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Marine Pollution Bulletin 54 (2007) 1923–1931
MARINE POLLUTION BULLETIN
www.elsevier.com/locate/marpolbul

Coral bleaching indices and thresholds for the Florida Reef Tract, Bahamas, and St. Croix, US Virgin Islands

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Abstract

It is well established that elevated sea temperatures cause widespread coral bleaching, yet confusion lingers as to what facet of extreme temperatures is most important. Utilizing long-term in situ datasets, we calculated nine thermal stress indices and tested their effectiveness at segregating bleaching years *a posteriori* for multiple reefs on the Florida Reef Tract. The indices examined represent three aspects of thermal stress: (1) short-term, acute temperature stress; (2) cumulative temperature stress; and (3) temperature variability. Maximum monthly sea surface temperature (SST) and the number of days >30.5 °C were the most significant; indicating that cumulative exposure to temperature extremes characterized bleaching years. Bleaching thresholds were warmer for Florida than the Bahamas and St. Croix, US Virgin Islands reflecting differences in seasonal maximum SST. Hind-casts showed that monthly mean SST above a local threshold explained all bleaching years in Florida, the Bahamas, and US Virgin Islands.
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Keywords: Coral bleaching threshold; Thermal stress indices; SST; Florida Reef Tract; Lee Stocking Island, Bahamas; St. Croix, US Virgin Islands

1. Introduction

Coral bleaching (loss of symbiotic zooxanthellae and/or their pigments) is a stress response that can be caused by many adverse environmental conditions; however, high sea temperature has been repeatedly identified as the most important causal factor at large spatial scales (Glynn, 1993; Brown, 1997; Hoegh-Guldberg, 1999; Berkelmans, 2002a). Coral bleaching events have been reported with increasing frequency on the Florida Reef Tract over the past 25 years. Isolated bleaching events occurred in 1911, 1961, 1973, and 1983 (Mayer, 1914; Shinn, 1966; Jaap, 1979, 1985), whereas the first event spanning the entire reef tract occurred in 1987 (Causey, 2001). Bleaching events in the 1980s were limited to the offshore reef tract, but in 1990 hydrocorals (*Millepora* spp.) on inshore patch reefs and the outer reef tract bleached (Causey, 2001). The most widespread and severe bleaching events have occurred during the past 10 years in 1997, 1998, and 2005, punctuated by mild and more localized bleaching events in the interim.

The variability in severity of bleaching both within and between sites is understandable given the complexity of the bleaching response. There is a broad continuum of pigment state (color) in zooxanthellate corals that is a function of temperature, light, and exposure time (Fitt et al., 2001), as corals naturally go through seasonal changes in zooxanthellae densities (Fitt et al., 2000). Although normal seasonal changes do occur in zooxanthellae densities, Warner et al. (2002) found that corals in the *Montastraea* species complex can lose up to 90% of their zooxanthellae without showing obvious signs of bleaching. Thus, visibly discernable paling in corals is a considerable metabolic stress to the coral host and should not be misinterpreted as normal just because zooxanthellae densities vary

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doi:10.1016/j.marpolbul.2007.08.009

seasonally. Furthermore, inter- and intra-specific variability exists in the susceptibility of the coral host (Knowlton et al., 1992; Edmunds, 1994) and zooxanthellae (Rowan et al., 1997) to temperature stress.

Although the response of corals to elevated temperatures is highly complex, a number of indicators have been generated with temperature data to hind-cast and forecast bleaching episodes. Monthly mean sea temperatures above a local threshold (Goreau et al., 1993; Brown et al., 1996) as well as cumulative heat stress have been used to explain bleaching events (Gleeson and Strong, 1995; Podesta and Glynn, 1997). Berkelmans et al. (2004) found that 3-day maximum temperatures best correlated with spatial patterns of bleaching on the Great Barrier Reef, whereas a log–log linear relationship existed between temperature and number of days above that temperature at which bleaching occurred in Puerto Rico (Winter et al., 1998). Sammarco et al. (2006) re-evaluated the Puerto Rico dataset and showed warm, bleaching years were characterized by high variance in bi-weekly sea temperature whereas a lower variance in temperature occurred during warm, non-bleaching years.

To assess which aspects of temperature best explained bleaching years on the Florida Reef Tract, we calculated nine separate indices representing three facets of thermal stress: (1) short-term, acute temperature stress; (2) cumulative temperature stress; and (3) temperature variability. In addition, daily and monthly anomalies were calculated from derived seasonal cycles for Florida reef sites. Lastly, estimated bleaching thresholds for Florida were compared with those for the Bahamas and St. Croix, US Virgin Islands.

2. Methods

2.1. SEAKEYS data

The SEAKEYS (sustained ecological research related to management of the florida keys seascape) program began in 1989 to complement the National Data Buoy Center's (NDBC) Coastal-Marine Automated Network (C-MAN) (Ogden et al., 1994). The SEAKEYS network was implemented for long-term monitoring of meteorological and oceanographic conditions along the 220-mile Florida Reef Tract and Florida Bay encompassing the Florida Keys National Marine Sanctuary (FKNMS). For the purpose of this study only those SEAKEYS stations that are situated on the Florida Reef Tract were of interest. These are Fowey Rocks (25.59 °N, 80.1 °W, at the northern terminus of the Florida Reef Tract), Molasses Reef (25.01 °N, 80.38 °W, east of Key Largo), Sombrero Reef (24.63 °N, 81.11 °W, south of Marathon), Sand Key (24.46 °N, 81.88 °W, south of Key West), and the Dry Tortugas (24.64 °N, 82.86 °W, at the western end of the Florida Reef Tract). From these stations hourly averages of bulk in situ sea surface temperature (SST) were obtained. Daily average SST was calculated from the beginning of data acquisition at each site through to 2005. The Molasses Reef site provided the most complete data set beginning in 1988 (Table 1). Data collection began at Sombrero Reef in 1988 as well, but data are limited at this site for some years. Data from the station at the Dry Tortugas is the least complete with large gaps during critical warm summer periods in 1997, 2004, and 2005. The remoteness of this station and the frequent impact of hurricanes in 2004 and 2005 explain why this site recorded only 82.7% of hourly data from 1992 to 2005 (Table 1). Nevertheless, all sites except the Dry Tortugas provide a record that is >90% complete for hourly, in situ SST from the time of their installation through 2005.

2.2. Thermal stress indices and anomalies

The annual maximum daily average and hourly SSTs were calculated to assess if short-term extreme temperatures were related to bleaching. Maximum monthly mean SST and degree-days were used as indices of cumulative heat stress per year. Degree-days were calculated according to Podesta and Glynn (1997). This index is similar to the degree-heating weeks of Gleeson (1994) and Gleeson and Strong (1995). The number of days per year that daily SSTs were >29.5, 30, 30.5, and 31 °C were calculated to assess their value as simple bleaching indices. These annual temperature variables were then logistically regressed with the presence–absence of bleaching. Only those years without missing data were used in the logistic regressions totaling 58 non-bleaching years and 12 bleaching years for Florida sites. The role of temperature variability was assessed by computing the coefficient of variation (CV) in bi-weekly mean SST from 1 July to 31 October and then comparing the CVs of warm, non-bleaching (WNB) and warm, bleaching (WB) years by site (Sammarco et al., 2006). WNB and WB compared by site were: Fowey Rocks, WNB (1993, 1999, 2004), WB (1997, 1998, 2005); Molasses Reef, WNB (1993, 1995, 2002), WB (1997, 1998, 2005); Sombrero Reef, WNB (2000, 2001, 2002), WB (1997, 1998, 2005); Sand Key, WNB (1995, 2001,

Table 1
Description and completeness of data by site

	Fowey Rocks	Molasses Reef	Sombrero Reef	Sand Key	Dry Tortugas
Start date	8/1/1991	1/1/1988	2/10/1988	5/19/1991	12/9/1992
N	5155	6460	5960	4994	4224
% Complete	94.2	98.3	90.7	91.2	82.7

N is number of days.

2004), WB (1993, 1997, 1998, 2005); Dry Tortugas, WNB (1999, 2000), WB (1997, 1998).

The seasonal SST cycle for each locale was estimated by taking the average of each day for the years of data available excluding warm years (1997, 1998, 2005 for all sites and 1993 for Sand Key only). For leap years, SST data for February 29 was not included in the estimate of the seasonal cycle. After determining the annual seasonal cycle for each site, the residuals (anomalies) from these values per year were determined daily and monthly. The time-series of monthly temperature anomalies were plotted during the warmest part of the year (July to September) for all sites, as these data were most pertinent to this study.

2.3. Time-integrated bleaching threshold curves

To determine thresholds for each site, beyond which community-wide bleaching is expected to commence, the cumulative number of days at each temperature (0.1 °C increments) were calculated each summer. These time–temperature curves represent the tail end of the cumulative frequency distributions of temperature for each year (Berkelmans, 2002a). A polynomial bleaching threshold curve was then interpolated through the average number of days at each 0.1 °C increment of the warmest, non-bleaching year and the coolest bleaching year for each site. Cumulative temperature curves that lie above the threshold line indicate bleaching years, whereas those that fall below the threshold line indicate non-bleaching years (Berkelmans, 2002a). This is a simplification of the methods previously described (Berkelmans, 2002a,b), because the bleaching data used here were highly qualitative as a result of the paucity of comprehensive studies documenting bleaching on the Florida Reef Tract. For Sand Key, the threshold curve was modified at the right tail so that it was above the non-bleaching year of 2004. This technique is hypothesized to be more robust than thresholds estimated as accumulated heat stress (i.e., degree–days threshold value) as time-integrated thresholds do not falsely assume linearity in exposure time and temperature (Berkelmans, 2002a). Furthermore, threshold curves allow daily estimates of thermal stress accumulation in near real-time.

Bleaching threshold curves were determined for Salt River Bay, St. Croix, US Virgin Islands (17.784 °N, 64.761 °W) and North Norman's Patch Reef, Lee Stocking Island, Bahamas (23.791 °N, 76.139 °W). SST was measured in situ with a Falmouth Scientific CTD affixed at 1 m depth (nominal) to the National Oceanic and Atmospheric Administration (NOAA) Integrated Coral Observing Network (ICON) stations in St. Croix (operational since 2002) and the Bahamas (operational since 2003). Due to the temporal constraints associated with the ICON data, seasonal cycles, anomalies, and thermal stress indices (excluding threshold estimates) were not calculated. Seasonal maximum SST was determined from advanced very high resolution radiometer (AVHRR) satellite data for all SEAKEYS and ICON sites. Satellite SST data were only used to estimate the seasonal maximum at all sites; all other SST values reported were measured in situ. Satellite data were used to determine the seasonal maximum given that the ICON datasets were not long enough to reliably estimate seasonal cycles. The cumulative frequency distribution of temperature from 2003 was used as the bleaching threshold curve for St. Croix as a partial bleaching event was documented during this year at this site (Manzello et al., 2006). The bleaching threshold for the Bahamas was estimated by averaging the number of days at each 0.1 °C increment for 2005 (bleaching year) and 2006 (warmest, non-bleaching year). Bleaching thresholds were also determined by taking the mean of the minimum monthly SST associated with bleaching and the maximum monthly SST not associated with bleaching for all SEAKEYS and ICON sites. Minimum monthly SST associated with bleaching refers to the coolest annual maximum monthly SST associated with a bleaching year, whereas the maximum monthly SST not associated with bleaching refers to the warmest annual maximum monthly SST not associated with a bleaching year.

2.4. Bleaching and coral community structure

Information on coral bleaching events for the Florida Reef Tract were obtained from an exhaustive search of the literature, available bleaching reports archived on the internet (Reefbase, 2006; CHAMP, 2006), and correspondence with local researchers. Given the spatial variability in environmental conditions and bleaching, a 15 km radius was chosen around each station and all bleaching reports made for reefs or coral communities within these bounds were compiled. Each bleaching observation was categorized based on severity (Table 2). A 'bleaching year' was identified when more than one bleaching report detailed moderate or mass bleaching (score of 2 or 3, respectively, in Table 2) or a local researcher corroborated an event. Mild bleaching (i.e., only a subset of coral species show paling and only a small proportion of all colonies (<25%) bleach; score of 1 in Table 2) observations were ignored because these reports may represent confusion with the normal seasonal patterns in zooxanthellae densities for some coral species (Fitt et al., 2000). Moderate bleaching is defined as >25%, but <50% of all coral colonies paling. Mass bleaching is when >50% of all coral colonies are bleached. NOAA ICON personnel on SCUBA have documented bleaching in St. Croix since 2003. Mass bleaching occurred in 2005, whereas a mild, partial bleaching event occurred in 2003 (Manzello et al., 2006). Mass coral bleaching was documented at North Norman's Patch Reef in 2005 (Mueller, unpub. data).

The structure of coral communities is an important determinant to the susceptibility and severity of bleaching at a site (Marshall and Baird, 2000; McClanahan et al., 2007). Hermatypic coral species abundance data were collected in 2003 and 2006 for Florida reef sites within 15 km of the SEAKEYS sites (Marks and Lang, 2006); 1999 for reefs near (<15 km) Salt River Bay, St. Croix (Marks and

Table 2
Bleaching events and severity within 15 km radius of SEAKEYS sites (1992–2005)

Year	Site	Bleaching category
1993	Sand Key	2
1997	Fowey Rocks	3
1997	Molasses Reef	3
1997	Sombrero Reef	3
1997	Sand Key	3
1997	Dry Tortugas	3
1998	Fowey Rocks	3
1998	Molasses Reef	3
1998	Sombrero Reef	3
1998	Sand Key	3
1998	Dry Tortugas	3
2001	Sombrero Reef	1
2004	Sombrero Reef	1
2005	Fowey Rocks	3
2005	Molasses Reef	2
2005	Sombrero Reef	3
2005	Sand Key	2

Lang, 2006); and 2005 before and during bleaching at North Norman's Patch Reef in the Bahamas (Mueller, unpub. data). Although these data are not directly comparable because they were collected in different years, they nonetheless provide an idea of the species composition at the sites for which bleaching thresholds were derived.

2.5. Community bleaching susceptibility index

The five most common coral species at all sites were given a score based on their reported susceptibility to bleaching: 1 = high susceptibility; and 2 = low susceptibility. *Millepora* spp., *Agaricia* spp., *Siderastrea siderea*, and *Montastraea annularis* (spp. complex) were assigned a score of 1, whereas all other coral species were assigned a score of 2 (Jaap, 1979, 1985; CARICOMP, 1997; McField, 1999). The five most abundant coral species by site were ranked so that the species with the highest abundance received a score of 5; the second most abundant species received a score of 4 and so on. For each site, the abundance ranks (1–5) of each species were multiplied by their respective susceptibility scores, and the resulting products were summed to produce a scaled estimate of reef-wide bleaching susceptibility. A low site susceptibility score (min. = 15) indicates a site with a community structure highly susceptible to bleaching whereas a high score (max. = 30) indicates a site resistant to bleaching.

3. Results

3.1. Florida Reef Tract: seasonal cycles and sea temperature anomalies

Anomalously warm temperatures coincided with every bleaching event examined (Fig. 1). Monthly anomalies coincident with bleaching in 2005 were not excessively high and were positive only during August for most sites. Bleaching in 2005 was associated with an August anomaly of 0.6 °C at Molasses Reef, 0.7 °C at Fowey Rocks and Sand Key, and 0.8 °C at Sombrero Reef. Bleaching occurred at Sand Key in August 1993 with an anomaly of only 0.5 °C, yet bleaching was not reported at Fowey Rocks or Sombrero Reef with the same anomaly in August 1993 or 2003, respectively (Fig. 1).

3.2. Florida Reef Tract: Bleaching indices and thresholds

Maximum monthly SST and the number of days >30.5 °C were the best indices of those examined (Table 3). The maximum monthly SST coincident with bleaching was variable by site; however it was always ⩾30.5 °C. Degree–days were very poor indicators of bleaching years (Table 3). The CVs of bi-weekly SST for warm bleaching years were not significantly different from warm, non-bleaching years (Mann–Whitney *U*-tests, *p*-values ranged from 0.47 to 0.98). Monthly SST bleaching thresholds were similar for Florida sites, although the threshold for Sombrero Reef was warmer than the other sites by 0.4–0.5 °C (30.4 °C for Fowey Rocks, Molasses Reef, and Sand Key; 30.5 °C for the Dry Tortugas; 30.9 °C for Sombrero Reef). The bleaching threshold curves are situated very near the warmest non-bleaching years for all sites (Fig. 2). The warmest non-bleaching years varied by site highlighting the patchiness of temperature disturbances. A threshold curve could not be determined with confidence for Sombrero Reef as the warm, non-bleaching summer of 2000 exceeded the time–temperature curves of bleaching years.

3.3. Comparison of bleaching thresholds for Florida, Bahamas, and St. Croix

Bleaching threshold curves constructed for the Bahamas and St. Croix, US Virgin Islands are shown alongside those for Florida in Fig. 3. Estimates of bleaching thresholds based on monthly SSTs and the intercept of the bleaching curves were correlated ($r^2 = 0.93$, $p = 0.0017$). The monthly SST bleaching thresholds were cooler for the Bahamas (29.8 °C) and St. Croix (29.4 °C) compared to Florida. There is a suggestion of an inverse latitudinal trend in the estimated monthly SST bleaching thresholds ($r^2 = 0.68$, $p = 0.02$), but a better relationship exists between bleaching thresholds and seasonal maximum SST ($r^2 = 0.80$, $p = 0.007$) (Fig. 4). The same trends were apparent when bleaching thresholds based on the intercept of the bleaching curves were regressed with latitude ($r^2 = 0.77$, $p = 0.0217$) and seasonal maximum SST ($r^2 = 0.90$, $p = 0.0038$).

Coral species abundance and bleaching susceptibility by site is listed in Table 4. The site with the community structure most resistant to bleaching was St. Croix and Sand Key, Florida whereas the site most susceptible was North

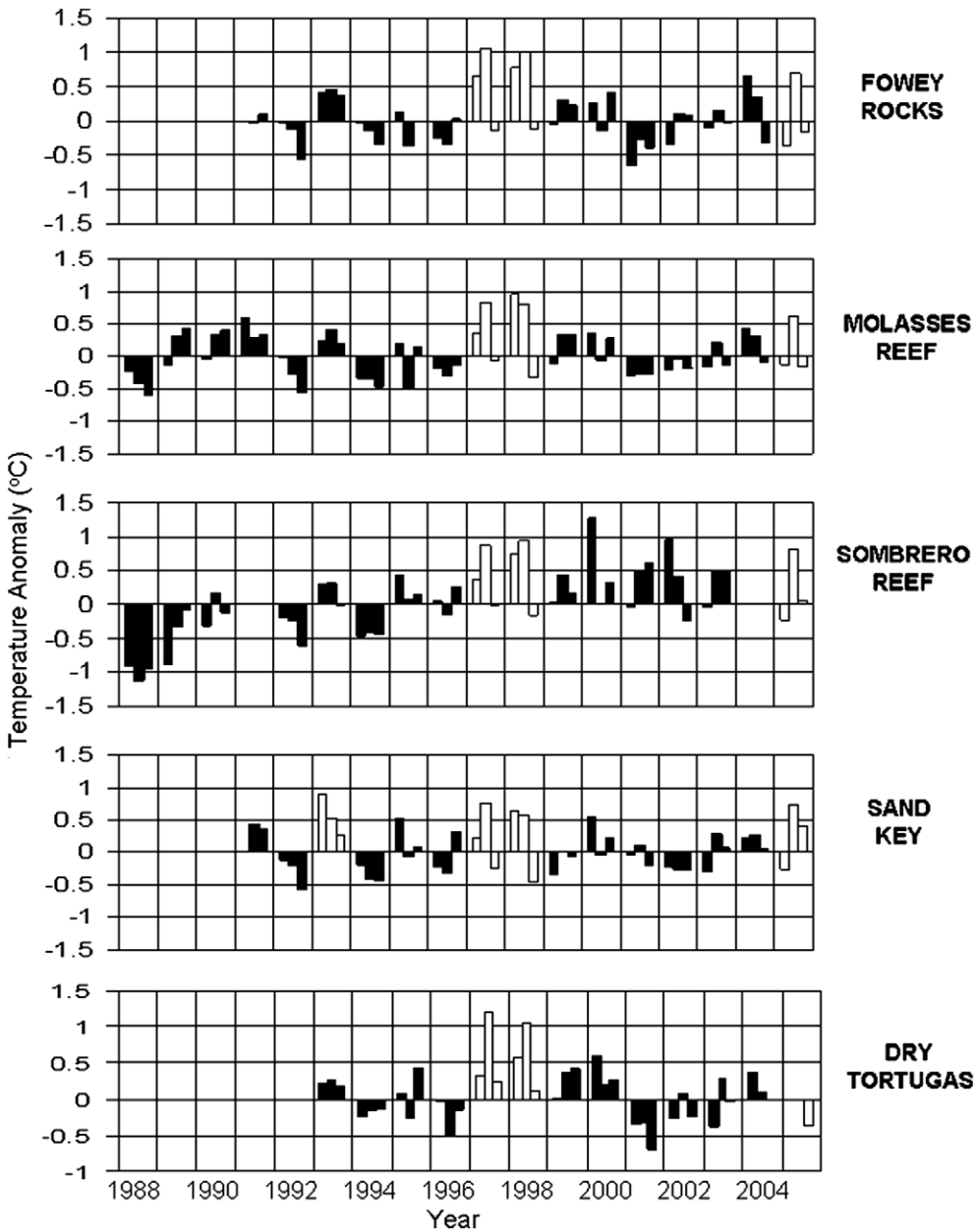

Fig. 1. Time series of monthly mean temperature anomalies at Florida sites for July–September. Each bar represents one month. Open bars identify bleaching years.

Table 3
Relevant statistics for logistic regression of bleaching indices with presence–absence of bleaching

Index	r^2	χ^2	p
Days > 29.5 °C	0.13	8.6	0.0033
Days > 30 °C	0.32	20.3	<0.0001
Days > 30.5 °C	0.42	27.1	<0.0001
Days > 31 °C	0.22	14.2	0.0002
Hourly Max. SST	0.12	7.5	0.0063
Daily Max. SST	0.2	12.8	0.0003
Monthly Max. SST	0.55	35.1	<0.0001
Degree–days	0.06	3.7	0.055

Norman's Patch Reef, Bahamas (Table 4). Community bleaching susceptibility was not related to the bleaching thresholds estimated as maximum monthly SST ($r^2 = 0.03$, $p = 0.73$), nor the intercepts of the bleaching curves ($r^2 = 0.06$, $p = 0.64$).

4. Discussion

Anomalously warm temperatures in excess of the bleaching thresholds estimated herein were associated with every bleaching year. Maximum monthly SST and the number of days >30.5 °C were the most significant; indicating that cumulative exposure to temperature extremes characterized bleaching years (Goreau et al., 1993; Brown et al., 1996; Berkelmans, 2002a). The CVs of the bi-weekly SSTs of warm, bleaching years were no different than those

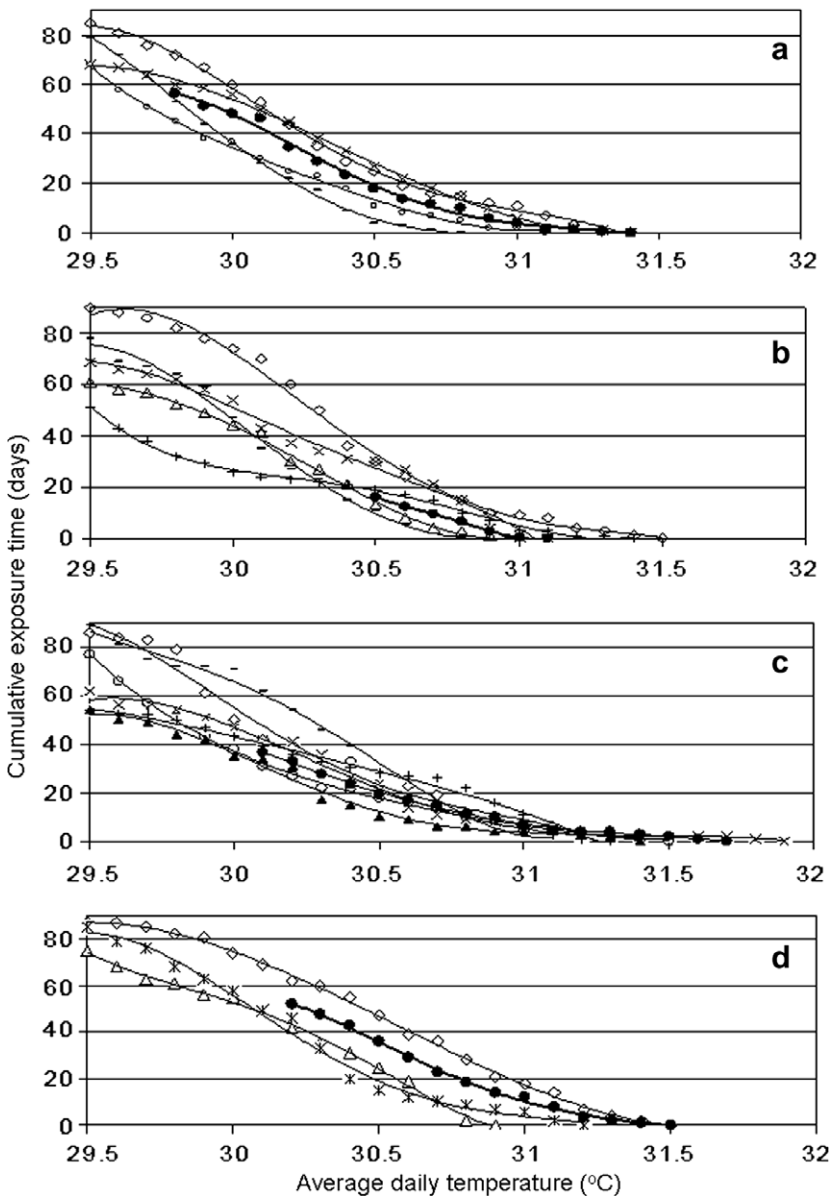

Fig. 2. Bleaching threshold curves for Florida reef sites: (a) Fowey Rocks, (b) Molasses Reef, (c) Sand Key, and (d) the Dry Tortugas. Bleaching curves fitted with polynomial trend lines. (–) 1993; (×) 1997; (◊) 1998; (ж) 1999; (∗) 2000; (▲) 2001; (○) 2004; (+) 2005. (●) Estimated bleaching curve. Cool, non-bleaching years were removed for clarity.

of warm, non-bleaching years showing that bi-weekly SST variability during summer months did not characterize bleaching years at any Florida sites, as shown for Puerto Rico (Winter et al., 1998; Sammarco et al., 2006). Our data re-confirms that the thermal shock of fluctuating temperature does not cause or correlate with widespread bleaching, but rather the prevailing mean temperatures are most critical (e.g., Jokiel and Coles, 1990; Craig et al., 2001). Bleaching thresholds were not related to community susceptibility using the index herein, but were significantly related to seasonal maximum SST (Coles et al., 1976).

The bleaching curve technique was good for estimating thresholds as shown by the significant correlation between the intercepts of the bleaching curves and thresholds estimated as monthly SST. This technique was not applicable at Sombrero Reef due the overlap observed between bleaching and non-bleaching year curves. Thermal conditions appeared favorable for bleaching at Sombrero Reef in 2000, as maximum monthly SST (31.1 °C) was greater than the threshold (30.9 °C), yet bleaching was not reported. The apparent absence of bleaching was not explained by low variance in bi-weekly SST relative to bleaching years. It is important to note that this was the only false positive (i.e., temperatures in excess of threshold without bleaching) for all sites totaling 77 years of data analyzed. The possibility of a community shift to more bleaching tolerant taxa following the temperature disturbances of 1997 and 1998 at Sombrero Reef was considered as a potential reason why bleaching was not reported in 2000 (McClanahan et al., 2007). Whether or not a commu-

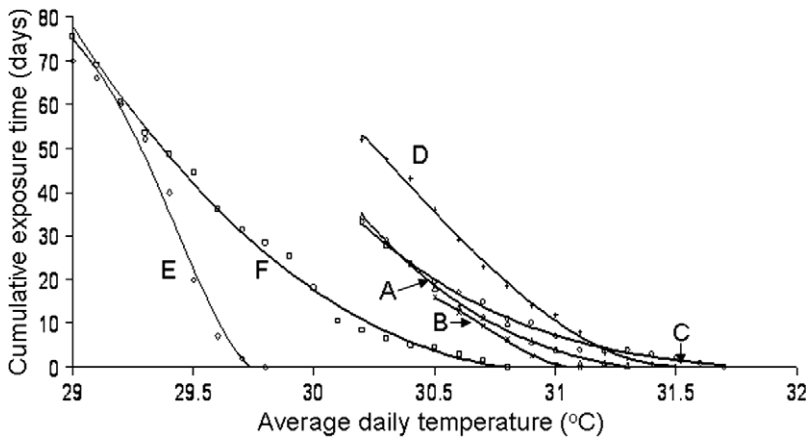

Fig. 3. Comparison of bleaching threshold curves for: (A) Fowey Rocks, FL (B) Molasses Reef, FL (C) Sand Key, FL, (D) Dry Tortugas, FL, (E) St. Croix, (F) Bahamas.

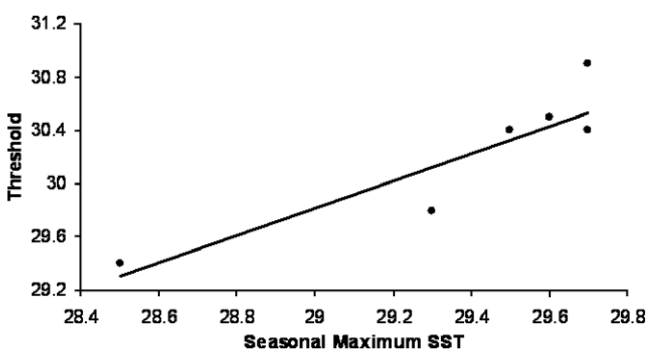

Fig. 4. Seasonal maximum SST plotted against bleaching thresholds for Florida, Bahamas, and St. Croix ($r^2 = 0.80$, $p = 0.007$).

nity shift occurred is unknown, but maximum monthly SST for 2005 was the same as previous bleaching years (all 31.0 °C) implying that the bleaching threshold of the taxa at Sombrero Reef did not change with time or repeated bleaching.

We hypothesize that the local-scale oceanographic conditions and their influence on the subsurface light field experienced by coral colonies may partially explain the false positive at Sombrero Reef in 2000. Sombrero Reef is located adjacent to the wide channels between islands in the middle Florida Keys where there is a strong net outflow of turbid and sometimes 'green' Florida Bay waters to the reef tract (Smith, 1994; Porter et al., 1999; Lee and

Table 4
Relative abundance and bleaching susceptibility score of coral communities within 15 km of stations

		LSI (2005)	FR (2003)	MR (2006)	SR (2003)	SK (2003)	DT (2004)	STX (1999)
No. sites surveyed		2	1	2	2	3	16	3
Mean depth (±s.e.m.)		6 (0)	5.2 (0)	6.7 (1.27)	6.7 (1.31)	4.5(0.76)	7.9 (0.27)	11.1 (0.66)
Total no. of corals		616	34	79	118	209	845	288
Coral species	Suscept. index	% of total						
A. cervicornis	2	0.3	–	–	–	4.3	3.2	0.3
A. palmata	2	–	–	1.3	8.5	18.2	–	–
C. natans	2	–	2.9	–	6.8	1.9	7.7	3.1
Agaricia spp.	1	20.6	8.8	12.7	2.5	1.0	0.4	3.8
M. annularis spp. complex	1	3.9	5.9	13.9	6.8	7.7	30.2	28.5
S. siderea	1	6.5	26.5	2.5	21.2	7.2	9.2	12.5
P. astreoides	2	12.0	8.8	22.8	11.9	44.0	6.4	3.1
D. strigosa	2	2.9	–	1.3	3.4	0.5	3.2	3.1
D. labyrinthiformis	2	0.5	2.9	5.1	2.5	1.0	1.2	1.4
D. clivosa	2	–	2.9	–	4.2	0.5	0.7	–
M. cavernosa	2	1.9	2.9	6.3	12.7	5.7	21.3	42.7
M. meandrites	2	1.6	–	–	–	–	–	–
Millepora spp.	1	48.9	8.8	30.4	9.3	5.3	10.5	–
S. intersepta	2	0.8	2.9	1.3	4.2	2.4	3.3	–
P. porites	1	0.0	26.5	2.5	5.9	0.5	2.7	1.4
Site susceptibility score		18	22	20	22	25	19	25

LSI, Lee Stocking Island, Bahamas; FR, Fowey Rocks, Florida; MR, Molasses Reef, Florida; SR, Sombrero Reef, Florida; SK, Sand Key, Florida; DT, Dry Tortugas, Florida; STX, St. Croix, US Virgin Islands. Year that surveys were performed is in parentheses following site abbreviation.

Smith, 2002). Jokiel and Brown (2004) reported that corals in areas of high turbidity in Hawaii suffered little or no bleaching even though they experienced identical temperatures to bleached corals in clear waters and suggested that reduced light penetration likely explained these observations. A thermal bleaching threshold was exceeded without bleaching for a coral community inhabiting turbid intertidal waters in Phuket, Thailand (Dunne and Brown, 2001). The recent history of photosynthetically active radiation (PAR, 400–700 nm) experienced at the coral surface prior (~1 month) to thermal stress shaped the bleaching response (Brown et al., 2000, 2002). These studies highlight the ongoing need for a comprehensive understanding of the underwater light field (unavailable for this study) experienced by corals prior to and during thermal stress (see Dunne and Brown, 2001; Fitt et al., 2001; Brown et al., 2002).

A temperature anomaly of ~1 °C above the mean monthly summer maximum is a frequently used threshold thought to explain severe bleaching (Goreau and Hayes, 1994; Gleeson and Strong, 1995; Hoegh-Guldberg, 1999). A monthly anomaly of ⩾0.6 °C above the seasonal maximum was coincident with moderate to severe bleaching on Florida reefs in 2005, which agrees with findings from Thailand (Brown et al., 1996). Hence, the commonly used ~1 °C anomaly may be too conservative to identify all bleaching events.

5. Conclusions

The bleaching thresholds presented in this study will refine expert systems that generate automated warnings in near real-time when conditions are conducive to bleaching (Hendee et al., 2001). These systems augment the large-scale NOAA satellite based 'hotspot' early warning system (Strong et al., 1997), which lacks fine temporal and spatial resolution (McClanahan et al., 2007). Additionally, sea temperature data obtained through in situ monitoring stations are more accurate at local scales than that obtained via satellites (Berkelmans, 2002a). Continued environmental monitoring, specifically of the underwater light field (PAR and UV, see Dunne and Brown, 2001) in concert with field studies (see McClanahan et al., 2007) is required to test the future validity of the thresholds presented here. Hind-casts showed that monthly mean SST in excess of the local threshold explained all bleaching years, thus future refinements are expected to be minimal.

Acknowledgements

The National Oceanic and Atmospheric Administration's Coral Reef Conservation Program is gratefully acknowledged for support of the SEAKEYS program and related research. Acknowledgment is due to M. Shoemaker, J. Craynock, J. Absten, C. Humphrey, J. Fajans, C. Jeffris, M. Gurnee, L. Gramer, L. Florit and others for work on the SEAKEYS project. D.P.M. thank B. Causey, D. DiResta, D. Lirman, E. Mueller, D. Swanson, and A. Szmant for clarification on the timing of bleaching events. The authors thank D. Ward and E. Mueller for documentation of bleaching in St. Croix and the Bahamas, respectively. G. Liu of NOAA's coral reef watch provided AVHRR SST data. D.P.M. is indebted to M. Brandt whose work provided the motivation necessary to complete this study. M. Brandt, L. Duncan and D. Lirman provided helpful feedback on an early version of this manuscript.

References

Berkelmans, R., 2002a. Time-integrated thermal bleaching thresholds of reefs and their variation on the Great Barrier Reef. Marine Ecology Progress Series 229, 73–82.

Berkelmans, R., 2002b. Reply to Comment on Berkelmans, R. 2002a. Marine Ecology Progress Series 237, 309–310.

Berkelmans, R., De'ath, G., Kininmonth, S., Skirving, W.J., 2004. A comparison of the 1998 and 2002 coral bleaching events on the Great Barrier Reef: Spatial correlation, patterns and predictions. Coral Reefs 23, 74–83.

Brown, B.E., Dunne, R.P., Chansang, H., 1996. Coral bleaching relative to elevated seawater temperature in the Andaman Sea (Indian Ocean) over the last 50 years. Coral Reefs 15, 151–152.

Brown, B.E., 1997. Coral bleaching: causes and consequences. Coral Reefs 16 (Suppl.), 129–138.

Brown, B.E., Dunne, R.P., Goodson, M.S., Douglas, A.E., 2000. Bleaching patterns in reef corals. Nature 404, 142–143.

Brown, B.E., Dunne, R.P., Goodson, M.S., Douglas, A.E., 2002. Experience shapes the susceptibility of a reef coral to bleaching. Coral Reefs 21, 119–126.

CARICOMP, 1997. Studies on Caribbean coral bleaching, 1995–1996. Proceedings of the 8th International Coral Reef Symposium, vol. 1, pp. 673–678.

Causey, B.D., 2001. Lessons learned from the intensification of coral bleaching from 1980–2000 in the Florida Keys, USA. In: Salm, R.V., Coles, S.L. (Eds.), Proceedings of the Workshop on Mitigating Coral Bleaching Impact Through MPA Design. The Nature Conservancy, Honolulu, Hawaii, USA, pp. 60–66.

CHAMP, 2006. Coral-list archived bleaching reports. Coral Health and Monitoring Program, Atlantic Oceanographic and Meteorological Laboratories, National Oceanic and Atmospheric Administration, Miami, FL, USA. <www.coral.noaa.gov>.

Coles, S.L., Jokiel, P.L., Lewis, C.R., 1976. Thermal tolerance in Tropical versus Subtropical Pacific reef corals. Pacific Science 30, 159–166.

Craig, P., Birkeland, C., Belliveau, S., 2001. High temperatures tolerated by a diverse assemblage of shallow-water corals in American Samoa. Coral Reefs 20, 185–189.

Dunne, R.P., Brown, B.E., 2001. The influence of solar radiation on bleaching of shallow water reef corals in the Andaman Sea, 1993–1998. Coral Reefs 20, 201–210.

Edmunds, P.J., 1994. Evidence that reef-wide patterns of coral bleaching may be the result of the distribution of bleaching susceptible clones. Marine Biology 121, 137–142.

Fitt, W.K., McFarland, F.K., Warner, M.E., Chilcoat, G.C., 2000. Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. Limnology and Oceanography 45, 677–685.

Fitt, W.K., Brown, B.E., Warner, M.E., Dunne, R.P., 2001. Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in tropical corals. Coral Reefs 20, 51–65.

Gleeson, M.W., 1994. Correlation of coral bleaching events and remotely-sensed sea surface temperatures. Trident Scholar Project, Report number 215, United States Naval Academy, Annapolis, MD.

Gleeson, M.W., Strong, A.E., 1995. Applying MCSST to coral reef bleaching. Advances in Space Research 16, 151–154.

Glynn, P.W., 1993. Coral reef bleaching: ecological perspectives. Coral Reefs 12, 1–17.

Goreau, T.J., Hayes, R.L., Clark, J.W., Basla, D.J., Robertson, C.N., 1993. Elevated sea surface temperatures correlate with Caribbean coral reef bleaching. In: Geyer, R.A. (Ed.), A Global Warming Forum: Scientific, Economic and Legal Overview. CRC Press, Boca Raton, FL, pp. 225–255.

Goreau, T.J., Hayes, R.L., 1994. Coral bleaching and ocean 'Hot Spots'. Ambio 3, 176–180.

Hendee, J.C., Mueller, E., Humphrey, C., Moore, T., 2001. A data-driven expert system for producing coral bleaching alerts at Sombrero Reef in the Florida Keys, USA. Bulletin of Marine Science 69, 673–684.

Hoegh-Guldberg, O., 1999. Climate change, coral bleaching and the future of the world's coral reefs. Marine and Freshwater Research 50, 839–866.

Jaap, W.C., 1979. Observation on zooxanthellae expulsion at Middle Sambo Reef, Florida Keys. Bulletin of Marine Science 29, 414–422.

Jaap, W.C., 1985. An epidemic zooxanthellae expulsion during 1983 in the lower Florida Keys coral reefs: hyperthermic etiology. Proceedings of the 5th International Coral Reef Symposium, vol. 6, pp. 143–148.

Jokiel, P.L., Coles, S.L., 1990. Response of Hawaiian and other Indo-Pacific reef corals to elevated temperatures associated with global warming. Coral Reefs 8, 155–162.

Jokiel, P.L., Brown, E.K., 2004. Global warming, regional trends and inshore environmental conditions influence coral bleaching in Hawaii. Global Change Biology 10, 1627–1641.

Knowlton, N., Weil, E., Weigt, L.A., Guzman, H., 1992. Sibling species in *Montastraea annularis*, coral bleaching, and the coral climate record. Science 255, 330–333.

Lee, T.N., Smith, N.P., 2002. Volume transport variability through the Florida Keys tidal channels. Continental Shelf Research 22, 1361–1377.

Manzello, D., Hendee, J.C., Ward, D., Hillis-Starr, Z., 2006. An evaluation of environmental parameters coincident with the partial bleaching event in St. Croix, US Virgin Islands 2003. Proceedings of the 10th International Coral Reef Symposium, vol. 1, pp. 709–717.

Marks, K.W., Lang, J.C., 2006. AGRRA Summary Products, version (09/2006). <www.agrra.org/Release_2006-09/>.

Marshall, P.A., Baird, A.H., 2000. Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 19, 155–163.

Mayer, A.G., 1914. The effects of temperature upon marine animals. Carnegie Institute of Washington Papers in Marine Biology 6, 3–24.

McClanahan, T.R., Ateweberhan, M., Ruiz Sebastian, C., Graham, N.A.J., Wilson, S.K., Bruggemann, J.H., Guillaume, M.M.M., 2007. Predictability of coral bleaching from synoptic satellite and in situ temperature observations. Corals Reefs, doi:10.1007/s00338-006-0193-7.

McField, M.D., 1999. Coral response during and after mass bleaching in Belize. Bulletin of Marine Science 64, 155–172.

Ogden, J.C., Porter, J.W., Smith, N.P., Szmant, A.M., Jaap, W.C., Forcucci, D., 1994. A long-term interdisciplinary study of the Florida Keys SEASCAPE. Bulletin of Marine Science 54, 1059–1071.

Podesta, G.P., Glynn, P.W., 1997. Sea surface temperature variability in Panama and Galapagos: extreme temperatures causing coral bleaching. Journal of Geophysical Research 102, 15749–15759.

Porter, J.W., Lewis, S.K., Porter, K.G., 1999. The effect of multiple stressors on the Florida Keys coral reef ecosystem: a landscape hypothesis and a physiological test. Limnology and Oceanography 44, 941–949.

Reefbase, 2006. Archived online bleaching reports. <www.reefbase.org>.

Rowan, R., Knowlton, N., Baker, A.C., Jara, J., 1997. Landscape ecology of algal symbiont communities explains variation in episodes of coral bleaching. Nature 388, 265–269.

Sammarco, P.W., Winter, A., Steward, J.C., 2006. Coefficient of variation of sea surface temperature (SST) as an indicator of coral bleaching. Marine Biology 149, 1337–1344.

Shinn, E.A., 1966. Coral growth-rate, an environmental indicator. Journal of Paleontology 40, 233–241.

Smith, N.P., 1994. Long-term Gulf-to-Atlantic transport through tidal channels in the Florida Keys. Bulletin of Marine Science 54, 602–609.

Strong, A.E., Barrientos, C.S., Duda, C., Sapper, J., 1997. Improved satellite techniques for monitoring coral reef bleaching. Proceedings of the 8th International Coral Reef Symposium, vol. 2, pp. 1495–1498.

Warner, M.E., Chilcoat, G.C., McFarland, F.K., Fitt, W.K., 2002. Seasonal fluctuations in the photosynthetic capacity of photosystem II in symbiotic dinoflagellates in the Caribbean reef coral *Montastraea*. Marine Biology 141, 31–38.

Winter, A., Appeldorn, R.S., Bruckner, A., Williams Jr., E.H., Goenaga, C., 1998. Sea surface temperatures and coral reef bleaching off La Parguera, Puerto Rico (northeastern Caribbean Sea). Coral Reefs 17, 377–382.