Hurricanes benefit bleached corals

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Recent, global mass-mortalities of reef corals due to record warm sea temperatures have led researchers to consider global warming as one of the most significant threats to the persistence of coral reef ecosystems. The passage of a hurricane can alleviate thermal stress on coral reefs, highlighting the potential for hurricane-associated cooling to mitigate climate change impacts. We provide evidence that hurricane-induced cooling was responsible for the documented differences in the extent and recovery time of coral bleaching between the Florida Reef Tract and the U.S. Virgin Islands during the Caribbean-wide 2005 bleaching event. These results are the only known scenario where the effects of a hurricane can benefit a stressed marine community.

coral bleaching | hurricane cooling | thermal stress

Coral bleaching is the loss of endosymbiotic algae (zooxanthellae) and/or a reduction in the photosynthetic pigment concentrations within the zooxanthellae that can be caused by many adverse environmental conditions (1); however, high sea temperature has been found to be the most important causal factor at large spatial scales (1–3). Worldwide, coral reefs are in a state of decline as a result of many local and regional-scale factors, and one of the greatest threats to the persistence of coral reef ecosystems over the next century is sea temperature warming (4, 5). Hurricane development is dependent on warm (>26°C) sea temperatures (6) and often correlated with widespread bleaching events. A common physical effect of hurricane passage is a reduction in sea temperature (up to 5°C) caused by wind-forced vertical mixing (7–9). It is well documented that physical impacts from storms can be devastating to coral reef ecosystems (10), but the damage caused by storms is highly variable between and within affected reefs (11). Severe damage to coral reefs has been observed and predicted to occur on reefs up to 30–90 km from a storm's center (12–14). Based on the spatial and temporal correlation between coral bleaching events and hurricanes, it has been hypothesized that bleached corals may benefit from hurricane passage (15). To better understand this potential feedback, the magnitude and duration of sea temperature cooling coincident with the passage of hurricanes and tropical storms was assessed for five reef sites on the Florida Reef Tract from 1998 to 2005. We provide evidence that hurricane-induced cooling was responsible for the documented differences in the extent and recovery time of coral bleaching between the Florida Reef Tract and the U.S. Virgin Islands (USVI) during the Caribbean-wide 2005 bleaching event.

Results and Discussion

Decreases in sea temperatures associated with high winds coincided with all hurricanes and tropical storms that passed within 700 km of the Florida Reef Tract (Table 1). Sea temperatures were cooled by 0.3–3.2°C (mean ± SEM = 1.5°C ± 0.10, n = 53) by hurricanes or tropical storms whose tracks passed within 400 km of a site, which is consistent with observations made in Okinawa (15, 17). When storms were >400 km from a site, Δ°C (magnitude of cooling) ranged from 0.1 to 0.9°C (mean ± SEM = 0.5°C ± 0.09, n = 10). Δ°C was significantly related to the nearest distance a storm track passed from a site and was greater when a site was to the left of the storm track (Fig. 1 and Table 2). The most intense surface seawater cooling in the open ocean occurs to the right of a storm's track in the Northern Hemisphere (7–9, 18, 19), but the dynamics of hurricane-induced cooling for reef sites, and complex coastal and shelf environments, are poorly understood (9). The evidence presented here and elsewhere (15) suggests that the coastal cooling response may differ from that in the open ocean. Wind speeds at the sites were significantly correlated with their distance from the storm track and therefore related to Δ°C (Table 2). For the same wind speed, Δ°C was greater for sites to the left of the storm track than the right (Table 2).

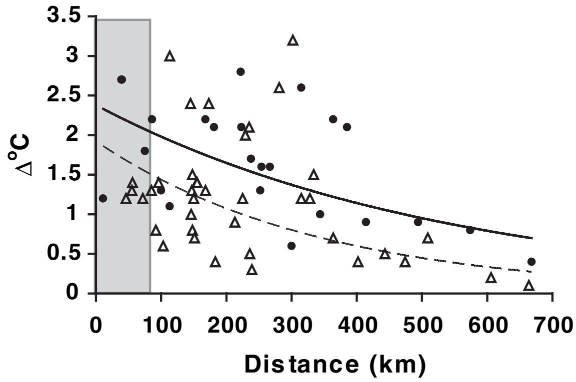

Fig. 1. Effect of distance from storm on magnitude of cooling (Δ°C), Florida Reef Tract (1998–2005). Data points for site being left (filled circles) or right (open triangles) of storm track are indicated. Separate regression lines are shown for site being on left (solid line) or right (dashed line) of storm track. Shaded box indicates range of physical damage swath.

The duration of sea temperature decrease to levels below average ranged from 1 to 40 days (mean ± SEM = 11 days ± 1.2, n = 49) for storms within 400 km, and from 0 to 6 days for storms >400 km from reef sites on the Florida Reef Tract (mean ± SEM = 2 days ± 0.9, n = 10) (Table 3). The duration of cooling was significantly related to Δ°C (correlation analysis, r = 0.49, n = 59, P < 0.0001), distance from the storm track, and wind speed (Table 2). Unlike Δ°C, the duration of cooling was not significantly related to the side of storm passage (Table 2).

In 2005, instances of bleaching in Florida and the USVI coincided with sea temperatures that were warmer than average (Fig. 2) and with the accumulation of thermal stress estimated by the degree heating weeks (DHW) (20) index (Fig. 3). Bleaching was considerably less prevalent and of shorter duration on the Florida Reef Tract compared with the USVI. In September

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Abbreviations: Δ°C, magnitude of cooling; USVI, U.S. Virgin Islands; DHW, degree heating weeks, NOAA, National Oceanic and Atmospheric Administration.

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Table 1. Nearest distance from and magnitude of cooling (Δ°C: max., min.) associated with named storms that affected the Florida Reef Tract from 1998 to 2005

Year	Storm name	Cat	Distance, value (site)	Max. Δ°C, value (site)	Min. Δ°C, value (site)
1998	H Georges	2	46 (DT)	1.4 (MR, SK)	1.2 (FR, DT)
1999	H Floyd	4	300 (FR)	0.9 (MR, SR)	0.4 (DT)
1999	TS Harvey	TS	146 (FR)	1.3 (SR, SK)	0.7 (DT)
1999	H Irene	1	11 (SK)	1.3 (SR)	0.8 (MR)
2001	TS Gabrielle	TS	148 (DT)	3.2 (FR)	1.5 (MR, DT)
2001	H Michelle	1	222 (SR)	2.8 (SR)	1.6 (FR, SK)
2004	H Charley	2	29 (DT)	0.6 (SK)	0.3 (FR)
2004	H Frances	2	168 (FR)	2.2 (FR)	1.7 (MR)
2004	H Ivan	4	368 (DT)	0.5 (SK)	0.1 (FR)
2004	H Jeanne	3	181 (FR)	2.1 (FR)	1.0 (SK)
2005	TS Arlene	TS	226 (DT)	1.2 (SK)	0.4 (MR)
2005	H Dennis	1	66 (DT)	2.1 (SR)	0.7 (FR)
2005	H Katrina	1	39 (FR)	2.7 (DT)	1.3 (MR)
2005	H Rita	2	62 (DT)	1.4 (SR)	0.8 (MR)
2005	H Wilma	3	46 (DT)	3.0 (FR)	2.4 (MR, SR)

Cat, Category of storm [Saffir-Simpson scale (16)] when it was noted distance from site; H, hurricane; TS, tropical storm; FR, Fowey Rocks; MR, Molasses Reef; SR, Sombrero Reef; SK, Sand Key; DT, Dry Tortugas.

2005, bleaching prevalence on the Florida Reef Tract was nearly identical to that observed in the USVI (Fig. 3). However, in October, it began to decline in Florida and continued to increase in the USVI (Fig. 3). Cooling due to Hurricane Rita (September 21–27, 2005) appears to have facilitated the recovery of corals in Florida as the accumulation of DHW ceased. Then, in late October the passage of Hurricane Wilma caused a large decrease in temperature (mean ± SEM = 2.6 ± 0.2, n = 3), followed by rapid bleaching recovery (within ≈2 weeks; Fig. 4), as evidenced by a dramatic decline of prevalence in early November to levels near those observed at the start of monitoring (Fig. 2). Conversely, in the USVI, bleaching peaked at that time with nearly 90% of all coral colonies bleached (Fig. 2). Interestingly, if a decrease in sea temperature comparable with that caused by Wilma in Florida occurred in the USVI in late October, temperatures there would have dropped to values observed in January when recovery was underway. Despite the high frequency of hurricanes in the North Atlantic in 2005, the closest storm to pass near the USVI was tropical depression Alpha (October 22–24; maximum sustained winds = 45 knots), which was >400 km away. In the absence of storm-induced cooling pulses, only the general seasonal decline in sea temperature was recorded. Consequently, the thermal stress accumulation continued longer (3 months in the USVI vs. 2 in Florida), bleaching prevalence was higher, and recovery from bleaching was greatly delayed into 2006 in the USVI.

Approximately 81 hurricanes have made landfall in either southeast or southwest Florida from 1851 to 2005 [$f_{\text{hurricane-(1851–2005)}} = 0.53$ hurricanes yr^{-1}] [ref. 21; see also www.aoml.noaa.gov/hrd/tcfaq/tcfaqHED.html for updated information regarding number of hurricane landfalls in south Florida (1851–2004) and discussion of factors that lead to hurricane formation], whereas five widespread coral bleaching events have impacted the Florida Reef Tract from 1987 to 2005 [$f_{\text{bleaching-(1987–2005)}} = 0.26$ events yr^{-1}] (22). If we use these frequencies as a baseline for the expected rate of future events, we find that the chance of a hurricane landfall and a bleaching event co-occurring in any given year is low ($P = 0.14$). If we assume the rate of bleaching in the future will be more representative of that observed from 1997 to 2005 [$f_{\text{bleaching-(1997–2005)}} = 0.33\ \text{yr}^{-1}$], the probability of these two phenomena co-occurring in the same year increases slightly [$P = f_{\text{bleaching-(1997–2005)}} \times f_{\text{hurricane-(1851–2005)}} = 0.17$]. The benefit that temperature-stressed corals may derive from proximal hurricane passage increases proportionally with the number of hurricanes in a given year, but multiple hurricane impacts at the same site in 1 year becomes less likely with each additional storm. For instance, the likelihood of four hurricanes impacting the Florida Reef Tract, which occurred in 2005, coincident with a bleaching event is rare ($P = 0.02$). The factors conducive to coral bleaching and hurricane formation are not entirely independent (i.e., warm water, low vertical wind shear; see www.aoml.noaa.gov/hrd/tcfaq/tcfaqHED.html), and the historical data of hurricane events only considers storms that made landfall

Table 2. *F* statistics, *P* values, and r^2 for linear regression and ANCOVA tests of the relationship between Δ°C and duration of cooling with distance from storm center, wind speed, and side of storm passage (left or right)

	Δ, °C			Duration of cooling		
Parameter	F	r^2	P value	F	r^2	P value
Distance	24.4	0.29	<0.0001	14.0	0.20	0.0001
Wind speed	22.6	0.27	<0.0001	12.4	0.18	0.001
Side of passage	5.8	0.09	0.01	0.19	0.003	NS
Distance × side of passage	19.9	0.40	<0.0001	7.1	0.20	0.001
Wind × side of passage	17.9	0.37	<0.0001	6.3	0.18	0.001

ANCOVA tests represent results from test for equal slopes as all tests for unequal slopes were not significant (NS). Δ°C was log transformed [ln(Δ°C)] and duration of cooling was square-root-transformed for regression analyses.

Table 3. Duration (days: max., min.) of cooling associated with named storms that affected the Florida Reef Tract from 1998 to 2005

Year	Storm name	Max. duration of cooling, value (site)	Min. duration of cooling, value (site)
1998	H Georges	9 (MR*, SK*)	7 (FR, SR)
1999	H Floyd	1 (FR)	0 (MR, SR, SK, DT)
1999	TS Harvey	12 (SK)	3 (FR)
1999	H Irene	9 (FR)	5 (MR)
2001	TS Gabrielle	15 (FR)	2 (SR)
2001	H Michelle	40 (MR)	5 (SR)
2004	H Charley	7 (SK)	1 (FR)
2004	H Frances	11 (FR)	3 (MR, SK)
2004	H Ivan	5 (SK)	0 (FR, MR)
2004	H Jeanne	26 (FR)	5 (SK)
2005	TS Arlene	8 (SK)	4 (MR*)
2005	H Dennis	23 (SR)	8 (MR)
2005	H Katrina	21 (DT)	4 (FR)
2005	H Rita	8 (FR)	3 (MR)
2005	H Wilma	22 (FR)	11 (SR)

Value refers to number of days it took for sea temperature to warm to prestorm value. Abbreviations are defined in Table 1.
*Indicates that site was below long-term average before impact of storm.

in south Florida. Hurricanes Dennis and Rita did not make landfall in south Florida in 2005, yet cooling along the entire Florida Reef Tract was observed as a result of these storms (Table 1). Thus, these factors likely make the probabilities reported an underestimate of the chances of these two events occurring at the same time.

Hurricane cooling is not expected to completely nullify the proposed effects of climate change on coral reefs (4, 5); however, instances in which hurricane and bleaching events co-occur can have a significant effect on coral reef persistence. We have shown that the area of cooling extends substantially outside the

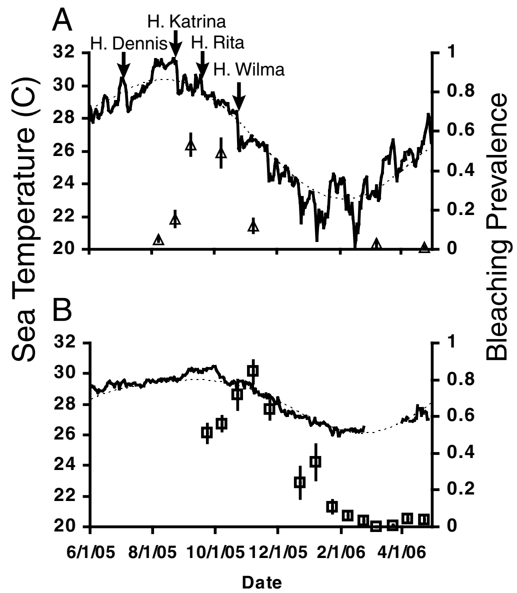

Fig. 2. Daily average sea temperature and bleaching prevalence from June 2005 through April 2006. (*A*) Florida Reef Tract. (*B*) USVI. Data points represent mean ± SEM bleaching prevalence. Solid and dashed lines represent the daily average and seasonal cycle for sea temperature, respectively. Arrows indicate timing of hurricane impacts clearly showing the cooling effect.

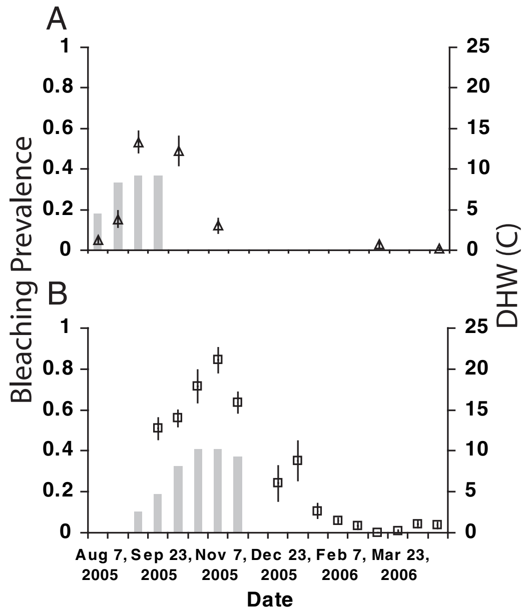

Fig. 3. Bleaching prevalence and DHW. (*A*) Florida Reef Tract. (*B*) USVI. Data points represent mean ± SEM bleaching prevalence. Gray bars represent DHW.

narrow swath of physical damage, providing empirical evidence that the passage of a hurricane can proportionally benefit a much greater area than it disturbs when reef corals are thermally stressed. During the 2005 Caribbean-wide bleaching event, the Florida Reef Tract was impacted by multiple hurricanes, whereas no major storms passed within 400 km of the USVI. Consequently, the prevalence of bleaching was considerably less, and recovery occurred more rapidly on Florida reefs compared with those in the USVI. Hurricane-induced cooling on Florida reefs depressed the accumulation of thermal stress, which likely explains the differences in bleaching between Florida and the USVI. Single, severe bleaching events can have dramatic, long-lasting impacts on the structure and function of coral reefs (23), and the cooling benefit of a hurricane can have substantial mitigative effects as documented in this study.

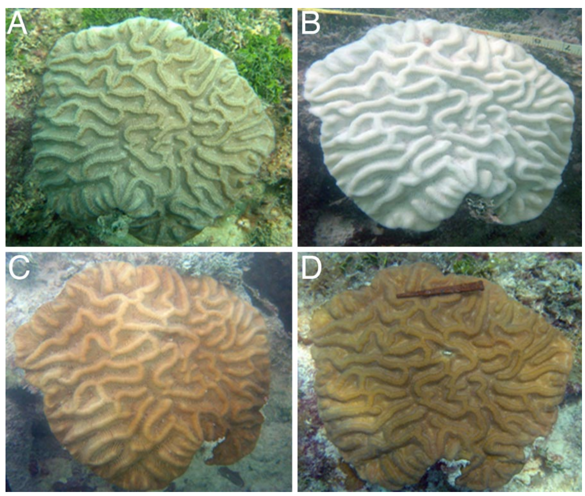

Fig. 4. Time-series of bleached coral (*Colpophyllia natans*) at Coral Gardens, Florida Reef Tract. (*A*) Prebleaching (August 11, 2005). (*B*) Bleached (September 6, 2005). (*C*) Nearly recovered (November 9, 2005). (*D*) Recovered with normal pigmentation (March 2, 2006). Nail in *D* is 8.3 cm long.

Table 4. Location, depth, and timing of surveys in USVI

Site	*Z*, m	Latitude	Longitude	Survey periods
Benner, ST	6	17°47′2.70″N	64°45′41.34″W	1, 13
Black Pt, ST	12	18°20′40.20″N	64°59′9.42″W	1, 14
Botony, ST	11	18°21′30.42″N	65°1′59.88″W	2, 10, 13
Buck Is, ST	14	18°16′43.79″N	64°53′53.99″W	1, 13
Buck Is, SC	14	17°47′7.33″N	64°36′33.01″W	8, 12
Cane Bay, SC	12	17°46′25.98″N	64°48′48.60″W	3, 5, 10
Eagle Ray, SC	13	17°45′41.40″N	64°41′55.68″W	4, 11
Fish Bay, SJ	6	18°19′51.01″N	64°45′50.69″W	2, 15
Flat Cay, ST	14	18°19′5.59″N	64°59′27.74″W	1, 14
Frenchman's, ST	11	18°19′8.15″N	64°55′26.83″W	7
Great Pond, SC	5	17°42′39.49″N	64°39′7.96″W	5
Jack's Bay, SC	13	17°44′36.13″N	64°34′17.76″W	5
King's Corner, SC	16	17°40′30″N	64°53′33″W	12
Lang Bank, SC	30	17°49′25.39″N	64°26′57.95″W	8, 11
Megan's, ST	10	18°22′27.30″N	64°56′3.77″W	3, 11, 13
Rupert's, ST	5	18°19′41.66″N	64°55′35.51″W	7
S Capella, ST	21	18°15′45.60″N	64°52′20.52″W	1, 14
S Fish, SJ	30	18°14′39.59″N	64°45′29.95″W	2, 15
S Water, ST	21	18°16′50.45″N	64°56′45.31″W	2, 14
Salt River, SC	9	17°47′7.08″N	64°45′33.84″W	2, 11
Savana, ST	7	18°20′26.30″N	65°4′55.38″W	2
Seahorse, ST	16	18°17′40.80″N	64°52′30.00″W	2, 15
Sprat Hall, SC	14	17°44′2.40″N	64°53′43.44″W	9
St James, ST	15	18°17″40.52″N	64°49′56.57″W	2, 14

SC, St. Croix; SJ, St. John; ST, St. Thomas; *Z*, depth. Survey periods are as follows: 1, Sep. 16–30, 2005; 2, Oct. 1–15, 2005; 3, Oct. 16–31, 2005; 4, Nov. 1–15, 2005; 5, Nov. 16–30, 2005; 6, Dec. 1–15, 2005; 7, Dec. 16–31, 2005; 8, Jan. 1–15, 2006; 9, Jan. 16–31, 2006; 10, Feb. 1–14, 2006; 11, Feb. 15–28, 2006; 12, Mar. 1–15, 2006; 13, Mar. 16–31, 2006; 14, Apr. 1–15, 2006; 15, Apr. 16–30, 2006.

Materials and Methods

Environmental Data Analysis. The SEAKEYS (Sustained Ecological Research Related to Management of the Florida Keys Seascape) program began long-term monitoring of meteorological and oceanographic conditions along the Florida Reef Tract in 1989 to complement the National Data Buoy Center's (NDBC) Coastal-Marine Automated Network (C-MAN) (24). For the purpose of this study only, those SEAKEYS stations situated on the Florida Reef Tract were of interest. These are Fowey Rocks (25°35′24″N, 80°5′60″W, at the northern terminus of the Florida Reef Tract), Molasses Reef (25°0′36″N, 80°22′48″W, east of Key Largo), Sombrero Reef (24°37′48″N, 81°6′36″W, south of Marathon), Sand Key (24°26′60″N, 81°52′48″W, south of Key West), and the Dry Tortugas (24°38′24″N, 82°51′36″W, at the western end of the Florida Reef Tract). From these stations, hourly averages of *in situ* sea temperature, measured with a thermistor (Model 44212, YSI, Yellow Springs, OH) at the surface, and wind speed, measured with an anemometer (Model 05106, R. M. Young, Traverse City, MI), were obtained (see www.ndbc.noaa.gov/instr.shtml for description of sensor calibration at National Data Buoy Center sites). Daily average sea temperature and daily average wind speed were determined from 1998 to 2005 for the five reef sites on the Florida Reef Tract. Δ°C (difference between prestorm and poststorm daily average sea temperature), the duration of cooling (number of days that sea temperature remained below the seasonal average), and the daily maximum wind speed due to storms was determined. The seasonal sea temperature cycle was estimated by taking the average of each day for the years of data available at each site and was smoothed by interpolating a sixth-order polynomial by using least squares. Data acquisition began in 1988 at Molasses and Sombrero Reef, in 1991 at Fowey Rocks and Sand Key, and in 1992 at the Dry Tortugas. Daily average sea temperature from Sombrero Reef was used in Fig. 2 because this site was near those monitored for bleaching and is located roughly in the middle of the Florida Reef Tract.

Regression analysis was used to evaluate the relationship between both Δ°C and the duration of cooling with distance from the storm center and wind speed. Distance from the storm center was estimated as the nearest distance that the plotted coordinates of a storm track passed to a site (see weather.unisys.com/hurricane/atlantic for Atlantic Tropical Storm tracking by year). The relationship between cooling patterns and the location of a site with respect to the track of the storm was tested with analysis of covariance (ANCOVA; tests for equal and unequal slopes). An α level of 0.05 was used for significance in all tests.

Sea temperature in the USVI was measured with an *in situ* Conductivity, Temperature, and Depth (CTD) instrument (part NXIC-CTD-BIO-AUTO, Falmouth Scientific, Cataumet, MA) affixed at 1-m depth to the National Oceanic and Atmospheric Administration (NOAA) Integrated Coral Observing Network (ICON) station at Salt River Bay, St. Croix, USVI (17°47′2.7″N, 64°45′41.34″W) that has been operational since 2002. The seasonal temperature cycle at this site was estimated in the aforementioned way, but we caution that this likely does not represent a true climatology given the short time frame over which data were acquired. Accumulated thermal stress was estimated by DHW, and values for Florida and the USVI were obtained online (see coralreefwatch.noaa.gov/satellite/current/sst_series_24reefs.html for NOAA Coral Reef Watch SST/DHW Time Series and Satellite Bleaching Alerts). DHW are the number of weeks that sea surface temperatures are 1°C greater than the expected annual maximum and represent the accumulation of thermal stress for the past 12 weeks (ref. 20 and http://coralreefwatch.noaa.gov/satellite/current/sst_series_24reefs.html).

Coral Bleaching Documentation. Corals within permanent quadrats (16 m^2, n = 5 per site) were surveyed for bleaching approximately biweekly on the Florida Reef Tract at French Reef (depth = 5–10 m, 25°2′1.32″N, 80°20′59.82″W), Little Grecian Reef (depth = 5 m, 25°7′8.40″N, 80°18′1.20″W), Cheeca Rocks (depth = 5 m, 24°53′49.56″N, 80°36′56.82″W), and Coral Gardens (depth = 5 m, 24°50′9.42″N, 80°43′39.42″W) from August through November 2005 and twice more in the spring of 2006. In the USVI, surveys of coral communities occurred at reef sites (n = 24, depth <30 m) adjacent to St. Thomas, St. Croix, and St. John from September 2005 through April 2006 (Table 4). Corals intercepted by a 10-m transect line (n = 6 transects per site) were assessed for bleaching at biweekly intervals from mid-September 2005 to the end of April 2006.

At each location, prevalence of bleaching was calculated as the mean proportion of coral colonies >10 cm in maximum diameter within sampling units (quadrats or transects) exhibiting bleaching on >10% of the colony's surface area. Bleaching prevalence values were averaged over all sampling units at all sites for each region. Bleaching-induced, complete colony mortality was rare during the recovery period in the USVI and was not observed for any corals monitored in Florida, ensuring that decreases in bleaching prevalence represented recovery. Recovery was deemed complete when bleaching prevalence declined to <10%, which was similar to ambient levels of bleaching before temperature disturbance.

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1. Glynn PW (1993) *Coral Reefs* 12:1–17.
2. Brown BE (1997) *Coral Reefs* 16S:129–138.
3. Berkelmans R (2002) *Mar Ecol Prog Ser* 229:73–82.
4. Hoegh-Guldberg O (1999) *Mar Freshwat Res* 50:839–866.
5. Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, *et al.* (2003) *Science* 301:929–933.
6. Gray WM (1979) in *Meteorology Over the Tropical Oceans*, ed Shaw DB (R Meteorol Soc, Berkshire, UK), pp 155–218.
7. Cornillon P, Stramma L, Price JF (1987) *Nature* 326:373–375.
8. Price JF, Sanford TB, Forristall GZ (1994) *J Phys Oceanogr* 24:233–260.
9. Xie L, Pietrafesa LJ, Bohm E, Zhang C, Li X (1998) *Geophys Res Lett* 25:769–772.
10. Harmelin-Vivien ML (1994) *J Coast Res Spec Issue* 12:211–231.
11. Lirman D, Fong P (1997) *Proc 8th Int Coral Reef Symp* 1:561–566.
12. Done TJ (1992) *Cont Shelf Res* 12:859–872.
13. Woodley JD (1992) *Hydrobiologia* 247:133–138.
14. Scoffin TP (1993) *Coral Reefs* 12:203–221.
15. Glynn PW (1996) *Galaxea* 13:143.
16. Simpson RH, Reihl H (1981) *The Hurricane and its Impact* (Louisiana State Univ Press, Baton Rouge, LA).
17. Nadaoka K, Nihei Y, Kumano R, Yokobori T, Omija T, Wakaki K (2001) *Coral Reefs* 21:387–398.
18. Price JF (1981) *J Phys Oceanogr* 11:153–175.
19. Stramma L, Cornillon P, Price JF (1986) *J Geophys Res* 91:5031–5035.
20. Gleeson MW, Strong AE (1995) *Adv Space Res* 16:151–154.
21. Jarrell JD, Mayfield M, Rappaport EN, Landsea CW (2001) *The Deadliest, Costliest, and Most Intense United States Hurricanes from 1900 to 2000 (and other Frequently Requested Hurricane Facts)* (Natl Oceanic and Atmos Administration, Miami), NOAA Tech Memo NWS TPC-1.
22. Causey BD (2001) in *Proceedings of the Workshop on Mitigating Coral Bleaching Impact Through MPA Design*, eds Salm RV, Coles SL (Nature Conservancy, Honolulu), pp 60–66.
23. Glynn PW (1988) *Galaxea* 7:129–160.
24. Ogden JC, Porter JW, Smith NP, Szmant AM, Jaap WC, Forcucci D (1994) *Bull Mar Sci* 54:1059–1071.