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Influence of water-temperature variability on stony coral diversity in Florida Keys patch reefs

M. Vega-Rodriguez[1,*], F. E. Müller-Karger[1], P. Hallock[1], G. A. Quiles-Perez[1], C. M. Eakin[2], M. Colella[3], D. L. Jones[1], J. Li[2], I. Soto[1], L. Guild[4], S. Lynds[5], R. Ruzicka[3]

[1]College of Marine Science, University of South Florida, 140 Seventh Avenue South, St. Petersburg, Florida 33701, USA
[2]Coral Reef Watch, Center for Satellite Applications and Research, NOAA National Environmental Satellite, Data, and Information Service, 5830 University Research Ct., E/RA32, College Park, Maryland 20740, USA
[3]Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, 100 Eighth Avenue Southeast, St. Petersburg, Florida 33701, USA
[4]Earth Science Division, NASA Ames Research Center, Moffett Field, California 94035, USA
[5]Cooperative Institute for Research in Environmental Sciences, University of Colorado, Boulder, Colorado 80309, USA

ABSTRACT: Annual surveys conducted by the Coral Reef Evaluation and Monitoring Project (CREMP) reported that average benthic cover of stony corals in the Florida Keys National Marine Sanctuary, USA declined from ~13% in 1996 to 8% in 2009. Keys-wide, mean species richness (SR) declined by ~2.3 species per station. Stress due to temperature extremes is suspected to be a major driver of this trend. We tested the potential for sea surface temperature (SST) variability and acute warm-temperature events (assessed with Degree Heating Weeks) to affect stony coral diversity in the Florida Keys. Benthic cover of 43 stony coral species was examined with respect to SST variability and habitat type (patch, offshore shallow, and offshore deep reefs). For each CREMP site, SST annual variance was classified as low ($<7.0°C^2$), intermediate (7.0 to $10.9°C^2$), or high ($\geq 11.0°C^2$). Nonparametric MANOVA analyses showed that in the Upper, Middle, and Lower Keys regions, massive-type stony coral species (e.g. *Siderastrea siderea*, *Pseudodiploria strigosa*, *Orbicella annularis* complex, *Montastraea cavernosa*, and *Colpophyllia natans*) were prevalent in the patch reef habitats exposed to intermediate to high SST variability. Intermediate SST variability was also correlated with higher Shannon diversity means in patch reefs in the Upper Keys and higher SR means in the Middle Keys, indicating either that the stony coral species in these habitats are adapted to an intermediate temperature range or that individual colonies have acclimatized to that range. No significant relationships were found between stony coral diversity and SST variability in the Dry Tortugas region.

KEY WORDS: Coral reef · Florida Keys · Sea surface temperature · Degree Heating Weeks · Species richness · Shannon diversity

INTRODUCTION

Biological diversity of coral reef communities depends on many variables, including the pool of available species, disturbance (e.g. hurricane frequency, fishing pressure, or recreational diving), changes in environmental parameters (e.g. temperature, nutrients, or light), and bottom topography (Connell 1978, Hallock 1987, Aronson & Precht 1995, Kleypas et al. 1999). While local declines of stony coral populations have been linked to extreme or prolonged changes in many of these variables, temperature-induced coral bleaching is considered one of the most important stressors responsible for worldwide declines in reef

*Corresponding author: mariavegarod@mail.usf.edu

health (Precht & Aronson 2004, Baker et al. 2008, Hoegh-Guldberg & Bruno 2010). Extreme water temperatures negatively influence coral colonies by disrupting their relationships with symbiotic dinoflagellates (*Symbiodinium*), causing coral bleaching, increased incidences of diseases, and coral mortality (Porter et al. 2001, Eakin et al. 2010).

Conversely, in some regions, exposures to recurrent thermal stress events have led to increased prevalence of more thermally tolerant coral species or acclimatization of surviving colonies. For example, in the tropical Pacific and Indian oceans, coral reefs exposed to high frequency in sea surface temperature (SST) anomalies displayed less bleaching and mortality in 2005 compared with 1998, despite experiencing higher thermal stress in 2005 (Thompson & van Woesik 2009). A working hypothesis motivating this study is that exposure to historically high SST variability should result in stony coral communities with species better adapted to extreme changes in temperature. A related hypothesis is that coral colonies that survive an extreme thermal event can acclimate to survive more thermal variability.

The Florida Keys is a subtropical barrier reef system formed ~4 to 8 ka BP (Shinn et al. 1989, Precht & Miller 2007). Massive reef-building species defined much of the geomorphology of the Upper and Middle Keys (e.g. *Orbicella annularis* complex [formerly *Montastraea annularis*; Budd et al. 2012], *Colpophyllia natans*). Branching species were abundant in the Upper and Lower Keys (*Acropora* spp.; Shinn et al. 1989, Precht & Miller 2007). Coral species distributions were influenced by changes in sea level and exposure to waters that flowed seaward from the Florida Bay through tidal passes in the Middle Keys. These waters had temperatures as low as 9°C and as high as 37°C, salinity from 30 to 40 ppt, and high suspended sediment load (Neumann & Macintyre 1985, Shinn et al. 1989, Lidz & Shinn 1991). Recurrent exposure to these waters has led to poor outer reef development associated with reduced recruitment and cover of fast-growing branching coral species (e.g. *Acropora palmata*) in the Middle Keys (Shinn et al. 1989, Lidz & Shinn 1991). Today, the most abundant reef features are patch reefs constructed by massive framework corals such as *Orbicella* spp., *M. cavernosa*, *Siderastrea siderea*, and *Diploria* spp. (Jaap et al. 2008). Well-developed spur and groove systems that are structural remnants from reef growth during the last interglacial period (formerly inhabited by *Acropora* spp. but now predominated by 'weedier' species like *Porites astreoides*) are conspicuous in the outer reefs (Jaap et al. 2008).

Over the last 50 yr, reefs in the Florida Keys have experienced numerous disturbances. Thermal anomalies have contributed to changes in scleractinian composition and cover on reefs. Massive coral mortality on inshore patch reefs after short-term exposure (8 d) to water temperatures <16°C was first reported in 1977 (Roberts et al. 1982). Record-breaking cold anomalies in 2010 led to the highest coral mortality reported for the Upper and Middle Keys in recent years (Kemp et al. 2011, Lirman et al. 2011, Colella et al. 2012). Tissue discolorations have also been observed in *A. palmata* and the *O. annularis* complex when exposed to summer high water temperatures (Jaap 1979). Warm thermal anomalies in the late 1980s and early 1990s led to bleaching and white-band disease and to complete or partial mortality of affected scleractinian corals, especially *A. palmata* and *A. cervicornis* (Porter & Meier 1992, Jaap et al. 2008, Somerfield et al. 2008). Widespread diseases including black-band, white-band, and others have been reported for important reef-building species such as *O. annularis* complex and *Pseudodiploria strigosa* (formerly *Diploria strigose*; Porter et al. 2001). These episodes have reduced total coral cover and led to changes in species composition for most of the Keys reefs (Porter & Meier 1992, Jaap et al. 2008, Somerfield et al. 2008).

The Coral Reef Evaluation and Monitoring Project (CREMP), led by the Florida Fish and Wildlife Research Institute, has collected data throughout the Keys since 1996. These observations show that average benthic cover of stony corals in the Florida Keys National Marine Sanctuary (FKNMS) has declined from ~13% in 1996 to 8% in 2009 (Ruzicka et al. 2013). Keys-wide, mean species richness (SR) has declined by ~2.3 species per station since 1996 (Ruzicka et al. 2010). While loss of *O. annularis* complex has driven a Keys-wide decline in coral cover, no significant changes were observed in abundance of species such as *S. siderea* (one of the most widespread coral species) between 1999 and 2009 (Ruzicka et al. 2010, 2013).

Several research teams have hypothesized that warm water temperature anomalies in the Pacific led to shifts in coral communities toward heat-tolerant species, resulting in changes to overall reef diversity and community structure (Guest et al. 2012). Studies conducted in Sesoko Island showed that long-term 'winners' or survivors of coral bleaching were (1) thermally tolerant species, (2) colonies of locally persistent species that grew rapidly, and (3) regionally persistent species that successfully recruited (van Woesik et al. 2011). Soto et al. (2011) suggested that in the Florida Keys, patch reef coral communities exposed to moderate SST variability exhibited higher percent live coral cover than those exposed to lower variability.

We tested the null hypothesis that differences in stony coral diversity in Florida Keys patch reefs were not correlated with SST variability or acute warm-temperature events between 1996 and 2010. The central question addressed in this paper is whether the SST variance (which accounts for the entire temperature spectrum including the cold and warm ends) can be used to predict changes in stony coral diversity in the Florida Keys? We report the results of an analysis that used CREMP coral survey data and satellite-derived SST data between 1996 and 2010.

MATERIALS AND METHODS

Study sites

The CREMP has conducted summer habitat surveys annually at permanently marked sites throughout the FKNMS (USA) since 1996 (Ruzicka et al. 2010). The CREMP sites used for this study (Fig. 1, Table S1 in the Supplement at www.int-res.com/articles/suppl/m528p173_supp.pdf) are distributed throughout the Upper Keys (10 sites between Turtle Key and Conch Key), the Middle Keys (8 sites between West Turtle Shoal and Sombrero Reef), and the Lower Keys (15 sites between West Washerwoman reef and Sand Key). The 3 CREMP sites located in the Dry Tortugas were grouped into a fourth region.

Satellite-derived SST variability

Satellite-derived SST observations provide a means to synoptically examine temperature variations. Daytime and nighttime SSTs were measured by the Advanced Very High Resolution Radiometer (AVHRR) at 1 km^2 resolution from 1995 to 2010. Data processing details are included in the Supplement. At 15 of the 36 CREMP sites (Fig. 1, Table S1 in the Supplement), bottom thermographs (Sea-Bird Electronics) recorded water temperature at 2 h intervals. The instruments were typically at depths shallower than 20 m; most were shallower than 10 m. For each pixel in the satellite images that included one of the 15 CREMP sites for which thermograph data were available, daily SST composites were extracted, and weekly means were calculated to minimize autocorrelation in the thermal data. To validate the satellite-derived temperatures, the weekly SST means and corresponding weekly *in situ* temperature means were compared using a linear Pearson regression analysis in IDL 7.0 (Exelis Visual Information Solutions).

For all 36 sites, weekly SST means were calculated, and annual SST variances were calculated as the average of the squared differences from the weekly means (Soto et al. 2011). These are herein referred to as SST variability. Partitioning of the data was done *a priori* to accommodate for 3 levels of SST variability categorized as low (annual variance <7.0°C^2), intermediate (annual variance of 7.0 to 10.9°C^2), and high (annual variance ≥11.0°C^2). Regional means were obtained by averaging all sites within a region (i.e. Upper Keys, Middle Keys, Lower Keys, and Dry Tortugas). Regional seasonal means were also computed (winter [December to February] and the following summer [June to October]).

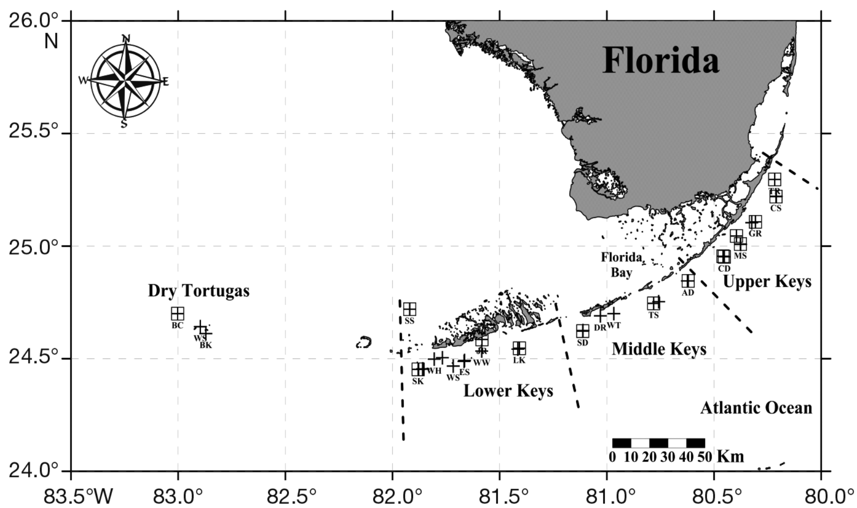

Fig. 1. Florida reef tract with 36 Coral Reef Evaluation and Monitoring Project (CREMP) stations included in this study. Crosses represent stations for which sea surface temperature and CREMP annual survey data were available. Boxes indicate the 15 stations where *in situ* temperature data were also available. Station codes are defined in Table S1 in the Supplement, available at www.int-res.com/articles/suppl/m528p173_supp.pdf

Percent live stony coral cover estimations

Percent live coral cover was used as a proxy for abundance and estimated for each of 43 different stony coral species using CREMP benthic cover data from annual surveys as described in Porter et al. (2002), Somerfield et al. (2008), and Ruzicka et al. (2013). All 36 sites were stratified across 3 habitat types (Table S1 in the Supplement): patch reefs (2 to 11 m depth), shallow spur and groove reefs (herein referred to as 'offshore shallow'; 4 to 8 m depth), and deep spur and groove reefs (herein referred to as 'offshore deep'; 11 to 23 m depth). At all sites, 2 to 4 stations were surveyed with 22 m × 40 cm transects (total survey area = 27 m^2) and filmed with a Sony Handycam DCR-TRV900 video camera. Approximately 210 sequential images were extracted for each station. Each image was overlain with 15 random points and analyzed for coral cover estimates using a custom software package (Point Count'99, http://prosper.cofc.edu/~coral/corallab.htm).

Coral diversity, SST variability, and habitat types: a multivariate statistical approach

Stony coral percent cover (i.e. abundance) data and annual SST variability were analyzed statistically using permutation-based nonparametric MANOVA (np-MANOVA or PERMANOVA; Anderson 2001). This permutation-based nonparametric test is appropriate when analyzing community composition data (Anderson 2001). The null hypothesis that no differences in stony coral diversity (coral species composition and abundance) existed among the 3 different categories of SST variability (low, intermediate, and high) was tested using an np-MANOVA. For this analysis, species-specific percent cover data (transformed using the square root to downweight species with the highest coral cover; Somerfield et al. 2008) were used to construct Bray-Curtis distance matrices, which served as input for the nonparametric multivariate analyses. To test for differences in diversity among all possible pairs of SST categories, pairwise multiple comparisons followed the np-MANOVA. A distance-based canonical analysis of principal coordinates (CAP; Anderson & Willis 2003) was used to create ordination plots for visualizing differences in stony coral diversity among SST variability categories. Success rates for reclassification of sites to SST categories generated by the CAP analysis provided a relative measure of distinctiveness in species among each SST category. The same statistical approaches were used to test for differences in coral diversity among habitats (patch, offshore shallow, and offshore deep reefs). Sites at the Dry Tortugas were analyzed separately but using the same approach, because those CREMP annual surveys did not start until 1999. All multivariate statistics were processed using the Fathom Toolbox for Matlab (Jones 2014) with 1000 permutation iterations and $\alpha = 0.05$.

Shannon diversity, SR, and warm thermal stress: a univariate approach

To characterize stony coral diversity through univariate metrics, annual Shannon diversity indices (H'; Magurran 1988, Connell et al. 2004) and stony coral SR were computed for each site. The Shannon index was calculated as $H' = -\sum p_i \ln p_i$, where p_i was the raw percent live coral cover. A species inventory dataset provided the data used for SR estimations. The inventories were collected simultaneously by 2 divers, who recorded the presence or absence of every stony coral species along ~20 min transects. After completing a survey, the divers compared all observations for confirmation and validation (Ruzicka et al. 2010). SR was calculated as the total number of species recorded per site. Regional annual means for both biodiversity metrics were calculated by averaging all sites within each region (Upper Keys, Middle Keys, Lower Keys, and Dry Tortugas). Time series of H' and SR regional annual means were thus constructed. Within each region, means for each habitat type were also calculated by averaging all sites in each habitat.

Degree Heating Weeks (DHWs), defined as the sum of all SSTs that exceeded maximum summer means by ≥1°C in a 12 wk window, were processed and interpreted using the NOAA Coral Reef Watch methodology as described in the Supplement. We used high-spatial-resolution (1 km^2) annual summer maximum DHWs (DHW_{max}) to better understand yearly changes at the scale relevant to the CREMP observations (Fig. 2). When DHW values are ≥4 but <8°C-weeks, significant coral bleaching is likely. Values ≥8 show conditions where mass coral bleaching and significant mortality are likely (Liu et al. 2013). Within each region, the DHW_{max} habitat means (patch, offshore shallow, and offshore deep reefs) were estimated.

Changes in diversity between years (Δ_y) were expressed in terms of differences during sequential years $y - 1$ and y. Between-year variations for H' were given by $H'_{\Delta y} = [(H'_y - H'_{y-1})/(H'_{y-1})] \times 100\%$. Between-year variations for SR ($SR_{\Delta y}$) were similarly calculated. To examine the effects of annual water temperature variability and heat stress on stony coral diversity, the SST variance, DHW_{max}, and coral diver-

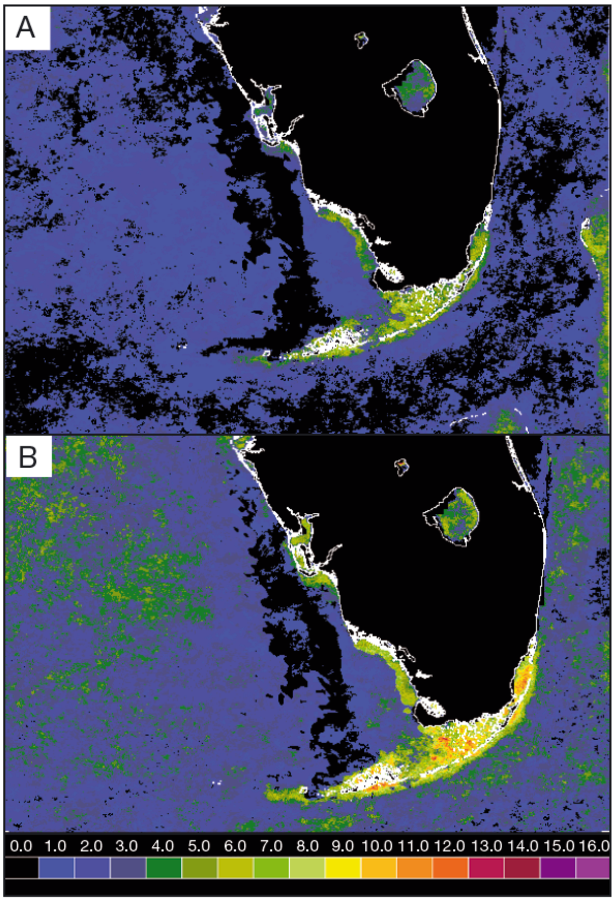

Fig. 2. High spatial resolution (1 km^2) Degree Heating Week (°C-weeks) images for (A) August 2, 2010, and (B) August 26, 2010

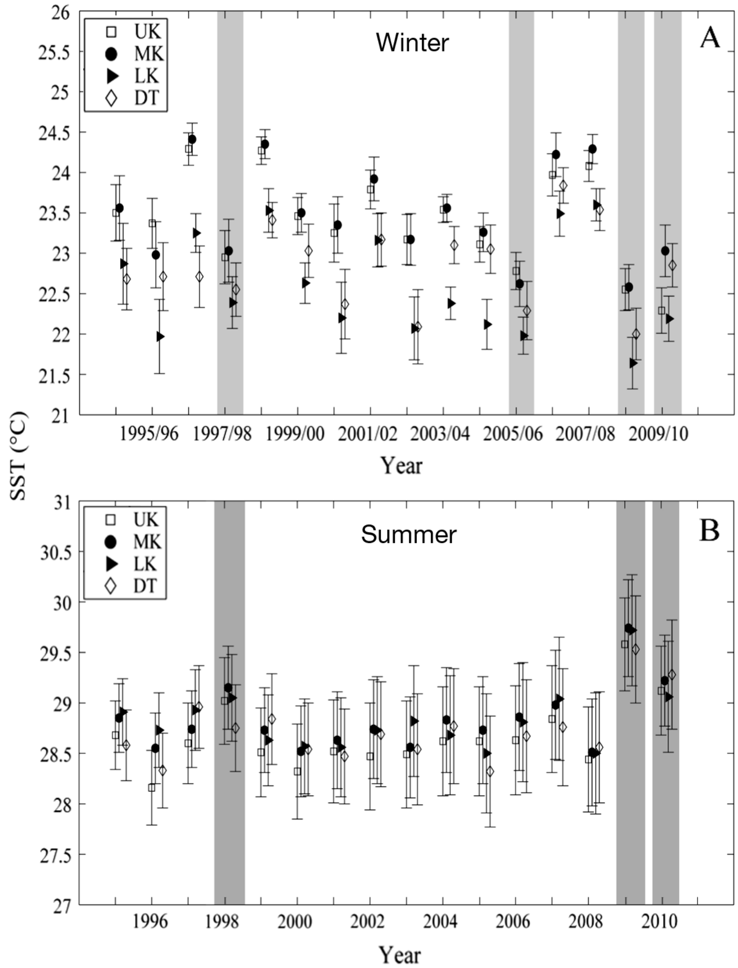

Fig. 3. Advanced Very High Resolution Radiometer sea surface temperature (SST) seasonal means by region for (A) winters and (B) the following summers in the Florida Keys. UK: Upper Keys; MK: Middle Keys; LK: Lower Keys; DT: Dry Tortugas. Shaded boxes highlight the coolest winters (when most regions were <23°C) and the warmest summers (when most regions were >29°C). Two-sided error bars denote standard errors of the mean

sity metrics (H', SR, $H'_{\Delta y}$, and $SR_{\Delta y}$) were compared. We used second-order polynomial regressions (Aronson & Precht 1995) to examine how the diversity indices in a particular habitat varied with SST variability and DHW_{max}. To test whether changes in habitat diversity were related to warm thermal stress accumulation, the DHW_{max} habitat means of each year were examined relative to the $SR_{\Delta y}$ and $H'_{\Delta y}$ habitat means of the following year. One-way ANOVAs were used to determine significance levels at $\alpha = 0.05$ for all regressions.

RESULTS

SST variability

The AVHRR SST and *in situ* water temperature measurements (5457 paired weekly mean measurements from 15 sites over 15 yr) showed a significant and positive correlation ($y = 0.78x + 5.70$; $r = 0.93$, $p = 0.004$, $\alpha = 0.05$; Fig. S1 in the Supplement).

The coolest winters (i.e. winters [December to February] for which most regions experienced seasonal SST means of <23.0°C) were observed in 1997/1998, 2005/2006, 2008/2009, and 2009/2010 (Fig. 3A). In general, the Lower Keys and Dry Tortugas experienced cooler winters (21.6 to 23.0°C) compared with those in the Middle and Upper Keys. However, during the record-breaking winter of 2009/2010, the Upper and Lower Keys experienced the coldest temperatures. In all regions, the coolest winters of 1997/1998, 2008/2009, and 2009/2010 preceded some of the warmest summer mean temperatures (Fig. 3). Summer SSTs >29.0°C (warm thermal threshold for

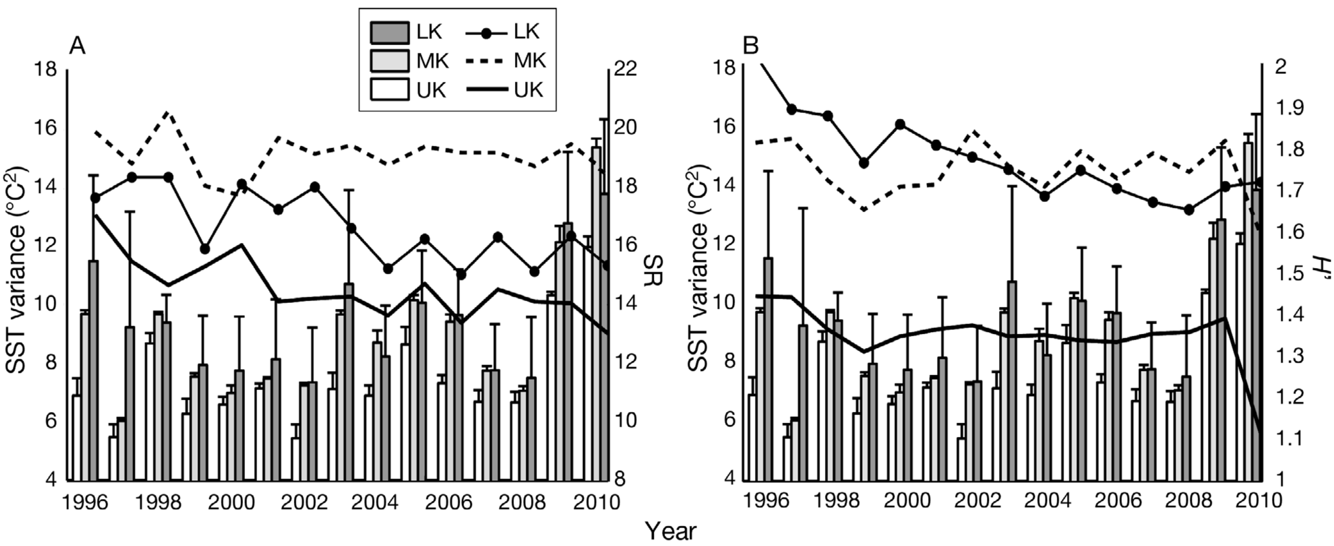

Fig. 4. Annual sea surface temperature (SST) variance means (°C^2, represented in bars) with (A) species richness (SR) annual means and (B) Shannon diversity index (H') annual means (represented by lines) for patch reefs in the Upper Keys (UK), Middle Keys (MK), and Lower Keys (LK). Error bars represent standard errors of the mean

corals) were observed in 1998, 2009, and 2010 in most regions (Fig. 3B). The Dry Tortugas exceeded this threshold in 2009 and 2010. All regions exhibited lower seasonal SST variability in summer than in winter. Within the Upper, Middle, and Lower Keys, the highest SST variability was observed at patch reef sites followed by those in the offshore shallow and deep reefs (Fig. 4, Fig. S2 in the Supplement).

Stony coral diversity, habitat types, and SST variability

Results from the multivariate analyses revealed that stony coral diversity varied significantly with SST variability and habitat (Table 1). Distance-based CAP ordination plots revealed that massive-type coral species such as *Orbicella annularis* complex, *Siderastrea siderea*, *Colpophyllia natans*, and *Pseudodiploria strigosa* were predominant in waters with intermediate to high SST variability (Fig. 5). *Acropora palmata* was more characteristic of sites with low to intermediate SST variability. Results from the CAP classifier indicated lower stony coral diversity in reefs exposed to low SST variability compared to those exposed to intermediate and high SST variability. Sites characterized by stony coral diversity were successfully classified to low or high SST variability, but overlap was evident for the intermediate SST category (Table 2).

Stony coral diversity also varied significantly with respect to habitat types (patch, offshore shallow, and offshore deep) (Table 1). Based on the CAP ordination plots, *Montastraea cavernosa*, *O. annularis* complex, *S. siderea*, *C. natans*, and *Stephanocoenia intersepta* were more characteristic of patch reefs, while

Table 1. Two-way permutation-based nonparametric MANOVA on the distribution of stony coral diversity among sites in all regions (Upper, Middle, and Lower Keys) with respect to sea surface temperature (SST) variability categories, habitat types, and the interaction between both factors. F^* = pseudo F-ratio, p = permuted p-value at $\alpha = 0.05$

Factor (1000 permutations)	df	F^*	p
Habitats (patch, offshore shallow, and deep reefs)	2	61.36	0.001
SST variability (low, intermediate, and high)	2	10.22	0.001
SST variability vs. Habitats	4	2.4	0.001

Table 2. Reclassification success of sites, characterized by specific coral diversity, to sea surface temperature (SST) variability categories obtained from the canonical analysis of principal coordinates discriminant analysis. Percentages indicate the success of associating sites with specific coral species compositions and abundances to specific SST categories. For example, 69% of sites by species were correctly assigned to the low SST variability category, whereas ~9% were erroneously assigned to the high SST variability category

SST variability	Low	Intermediate	High
Low	69	22	9
Intermediate	35	33	31
High	10	20	70

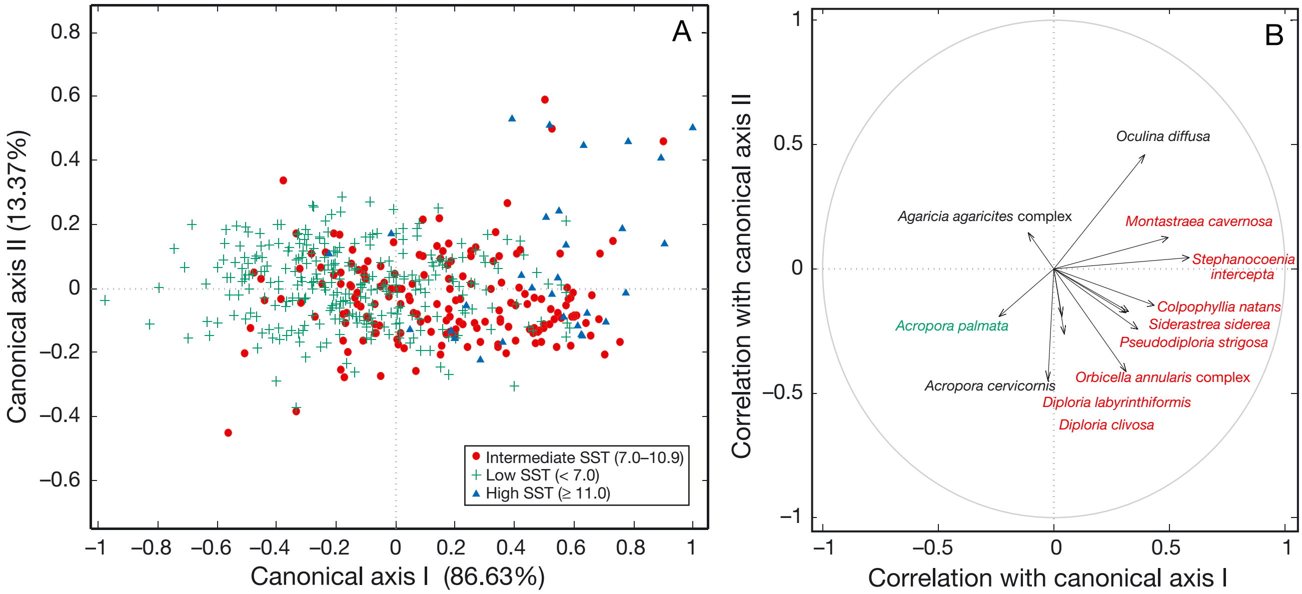

Fig. 5. Distance-based canonical discriminant analysis. (A) Ordination plots of the spatial variation of coral species as a function of sea surface temperature (SST) variability (°C^2) and (B) vector plot based on indicator species among each SST variability category along the first 2 canonical axes depicted in (A). Species are color coded to match SST variability and habitats from Fig. 6. Species in black are those for which habitats and SST variability color codes did not match

A. palmata was more representative of offshore shallow reefs, and *Agaricia agaricites* was more representative of offshore deep reefs (Fig. 6). Across habitat types, misclassifications of sites by stony coral diversities were low (Table 3), suggesting that coral composition was distinct among habitats. Stony coral diversity was significantly influenced by SST variability only in patch reefs (Table 4).

Although CREMP sites in the Dry Tortugas displayed significant differences in stony coral diversity among habitats (1 patch reef site and 2 offshore deep reefs sites; $F^* = 69.21$, $p = 0.001$, df = 2), no significant differences were related to SST variability ($F^* = 0.67$, $p = 0.58$, df = 2). Therefore, no further tests regarding SST and univariate diversity indices (i.e. H', SR) were performed for this region.

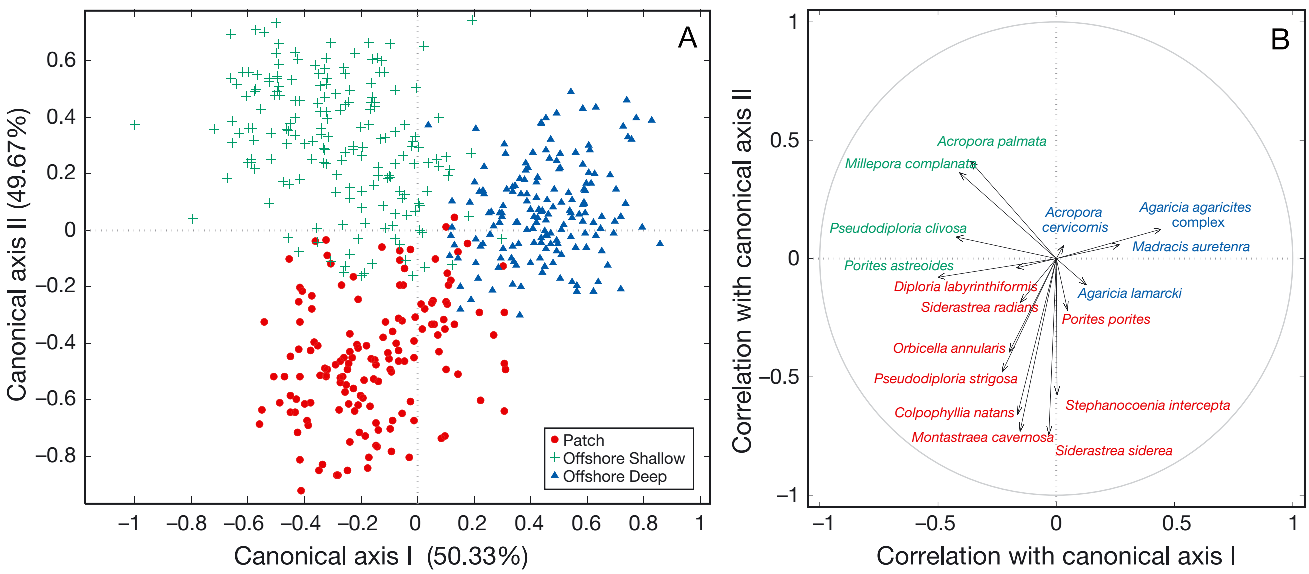

Fig. 6. Canonical analysis of principal coordinates. (A) Ordination plots of the spatial variation of coral species for 3 habitats in the Florida Keys (patch, offshore shallow, offshore deep reefs) and (B) vector plot based on indicator species within each habitat along the first 2 canonical axes depicted in (A). Species are color coded to match habitats

Table 3. Reclassification success of sites, characterized by specific coral diversity, to reef habitats obtained from the canonical analysis of principal coordinates discriminant analysis. Percentages indicate the success of associating sites with specific coral species compositions and abundances to specific habitats. For example, 89% of sites by species were correctly assigned to patch reefs, whereas 3% were erroneously assigned to offshore shallow reefs

Reef habitat	Patch	Offshore shallow	Offshore deep
Patch	89	3	8
Offshore shallow	7	89	4
Offshore deep	1	1	99

H′, SR, SST variability, and warm thermal anomalies

Regional means for H' and coral SR exhibited significant differences (Fig. S3 in the Supplement). The range of regional means for H' was 1.2 ± 0.04 to 1.7 ± 0.1 (mean ± SE), with the highest values seen in the Lower Keys (Fig. S3A in the Supplement). Regional means for SR ranged from 12.0 ± 1.0 to 19.0 ± 1.3 (mean ± SE). Data from the Middle and Lower Keys had values of ~16 or less, which was higher than values observed in the Upper Keys (Fig. S3B in the Supplement). Likewise, the highest H' values were observed in the data from the Middle and Lower Keys (Fig. S3A in the Supplement). Overall, CREMP sites in patch reefs (Fig. 4) exhibited the highest coral diversity followed by those in offshore shallow and deep reefs (Fig. 4, Fig. S2 in the Supplement). In general, decreases in diversity were observed in data from the year following the highest temperature variances (e.g. 1999 and 2010).

Annual means of H' were significantly related to SST variability only in patch reefs of the Upper Keys. This was confirmed with a second-order polynomial regression (R^2 = 0.59, $p < 0.05$) (Fig. 7A). Annual means in SR were significantly related to SST variability in patch reefs of the Middle Keys (R^2 = 0.39, $p = 0.05$) (Fig. 7B). There were no significant relationships either between diversity index (H', SR) and SST variability in Lower Keys patch reefs or between these indices and SST variability in any offshore shallow or deep reefs in any region.

Warm-temperature thermal stress exceeded the bleaching threshold of 4°C-weeks at patch reefs of the Middle and Lower Keys in 1997, 1998, 2005, 2007, 2009, and 2010 (Fig. 8). In 1998, 2009, and 2010, the 4°C-weeks threshold was exceeded in the Upper Keys as well. Offshore shallow reefs in the

Table 4. One-way permutation-based nonparametric MANOVA that independently tested the distribution of stony coral diversity with respect to sea surface temperature variability for each habitat among all regions. F^* = pseudo F-ratio, p = permuted p-value, bold = significant at α = 0.05

Factor (1000 permutations)	df	F^*	p
Patch reefs	2	3.29	**0.005**
Offshore shallow reefs	2	1.21	0.26
Offshore deep reefs	2	0.99	0.45

Middle Keys had DHW_{max} > 4°C-weeks in years 1997, 2009, and 2010 (Fig. S4A in the Supplement). Offshore deep reefs always had DHW_{max} ≤ 4°C-weeks (Fig. S4B in the Supplement).

To evaluate the change in diversity after a warm year, between-year variations in H' and SR ($H'_{\Delta y}$ and $SR_{\Delta y}$, respectively) were examined as a function of the maximum thermal stress (DHW_{max}) of the previous year. The $H'_{\Delta y}$ in the Upper and Middle Keys patch reefs declined significantly in 1998 following the

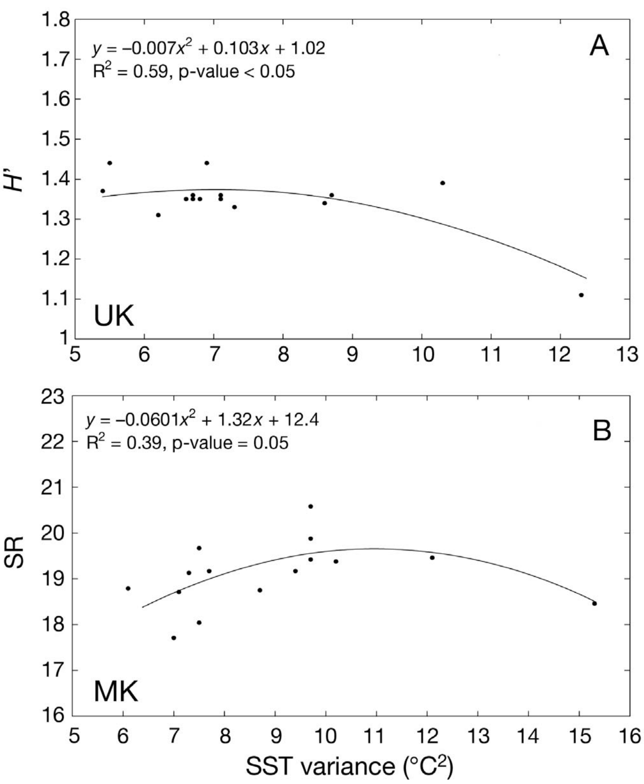

Fig. 7. (A) Relationship between annual sea surface temperature variance (SST, °C^2) means and annual Shannon diversity index (H') means for patch reefs in the Upper Keys (UK). (B) Relationship between annual SST variance (°C^2) means and annual species richness (SR) means for patch reefs in the Middle Keys (MK)

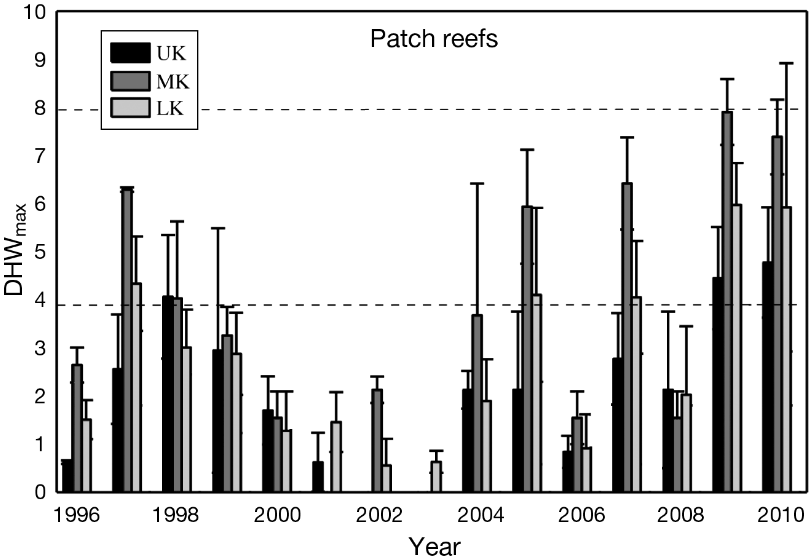

Fig. 8. Annual summer maximum Degree Heating Week (DHW_{max}) means for patch reefs in the Upper Keys (UK), Middle Keys (MK), and Lower Keys (LK) during 1996 to 2010. The intermittent dashed lines represent DHW thresholds (4 and 8°C-weeks), above which significant coral bleaching and mortality are likely to occur. Error bars denote standard deviations

warmer waters in 1997 (Fig. 9). In 1998, the $H'_{\Delta y}$ in the Middle Keys declined about 5% despite being exposed to DHW_{max} of ~6.3°C-weeks in 1997, whereas the Upper Keys had a similar decline but were exposed to DHW_{max} of ~2.8°C-weeks. Offshore shallow and deep reefs also exhibited significant $H'_{\Delta y}$ declines after exposure to DHW_{max} of ~2.5°C-weeks (R^2 = 0.41, p = 0.05 for offshore shallow sites; R^2 = 0.35, p = 0.05 for offshore deep sites). Middle Keys patch reefs had similar patterns (R^2 = 0.50, $p < 0.05$) (Fig. 9B). Following warm anomalies in 2005, the $H'_{\Delta y}$ for patch reefs in the Upper and Middle Keys changed only slightly. A sharp decline in diversity was observed in 2010 at the patch reefs of the Upper and Middle Keys after the DHW_{max} of 2009 (>4.0°C-weeks in the Upper Keys, DHW_{max} of >7.0°C-weeks in the Middle Keys; Fig. 9). No significant relationships were found between DHW_{max} and $H'_{\Delta y}$ in the Lower Keys. Similarly, there was no relationship between DHW_{max} and SR for any of the habitats in any of the regions.

DISCUSSION

Seasonal and interannual variations in insolation, air masses, wind mixing, and ocean circulation influence SST and *in situ* temperatures in waters around the Florida Keys. Our data showed that, on average, *in situ* temperature measurements were slightly cooler than satellite-derived estimates. The slight bias likely is because the satellite-derived SST represents the 'skin' of the ocean, while the *in situ* observations represent water temperatures within the water column at depths of up to 23 m. Nevertheless, the strong correlation between the datasets confirms that satellite-derived SSTs can provide reliable estimates of temperature ranges to which shallow-water reefs are exposed.

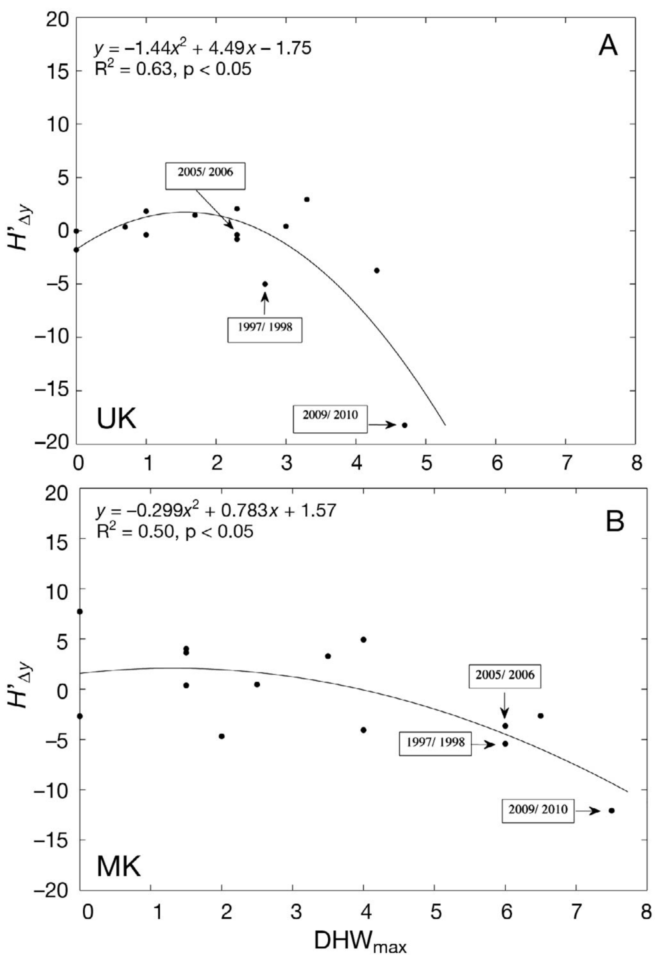

Fig. 9. Relationship of the change in Shannon diversity ($H'_{\Delta y}$; percent difference) means of 1 yr as a function of the maximum Degree Heating Week (DHW_{max}) means of the previous year for patch reefs of the (A) Upper Keys (UK) and (B) Middle Keys (MK). Highlighted in the boxes are years of warm thermal anomalies in the Florida Keys (left of the slash) and years of diversity change (right of the slash)

Seasonal (winter vs. summer) SST differences were consistently greater for data from the Dry Tortugas than elsewhere in the Keys. When the Loop Current extends north into the Gulf of Mexico, the Dry Tortugas Gyre is typically better developed and leads to periodic recirculation of cooler waters off the Dry Tortugas. This large feature (~200 km diameter) may persist for 100 d and extend toward the Lower Keys (Lee et al. 1994, Fratantoni et al. 1998). Thus, high SST variability was also observed around the Lower Keys, with somewhat less variability in the Middle Keys and the least variability in the Upper Keys. The Middle Keys reefs are also exposed to outflows of Florida Bay waters, which can be cooler than deeper offshore waters in winter and warmer in summer (Shinn et al. 1989, Smith & Lee 2003, Jaap et al. 2008). The Upper Keys have alongshore currents driven by the Florida Current; herein, the reefs experience cool, deep-water incursions through upwelling during summer and often are affected by cold polar air masses during winter (Lirman et al. 2011, Stokes et al. 2011, Chollett et al. 2012).

Among regions in the Florida Keys, the different habitat types were characterized by specific stony coral diversity (coral species composition and abundance). Shallow-water patch reefs were typically dominated by massive-type corals (e.g. *Montastraea cavernosa, Orbicella annularis* complex, *Siderastrea siderea, Colpophyllia natans*), while *Acropora palmata* was representative of offshore shallow reefs, and *Agaricia agaricites* was representative of offshore deep reefs. Among habitat types, patch reefs experienced the highest SST variability and therefore the coolest and warmest SSTs. The trend was consistent with that described above, with patch reefs in the Lower Keys experiencing the most variability, and those in the Upper Keys experiencing the least.

We expected stony coral diversity at the CREMP stations to differ along this gradient in SST variability (representing β-diversity; Whittaker 1972). Our results indeed revealed differences in species composition and abundance on patch reefs among the 3 different categories of SST variability (low, intermediate, and high). Faviid (e.g. *Orbicella* spp., *M. cavernosa*, *C. natans*) and siderastreid (e.g. *S. siderea*) massive-type corals were relatively more abundant where exposed to intermediate and high SST variability. The overlap in the characterization of sites by stony coral diversity, achieved with the CAP discriminant analysis, suggests that diversities were similar at patch reefs of the Middle and Lower Keys. Coral species that characterize patch reef environments are consistently exposed to wider ranges of temperature and therefore either adapted or at least acclimatized to greater temperature variability better than those found in offshore reef habitats. Most acroporid corals were found on offshore shallow or offshore deep reefs (e.g. Wirt et al. 2013), in waters with low to intermediate SST variability. Individuals of these species, especially *A. palmata*, appear to be more sensitive to extreme temperature changes, and they may lack the ability to acclimatize as readily to increased temperature variability.

Further thermal acclimatization of already more eurythermal coral species could partially explain why percent cover of scleractinians at patch reefs did not decline after the 1997/1998 El Niño-Southern Oscillation events (Ruzicka et al. 2013). Coral acclimatization to water temperature variability has been documented in other reef systems (Gates & Edmunds 1999, LaJeunesse 2002, Berkelmans & van Oppen 2006, Grottoli et al. 2006, Maynard et al. 2008, Thompson & van Woesik 2009, Oliver & Palumbi 2011, Silverstein et al. 2012, Palumbi et al. 2014).

We were unable to detect any correlation between SST and stony coral diversity among the Dry Tortugas sites, very likely a consequence of the inherent differences among the 3 sites in the CREMP database. The single patch reef site in the Dry Tortugas is an old stand of mostly dead *A. cervicornis*. One of the offshore deep sites is located in a deep pinnacle at ~23 m, and the other is a relatively high-relief spur and groove system.

Annual H' and SR measurements at the scale of individual habitats (representing α diversity; e.g. Whittaker 1972) are consistent with reports from previous studies of Florida reefs. For example, H' values, although based on percent cover as a proxy for abundance of each species, are consistent with those previously reported for Florida Keys sites by Santavy et al. (2011), which were based on total colony counts (1.1 ± 0.13 to 1.5 ± 0.13, mean ± SE). Our SR data are also similar to those reported by Rutten et al. (2008) for the Florida Keys (12.1 ± 0.8 to 19.7 ± 0.4, mean ± SE) as well as for patch reefs in Biscayne National Park (Dupont et al. 2008 and references therein). Dupont et al. (2008) demonstrated that despite the widespread loss of coral cover, overall SR along the Florida reef tract (representing γ diversity) has not declined and falls within historic norms for Florida and the Caribbean.

The highest H' and SR values overall were found at patch reefs in the Lower (mean $H' \approx 2$ in 1996) and Middle (mean SR ≈ 20) Keys. The SR and H' values at patch reefs in the Middle Keys, which are typically exposed to intermediate temperature variability, remained relatively consistent throughout the time series, despite drops in 1999 and 2010. In contrast, in both the Lower and Upper Keys patch reefs, which were exposed to higher and lower SST variability, respectively, the diversity indices declined over the 14 yr of the study. Although no correlations with SST variability were evident, diversity data for offshore shallow and deep reefs revealed overall declines in H' and SR between 1996 and 2010, especially following years with water temperature anomalies (Fig. S2 in the Supplement). These trends are consistent with the working hypothesis that reef communities exposed to intermediate temperature variability should be less affected by temperature anomalies than reef communities living under either high or low SST variability. In this study, patch reef habitats were those exposed to intermediate to high thermal variability and which hosted the species that have declined the least. Moreover, the intermediate-exposed (Middle Keys) patch reefs have fared the best overall. Our findings are consistent with those of Soto et al. (2011), who found higher stony coral cover at sites exposed to moderate variability in water temperatures.

Marked reductions in stony coral diversity at Florida Keys patch reefs occurred when the coolest and warmest temperatures coincided in consecutive seasons (e.g. in 1998 and 2010). Indeed, many studies have attributed severe coral bleaching or mortality to either warm- or cold-water events (Roberts et al. 1982, Manzello et al. 2007, Jaap et al. 2008, Lirman et al. 2011, Colella et al. 2012). Fewer studies have considered how coral communities may respond to temperature extremes occurring in consecutive winter–summer periods (Heron et al. 2010, Roth et al. 2012). Our results show that between 1996 and 2010, the coolest winters were followed by the warmest summers. In 1997 to 1998, the coolest seasonal SST mean (22.4°C) was observed in the Lower Keys. This was followed by a maximum summer mean of 29.1°C in 1998. Decreases in diversity were observed in 1999 at the Middle and Lower Keys. Recovery was observed in patch reefs of the Middle Keys between 2001 and 2010, despite small decreases after extreme thermal events in 2005 and 2009. This suggests that within the time frame of our study, individuals of more eurythermal faviid and siderastreid species were capable of resisting greater temperature ranges within patch reefs of the Middle Keys.

The coolest and subsequent warmest seasonal mean temperatures of the time series were recorded in 2009 to 2010. After the cold-water event that occurred in the Upper and Middle Keys in January 2010, extensive mortality was reported for *O. annularis* complex and *Porites* spp. on many patch reefs (Kemp et al. 2011, Lirman et al. 2011, Colella et al. 2012). Those in the Upper Keys were especially sensitive to extreme fluctuations in temperature, especially in 2010, likely because these reefs normally experience a narrower range of temperature variance than those further south. Thus, severe cold-water events may indeed be more important than previously thought in controlling the community structure on patch reefs in the Keys.

DHW, defined as the sum of all SSTs that exceeded maximum summer means by ≥1°C in a 12 wk window, is a methodology developed by the NOAA Coral Reef Watch to predict mass coral bleaching events (Liu et al. 2013). Between 1996 and 2010, high temperature anomalies occurred every ~5 to 7 yr (1998, 2005, 2010) (Fig. 8). Following exposure to the warm thermal anomalies in 1997, the diversity (H') in patch reefs of the Upper and Middle Keys declined significantly. Offshore shallow and deep patch reefs in the Upper Keys also exhibited significant declines in H' in 1997 to 1998. The change in the Middle Keys was smaller than that in the Upper Keys in spite of a higher thermal stress index in the Middle Keys (DHW_{max} ~6 vs. 3°C-weeks). This suggests that the corals in patch reefs of the Middle Keys were better suited to withstand acute warm-water events (~6 to 15.5 SST variance; Fig. 9). Guest et al. (2012) hypothesized that stony coral communities exposed to greater SST variability (and therefore more frequent acute thermal events) may develop greater resilience. However, observations by Soto et al. (2011), consistent with our results, revealed that a decline in coral cover occurred at the highest variability sites as well as the lowest variability sites, with the intermediate-variability sites exhibiting the least decline.

Certainly, a variety of environmental factors, in addition to thermal stress, have influenced Florida Keys coral populations since the 1990s. White-band disease decimated the acroporid populations long before the CREMP monitoring began (Gladfelter 1982, Patterson et al. 2002), and its continued presence may be limiting the recovery of these taxa. A variety of other diseases have also become prevalent, with anthropogenically associated microbes implicated in some cases, but with temperature stress clearly a complicating factor (e.g. Porter et al. 2001, Eakin et al. 2010). Ruzicka et al. (2013) proposed that increasing octocoral populations might be limiting stony coral recovery. Octocorals rapidly colonize open spaces (e.g. fragments and rubble left behind by dead *A. cervicornis* colonies), shade surfaces where young corals settle, and increase competition for food resources (Connell et al. 2004, Ruzicka et al. 2013). The passage of 12 hurricanes since the early 1990s also stressed stony coral communities (Precht & Miller 2007, Ruzicka et al. 2010 and references therein) by decreasing water clarity in the Middle and Lower Keys while adding extremely turbid and nutrient-rich waters from Florida Bay (Barnes et al. 2013). Phytoplankton-rich 'blackwater' events observed between late 2001 and early 2002 resulted in the sharp decline in percent cover and SR at Smith Shoal, a patch reef in the Lower Keys (Hu et al. 2003). A question for future studies is whether thermally tolerant coral taxa are better able to survive other stressors as well.

We conclude that coral diversity on patch reefs in the Florida Keys has been influenced by temperature variability. The stony coral assemblages most common in the Middle Keys patch reefs, which have historically been exposed to intermediate SST variability, have survived or recovered from thermal anomalies that have occurred over the past 2 decades. In contrast, stony corals in the Upper Keys patch reefs, typically exposed to lower temperature variability, and those in the Lower Keys, where temperature variability is higher, have experienced losses in coral cover and SR. In addition, we recommend close attention to years in which cold and warm water temperature anomalies coincide. Severe winters should receive more scrutiny as important contributors to the long-term decline of *Acropora* spp. and *O. annularis* complex in the Florida Keys reefs.

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