

# Species composition, habitat, and water quality influence coral bleaching in southern Florida

Daniel E. Wagner<sup>1,\*</sup>, Philip Kramer<sup>2</sup>, Robert van Woesik<sup>1</sup>

<sup>1</sup>Department of Biological Sciences, Florida Institute of Technology, 150 West University Blvd, Melbourne, Florida 32901, USA

<sup>2</sup>The Nature Conservancy, Florida Keys Office, PO Box 420237, Summerland Key, Florida 33042, USA

**ABSTRACT:** The present study examines coral bleaching along the Florida Keys reef tract (USA) during a major thermal-stress event in the summer of 2005, and during the summers of 2006 and 2007, which were mild thermal stress years. The primary objectives were to (1) examine the spatial pattern of coral bleaching and its relationship to coral community composition and habitat and (2) determine the relationship between environmental parameters and coral-bleaching prevalence (i.e. the proportion of colonies that bleached within each population). Over 50 % of all coral species bleached along much of the reef tract in 2005. The Lower Keys supported more colonies per unit area than elsewhere and showed the highest number of bleached coral colonies; Biscayne and the Middle Keys showed the highest coral-bleaching prevalence. The most thermally sensitive corals were *Porites furcata*, *Millepora complanata*, *Siderastrea radians*, *Porites divaricata*, *Agaricia agaricites*, *Millepora alcicornis*, and *Porites porites*. The most extensive bleaching was recorded for large colonies,  $\geq 30$  cm, except in 2005 when small branching *Porites* colonies ( $< 30$  cm) showed higher bleaching prevalence. Shallow-water coral colonies and corals at localities with high productivity, in the form of chlorophyll *a* and dissolved inorganic nitrogen concentration, showed higher bleaching prevalence than both deep coral colonies and corals at localities with low productivity. By locally regulating waste-water discharge from the land, and thereby reducing local primary productivity, the severity of coral bleaching may be reduced when subjected to high regional water temperatures.

**KEY WORDS:** Bleaching · Temperatures · Corals · Coral reefs · Nutrients · Florida

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

Coral bleaching, or the loss of symbiotic zooxanthellae and pigments in reef corals, has recently become commonplace in the world's tropical oceans (Brown 1997, Hoegh-Guldberg 1999, Coles & Brown 2003, Douglas 2003, Hoegh-Guldberg et al. 2007) because of worldwide increases in sea temperatures (Webster et al. 2005). Bleaching is an end product of multiple stresses, of which anomalous thermal stress is one (Glynn 1993, 1996, Coles & Brown 2003). Yet, temperature and irradiance are strongly related physiologically; an increase in temperature under lighted conditions is perceived by the corals' symbionts as an increase in light pressure (Iglesias-Prieto & Trench

1994, Takahashi et al. 2004). The photosynthetic machinery of most coral species is susceptible to moderate increases in temperature and irradiance, enhancing chronic photoinhibition in the symbiotic algae within corals, which leads to bleaching (Iglesias-Prieto & Trench 1994, 1997, Warner et al. 1996, 1999, Jones et al. 1998, Takahashi et al. 2004). The cause-and-effect relationship is, however, complicated by varying susceptibilities to thermal and irradiance stress by (1) different coral species (Marshall & Baird 2000, Loya et al. 2001, McClanahan et al. 2002, Weis 2008), (2) temperature differences among habitats (McClanahan et al. 2007), (3) depth differences (Baker et al. 2008), (4) differential water-flow rates of habitats interacting with temperature (Nakamura & van Woesik 2001, Castillo &

\*Email: dwagner1993@my.fit.edu

Helmuth 2005, Finelli et al. 2006), and (5) the potential adjustments of gene pools to thermal stresses through time (Stat et al. 2008, Thompson & van Woesik 2009).

While both the seasonal highpoints of temperature and irradiance stress interact to induce coral bleaching (Jones & Hoegh-Guldberg 2001), the interactions of a variety of lesser known environmental conditions also influence bleaching (Nakamura & van Woesik 2001, Fabricius 2006). For example, low salinity causes osmotic shock that leads to host-cell detachment of symbionts after heavy rains (van Woesik et al. 1995), yet, thermal stress also changes the osmotic capacity of corals (Mayfield & Gates 2007), and both disturbances can, in extreme cases, lead to host-cell detachment, although the causative agents differ (Gates et al. 1992). It is likely that habitat differences, or seasonal changes in salinity, affects the osmotic capacity of corals, which, in turn, also influences their susceptibility to thermal stress. In addition, elevated nutrient concentrations seem to change the sensitivity of corals to other environmental stresses, including temperature (Bruno et al. 2003, Nordemar et al. 2003, Schloder & D'Croz 2004). Indeed, elevated nutrients increase pigmentation in coral symbionts (Muscatine et al. 1998), which elicits darkening in corals, making them more sensitive to elevated irradiance and temperature (Fabricius 2006). Understanding the interaction between temperature stress and water quality is critical in a time of rapid climate change, especially if improving water quality increases coral-community resilience to regional thermal stress (Dodge et al. 2008).

The Florida Keys have experienced both minor (2006) and moderate to major (1983, 1987, 1998, 2005) bleaching episodes over the last several decades (Manzello et al. 2007). Here we examine the effect of multiple environmental stressors on the magnitude of bleaching during a major thermal stress event in 2005, when the sea surface temperatures were from 2 to 3°C above the regional average, and, during the summers of 2006 and 2007, when temperatures were closer to the seasonal average. The principle objectives were to (1) examine the spatial pattern of coral bleaching and its relationship to the composition and habitat of the coral community and (2) determine the relationship between the environmental parameters and coral-bleaching prevalence.

## METHODS

**Study sites.** The study area extends from Martin County in the northeast (27° N, 80° W), down Florida's east coast westward along the Florida Keys reef tract to the beginning of the Marquesas (24.5° N, 82° W) in the south west (Fig. 1). This ~500 km expanse represents a

vast array of environmental conditions, from extreme wave exposure in the north to more sheltered conditions in the Lower Florida Keys (Murdoch & Aronson 1999, Precht & Miller 2007). The northern reefs support few corals, and reef growth appears to have ceased approximately 4000 yr ago (Banks et al. 2007). The Florida Keys reef tract is made up of bank-barrier reefs interspersed with seagrass beds, barren carbonate (hard-bottom) habitats, and patch reefs. The cross-shelf zonation (Fig. 1, inset) is characterized by patch reefs in the mid-channel (Hawk Channel) and offshore sub-regions, with a well-developed spur-and-groove bank-reef system at the reef's margin. The Caribbean-facing Middle Keys are sheltered from large ocean swells, but are bathed continuously by the highly variable waters of Florida Bay and the Gulf of Mexico.

**Environmental data.** *In situ* water quality datasets were obtained from the Southeast Environmental Research Center (SERC), Florida International University. Water quality parameters were monitored at 151 sites along the Florida Keys reef tract on a rolling basis, such that each site was sampled quarterly. The data used in the present study covered the sampling period from January 1995 to December 2006. Data for all years were validated for usability through semi-variogram analysis (Wagner et al. 2008). Interpolation using 'ordinary kriging' was performed to predict the values of each water quality parameter at coral-monitoring locations along the Florida Keys reef tract. Cross-validation of subsequent (value) predictions was applied by alternately removing each 'measured' value at each site and predicting the value from its neighboring sites. These values were then tested for consistency using chi-squared tests by comparing measured versus predicted values. Near-substrate temperature, salinity, dissolved inorganic nitrogen, and chlorophyll *a* (chl *a*) were spatially predictable (Wagner et al. 2008) and were used in the present study to examine relationships with coral composition and coral bleaching. Other water-quality parameters, namely many nitrogen species and turbidity, although potentially influential, were not spatially predictable (Wagner et al. 2008) and were therefore not used for comparative purposes.

**Coral data.** Data for the present study were drawn from the disturbance response monitoring program established in 2005 as part of the Florida Reef Resilience Program (FRRP). A 2-stage stratified, randomized sampling design was employed (after Ault et al. 2006); oceanographic and geomorphologic features were used to stratify habitats into 7 sub-regions and a number of cross-shelf zones (strata) (Fig. 1). The study area was gridded, using GIS, into 200 m × 200 m cells, which were designated as the primary sampling units (hereinafter called a 'site') if they contained >50% reef habitat. Random primary units were chosen for field

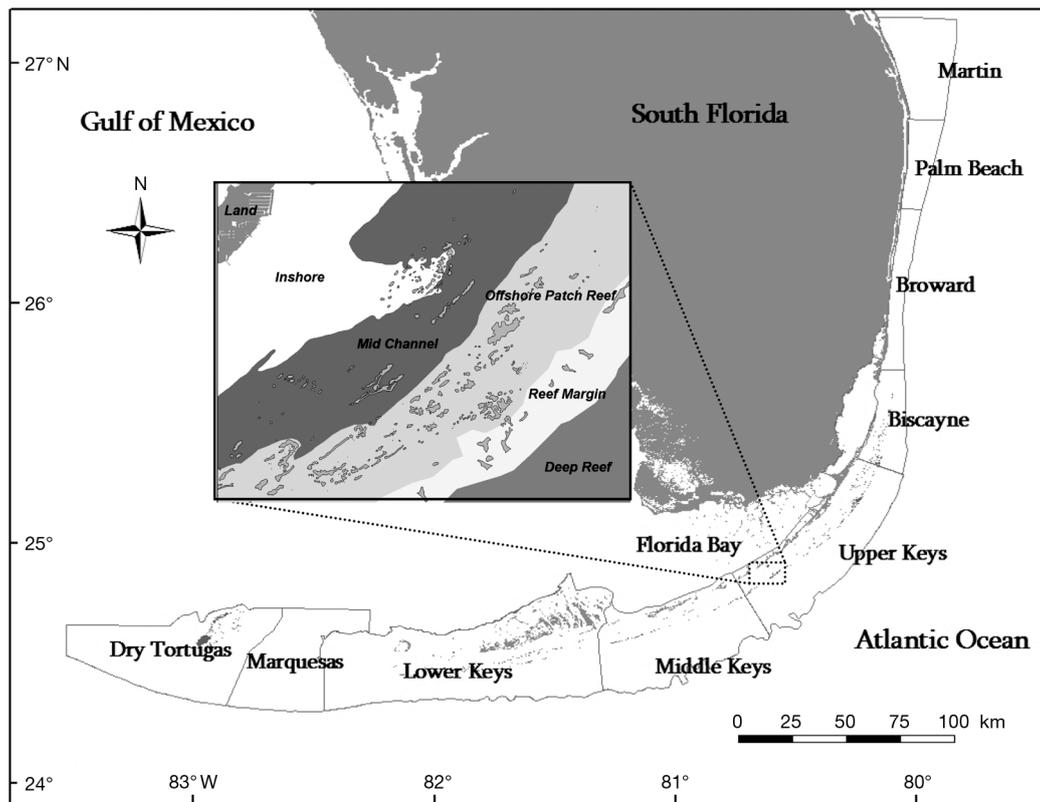


Fig. 1. Southern Florida showing The Nature Conservancy sub-regions and (inset) cross-shelf zones along the Florida Keys reef tract

assessments from each stratum. Sampling teams were assigned pre-selected sub-regions and randomly chosen sampling sites each year. Boat drivers were given primary, secondary, and tertiary GPS coordinates, within each stratum unit, to provide alternatives in case non-reef localities were (randomly) selected. Two, 10 m × 1 m belt-transects were haphazardly laid within each site, recording 0.5 m on either side of each transect line. All scleractinian corals  $\geq 4$  cm in maximum diameter were measured for maximum width, partial mortality, percentage bleaching, and disease. Bleaching was characterized by severity of discoloration, as in McClanahan et al. (2005). Sampling was re-randomized for every sampling period. Sampling was performed at 432 sites during 3 separate sampling efforts, in the summers of 2005, 2006, and 2007. The summer dates were chosen to best coincide with maximum irradiance and seasonal high water temperatures.

**Data analysis.** The Bray-Curtis similarity index was applied to the bleaching datasets prior to analysis. Similarity percentages (SIMPER) (Primer5) analysis was used to determine the percent contribution of each coral species to the average resemblances among sub-regions and zones. Analysis of similarity (ANOSIM) (Primer5) was used to examine the general null

hypothesis that there were no differences in coral-bleaching prevalence among sub-regions and zones. To examine the effect of colony size on bleaching prevalence, coral species were assigned to a growth form, as either foliose, branching, massive, or encrusting. Each coral colony was allocated to 1 of 4 size classes (4 to 9.9, 10 to 19.9, 20 to 29.9, and  $\geq 30$  cm), nested within each growth form.

Canonical correspondence analyses (CCA) was used to assess relationships between a suite of environmental and biotic matrices that were measured or interpolated, via kriging, for each site. The environmental matrix used the means of (1) water temperature, (2) salinity, (3) dissolved inorganic nitrogen (DIN), and (4) chl *a*, all sampled from the SERC water-quality dataset collected over 12 yr (1995 to 2007), and (5) water depth recorded during surveys. To derive predicted water-quality concentrations at the coral-monitoring sites, the water-quality dataset was interpolated using kriging (Wagner et al. 2008). The environmental data obtained from SERC did not include the most northeastern sub-regions (Martin, Palm Beach, and Broward; Fig. 1); therefore, sites within these sub-regions were excluded from the CCA. The biotic matrices used for the CCAs were (1) coral-

Table 1. Percent species contributions (SIMPER) for sub-regions and zones along the Florida Keys reef tract using abundance data pooled from 2005 to 2007. Type—f: foliose; m: massive; b: branching; e: encrusting; a: potentially all coral growth forms. Sub-regions and zones are identified in Fig. 1, with incipient reefs, ridge complex, and outer reef zones primarily located in and north of Broward, and fore reefs located south of Broward

Coral	Type	Sub-region						
		Martin	Palm Beach	Broward	Biscayne	Upper Keys	Middle Keys	Lower Keys
<i>Siderastrea radians</i>	e	74.5	12.8	1.2	3.8	1.7	1.0	0.9
<i>Siderastrea siderea</i>	m	15.4	12.4	18.0	27.3	22.7	26.8	27.5
<i>Diploria clivosa</i>	m	6.9	0.1	0.2	0.2	0.3	0.3	0.1
<i>Oculina diffusa</i>	b	2.8	–	–	–	0.0	–	0.2
<i>Diploria strigosa</i>	m	0.2	0.2	0.3	0.2	0.4	0.1	0.7
<i>Millepora alcicornis</i>	a	0.2	22.6	18.1	20.1	42.1	36.6	22.1
<i>Porites astreoides</i>	b	–	1.0	12.2	21.5	9.8	10.3	17.8
<i>Stephanocoenia intersepta</i>	e	–	0.3	20.0	2.3	2.2	9.7	9.9
<i>Montastraea faveolata</i>	m	–	–	0.2	0.5	1.1	0.7	2.2
<i>Agaricia agaricites</i>	f	–	0.1	0.2	6.4	4.8	3.4	3.6
<i>Porites porites</i>	b	–	–	1.2	6.8	7.7	1.8	1.5
<i>Montastraea cavernosa</i>	m	–	39.1	17.1	1.8	1.2	5.6	7.5
<i>Dichocoenia stokesi</i>	m	–	5.9	3.9	7.0	4.0	1.8	3.0
<i>Solenastrea bournoni</i>	m	–	2.9	2.4	0.3	0.5	0.6	0.8
<i>Meandrina meandrites</i>	m	–	2.5	4.1	0.5	0.1	0.2	0.2
<i>Mussa angulosa</i>	m	–	0.1	–	–	–	<0.1	0.1
<i>Eusmilia fastigiata</i>	m	–	–	0.1	0.1	<0.1	0.1	0.1
<i>Montastraea franksi</i>	m	–	–	–	<0.1	0.1	0.1	0.2
<i>Montastraea annularis</i>	m	–	–	–	<0.1	0.2	–	0.2
<i>Colpophyllia natans</i>	m	–	–	0.1	0.1	0.1	0.5	0.6
<i>Acropora cervicornis</i>	b	–	–	0.1	0.1	<0.1	–	<0.1
<i>Isophyllia sinuosa</i>	m	–	–	–	–	–	–	<0.1
<i>Millepora complanata</i>	a	–	–	<0.1	0.1	<0.1	0.1	0.1
<i>Madracis decactis</i>	b	–	–	0.7	–	<0.1	–	<0.1
<i>Agaricia lamarcki</i>	f	–	–	0.1	<0.1	<0.1	<0.1	<0.1
<i>Favia fragum</i>	m	–	–	<0.1	–	–	0.1	<0.1
<i>Agaricia fragilis</i>	f	–	–	<0.1	–	–	–	–
<i>Mycetophyllia</i> sp.	m	–	–	<0.1	–	–	<0.1	0.1
<i>Porites divaricata</i>	b	–	–	<0.1	0.2	0.4	<0.1	0.2
<i>Porites furcata</i>	b	–	–	–	0.4	0.2	0.1	<0.1
<i>Diploria labyrinthiformis</i>	m	–	–	–	0.3	0.4	0.2	0.2
<i>Porites branneri</i>	e	–	–	–	<0.1	–	–	–
<i>Solenastrea hyades</i>	m	–	–	–	–	0.1	–	0.1
<i>Leptoseris cucullata</i>	e	–	–	–	–	<0.1	–	–
<i>Madracis mirabilis</i>	b	–	–	–	–	–	<0.1	<0.1
<i>Manicina areolata</i>	m	–	–	–	–	–	<0.1	0.1
<i>Cladacora arbuscula</i>	b	–	–	–	–	–	–	<0.1
<i>Madracis formosa</i>	b	–	–	–	–	–	–	<0.1

Coral	Type	Reef zone							
		Incipient	Ridge complex	Outer	Inner	Offshore patch	Inshore	Forereef	Mid-channel
<i>Siderastrea radians</i>	e	74.5	8.4	0.7	0.8	1.3	3.3	1.9	2.1
<i>Siderastrea siderea</i>	m	15.4	4.3	17.2	24.9	21.1	18.8	21.0	38.5
<i>Millepora alcicornis</i>	a	0.2	27.3	20.2	13.3	40.4	15.1	39.5	11.3
<i>Montastraea cavernosa</i>	m	–	46.2	21.4	17.2	2.2	11.6	3.4	3.5
<i>Porites astreoides</i>	b	–	1.9	6.9	8.0	12.1	18.2	16.3	15.2
<i>Diploria clivosa</i>	m	6.9	–	–	0.0	0.3	0.7	0.3	0.3
<i>Oculina diffusa</i>	b	2.8	–	–	–	–	0.1	–	0.2
<i>Diploria strigosa</i>	m	0.2	0.1	0.1	0.3	0.4	0.5	0.3	0.7
<i>Agaricia agaricites</i>	f	–	0.1	0.3	0.2	2.7	0.2	6.9	2.7
<i>Porites porites</i>	b	–	–	0.9	0.7	5.6	1.0	3.2	5.4
<i>Meandrina meandrites</i>	m	–	3.8	7.2	6.9	0.1	0.7	0.3	0.2
<i>Stephanocoenia intersepta</i>	e	–	0.7	20.4	24.0	5.7	11.0	3.5	6.2
<i>Montastraea faveolata</i>	m	–	–	0.3	0.2	0.5	0.3	0.7	3.2
<i>Dichocoenia stokesi</i>	m	–	5.1	1.5	2.1	5.9	8.4	1.8	7.1
<i>Solenastrea bournoni</i>	m	–	1.9	0.1	0.6	0.7	8.7	0.2	0.6

Table 1 (continued)

Coral	Type	Reef zone							
		Incipient	Ridge complex	Outer	Inner	Offshore patch	Inshore	Forereef	Mid-channel
<i>Mussa angulosa</i>	m	–	0.1	–	–	<0.1	<0.1	–	0.1
<i>Montastraea franksi</i>	m	–	–	–	<0.1	0.1	–	0.1	0.1
<i>Eusmilia fastigiata</i>	m	–	–	0.4	0.1	0.1	<0.1	<0.1	0.2
<i>Colpophyllia natans</i>	m	–	–	<0.1	0.1	0.2	0.6	0.1	0.8
<i>Millepora complanata</i>	a	–	–	0.1	<0.1	–	–	0.1	–
<i>Madracis decactis</i>	b	–	–	2.0	0.5	0.0	0.1	<0.1	–
<i>Agaricia lamarcki</i>	f	–	–	0.3	0.1	–	<0.1	<0.1	<0.1
<i>Porites divaricata</i>	b	–	–	–	<0.1	0.4	0.3	0.1	0.2
<i>Porites furcata</i>	b	–	–	–	<0.1	0.1	0.1	0.1	0.1
<i>Favia fragum</i>	m	–	–	–	<0.1	<0.1	0.1	<0.1	<0.1
<i>Diploria labyrinthiformis</i>	m	–	–	–	–	0.1	0.2	0.1	0.7
<i>Montastraea annularis</i>	m	–	–	–	–	<0.1	0.1	<0.1	0.5
<i>Acropora cervicornis</i>	b	–	–	–	–	<0.1	0.2	<0.1	0.1
<i>Solenastrea hyades</i>	m	–	–	–	–	<0.1	<0.1	<0.1	<0.1
<i>Mycetophyllia</i> sp.	m	–	–	–	–	<0.1	–	<0.1	0.1
<i>Cladacora arbuscula</i>	b	–	–	–	–	–	<0.1	–	<0.1
<i>Isophyllia sinuosa</i>	m	–	–	–	–	–	<0.1	–	<0.1
<i>Madracis mirabilis</i>	b	–	–	–	–	–	–	<0.1	<0.1
<i>Agaricia fragilis</i>	f	–	–	0.1	–	–	–	–	–
<i>Manicina areolata</i>	m	–	–	–	–	–	<0.1	–	–
<i>Porites branneri</i>	e	–	–	–	–	–	–	<0.1	–

bleaching prevalence for 2005, 2006, and 2007, which was the total number of bleaching cases in each population divided by the number of individuals in the population, and (2) the coral-bleaching prevalence data for each species further assigned to the 4 size classes (4 to 9.9, 10 to 19.9, 20 to 29.9, and  $\geq 30$  cm).

## RESULTS

Coral diversity was highest in the Lower Keys, with species richness decreasing northward along the reef tract up through Martin County (Table 1). Some species were found in all sub-regions, including *Siderastrea siderea*, *Millepora alcicornis*, *Diploria clivosa*, and *Diploria strigosa* (Fig. 2), but their relative abundances varied across localities (Table 1). Bleaching was highly variable at regional and zonal scales during the summer of 2005. The Lower Florida Keys showed the highest number of bleached corals (with 70% of the total number of coral colonies bleached), which was primarily because the reefs supported more colonies per unit area than elsewhere (Table 2). The Biscayne sub-region, and the Middle and Upper Keys showed the highest degree of bleaching prevalence (Table 2). Highest bleaching prevalence was recorded for *Siderastrea siderea*, *Millepora alcicornis*, *Agaricia agaricites*, and *Siderastrea radians*, which were also among the most common corals (Table 3, Fig. 3).

While all sub-regions showed similar bleaching patterns (ANOSIM,  $R < 0.100$ ,  $p > 0.05$ ), each sub-region differed with respect to bleaching prevalence (Table 3), with more coral species bleaching in Biscayne, followed by the Lower Keys and Upper and Middle Keys. This pattern was primarily a consequence of the hierarchically nested relationship of coral species composition (Fig. 4). Similarly, the mid-channel zone (2 to 10 m) showed higher bleaching prevalence than the forereef (2 to 20 m), offshore patch reefs (2 to 12 m) or the inshore areas (2 to 6 m). The cross-shelf patterns had a similar nested composition that was not simply a consequence of depth-range differences; the most prolific coral communities were found in the mid-channel zone (Fig. 5). The greatest proportion of bleached coral species, and the highest bleaching prevalence in all years, occurred within the mid-channel, forereef, and inshore reef zones (Table 2). There was a significant difference in the extent of bleaching between inshore and forereef habitats, with more species bleaching on forereefs than on inshore reefs (ANOSIM,  $R = 0.700$ ,  $p < 0.05$ ).

During the summer of 2005, a severe bleaching year, the largest coral colonies, for all growth forms except branching *Porites* spp., bleached more frequently and extensively than the small coral colonies (Table 4). The only exception was in Biscayne, where bleaching showed no size preference. *Porites* spp. in 2005 showed more extensive bleaching of small colonies (<30 cm). During the summer of 2007, a relatively mild

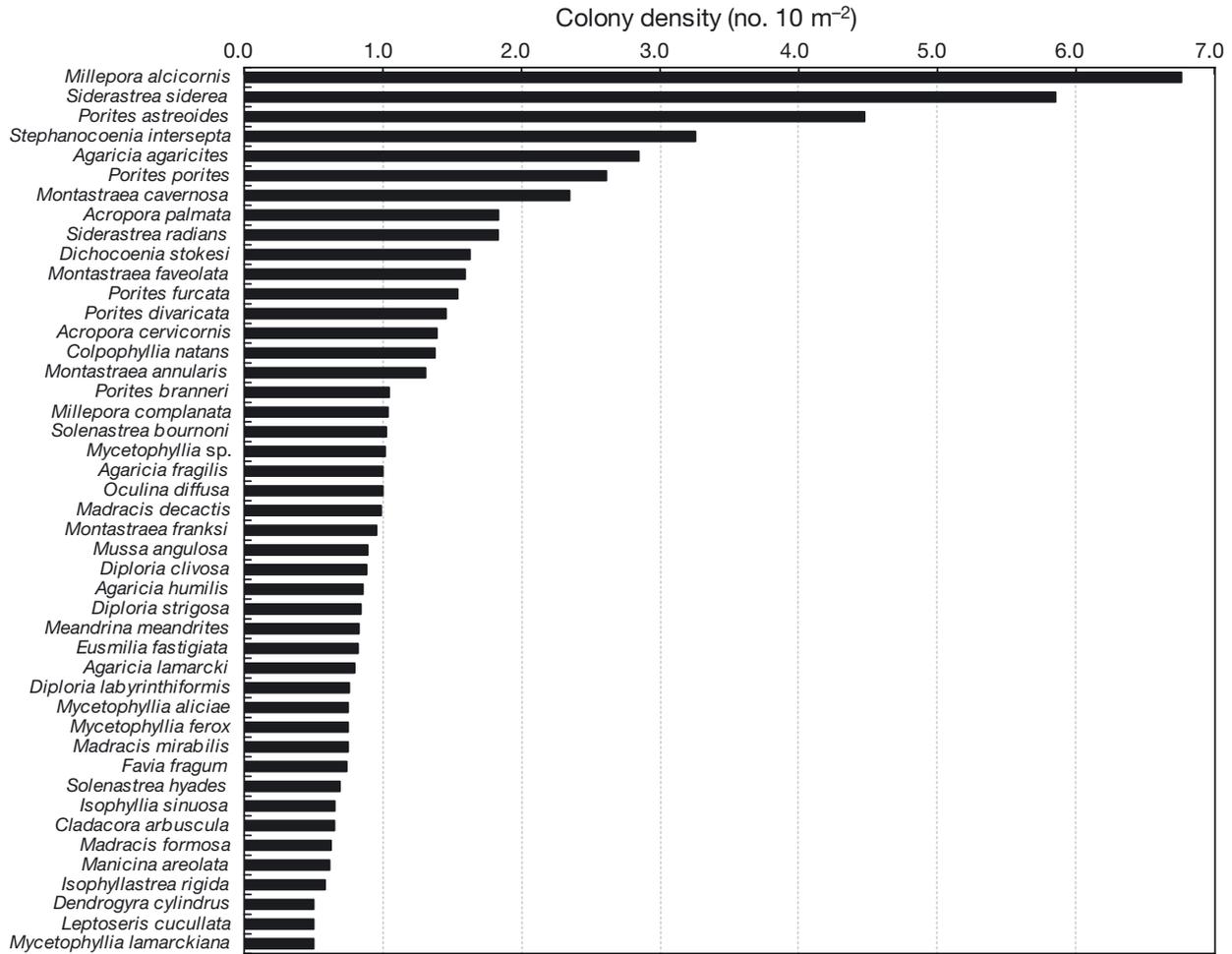


Fig. 2. Mean colony densities (2005 to 2007) for individual coral species along the Florida Keys reef tract

Table 2. Total observed colonies, number of bleached coral colonies, percentages of species bleached and mean bleaching prevalence for Florida Keys and southeast Florida sub-regions and zones during the summer of 2005

	Total no. of colonies	Colonies bleached	% species bleached	% colonies bleached
<b>Sub-regions</b>				
Martin	76	26	0.50	0.34
Palm Beach	46	3	0.00	0.07
Broward	790	263	0.65	0.33
Biscayne	547	314	0.87	0.57
Upper Keys	712	350	0.70	0.49
Middle Keys	438	251	0.71	0.57
Lower Keys	1666	579	0.63	0.35
<b>Zones</b>				
Incipient reef	76	26	0.50	0.34
Outer reef	244	66	0.45	0.27
Inner reef	277	82	0.64	0.30
Offshore patch reef	1025	366	0.64	0.36
Inshore	335	132	0.47	0.39
Forereef	1485	655	0.66	0.44
Mid-channel	833	459	0.75	0.55

bleaching year, all large colonies showed higher bleaching prevalence than small colonies for all sub-regions and zones (Table 4).

There was a strong relationship between coral-bleaching prevalence and depth (Table 5), with fewer colonies bleaching on the deep reefs than on the shallow reefs. There was a clear relationship between bleaching and high water temperature, high DIN concentrations, and high chl *a* concentrations in the water column (Table 5). In 2006 and 2007, which were relatively mild bleaching years, the variance in bleaching was explained largely by differences in chl *a* and DIN (Table 5). When the means of the environmental variables, taken over the 12 yr period (i.e. from 1995 to 2007), were tested against colony-size-specific bleaching, pooled over all 3 yr (2005 to 2007), 60% of the variance was explained by chl *a*, temperature, and depth (on the first CCA species axis) and 45% of the variance was explained by temperature and DIN in the water column on the second CCA axis

(Table 6). The variance in temperature for each site explained 44% of the total variance (on the first CCA species axis), whereas 74% of the variance was explained by differences in salinity (on the second CCA species axis; Table 6).

## DISCUSSION

The present study has clearly shown that coral assemblages in the Florida Keys are not totally random assortments of corals. While it has long been known

Table 3. Percent species contribution (SIMPER) for sub-regions and zones along the Florida Keys reef tract (see Fig. 1) using bleaching prevalence data from the summer of 2005. Type—f: foliose; m: massive; b: branching; e: encrusting; a: potentially all coral growth forms

Coral	Type	Sub-region						
		Palm Beach	Martin	Middle Keys	Broward	Biscayne	Upper Keys	Lower Keys
<i>Siderastrea radians</i>	e	–	93.0	3.2	0.2	20.5	6.0	9.6
<i>Siderastrea siderea</i>	m	–	7.0	22.4	17.8	10.2	13.0	16.6
<i>Agaricia agaricites</i>	f	–	–	14.4	0.3	17.2	13.0	21.1
<i>Stephanocoenia intersepta</i>	e	–	–	18.2	59.3	0.5	3.2	7.1
<i>Millepora alcicornis</i>	a	–	–	7.3	1.1	12.8	44.2	18.0
<i>Porites porites</i>	b	–	–	9.4	0.6	16.6	10.4	2.1
<i>Porites asteroides</i>	b	–	–	4.7	11.0	9.7	1.8	9.3
<i>Montastrea cavernosa</i>	m	–	–	0.6	4.6	0.2	1.4	6.1
<i>Solenastrea bournoni</i>	m	–	–	3.2	2.9	2.6	1.6	1.5
<i>Colpophyllia natans</i>	m	–	–	6.2	–	–	0.6	0.7
<i>Diploria clivosa</i>	m	–	–	3.4	–	–	1.0	–
<i>Montastraea faveolata</i>	m	–	–	7.1	–	–	1.4	1.1
<i>Dichocoenia stokesi</i>	m	–	–	–	0.3	–	1.3	0.3
<i>Diploria strigosa</i>	m	–	–	–	0.2	–	0.6	2.5
<i>Millepora complanata</i>	a	–	–	–	0.1	2.3	–	0.2
<i>Meandrina meandrites</i>	m	–	–	–	1.5	0.3	–	–
<i>Porites divaricata</i>	b	–	–	–	–	1.7	0.5	2.6
<i>Porites furcata</i>	b	–	–	–	–	5.5	–	–
<i>Montastraea annularis</i>	m	–	–	–	–	–	0.2	0.3
<i>Agaricia lamarcki</i>	f	–	–	–	–	–	–	0.2
<i>Eusmilia fastigiata</i>	m	–	–	–	–	–	–	<0.1
<i>Solenastrea hyades</i>	m	–	–	–	–	–	–	0.9
Coral	Type	Reef zone						
		Incipient	Outer	Inshore	Inner	Offshore patch	Mid-channel	Forereef
<i>Siderastrea radians</i>	e	93.0	–	–	–	8.3	12.7	9.8
<i>Siderastrea siderea</i>	m	7.0	5.6	9.8	37.4	14.9	13.2	17.2
<i>Stephanocoenia intersepta</i>	e	–	84.7	39.6	48.8	7.1	4.9	5.6
<i>Montastrea cavernosa</i>	m	–	5.8	5.4	3.2	1.7	2.0	2.5
<i>Porites asteroides</i>	b	–	3.3	25.0	4.9	8.8	9.0	5.2
<i>Millepora alcicornis</i>	a	–	0.6	–	1.3	24.2	22.5	20.8
<i>Solenastrea bournoni</i>	m	–	–	17.5	0.4	6.5	0.9	1.5
<i>Meandrina meandrites</i>	m	–	–	1.4	0.9	–	–	0.1
<i>Agaricia agaricites</i>	f	–	–	1.3	–	8.9	9.0	27.4
<i>Porites porites</i>	b	–	–	–	1.8	7.9	11.7	6.2
<i>Diploria strigosa</i>	m	–	–	–	1.4	3.3	0.4	0.8
<i>Montastraea faveolata</i>	m	–	–	–	–	2.0	2.9	0.5
<i>Porites divaricata</i>	b	–	–	–	–	1.8	3.4	0.3
<i>Colpophyllia natans</i>	m	–	–	–	–	1.8	0.7	0.6
<i>Diploria clivosa</i>	m	–	–	–	–	1.1	0.3	0.2
<i>Dichocoenia stokesi</i>	m	–	–	–	–	1.5	1.9	–
<i>Eusmilia fastigiata</i>	m	–	–	–	–	0.1	–	–
<i>Montastrea annularis</i>	m	–	–	–	–	–	0.3	0.2
<i>Solenastrea hyades</i>	m	–	–	–	–	–	4.0	–
<i>Diploria labyrinthiformis</i>	m	–	–	–	–	–	0.3	–
<i>Porites furcata</i>	b	–	–	–	–	–	–	0.7
<i>Millepora complanata</i>	a	–	–	–	–	–	–	0.4
<i>Agaricia lamarcki</i>	f	–	–	–	–	–	–	0.1

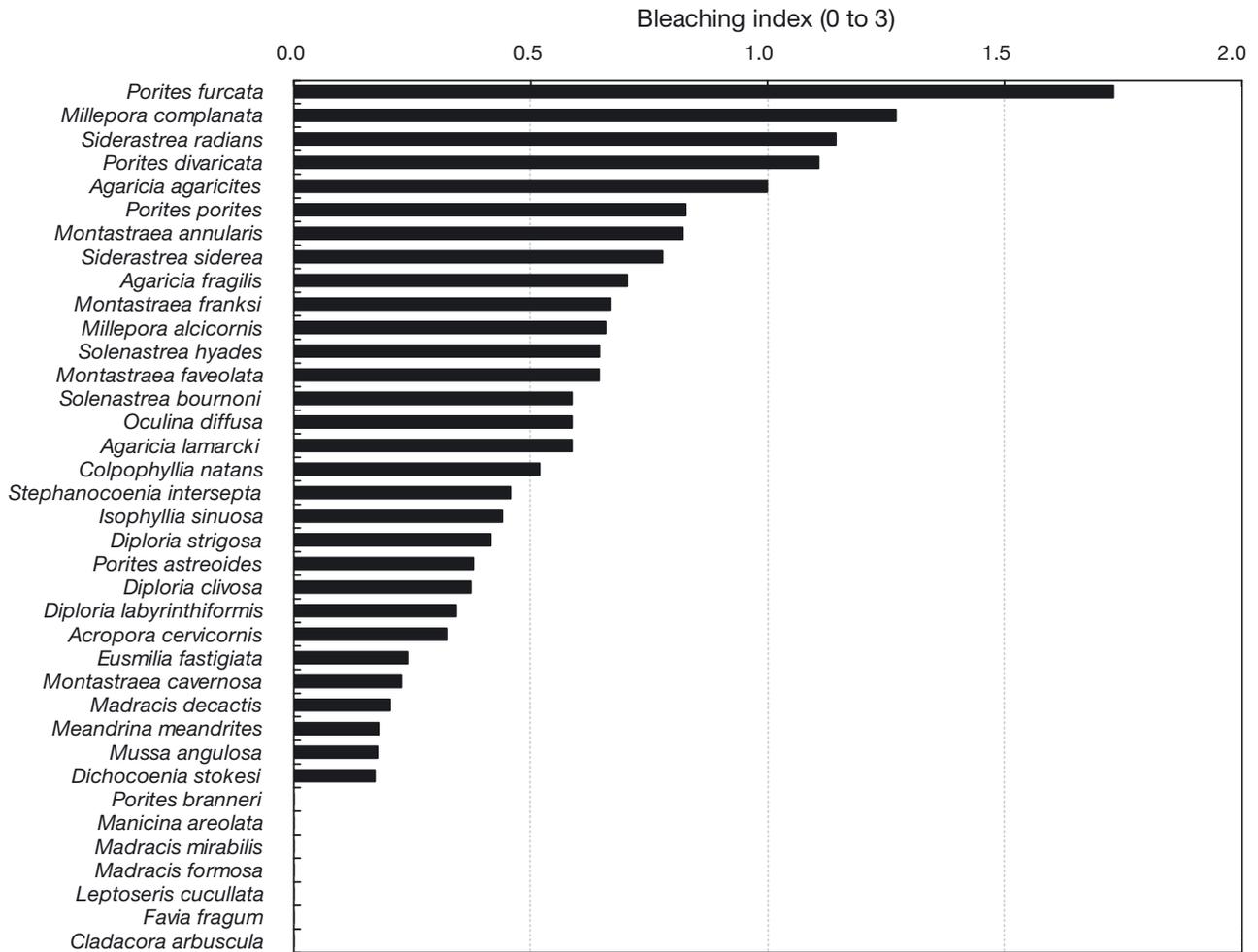


Fig. 3. Mean bleaching indices (2005 to 2007) for individual coral species along the Florida Keys reef tract; species without an index were not recorded as bleached throughout the surveys

that coral assemblages vary in diversity and relative abundance in accordance with habitat, we have shown a hierarchically nested arrangement of the coral assemblages. The sparse local coral assemblages were sub-sets of the more diverse regional assemblages. The nested assemblages were not simply a consequence of differences in depth ranges, because the forereef assemblages, ranging from 2 to 20 m in depth, were nested within the 2 to 12 m deep offshore patch reefs, which, in turn, were nested in the 2 to 10 m deep mid-channel reefs. These results agree with work previously carried out on the Great Barrier Reef (van Woesik & Done 1997), off the Mariana Islands (Houk & van Woesik 2010), and in the western Pacific Ocean in general (Karlson et al. 2004), which all show high-diversity assemblages concentrically arranged around depauperate assemblages. These species-poor assemblages, associated, for example, with inshore reefs or reefs in Martin County, were the result of consistently harsh environmental conditions most likely selecting against

environmentally sensitive, more vulnerable, coral species (Figs. 4 & 5).

Coral-bleaching prevalence was higher on forereefs than on near-shore reefs (Table 2), and shallow corals had a higher bleaching prevalence than deep corals. These results agree with ecological (Fitt et al. 2001, McClanahan et al. 2007) and physiological studies (Hoegh-Guldberg & Smith 1989, Iglesias-Prieto & Trench 1994, 1997) showing that high irradiance, characteristic of both shallow reefs and forereefs, enhances coral bleaching under elevated temperatures. Water temperatures were regionally high in the Florida Keys during the summer of 2005 (Wagner et al. 2008). Comparative analyses, however, detected weaker relationships between coral bleaching and temperature differences in 2005 than in 2006 and 2007, most likely because of the homogenous nature and large spatial extent of the anomalously high water temperatures in 2005 (Wagner et al. 2008). Despite the relative homogeneity of high water tem-

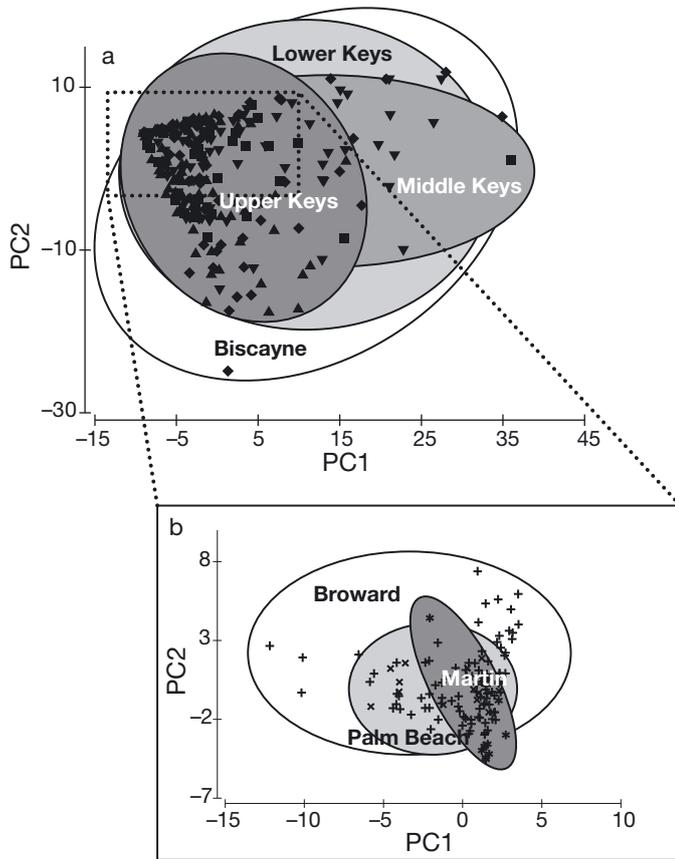


Fig. 4. Principal components (PC) analysis ordination plots for sub-regions along the (a) Florida Keys reef tract and (b) South Florida reef tract, indicating colony density for the top 12 dominant species. ◆: Biscayne (2 to 20 m); ▲: Upper Keys (1 to 18 m); ■: Middle Keys (2 to 16 m); ▼: Lower Keys (1 to 19 m); \*: Martin (4 to 7 m); x: Palm Beach (3 to 22 m); +: Broward (4 to 29 m)

peratures in 2005, there was considerable spatial variability in coral-bleaching prevalence (i.e. the proportion of colonies that bleached within each population). For example, while massive species such as *Montastrea*, *Siderastrea*, and *Diploria* tended to bleach more in the Middle Keys, localities with high densities of *Millepora alcicornis* and *Agaricia agaricites* had higher bleaching prevalence than localities where these species were absent. Similarly, the ubiquitous *Siderastrea siderea* accounted for a relatively high percentage of bleaching in all sub-regions and zones. Conversely, the presence of *Porites asteroides* reduced bleaching prevalence.

Colony size also played an important role in coral-bleaching prevalence during high-temperature periods. For example, in the mild thermal-stress year of 2007, coral-bleaching prevalence was not related to coral colony size. In contrast, during the summer of 2005, a high thermal-stress year, large coral colonies of

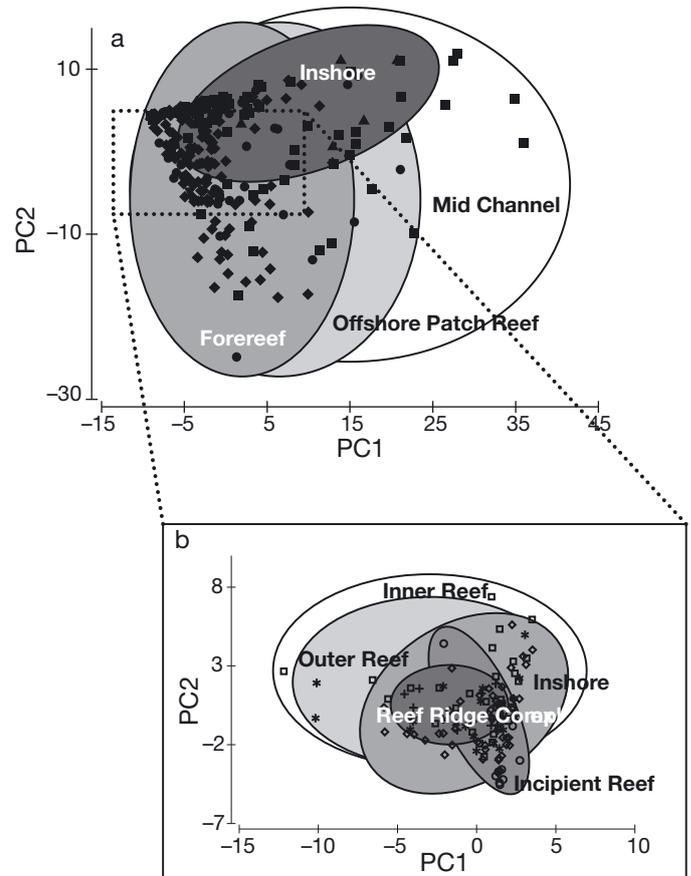


Fig. 5. Principal components (PC) analysis ordination plots for zones along the (a) Florida Keys reef tract and (b) South Florida reef tract, indicating colony density for the top 12 dominant species. ▲: inshore (2 to 6 m); ■: mid-channel (2 to 10 m); ●: offshore patch reef (2 to 12 m); ◆: foreereef (2 to 20 m); □: inner reef (8 to 19 m); \*: outer reef (6 to 29 m); +: reef ridge complex (15 to 22 m); ○: incipient reef (4 to 7 m)

foliose, massive, and encrusting growth forms exhibited higher bleaching prevalence than small colonies. However, during the same summer, there was a noticeable reversal in these trends for the branching growth forms, which were primarily composed of *Porites* spp., with small *Porites* colonies showing higher sensitivity to thermal stress than large colonies. It is well known that large *Acropora* colonies are more likely to bleach and die than large *Porites* colonies, which can bleach and recover (van Woesik et al. 2004). However, earlier studies by Loya et al. (2001) and Nakamura & van Woesik (2001) (in the Pacific Ocean) have shown that small branching *Acropora* colonies are less susceptible to thermal stress than large colonies of the same species. These contrasting results, whereby small branching *Porites* colonies, in the present study, were more susceptible to irradiance and thermal stress than small *Acropora* colonies, in previous studies in the Pacific Ocean (Bena & van Woesik 2004), could stem in part

Table 4. Bleaching prevalence during the summers of 2005 and 2007 for 4 size classes (4 to 9.9, 10 to 19.9, 20 to 29.9, and  $\geq 30$  cm) of 4 coral growth forms (foliose, branching, massive, and encrusting) by sub-region and zone along the Florida Keys reef tract

	2005				2007			
	4–9.9 cm	10–19.9 cm	20–29.9 cm	$\geq 30$ cm	4–9.9 cm	10–19.9 cm	20–29.9 cm	$\geq 30$ cm
<b>Sub-region</b>								
Foliose								
Biscayne	0.90	0.83	0.50	–	0.34	0.65	0.33	0.86
Upper Keys	0.65	0.61	0.67	–	0.54	0.74	0.54	0.50
Middle Keys	0.42	0.69	0.80	1.00	0.47	0.83	1.00	–
Lower Keys	0.67	0.59	0.60	–	0.52	0.52	0.40	–
Branching								
Biscayne	0.80	0.81	0.59	0.29	0.06	0.14	0.22	0.36
Upper Keys	0.54	0.65	0.45	0.48	0.15	0.18	0.18	0.27
Middle Keys	0.37	0.40	0.25	0.00	0.14	0.18	0.30	–
Lower Keys	0.80	0.83	0.40	0.37	0.26	0.24	0.22	0.40
Massive								
Biscayne	0.52	0.36	0.56	0.25	0.10	0.18	0.11	0.12
Upper Keys	0.34	0.46	0.52	0.57	0.31	0.20	0.19	0.24
Middle Keys	0.37	0.68	0.76	0.80	0.10	0.13	0.11	0.21
Lower Keys	0.21	0.35	0.42	0.53	0.16	0.27	0.31	0.40
Encrusting								
Biscayne	0.75	0.60	–	–	0.10	0.09	0.14	0.20
Upper Keys	0.61	0.69	0.33	1.00	0.36	0.00	0.50	0.00
Middle Keys	0.37	0.36	0.83	0.75	0.20	0.09	0.20	0.67
Lower Keys	0.31	0.33	0.28	0.43	0.30	0.30	0.43	0.50
<b>Zone</b>								
Foliose								
Offshore patch reef	0.75	0.54	0.40	–	0.41	0.86	0.80	–
Inshore	–	–	–	–	–	0.50	1.00	–
Forereef	0.60	0.65	0.58	1.00	0.47	0.62	0.40	0.86
Mid-channel	0.73	0.80	0.88	–	0.43	0.63	0.42	0.50
Branching								
Offshore patch reef	0.73	0.77	0.29	0.25	0.12	0.12	0.00	0.00
Inshore	0.29	0.37	0.00	0.00	0.17	0.19	0.50	0.29
Forereef	0.83	0.77	0.37	0.00	0.10	0.09	0.03	0.30
Mid-channel	0.65	0.82	0.69	0.61	0.22	0.30	0.33	0.38
Massive								
Offshore patch reef	0.25	0.35	0.55	0.40	0.12	0.12	0.18	0.18
Inshore	–	–	1.00	–	0.09	0.27	0.30	0.38
Forereef	0.36	0.49	0.45	0.60	0.19	0.36	0.30	0.34
Mid-channel	0.23	0.42	0.56	0.67	0.10	0.15	0.16	0.24
Encrusting								
Offshore patch reef	0.30	0.33	0.36	0.33	0.11	0.12	0.50	0.75
Inshore	–	–	–	–	1.00	1.00	1.00	1.00
Forereef	0.49	0.33	0.67	–	0.28	0.10	0.12	0.00
Mid-channel	0.41	0.50	0.29	0.73	0.94	1.00	1.00	1.00

from differences in the concentrations of protective pigments; small *Acropora* recruits support high concentrations of (photoprotective) fluorescent proteins that are reabsorbed under low-light treatments (Papina et al. 2002).

The strong relationship between coral bleaching and both chl *a* and DIN concentrations suggests that coral bleaching may be highly influenced by water-column productivity. High concentrations of DIN are not necessarily the same as high productivity, because water-flow rates are also critical (Atkinson &

Bilger 1992). Yet, chl *a* is a good proxy of water-column productivity and has previously been associated with coral-community shifts in general (Tomas-cik & Sander 1987, van Woessik et al. 1999) and in the Florida Keys in particular (Dustan 1977, Maliao et al. 2008). Although we could not infer a direct cause and effect from our results, other studies have shown that elevated productivity increases chlorophyll pigment concentrations in coral symbionts and increases population densities of symbionts (Muscatine et al. 1998). Moreover, these conditions are known to increase the

Table 5. Explained variance and correlation coefficients for canonical correspondence analysis between coral-bleaching prevalence and environmental parameters (mean values of temperature, salinity, dissolved inorganic nitrogen (DIN), chlorophyll *a* [chl *a*], and depth) in the summer wet season of 2005, 2006, and 2007. Cum % var. spec.-env. = cumulative percentage of the species–environment relationship. SPEC AX1 = Species Axis 1 and SPEC AX2 = Species Axis 2. Strong correlations are highlighted in bold

Environmental parameter	Mean 2005		Mean 2006		Mean 2007	
	SPEC AX1	SPEC AX2	SPEC AX1	SPEC AX2	SPEC AX1	SPEC AX2
Temperature	-0.2951	-0.1185	0.1077	<b>-0.5441</b>	<b>0.4835</b>	-0.3036
Salinity	-0.0862	-0.0538	-0.1616	0.367	0.3746	-0.0465
DIN	-0.0219	<b>0.6297</b>	-0.29	0.2304	-0.0913	<b>-0.4399</b>
Chl <i>a</i>	0.0352	<b>0.6582</b>	<b>0.8297</b>	0.1809	0.0236	<b>-0.5101</b>
Depth	<b>0.5804</b>	0.1541	0.1321	<b>0.4144</b>	<b>0.5593</b>	0.3107
Cum % var. spec.-env.	34.3	57.8	34.3	58.9	34.5	62.7
Σ all canonical eigenvalues	0.638		0.985		0.518	

Table 6. Explained variance and correlation coefficients for canonical correspondence analysis between coral-bleaching prevalence and coral-bleaching index, for colony-size-specific bleaching (4–9.9, 10–19.9, 20–29.9, and ≥30 cm), and the means of environmental parameters (temperature, salinity, DIN, chl *a*, and depth) in the wet season over a 12 yr period (1995 to 2007). Cum % var. spec.-env. = cumulative percentage of the species–environment relationship. SPEC AX1 = Species Axis 1 and SPEC AX2 = Species Axis 2. Strong correlations are highlighted in bold

Environmental parameter	Bleaching prevalence				Bleaching index			
	Environmental means		Environmental variance		Environmental means		Environmental variance	
	SPEC AX1	SPEC AX2	SPEC AX1	SPEC AX2	SPEC AX1	SPEC AX2	SPEC AX1	SPEC AX2
Temperature	<b>-0.5925</b>	<b>-0.4461</b>	<b>-0.4352</b>	-0.0863	<b>0.703</b>	-0.3389	<b>-0.4751</b>	-0.1661
Salinity	-0.3586	-0.2713	-0.22	<b>0.742</b>	<b>0.5085</b>	-0.2365	-0.3284	<b>0.6824</b>
DIN	-0.2474	<b>0.4437</b>	-0.0922	-0.2326	0.1382	<b>0.4087</b>	-0.0567	-0.3126
Chl <i>a</i>	<b>-0.6196</b>	0.0656	0.2066	-0.2367	<b>0.5989</b>	0.0949	0.1216	-0.2643
Depth	<b>-0.5939</b>	0.3015	<b>0.6004</b>	-0.3097	<b>0.5783</b>	<b>0.4458</b>	<b>0.6788</b>	-0.1214
Cum % var. spec.-env.	38.9	61.1	31.7	58.2	41	65.8	34.8	63.3
Σ all canonical eigenvalues	0.541		0.575		0.549		0.536	

vulnerability of corals to high irradiance, which leads to photoinhibition (Hoegh-Guldberg & Smith 1989, Iglesias-Prieto & Trench 1994, Jones & Hoegh-Guldberg 2001, Fabricius 2006).

The increased nutrient availability from storm-water runoff during South Florida's rainy season may stimulate the up-regulation of symbiont pigments and symbiont densities in corals. These results point to not only the well known interaction between temperature and light outlined above (Brown et al. 1999, Fitt et al. 2001), but also the interaction of those parameters with water quality. Previous experimental studies have specifically shown that nitrate enrichment exacerbates temperature stress (Nordemar et al. 2003, Schloder & D'Croz 2004). Nutrient enrichment has also been shown experimentally to increase the severity of coral diseases (Bruno et al. 2003). Other experimental studies have shown a link between temperature, light, coral bleaching, and diseases (Muller et al. 2008,

Muller & van Woesik 2009). Therefore, while we showed that depth was critical here, we could not assume a homogenous water column across the Florida Keys, when in fact turbidity was higher near shore and may well have reduced irradiance and bleaching.

Turbidity was not predictable, because it was collected at a spatial scale of  $10^3$  m and appears more homogenous at scales of from  $10^1$  to  $10^2$  m (Wagner et al. 2008). Therefore, the high spatial heterogeneity and ephemeral nature of turbidity precluded its present use in comparative analyses. Nevertheless, we did show that coral-bleaching prevalence was higher on reefs with high productivity (Table 5). Consistent with the present results and with physiological studies (Jones & Hoegh-Guldberg 2001), Lirman & Fong (2007) showed that near-shore patch reefs (<2 km from shore) supported higher coral cover and larger coral colonies than offshore patch reefs (>6 km from shore). We posit that reduced irradiance, through elevated

near-shore turbidity, also suppresses 'thermal' stress near shore. Similarly, Jokiel & Brown (2004) reported no coral bleaching on turbid reefs in Hawaii, whereas less turbid reefs showed extensive bleaching. Therefore, the spatial variation of turbidity (and the associated attenuation coefficient,  $k_d$ ) are critically important for distinguishing coral-bleaching prevalence differences at small spatial scales and may be the very key to resolving the unexplained variance in the present study.

While bleaching patterns are clearly dependent on near-substrate temperatures, the quality of Florida Bay-derived waters appeared most influential along the shoreline towards Biscayne Bay and northward along the South Florida coastline (Table 2). Other studies have shown that both the Florida current and the proximity of Florida Bay have a direct impact on water quality, which, in turn, affects coral-community structure (Marszalek et al. 1977). The close proximity of the reef tract to the passes interspersed throughout the Middle Keys allows water from Florida Bay to flow into the Atlantic, bathing the reef system in warmer, hyper-saline waters in the dry season (Precht & Miller 2007) and hypo-saline water in the wet season (Precht & Miller 2007, Wagner et al. 2008). During thermal stress events these osmotic extremes may couple to exacerbate the bleaching response (Mayfield & Gates 2007). Salinity concentrations distinctly explained some of the bleaching prevalence in the present study, during 2006 and 2007 (Table 6).

Understanding the interaction between temperature stress and more local stressors, such as water quality, is critical at a time of rapid climate change. It is also important to identify the environmental processes associated with the geographic positioning of coral reefs, such as ocean currents, temporal and spatial effects of cloud cover, turbidity, upwelling, rainfall, and salinity (Precht & Miller 2007). Coupling these variables with the inherent resistance of specific coral taxa to bleaching allows the predictive modeling necessary to identify future 'winners and losers' following wide-scale coral-bleaching events (Loya et al. 2001). In conclusion, the present study has clear management and policy implications that may increase local coral-community resilience to regional thermal stressors. We have shown a strong relationship between both chl *a* and DIN concentrations in the water column and the likelihood of coral bleaching. Therefore, locally regulating waste-water discharge from the land to minimize nutrients and reduce local water-column productivity may reduce coral bleaching when regional water temperatures are high. Such local actions will lead to benefits in the targeted area, at a time of rapid ocean warming.

*Acknowledgements.* We thank S. van Woesik for editorial comments on the manuscript. Special thanks to Chris Berg of The Nature Conservancy for endless support of this project and for the use of the Florida Reef Resilience Project dataset. Environmental data were provided by the SERC-FIU Water Quality Monitoring Network, which is supported by SFWMD/SERC Cooperative Agreements Nos. C-10244 and C-13178, as well as by EPA Agreement No. X994621-94-0. Additional thanks to H. Hudson, Florida Keys National Marine Sanctuary Biologist, for contributing the SERC data used in this manuscript. This is Contribution Number 32 from the Institute for Research on Global Climate Change at the Florida Institute of Technology.

#### LITERATURE CITED

- Atkinson MJ, Bilger RW (1992) Effects of water velocity in phosphate uptake in coral reef-flat communities. *Limnol Oceanogr* 37:273–279
- Ault JS, Smith SG, Bohnsack JA, Luo J, Harper DE, McClellan DB (2006) Building sustainable fisheries in Florida's coral reef ecosystem: positive signs in the Dry Tortugas. *Bull Mar Sci* 78(3):633–654
- Baker A, Glynn P, Riegl B (2008) Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. *Estuar Coast Shelf Sci* 80:435–471
- Banks KW, Riegl B, Shinn EA, Piller WE, Dodge RE (2007) Geomorphology of the Southeast Florida continental reef tract (Miami-Dade, Broward, and Palm Beach Counties, USA). *Coral Reefs* 26:617–633
- Bena C, van Woesik R (2004) The impact of two bleaching events on the survival of small-coral colonies. *Bull Mar Sci* 75:115–125
- Brown BE (1997) Coral bleaching: causes and consequences. *Coral Reefs* 16(Suppl):S129–S138
- Brown BE, Ambari I, Warner ME, Fitt WK, Dunne RP, Gibb SW, Cummings DG (1999) Diurnal changes in photochemical efficiency and xanthophyll concentrations in shallow water reef corals: evidence for photoinhibition and photoprotection. *Coral Reefs* 18:99–105
- Bruno JF, Petes LE, Harvell CD, Hettinger A (2003) Nutrient enrichment can increase the severity of coral diseases. *Ecol Lett* 6:1056–1061
- Castillo KD, Helmuth BST (2005) Influence of thermal history on the response of *Montastrea annularis* to short-term temperature exposure. *Mar Biol* 148:261–270
- Coles SL, Brown BE (2003) Coral bleaching—capacity for acclimatization and adaptation. *Adv Mar Biol* 46:183–215
- Dodge RE, Birkeland C, Hatzioles M, Kleypas J and others (2008) A call to action for coral reefs. *Science* 322:189–190
- Douglas AE (2003) Coral bleaching—How and why? *Mar Pollut Bull* 46:385–392
- Dustan P (1977) Vitality of reef coral populations off Key Largo, Florida: recruitment and mortality. *Environ Geol* 2: 51–58
- Fabricius KE (2006) Effects of irradiance, flow, and colony pigmentation on the temperature microenvironment around corals: Implications for coral bleaching? *Limnol Oceanogr* 51:30–37
- Finelli CM, Helmuth BST, Pentcheff ND, Wetthey DS (2006) Water flow influences oxygen transport and photosynthetic efficiency in corals. *Coral Reefs* 25:47–57
- Fitt WK, Brown BE, Warner ME, Dunne RP (2001) Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in tropical corals. *Coral Reefs* 20:51–65

- Gates RD, Baghdasarian G, Muscatine L (1992) Temperature stress causes host cell detachment in symbiotic cnidarians: implications for coral bleaching. *Biol Bull* 182:324–332
- Glynn PW (1993) Coral bleaching: ecological perspectives. *Coral Reefs* 12:1–17
- Glynn PW (1996) Coral reef bleaching: facts, hypotheses and implications. *Glob Change Biol* 2:495–509
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Mar Freshw Res* 50:839–866
- Hoegh-Guldberg O, Smith GJ (1989) The effect of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* Esper and *Seriatopora hystrix* Dana. *J Exp Mar Biol Ecol* 129:279–303
- Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS and others (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–1742
- Houk P, van Woesik R (2010) Coral assemblages and reef growth in the Commonwealth of the Northern Mariana Islands (Western Pacific Ocean). *PSZN I: Mar Ecol* 31: 318–329
- Iglesias-Prieto R, Trench RK (1994) Acclimation and adaptation to irradiance in symbiotic dinoflagellates. I. Responses of the photosynthetic unit to changes in photon flux density. *Mar Ecol Prog Ser* 113:163–175
- Iglesias-Prieto R, Trench RK (1997) Acclimation and adaptation to irradiance in symbiotic dinoflagellates. II. Responses of chlorophyll protein complexes to different light regimes. *Mar Biol* 130:23–33
- Jokiel PL, Brown EK (2004) Global warming, regional trends and inshore environmental conditions influence coral bleaching in Hawaii. *Glob Change Biol* 10:1627–1641
- Jones RJ, Hoegh-Guldberg O (2001) Diurnal changes in the photochemical efficiency of the symbiotic dinoflagellates (Dinophyceae) of corals: photoprotection, photoinactivation and the relationship to coral bleaching. *Plant Cell Environ* 24:89–99
- Jones RJ, Hoegh-Guldberg O, Larkum AWD, Schreiber U (1998) Temperature-induced bleaching of corals begins with impairment of the CO<sub>2</sub> fixation mechanism in zooxanthellae. *Plant Cell Environ* 21:1219–1230
- Karlson RH, Cornell HV, Hughes TP (2004) Coral communities are regionally enriched along an oceanic biodiversity gradient. *Nature* 429:867–870
- Lirman D, Fong P (2007) Is proximity to land-based sources of coral stressors an appropriate measure of risk to coral reefs? An example from the Florida Reef Tract. *Mar Pollut Bull* 54:779–791
- Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, van Woesik R (2001) Coral bleaching: the winners and losers. *Ecol Lett* 4:122–131
- Maliao R, Turigan RG, Linn J (2008) Phase-shift in coral reef communities in the Florida Keys National Marine Sanctuary (FKNMS), USA. *Mar Biol* 154:841–853
- Manzello DP, Berkelmans R, Hendee JC (2007) Coral bleaching indices and thresholds for the Florida Reef Tract, and St. Croix, US Virgin Islands. *Mar Pollut Bull* 54: 1923–1931
- Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs* 19:155–163
- Marszalek DS, Babashoff G Jr, Noel MR, Worley DR (1977) Reef distribution in South Florida. In: Taylor DL (ed) *Proc 3rd Int Coral Reef Symp.* University of Miami, FL, p 223–230
- Mayfield AB, Gates RD (2007) Osmoregulation in anthozoan-dinoflagellate symbiosis. *Comp Biochem Physiol* 147:1–10
- McClanahan T, Polunin N, Done T (2002) Ecological states and the resilience of coral reefs. *Conserv Ecol* 6:18. Available at: [www.consecol.org/vol6/iss2/art18/](http://www.consecol.org/vol6/iss2/art18/)
- McClanahan TR, Maina J, Moothien-Pillay R, Baker AC (2005) Effects of geography, taxa, water flow, and temperature variation on coral bleaching intensity in Mauritius. *Mar Ecol Prog Ser* 298:131–142
- McClanahan TR, Ateweberhan M, Muhando CA, Maina J, Mohammed MS (2007) Effects of climate change and seawater temperature variation on coral bleaching and mortality. *Ecol Monogr* 77:503–525
- Muller EM, van Woesik R (2010) Shading reduces coral disease progression. *Coral Reefs* 28:757–760
- Muller EM, Rogers CS, Spitzack AS, van Woesik R (2008) Bleaching increases likelihood of disease on *Acropora palmata* (Lamarck) in Hawksnest Bay, St John, US Virgin Islands. *Coral Reefs* 27:191–195
- Murdoch TJT, Aronson RB (1999) Scale-dependent spatial variability of coral assemblages along the Florida Reef Tract. *Coral Reefs* 18:341–351
- Muscatine L, Ferrier-Pagès C, Blackburn A, Gates RD, Baghdasarian G, Allemand D (1998) Cell-specific density of symbiotic dinoflagellates in tropical anthozoans. *Coral Reefs* 17:329–337
- Nakamura T, van Woesik R (2001) Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. *Mar Ecol Prog Ser* 212:301–304
- Nordemar I, Nystrom M, Dizon R (2003) Effects of elevated seawater temperature and nitrate enrichment on the branching coral *Porites cylindrica* in the absence of particulate food. *Mar Biol* 142:669–677
- Papina M, Sakihama Y, Bena C, van Woesik R, Yamasaki H (2002) Separation of highly fluorescent proteins by SDS-PAGE in Acroporidae corals. *Comp Biochem Physiol* 131: 767–774
- Precht WF, Miller SL (2007) Ecological shifts along the Florida reef tract: the past as a key to the future. In: Aronson RB (ed) *Geological approaches to coral reef ecology.* Springer-Verlag, New York, p 237–312
- Schloder C, D'Croz L (2004) Responses of massive and branching coral species to the combined effects of water temperature and nitrate enrichment. *J Exp Mar Biol Ecol* 313:255–268
- Stat M, Morris E, Gates RD (2008) Functional diversity in coral–dinoflagellate symbiosis. *Proc Natl Acad Sci USA* 105:9256–9261
- Takahashi S, Nakamura T, Sakamizu M, van Woesik R, Yamasaki H (2004) Repair machinery of symbiotic photosynthesis as the primary target of heat stress for reef-building corals. *Plant Cell Physiol* 45:251–255
- Thompson D, van Woesik R (2009) Corals escape bleaching in regions that recently and historically experienced frequent thermal stress. *Proc R Soc Lond Ser B Biol Sci* 276:2893–2901
- Tomascik T, Sander S (1987) Effects of eutrophication on reef-building corals. II. Structure of scleractinian coral communities on fringing reefs, Barbados, West Indies. *Mar Biol* 94:53–75
- van Woesik R, Done TJ (1997) Coral communities and reef growth in the southern Great Barrier Reef. *Coral Reefs* 16: 103–115
- van Woesik R, De Vantier LM, Glazebrook JS (1995) Effects of Cyclone 'Joy' on nearshore coral communities of the Great Barrier Reef. *Mar Ecol Prog Ser* 128:261–270

- van Woesik R, Tomascik T, Blake S (1999) Coral assemblages and physico-chemical characteristics of the Whitsunday Islands: evidence of recent community changes. *Mar Freshw Res* 50:427–440
- van Woesik R, Irikawa A, Loya Y (2004) Coral bleaching: signs of change in southern Japan. In: Rosenberg E, Loya Y (eds) *Coral health and disease*. Springer-Verlag, Heidelberg, p 119–141
- Wagner DE, Meilbrecht E, van Woesik R (2008) Application of landscape ecology to spatial variance of water-quality parameters along the Florida Keys reef tract. *Bull Mar Sci* 83:553–569
- Warner ME, Fitt WK, Schmidt GW (1999) Damage to Photosystem II in symbiotic dinoflagellates: a determinant of coral bleaching. *Proc Natl Acad Sci USA* 96: 8007–8012
- Webster PJ, Holland GJ, Curry JA, Chang HR (2005) Changes in tropical cyclone number, duration, and intensity in a warming environment. *Science* 309:1844–1846
- Weis VM (2008) Cellular mechanisms of Cnidarian bleaching: stress causes the collapse of symbiosis. *J Exp Biol* 211: 3059–3066

*Editorial responsibility: Otto Kinne,  
Oldendorf/Luhe, Germany*

*Submitted: July 21, 2009; Accepted: March 15, 2010  
Proofs received from author(s): May 20, 2010*