{15}N$, indicated that these HABs were supported by land-based sewage pollution (Lapointe et al. 2005b). The widespread invasion of the Mediterranean Sea by *Caulerpa taxifolia* has been linked to land-based nutrient discharges (Chisholm et al. 1997; Jaubert et al. 2003).

Although disturbance from hurricanes has facilitated phase shifts away from coral and towards

* Corresponding author; tele: 772/465-2400 ext 276; fax: 772/468-0757; e-mail: lapointe@hboi.edu

TABLE 1. *Caulerpa brachypus f. parvifolia* mean percent benthic cover at northern Palm Beach County study sites in August 2004, prior to hurricanes Frances and Jeanne. Data include site depths (m), locations (latitude, longitude) and means ± 1 S.D. Note that percent cover generally increases from north to south.

Latitude	Longitude	Site Name	Depth (m)	Cover (%)
26°86	80°01	N. Colonel's Ledge	25	40±20
26°83	80°00	The Bluffs	22	49±27
26°83	80°01	Zimm's Reef	21	49±17
26°82	80°02	Frank's Reef	21	54±20
26°79	79°98	Princess Anne	28	64±5
		Means ± 1 SD	23±3	51±9

macroalgal dominance on some reefs, hurricanes could also play a beneficial role, at least temporarily, by removing the excessive biomass of macroalgal blooms. The effects of wave action and currents from Hurricanes Edith in Puerto Rico (Glynn et al. 1964) and Andrew in south Florida (Blair et al. 1994) both had major effects on reef biota, especially removal of benthic macroalgae. Considering that macroalgal blooms have negative effects on recruitment and growth of hermatypic reef corals and associated biodiversity (Howarth et al. 2000), a reduction of excessive biomass by hurricanes could have positive effects on coral reef development. We had the opportunity to partially address this hypothesis during the late summer of 2004, when two hurricanes directly affected the macroalgal HAB and coral reef communities in northern Palm Beach County. The southern eye wall of Hurricane Frances (category 2 on the Saffir-Simpson scale) made landfall just north of Juno Beach, Florida on 4 September 2004. Shortly thereafter, Hurricane Jeanne (category 3) followed a very similar track to Frances, making landfall on September 24, 2004 at approximately the same location (Sallenger et al. 2006). Considering that the eye of each storm passed just north of two stations (North Colonel's Ledge, NCL; Princess Anne, PA) where the invasion of *C. brachypus* had been monitored between January 2003 and August 2004 (Lapointe et al. 2004), we took advantage of this opportunity to assess the effects of the twin hurricanes on the HAB populations and reef biota, especially *C. brachypus*. We report here the abundance of *C. brachypus* and other macroalgae at NCL and PA before and after the storms, as well as describe the overall physical effects of the twin hurricanes on coral reefs off Palm Beach County.

Methods

Quarterly biotic cover data were collected as part of an Environmental Protection Agency Ecology and Oceanography of Harmful Algal Blooms (ECOHAB) project between January 2003 and July 2004 (pre-hurricane) at the NCL (25 m depth) and PA (28 m depth) sites (Table 1) by SCUBA divers using replicate (n = 3) 50-m belt transects and digital underwater video. One diver slowly swam along each transect, demarcated with a Keson fiberglass survey tape, using a Sony TRV 900 digital camcorder in an Amphibico Navigator 900 underwater housing to obtain high resolution underwater imagery. The diver facilitated sharp imagery by holding the camera still, perpendicular to, and approximately 0.3 m off the reef surface. A second diver collected voucher specimens to allow for taxonomic identification of macroalgae in the laboratory. To quantify reef biota, ten video frames equally spaced along each of the three transects were grabbed and used as benthic quadrats (0.4 m^2). Using ten randomized points projected onto each quadrat with a high resolution monitor, two separate scorers used the randomized point count method to estimate benthic HAB coverage (%; Lapointe 1997). In July and August 2004, just prior to landfall of Hurricanes Frances and Jeanne, three additional reef sites (The Bluffs, Zimm's Reef, Frank's Reef) were surveyed in northern Palm Beach County for percent cover of *C. brachypus* (Table 1).

Following the twin hurricanes, the NCL and PA sites as well as 22 additional reef sites in Palm Beach County were surveyed in collaboration with Florida's Fish and Wildlife Research Institute. As part of this broader spatial assessment of hurricane effects, we had the opportunity to observe the effects of the hurricanes not only on HABs, but also on reef sedimentation and burial. To enable rapid assessments in this post-hurricane work, we collected video imagery from replicate (n = 2) 25-m belt transects at a total of 24 reefs sites in Palm Beach County, which included NCL, PA, The Bluffs, and Zimm's and Frank's Reefs where pre-hurricane surveys of *C. brachypus* cover (%) had been made. In the laboratory, 15 still images per transect were frame-grabbed from transect video at each site and each image was overlayed with a randomly generated pattern of ten points (dots) using PointCoint '99 software and analyzed for percent cover (Porter et al. 2002).

Results and Discussion

The coral reef communities in the northern Palm Beach County study area represent the northern extent of tropical reef coral growth in Florida. Historically, these coral reefs have had relatively low cover of hermatypic corals and higher cover of octocorals and sponges (Jaap and Hallock 1990), and all of these biota have faced increasing competition with macroalgae in recent decades (Lapointe et al. 2005a,b). Results of our ECOHAB monitoring at both the PA and NCL sites in 2003–2004 quantified the explosive invasion of *C.*

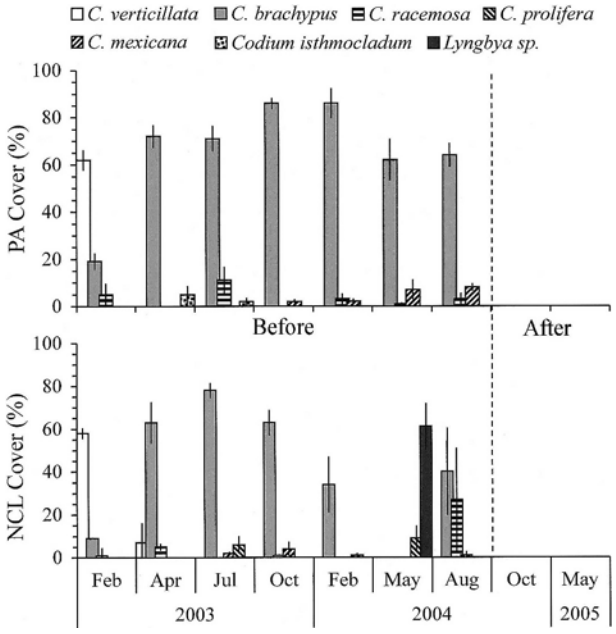

Fig. 1. Mean percent harmful algal bloom (HAB) cover at North Colonel's Ledge (NCL) and Princess Anne (PA) between January 2003 and May 2005. Values represent means ± 1 SD (n = 2–6). Dashed line indicates passage of Hurricanes Frances and Jeanne. Note that cover of *C. brachypus* forma *parvifolia* decreases to zero at both sites after landfall of Hurricanes Frances and Jeanne in September 2004.

brachypus into these reef communities. In February 2003, *C. verticillata* was the dominant HAB species at both the PA and NCL sites (Fig. 1). At this time, *C. brachypus* accounted for relatively low cover (~ 20%) at the PA site, and only trace amounts (< 1% cover) were observed at NCL. By April 2004, *C. brachypus* had increased to 60–70% cover at both PA and NCL, becoming the dominant space-occupying organism at both sites (Figs. 1 and 2A). Between April 2003 and August 2004, *C. brachypus* consistently occurred at 60% to 90% cover at PA. *C. brachypus* was more variable at NCL during this period, ranging from 38% to 80% cover, and was overgrown by a bloom of the cyanobacterium *Lyngbya* sp. in May 2004. In addition to *C. brachypus*, *C. racemosa* also formed extensive blooms on some reefs by August 2004 and, together with *Caulerpa mexicana*, *Caulerpa prolifera*, and *C. isthmocladum*, contributed to the macroalgal HAB communities at NCL and PA (Figs. 1 and 2B). In late August 2004, surveys at three other reef locations (The Bluffs, Zimm's Reef, Frank's Reef) in northern Palm Beach County indicated that *C. brachypus* covered from 40% to 64% of benthic reef communities in the northern Palm Beach County study area, with coverage generally decreasing from south to north (Table 1).

Extensive reef surveys at the 24 sites in Palm Beach County following Hurricanes Frances and Jeanne revealed virtually complete physical removal or burial of *C. brachypus* and other HAB species by the storms (see Fig. 1 for ECOHAB sites NCL and PA). No fragments or even traces of these chlorophyte HAB species were observed at any of the 24 reef sites in November 2004 or in May 2005 (Fig. 2C). Working from south to north in Palm Beach County in November 2004, complete reef burial by sand was first observed at a nearshore site in Boca Raton in southern Palm Beach County. Several mid depth reef sites (9–15 m) were covered by fine to coarse sediment layers 8–10 cm thick; many of the deep reef sites (to 43 m) were covered by a 1-cm thick layer of fine sediment and silt (Fig. 2D). We observed extensive drifting and scouring of coarse sand adjacent to deep reefs in water up to 43 m depths offshore northern Palm Beach County, confirming substantial physical effects to these deep reef communities (Fig. 2E). Physical effects of Hurricane Allen on August 6, 1980 were documented to 50 m depths on reefs at Discovery Bay, Jamaica, where platelike colonies of *Agaricia* spp. were damaged and sediments washed away (Woodley et al. 1981). On reefs off Jupiter, Florida, where beach renourishment projects were completed just prior to Hurricanes Frances and Jeanne, we observed accumulations of fine silt-clay deposits, some in excess of 1 m thick, along the western edge of reefs (Fig. 2F).

These observations suggest that removal of *C. brachypus* and other macroalgae by physical removal or burial was one of the most pronounced ecological effects of the twin hurricanes on southeast Florida's reefs. Similar observations have been made previously. A variety of macroalgae growing on *Porites furcata* in the shallow reef flat at La Parguera, Puerto Rico, were removed by strong wave action associated with Hurricane Edith on September 26–27, 1963; compared to the macroalgae, relatively little damage occurred to the *Porites* coral associations (Glynn et al. 1964). The macroalgal community consistently showed the greatest loss (40–90%) of all reef biota from Hurricane Andrew, a category 4 storm, that made landfall on 22 August 1992 in Dade County, Florida; compared to macroalgae, a lower loss of octocorals (50%) and hard corals (38%) occurred on the offshore reefs (Blair et al. 1994). Although we observed virtually complete removal of macroalgae on Palm Beach County's reefs following Hurricanes Frances and Jeanne, we also noted considerable detachment and loss of octocorals and sponges, as well as burial of hard corals by these storms.

The differential susceptibility of biota to physical effects from hurricanes has been reported for other south Florida ecosystems. Hurricane Georges passed over the middle and lower Florida Keys on 25

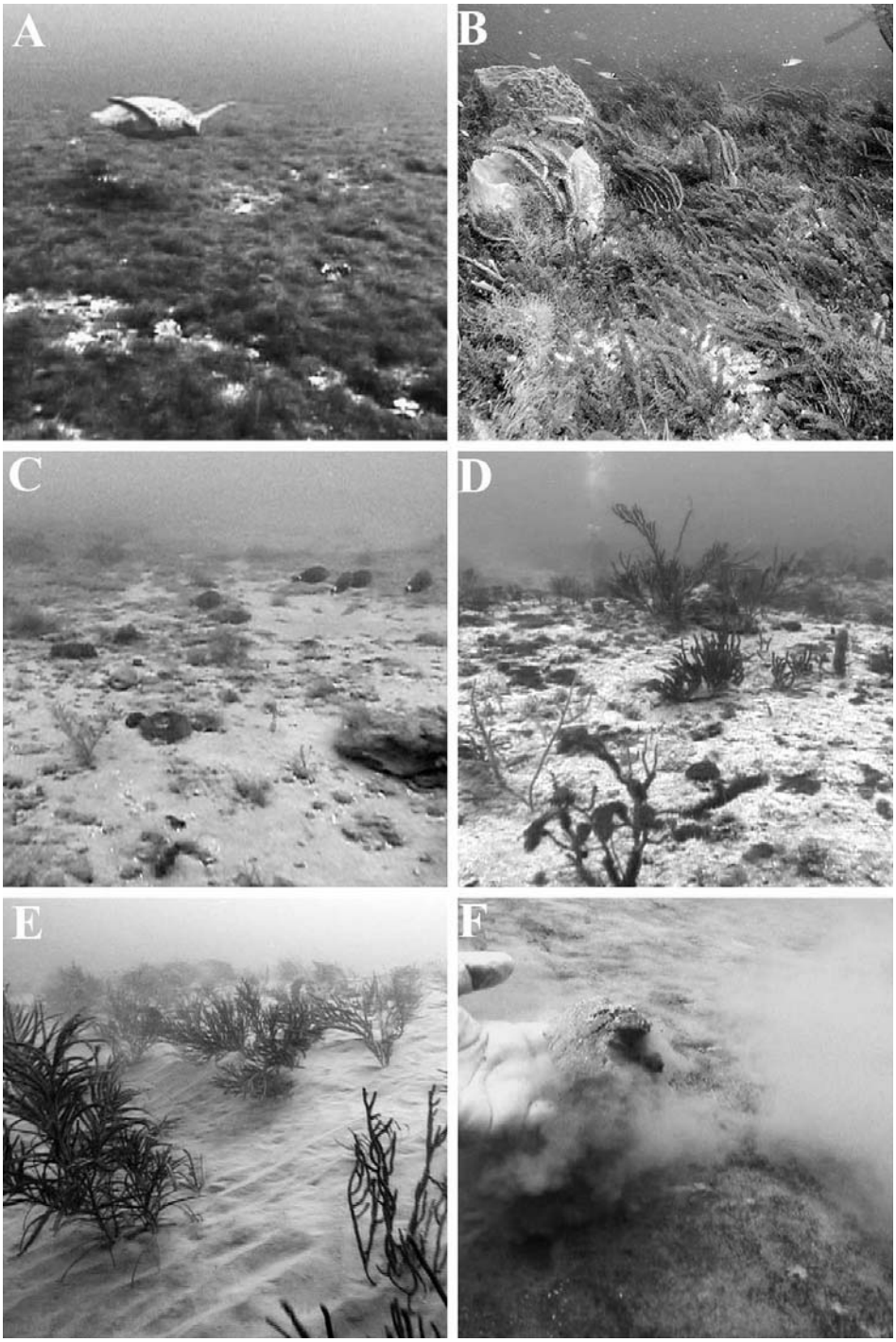

Fig. 2. Underwater images: A) thick mat of *Caulerpa brachypus* forma *parvifolia* overgrowing reef at Princess Anne, 10 February 2004; B) bloom of *Caulerpa racemosa* at North Colonel's Ledge, August 2004; C) Princess Anne site on November 9, 2004, following removal of *C. brachypus* bloom by Hurricanes Frances and Jeanne; D) thin sediment layer on reef (66% sediment cover over hard bottom (site BR 19) in Broward County on October 14, 2004; E) burial of reef (South Double Ledges, Palm Beach County) by coarse sand movement, October 9, 2004; and F) fine sediment deposit on west side of Jupiter Ledge, northern Palm Beach County, November 30, 2004.

September 1998, resulting in greater losses of calcareous green macroalgae (24%) compared to either *Thalassia testudinum* (3%) or *Syringodium filiforme* (19%) in back reef seagrass meadows (Fourqurean and Rutten 2004). Hurricane Andrew had devastating effects on mangrove forests in Everglades National Park (Smith et al. 1994) that varied with size and species of the mangroves. Maximum mortality occurred in the 20–25 cm diameter at breast height (DBH) class for *Rhizophora mangle* and *Avicennia germinans* compared to the 15–20 cm DBH class for *Laguncularia racemosa*; comparisons among species revealed that *A. germinans* had significantly less mortality than either *L. racemosa* or *R. mangle*. Compared to the major damage to the mangrove forests, Hurricane Andrew had relatively minor effects on adjacent seagrass meadows (Tilmant et al. 1994).

Over geological time scales, coral reefs have adapted to a broad spectrum of natural disturbances including changes in temperature, abundance of coral predators, sea level, and physical effects from tropical hurricanes and cyclones. This natural disturbance regime has been important for the development of species diversity, community structure, and dynamics of coral reefs (Nystrom et al. 2000). The prospects for recovery of coral reefs in southeast Florida from the twin hurricanes are uncertain. Anthropogenic nutrient enrichment of coastal waters has altered the natural disturbance regime affecting these reefs, which can prevent the recovery of coral reefs from the physical effects of hurricanes (Kinsey 1988; Bell and Elmetri 1995). Recent observations of reemerging HABs and other opportunistic biota support this hypothesis. Surveys off Jupiter in July 2005 indicated that small populations of *C. brachypus* were beginning to reemerge from deep reef habitats. On 24 October, the reefs were affected again by Hurricane Wilma. Following several months of turbid coastal water after Wilma's passage, reefs in northern Palm Beach County were rapidly colonized by the bryozoan *Scrupocellaria* sp. at levels up to 45% cover (at site PA). This bryozoan had not been abundant during any previous surveys since our observations began in 2001. More recently, thick mats of *Cladophora liniformis* overgrew octocorals and sponges on reefs in northern Palm Beach County at up to 47% cover (Zimm's Reef) in May 2006. Opportunistic biota (both heterotrophic and autotrophic) are competing for newly created space following the hurricane disturbance and their unusually high biomass levels further indicate nutrient stress. Recovery of these reefs from HABs and other opportunistic biota might be improved if the major anthropogenic nutrient sources supporting the blooms, i.e., sewage and agricultural runoff, could be moderated through improved wastewater treatment, reuse, and nonpoint source nutrient management (NRC 2000).

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Literature Cited

Bell, P. R. F. and I. Elmetri. 1995. Ecological indicators of large-scale eutrophication in the Great Barrier Reef lagoon. *Ambio* 24: 208–215.

Blair, S. M., T. L. McIntosh, and B. J. Mostkoff. 1994. Impacts of Hurricane Andrew on the offshore reefs systems of central and northern Dade County, FL. *Bulletin of Marine Science* 54:961–973.

Chisholm, J. R. M., F. E. Fernex, D. Mathieu, and J. M. Jaubert. 1997. Wastewater discharge, seagrass decline and algal proliferation on the Cote d' Azur. *Marine Pollution Bulletin* 34:78–84.

Connell, J. H. 1978. Diversity in tropical rainforests and coral reefs. *Science* 199:1302–1309.

Cribb, A. B. 1958. Records of marine algae from south-eastern Queensland—IV. Caulerpa. University of Queensland Papers, University of Queensland Press, Brisbane, Australia.

Fourqurean, J. W. and L. M. Rutten. 2004. The impact of Hurricane Georges on soft-bottom back reef communities: Site- and species-specific effects in south Florida seagrass beds. *Bulletin of Marine Science* 75:239–257.

Gardner, T. A., I. M. Cote, J. A. Gill, A. Grant, and A. R. Watkinson. 2005. Hurricanes and Caribbean coral reefs: Impacts, recovery patterns, and role in long-term decline. *Ecology* 86:174–184.

Geister, J. 1977. The influence of wave exposure on the ecological zonation of Caribbean reefs. *Proceedings of the 3rd International Coral Reef Symposium* 1:23–39.

Glynn, P. W., L. R. Almodóvar, and J. G. Gonzales. 1964. Effects of Hurricane Edith on marine life in la Parguera, Puerto Rico. *Caribbean Journal of Science* 4:335–345.

Goreau, T. J. and R. M. Hayes. 1994. Coral bleaching and ocean hot spots. *Ambio* 23:176–180.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching, and the future of the world's coral reefs. *Marine and Freshwater Research* 8:839–866.

Howarth, R., D. Anderson, J. Cloern, C. Elfring, C. Hopkinson, B. Lapointe, T. Malone, N. Marcus, K. McGlathery, A. Sharpley, and D. Walker. 2000. Nutrient pollution of coastal rivers, bays, and seas. *Issues in Ecology* 7:1–15.

Hughes, T. P. 1994. Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–1551.

Jaap, W. and P. Hallock. 1990. Coral reefs, p. 574–616. *In* R. Myers and J. J. Ewel (eds.), Ecosystems of Florida. University Press of Florida, Gainesville, Florida.

Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical over-fishing and the recent collapse of coastal ecosystems. *Science* 293:629–638.

JAUBERT, J. M., J. R. M. CHISHOLM, A. MINGHELLI-ROMAN, M. MARCHIORETTI, J. H. MORROW, AND H. T. RIPLEY. 2003. Re-evaluation of the extent of *Caulerpa taxifolia* development in the northern Mediterranean using airborne spectrographic sensing. *Marine Ecology Progress Series* 263:75–82.

JOHANNES, R. E. 1975. Pollution and degradation of coral reef communities, p. 13–51. *In* E. Wood and R. E. Johannes (eds.), Tropical Marine Pollution. Elsevier Oceanography Series 12, New York.

KINSEY, D. W. 1988. Coral reef response to some natural and anthropogenic stresses. *Galaxea* 7:113–128.

LAPOINTE, B. E. 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. *Limnology and Oceanography* 42:1119–1131.

LAPOINTE, B. E. 1999. Simultaneous top-down and bottom-up forces control macroalgal blooms on coral reefs (reply to the comment by Hughes et al.). *Limnology and Oceanography* 44: 1586–1592.

LAPOINTE, B. E., P. J. BARILE, M. M. LITTLER, D. S. LITTLER, B. J. BEDFORD, AND C. GASQUE. 2005a. Macroalgal blooms on southeast Florida coral reefs: I. Nutrient stoichiometry of the invasive green alga *Codium isthmocladum* in the wider Caribbean indicates nutrient enrichment. *Harmful Algae* 4:1092–1105.

LAPOINTE, B. E., P. J. BARILE, M. M. LITTLER, AND D. S. LITTLER. 2005b. Macroalgal blooms on southeast Florida coral reefs II. Cross-shelf discrimination of nitrogen sources indicates widespread assimilation of sewage nitrogen. *Harmful Algae* 4:1106–1122.

LAPOINTE, B. E., P. J. BARILE, AND C. S. YENTSCH. 2004. The physiology and ecology of macroalgal blooms (green tides) on coral reefs off northern Palm Beach County, Florida (USA). *Harmful Algae* 3:185–268.

NATIONAL RESEARCH COUNCIL (NRC). 2000. Clean Coastal Waters: Understanding and Reducing the Effects of Nutrient Pollution. Ocean Studies Board, Water Science and Technology Board, National Academy Press, Washington, D.C.

NYSTROM, M., C. FOLKE, AND F. MOBERG. 2000. Coral reef disturbance and resilience in a human-dominated environment. *Trends in Ecology and Evolution* 15:413–417.

PORTER, J. W., V. KOSMYNIN, K. L. PATTERSON, K. G. PORTER, W. C. JAAP, J. L. WHEATON, K. HACKETT, M. LYBOLT, C. P. TSOKOS, G. YANEV, D. M. MARCINEK, J. DOTTEN, D. EAKEN, M. PATTERSON, O. W. MEIER, M. BRILL, AND P. DUSTAN. 2002. Detection of coral reef change by the Florida Keys Coral Reef Monitoring Project, p. 749–769. *In* J. W. Porter and K. A. Porter (eds.), The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An Ecosystem Sourcebook. CRC Press, Boca Raton, Florida.

ROGERS, C. S. AND J. BEETS. 2001. Degradation of marine ecosystems and decline of fishery resources in marine protected areas in the US Virgin Islands. *Environmental Conservation* 24: 312–322.

SALLENGER, A. H., H. F. STOCKDON, L. FAUVER, M. HANSEN, D. THOMPSON, C. W. WRIGHT, AND J. LILLYCROP. 2006. Hurricanes 2004: An overview of their characteristics and coastal change. *Estuaries and Coasts* 29:880–888.

SMITH, III, T. J., M. B. ROBBLEE, H. R. WANLESS, AND T. W. DOYLE. 1994. Mangroves, hurricanes and lightning strikes. *BioScience* 44: 256–262.

TILMANT, J. T., R. W. CURRY, R. D. JONES, A. SZMANT, J. C. ZIEMAN, M. FLORA, M. B. ROBBLEE, D. SMITH, R. W. SNOW, AND H. WANLESS. 1994. Hurricane Andrew's effect on marine resources. *BioScience* 44:230–237.

WOODLEY, J. D., E. A. CHORNESKY, P. A. CLIFFORD, J. B. C. JACKSON, L. S. KAUFMAN, N. KNOWLTON, J. C. LANG, M. P. PEARSON, J. W. PORTER, M. C. ROONEY, K. W. RYLAARSDAM, V. J. TUNNICLIFFE, C. M. WAHLE, J. L. WULFF, A. S. G. CURTIS, M. D. DALLMEYER, B. P. JUPP, M. A. R. KOEHL, J. NEIGEL, AND E. M. SIDES. 1981. Hurricane Allen's impact on Jamaican coral reefs. *Science* 214: 749–755.