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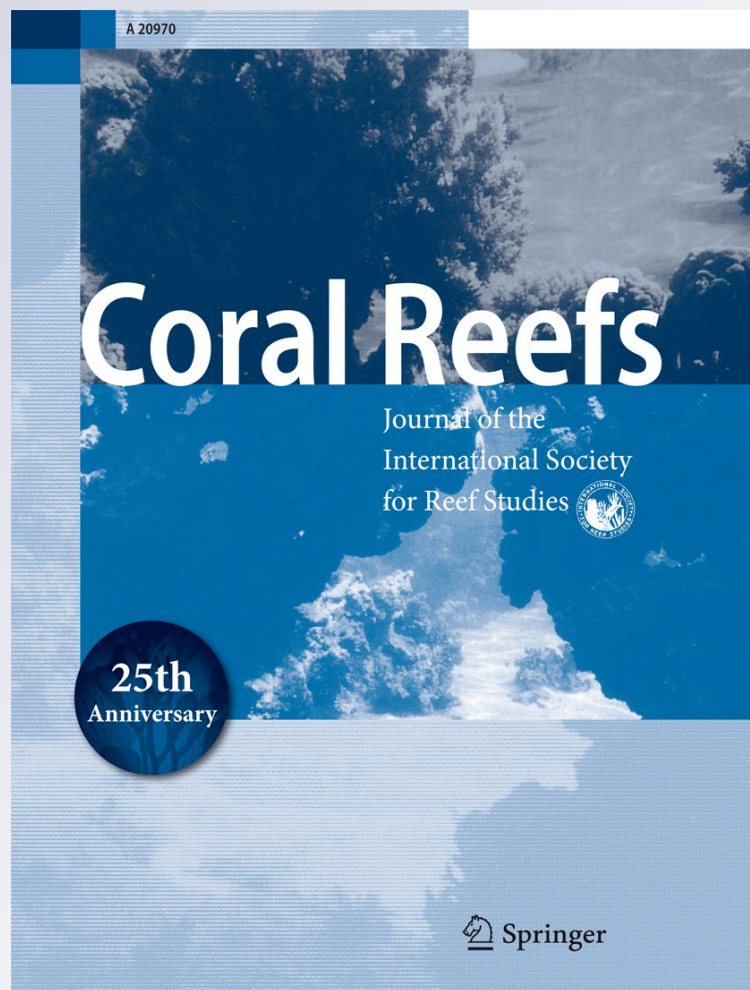
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Cold-water event of January 2010 results in catastrophic benthic mortality on patch reefs in the Florida Keys

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Abstract The Florida Keys are periodically exposed to extreme cold-water events that can have pronounced effects on coral reef community structure. In January 2010, the Florida Keys experienced one of the coldest 12-day periods on record, during which water temperatures decreased below the lethal limit for many tropical reef taxa for several consecutive days. This study provides a quantitative assessment of the scleractinian mortality and acute changes to benthic cover at four patch reefs in the middle and upper Keys that coincided with this cold-water event. Significant decreases in benthic cover of scleractinian corals, gorgonians, sponges, and macroalgae were observed between summer 2009 and February 2010. Gorgonian cover declined from $25.6 \pm 4.6\%$ (mean \pm SE) to $13.3 \pm 2.7\%$, scleractinian cover from $17.6 \pm 1.4\%$ to $10.7 \pm 0.9\%$, macroalgal cover from $8.2 \pm 5.2\%$ to $0.7 \pm 0.3\%$, and sponge cover from $3.8 \pm 1.4\%$ to $2.3 \pm 1.2\%$. Scleractinian mortality varied across sites depending upon the duration of lethal temperatures and the community composition. *Montastraea annularis* complex cover was reduced from $4.4 \pm 2.4\%$ to $0.6 \pm 0.2\%$, and 93% of all colonies surveyed suffered complete or partial mortality. Complete or partial mortality was also observed in >50% of all *Porites astreoides* and *Montastraea cavernosa* colonies and resulted in a significant reduction in cover. When compared with historical accounts of cold-water-induced mortality, our results suggest that the 2010 winter mortality was one of the most severe on record.

The level of coral mortality on patch reefs is of particular concern because corals in these habitats had previously demonstrated resistance against stressors (e.g., disease and warm-water bleaching) that had negatively affected corals in other habitats in the Florida Keys during recent decades.

Keywords Subtropical reefs · Community structure · Temperature thresholds · Hypothermic stress · Coral mortality · *Montastraea annularis*

Introduction

Cold-water-induced stress and mortality are important determinants of community structure for coral reef ecosystems (Glynn and Stewart 1973; Glynn 1976; Coles and Fadlallah 1991; Hoegh-Guldberg et al. 2005). In the Florida Keys, coral reefs are located near their northern latitudinal limit (Vaughan 1919). Because of its subtropical location, South Florida is periodically subjected to intrusions of cold, Arctic air masses that coincide with abnormally strong shifts in prevailing climatic patterns (e.g., Arctic Oscillation). During extended periods of extreme cold weather, seawater temperatures in shallow bay and bank environments can rapidly plummet below the thermal survival threshold of many tropical reef organisms (Voss 1973; Roberts et al. 1982). Ginsburg and Shinn (1964, 1994) hypothesized that the transport of inimical waters from Florida Bay into adjacent ocean basins is a major factor limiting reef development opposite large tidal passes and in nearshore waters of the Florida Keys. While the term “inimical” refers to a number of water quality parameters (e.g., turbidity, high salinity, and high temperatures) thought to be detrimental to coral survival, several studies have specifically examined the role of cold water in

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structuring nearshore coral communities in the upper and middle Florida Keys (Marszalek et al. 1977; Hudson 1981; Roberts et al. 1982; Walker et al. 1982; Jaap 1984; Burns 1985; Ginsburg et al. 2001; Precht and Miller 2007).

Sustained intrusions of polar air masses into South Florida have been associated with benthic mortality in marine communities (Voss 1973; Porter et al. 1982; Roberts et al. 1982). Although cold-tolerance thresholds vary between species, stony corals (Order Scleractinia) in general become physiologically impaired when water temperatures fall below 16°C and can only survive a few hours at temperatures below 14°C (Mayor 1914, 1915). One of the earliest observations linking the mortality of corals with hypothermic stress in Florida was made in 1970 at “Hens and Chickens”, a large, intensively studied patch reef in the upper Keys. Although in situ water temperature data were not available then, coral mortality at Hens and Chickens was estimated at 80% to 90% and many large *Montastraea annularis* complex colonies suffered near complete mortality (Voss 1973; Hudson et al. 1976). Cold-water-induced mortality in benthic communities also occurred in 1977 and 1981. In 1977, successive cold fronts passed through South Florida causing catastrophic mortality of shallow, nearshore acroporid populations in the Dry Tortugas and The Bahamas (Davis 1982; Porter et al. 1982; Roberts et al. 1982). A similar weather pattern developed in 1981 apparently causing mortality of various coral species along the outer Florida reef tract (Walker et al. 1982). Since then, prolonged influxes of cold Arctic air masses have not been documented in Florida.

The Coral Reef Evaluation and Monitoring Project (CREMP) has been monitoring benthic community composition at fixed survey sites throughout the Florida Keys National Marine Sanctuary since 1996. During this time period, CREMP has documented how both large-scale (e.g., 1997/1998 El Niño) and localized (e.g., harmful algal blooms) disturbances have changed coral community composition on reefs in the Florida Keys (Hu et al. 2003; Somerfield et al. 2008; Ruzicka et al. 2010). Despite widespread mortality along the outer bank reefs in the middle and upper Keys, nearshore patch reefs have demonstrated a marked resistance, with little or no coral mortality documented. Because of their persistence through severe disturbances, patch reefs were regarded as critical in maintaining the resilience of the greater Florida reef tract by providing essential habitat for fishes and benthic organisms and supplying a potential source of larvae to help replenish deteriorated offshore communities (Lirman and Fong 2007).

In January 2010, a prolonged intrusion of cold Arctic air lowered water temperatures in the Florida Keys below the thermal threshold for corals and other tropical organisms

for several consecutive days. Shortly after the coldest temperatures had abated, preliminary observations suggested that widespread coral mortality and bleaching was occurring on nearshore patch reefs throughout the Florida Keys. Lirman et al. (2011) provided a broad overview of the 2010 cold-water event and characterized the stony coral mortality across the entire Florida Reef Tract. Our study expands upon these findings by integrating in situ temperature data with percent cover and demographic measurements to describe the full extent of benthic community mortality at four long-term monitoring sites and establishes a baseline to assess recovery following the event. Although widespread coral bleaching and mortality are commonly associated with warm-water disturbances (Baker et al. 2008; Obura and Mangubhai 2011), the results presented here demonstrate that extreme cold-water events can be equally, if not more destructive.

Materials and methods

Site descriptions

Inner shelf margin patch reefs are some of the most ecologically diverse and topographically complex habitats in the Florida Keys (Lirman and Fong 2007). They are located between the Florida Keys archipelago and the outer reef tract in an area commonly referred to as Hawk Channel (Fig. 1). Hawk Channel patch reefs are generally composed of massive, long-lived, framework-building corals such as *Montastraea* spp., *Diploria* spp., *Colpophyllia natans*, and *Siderastrea siderea* and range from small coral assemblages to large structures with several meters of vertical relief.

Four patch reefs were surveyed in February 2010, approximately 3 weeks after the coldest temperatures subsided. The four sites are located 3–5 km from shore, vary in depth between 5 and 8 m, and vary in proximity to tidal exchanges with Florida Bay. A single patch reef, Burr Patch, was surveyed in the upper Keys, and three sites, Dustan Rocks, Thor Patch, and West Turtle Shoal, were surveyed in the middle Keys (Fig. 1). Sites in the middle and upper Keys were targeted because the greatest levels of cold-water mortality were reported from these areas. These reports were confirmed in Lirman et al. (2011).

Temperature data

HOBO® U22 (Onset, Pocasset, MA) temperature loggers are deployed at a subset of CREMP sites throughout the Florida Keys. Temperature loggers are attached to permanent station markers on the seafloor and record in situ water temperatures hourly. Loggers were collected from three of

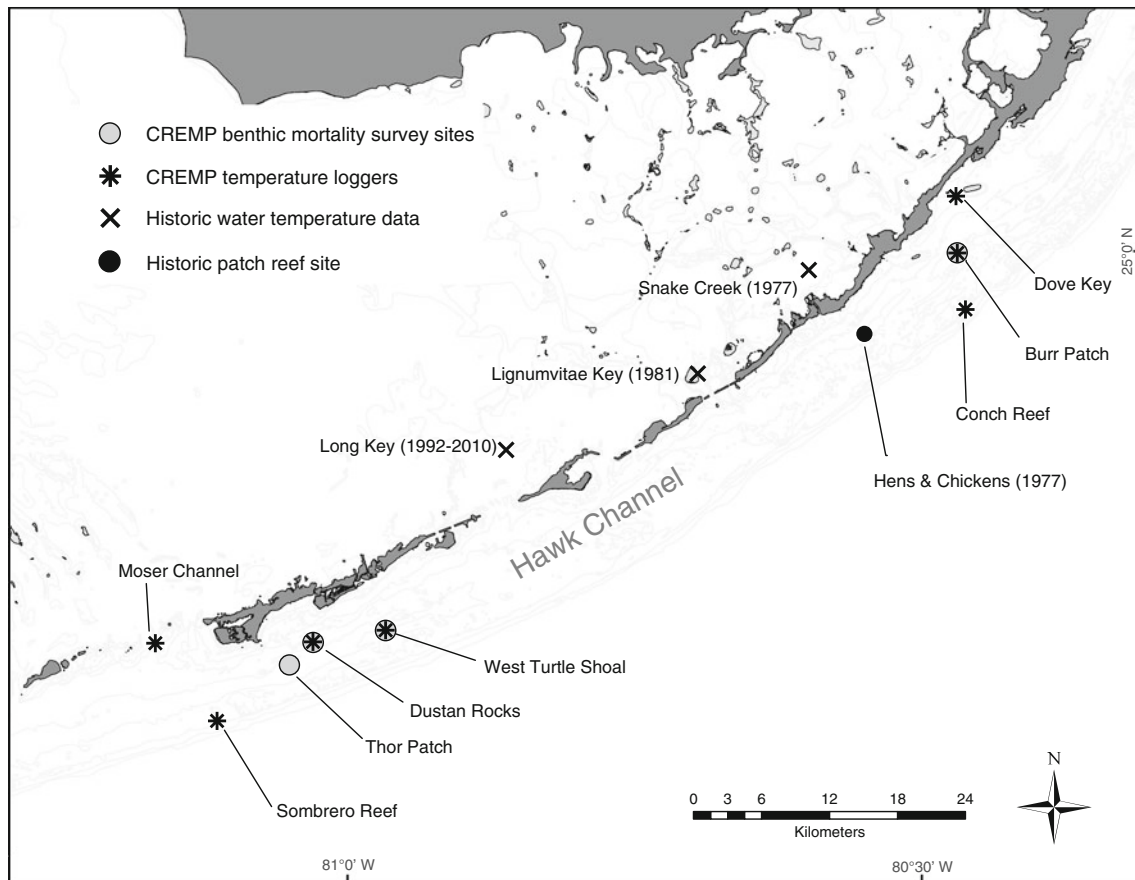


Fig. 1 Map of the *middle* and *upper* Florida Keys showing the location of coral reef evaluation and monitoring project (*CREMP*) survey sites, sites with temperature logger data, and historical sites where temperature data were collected

the four study sites: Burr Patch, Dustan Rocks, and West Turtle Shoal. A logger was not deployed at Thor Patch. Loggers were also retrieved from additional *CREMP* locations to compare bottom temperatures at nearshore and offshore environments. Two shallow nearshore areas, Moser Channel and Dove Key, and two shallow forereef sites, Sombrero Reef and Conch Reef, were selected (Fig. 1). For each site, the number of hours at <16 , <14 , and $<12^{\circ}\text{C}$ was calculated for the month of January. Data acquired from the National Data Buoy Center for the Long Key station were used to compare Florida Bay water temperatures from 1977 and 1981 to those observed during the 2010 event.

Video surveys

CREMP has used an established protocol to monitor benthic cover at fixed sites throughout the Florida Keys since 1996 (Porter et al. 2002; Ruzicka et al. 2010). For the present assessment, two marked sampling stations were surveyed at each site. Video transects are prepared by overlaying stainless steel poles atop each permanent stake

and securing three fiberglass tapes between the poles. Plastic chains are then laid underneath the tapes to mark the substratum for transect filming. Video was captured using a Sony[®] Handycam DCR-TRV900. For each station, video surveys covered three $\sim 22\text{ m} \times 40\text{ cm}$ transects, constituting a sampling area of $\sim 27\text{ m}^2$.

Images were analyzed using a custom software package, Point Count'99, to determine the percent cover of benthic organisms. Between 200 and 250, abutting frames were extracted from the video for each station and overlaid with 15 random points per image, resulting in $\sim 3,000$ points counted for each station. Scleractinian corals were identified to species and other benthic organisms to gross taxonomic levels (sponges, octocorals [Order Gorgonacea], and macroalgae). The octocoral category was selected if a random point fell on any part of the organism, including large branches that may have obscured other sessile organisms, and is therefore a measure of both canopy and benthic coverage (i.e., encrusting spp. such as *Briareum asbestinum* or *Erythropodium caribaeorum*). The category "macroalgae" was defined as any algae with recognizable structure (e.g., *Halimeda* spp., *Dictyota* spp., *Lobophora*

spp.) and also included large tufts/knobs of cyanobacteria. Crustose coralline algae and algae turfs were not recorded as macroalgae. A generalized linear mixed model ANOVA with year and site as fixed effects was used to compare changes in percent cover (mean \pm SE) of the major benthic groups and five common stony coral species (*Montastraea annularis* complex [includes *M. faveolata*, and *M. franksi*], *M. cavernosa*, *C. natans*, *S. siderea*, and *Porites astreoides*) between summer 2009 and February 2010. Percent cover data were pooled for each station, and square root transformed with stations nested within sites in the model. Because the number of stations sampled within a site ($N = 2$) limited the power of intra-site comparisons, only the effect of year is reported. All analyses were performed in SAS v9.2.

Demographic surveys

Demographic surveys were modeled after those used by the Atlantic and Gulf Rapid Reef Assessment Program (AG-RRA) and the Florida Reef Resilience Program (FRRP) (Lang et al. 2010; Wagner et al. 2010). Two 10 m \times 1 m belt-transect surveys were conducted at each site (i.e., one per station; $N = 8$). The maximum width, the presence of disease and bleaching, and the percentage of estimated tissue mortality were recorded for each scleractinian coral colony ≥ 4 cm in diameter. Mortality was identified as “recent” if the corallite structure could be clearly distinguished, and there was minimal overgrowth by algae or other fouling organisms. Otherwise, mortality was identified as “old”. Demographic surveys were not conducted in summer 2009.

Demographic data were used to provide a description of mortality by size class. Data concerning disease and bleaching were not reported because the incidence of both conditions was extremely rare. In order to characterize mortality associated with the 2010 cold-water event, only recent mortality was reported. Mortality was classified into four levels of severity: mild (<10% partial mortality), moderate (10–50% partial mortality), severe (51–90% partial mortality), and lethal (>91% partial mortality). Results were pooled in two ways: for all species within a site and for five common coral species (*M. annularis* complex, *M. cavernosa*, *C. natans*, *S. siderea*, and *P. astreoides*) across the four study sites. For the five common coral species, colonies were grouped into three size classes. For *M. annularis* complex, *M. cavernosa*, and *C. natans*, the following size classes were used: size class I (4–10 cm), size class II (10–50 cm), and size class III (>50 cm). To account for their relatively smaller size, the two larger size classes for *S. siderea* and *P. astreoides* were adjusted to 10–30 cm (size class II) and >30 cm (size class III).

Results

The coldest water temperatures were recorded on 7th and 8th January and between 10th and 15th January 2010 (Fig. 2). Of the three survey sites with loggers, the coldest temperatures and longest exposure to lethal temperatures were recorded at Burr Patch, in the upper Keys. Summed for the entire month of January, water temperatures at Burr Patch were <16°C for 150 h, <14°C for 66 h, and <12°C for 32 h (Table 1). The minimum temperature recorded was 11.2°C. Of the middle Keys sites, Dustan Rocks had the longest duration of temperatures <16 and <14°C (Table 1). Temperatures at Dustan Rocks and West Turtle Shoal dropped below 12°C but for only 2 h or less. Water temperatures in Florida Bay and shallow nearshore environments decreased more rapidly and reached lower minima than those of patch reefs (Table 1, Fig. 2). The Long

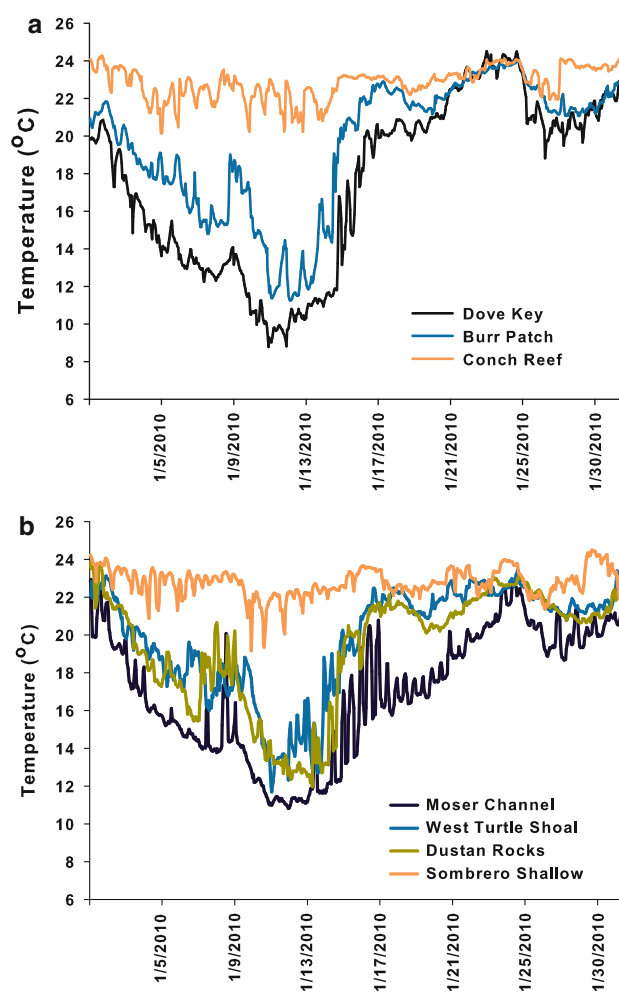


Fig. 2 Hourly in situ water temperature recordings from 1 to 30 January 2010. **a** Upper Keys sites: Dove Key, Burr Patch, and Conch Reef. **b** Middle Keys sites: Moser Channel, West Turtle Shoal, Dustan Rocks, and Sombrero Reef. Corresponding locations are shown in Fig. 1

Table 1 In situ water temperature data summarized from 1 to 30 January 2010 for three study sites, four reference sites, and historical data from 1977 and 1981

Sites	Logger depth (m)	January average (°C)	Minimum (°C)	Duration (h)		
				<16°C	<14°C	<12°C
Upper Keys						
Burr Patch	5.0	19.6	11.2	150	66	32
Dove Key	2.7	17.6	8.8	286	229	128
Conch Reef	5.3	22.8	20.1	0	0	0
Middle Keys						
West Turtle Shoal	8.0	19.9	11.7	89	49	2
Dustan Rocks	5.0	19.4	12.0	133	79	1
Moser Channel	4.0	17.1	10.8	275	154	83
Sombrero Reef	2.7	22.8	19.2	0	0	0
Historical data						
Lignumvitae (1981) ^a	1.7	^d	8.7	~156	^d	^d
Snake Creek (1977) ^b	2.0	^d	12.9	~192	^d	^d
Hens and Chickens (1977) ^b	4.7	^d	12.6	~192	~60	^d
Long Key (2010) ^c	2.0	16.5	8.7	316	252	127

The average temperature for January was calculated from hourly recordings.

Corresponding locations for all sites are shown in Fig. 1

^a Walker et al. (1982)

^b Roberts et al. (1982)

^c National Data Buoy Center

^d No data available

Key observing station in Florida Bay recorded the coldest temperature (8.7°C) and had the longest duration of temperatures <16, <14, and <12°C followed by Dove Key, the nearshore site in the upper Keys (Table 1). Water temperatures at Moser Channel were lower than those at adjacent middle Keys patch reef sites but were not as low at Long Key or Dove Key nor did low temperatures last as long. In contrast, water temperatures at the two shallow forereef sites, Conch Reef and Sombrero Reef, remained >16°C throughout January (Table 1; Fig. 2).

Averaged for all sites ($N = 4$), the mean percent live cover for all benthic groups (stony corals, octocorals, sponges, and macroalgae) decreased significantly between summer 2009 and February 2010 (mixed model ANOVA, $p < 0.011$). The largest decrease in cover was for octocorals, which declined from $25.6 \pm 4.6\%$ to $13.3 \pm 2.7\%$. The next largest change was for macroalgal cover ($8.2 \pm 5.2\%$ to $0.7 \pm 0.3\%$), followed by scleractinian corals ($17.6 \pm 1.4\%$ to $10.7 \pm 0.9\%$) and sponges ($3.8 \pm 1.4\%$ to $2.3 \pm 1.2\%$). Although mortality occurred across all four study sites, it was most severe at Burr Patch and Dustan Rocks. Octocoral cover was reduced by more than half its 2009 summer value at both sites, and stony coral cover declined from 20.3 to 8.1% at Burr Patch and from 19.6 to 11.1% at Dustan Rocks (Table 2). This pattern of decline was repeated for macroalgal cover, where percent cover was reduced to near zero at both locations (Table 2). A decline in sponge cover was consistent across all sites, but the largest decrease was observed at West Turtle Shoal, where it decreased from 6.3 to 2.5% (Table 2).

The change in cover for the five most common scleractinian species varied. Averaged for all sites ($N = 4$), a

significant decrease in cover was observed for *M. annularis* complex, *M. cavernosa*, and *P. astreoides* (mixed model ANOVA, $p < 0.021$). Percent cover of *M. annularis* complex declined from $4.4 \pm 2.4\%$ to $0.6 \pm 0.2\%$, *M. cavernosa* from $4.5 \pm 1.2\%$ to $2.6 \pm 1.0\%$, and *P. astreoides* from $0.6 \pm 0.1\%$ to $0.1 \pm 0.1\%$. The largest reduction in cover for these three species was observed at Burr Patch and Dustan Rocks (Table 2). A significant change in cover was not detected for *C. natans* ($p = 0.054$), and *S. siderea* significantly increased in cover ($3.0 \pm 0.6\%$ to $3.8 \pm 0.7\%$) between the sampling periods ($p = 0.026$).

The percentage of coral colonies (all scleractinian species) suffering lethal or severe mortality was greatest at Burr Patch and Dustan Rocks. At Burr Patch, 35% of all colonies suffered lethal mortality, 11% severe, 15% moderate, and 39% mild (Fig. 3). At Dustan Rocks, 14% of all colonies suffered lethal mortality, 8% severe, 15% moderate, and 63% mild (Fig. 3). At West Turtle Shoal, the incidence of lethal mortality (11%) was less compared to Burr Patch and Dustan Rocks, as were severe (4%) and moderate mortality (12%). Lethal mortality was not observed at Thor Patch, and 86% of all colonies only displayed mild mortality (Fig. 3).

The species with the highest levels of mortality across all sites were *Montastraea annularis* complex and *P. astreoides*. Spanning all size classes, 93% of all *M. annularis* complex colonies displayed some level of mortality with lethal and severe mortality occurring in >50% of all colonies regardless of size (Fig. 4a). All *P. astreoides* colonies measured were <30 cm in max diameter. Pooled for the two smaller size classes, 57% of all colonies had lethal mortality and 77% of all colonies displayed some level of

Table 2 Percent cover of the benthic taxa groups and the five selected stony coral species at each survey site as determined by video surveys

	Burr Patch		Dustan Rocks		West Turtle Shoal		Thor Patch		All sites		F value	P value
	2009	2010	2009	2010	2009	2010	2009	2010	2009	2010		
<i>Benthic groups</i>												
Stony Coral	20.3	8.1	19.6	11.1	15.6	11.6	14.7	11.8	17.6 ± 1.4	10.7 ± 0.9	20.40	0.011
Octocorals	17.3	5.1	36.9	15.9	29.1	16.0	18.9	16.3	25.6 ± 4.6	13.3 ± 2.7	90.10	0.001
Sponges	1.0	0.3	1.9	0.9	6.3	2.5	6.0	5.5	3.8 ± 1.4	2.3 ± 1.2	22.38	0.009
Macroalgae	23.7	0.2	5.2	0.2	2.3	1.5	1.7	1.1	8.2 ± 5.2	0.7 ± 0.3	51.97	0.002
<i>Stony coral species</i>												
<i>Montastraea annularis</i> complex	10.2	1.2	6.7	0.3	0.5	0.6	0.3	0.1	4.4 ± 2.4	0.6 ± 0.2	25.91	0.007
<i>Montastraea cavernosa</i>	1.0	0.3	4.6	1.7	6.0	3.3	6.5	5.1	4.5 ± 1.2	2.6 ± 1.0	13.91	0.020
<i>Colpophyllia natans</i>	3.6	2.9	1.4	1.4	3.3	2.7	3.5	2.2	2.9 ± 0.5	2.3 ± 0.3	7.29	0.054
<i>Siderastrea siderea</i>	3.0	3.2	4.5	5.8	2.9	3.5	1.8	2.6	3.0 ± 0.6	3.8 ± 0.7	11.90	0.026
<i>Porites astreoides</i>	0.8	0.0	0.5	0.0	0.4	0.1	0.7	0.4	0.6 ± 0.1	0.1 ± 0.1	73.97	0.001

Percent cover values for each site are the average of the two stations; no error estimate is given. Percent cover values for all sites ($N = 4$) are the average \pm SE. F values and P values are the results of the mixed model ANOVA test for each category ($df_{\text{num}} = 1$, $df_{\text{den}} = 4$). Values are from summer 2009 and February 2010

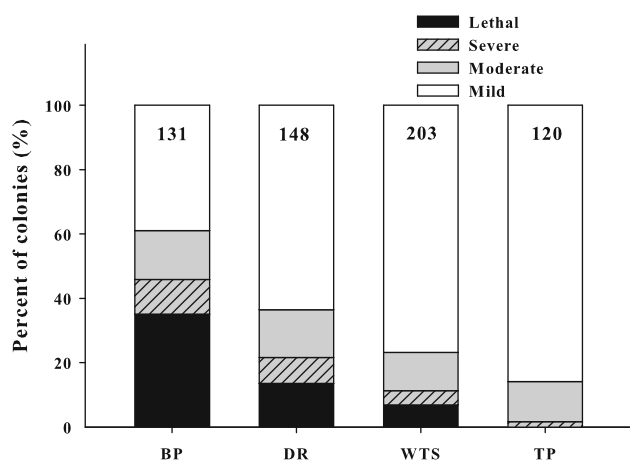


Fig. 3 Percentage of stony coral colonies categorized with mild (<10%), moderate (10–50%), severe (51–90%), and lethal (>90%) partial mortality during the 2010 cold-water event as determined by demographic surveys. Data for all coral species were pooled within a site. The total number of colonies surveyed is indicated at the top of each bar. BP Burr Patch, DR Dustan Rocks, WTS West Turtle Shoal, TP Thor Patch

partial mortality (e.g., lethal, severe, moderate; Fig. 4b). Lethal mortality was rarely observed in *M. cavernosa*, but this species had the highest occurrence of colonies with moderate to severe levels of partial mortality. Only three of 63 colonies (5%) had lethal mortality, but >60% of colonies in the two largest size classes had moderate or severe mortality (Fig. 4c). Lethal, severe, and moderate levels of mortality were low in *C. natans* and occurred in <15% of all colonies (Fig. 4d). Lethal mortality was not documented for *S. siderea*, and the incidence of severe or moderate mortality was extremely low with <5% recorded for any

size class (Fig. 4e). Figure 5 shows examples of partial and whole colony mortality on the stony corals *M. annularis* complex, *M. cavernosa*, and *C. natans*, and the encrusting octocoral *E. caribaeorum*.

Discussion

In January 2010, for the first time in nearly 30 years, South Florida experienced an extreme winter event. Low air temperatures recorded in Key West nearly matched a record set in 1886, and a new record was set for the longest duration of daily air temperatures <8°C, breaking a record set in 1876 (National Weather Service 2010). Although the paucity of in situ temperature data from previous events limits the number of direct comparisons, results presented here indicate that water temperatures during January 2010 were colder with lethal temperatures persisting longer than previous cold-water events in 1977 and 1981. For example, temperature data are available from Hens and Chickens patch reef from winter 1977. Hens and Chickens is located in the upper Keys ~10 km from Burr Patch, and the two sites are comparable in depth and distance from shore. In 2010, Burr Patch had a temperature profile similar to that at Hens and Chickens in 1977 and was subject to a similar number of hours at $\leq 14^\circ\text{C}$. However, at Hens and Chickens in 1977, the minimum temperature never dropped below 12°C . In contrast, the minimum temperature at Burr Patch in 2010 reached 11.2°C and was $\leq 12^\circ\text{C}$ for 32 consecutive hours (Table 1). The worst report of cold-induced mortalities at Hens and Chickens was in 1970, but temperature data are not available for that event (Roberts

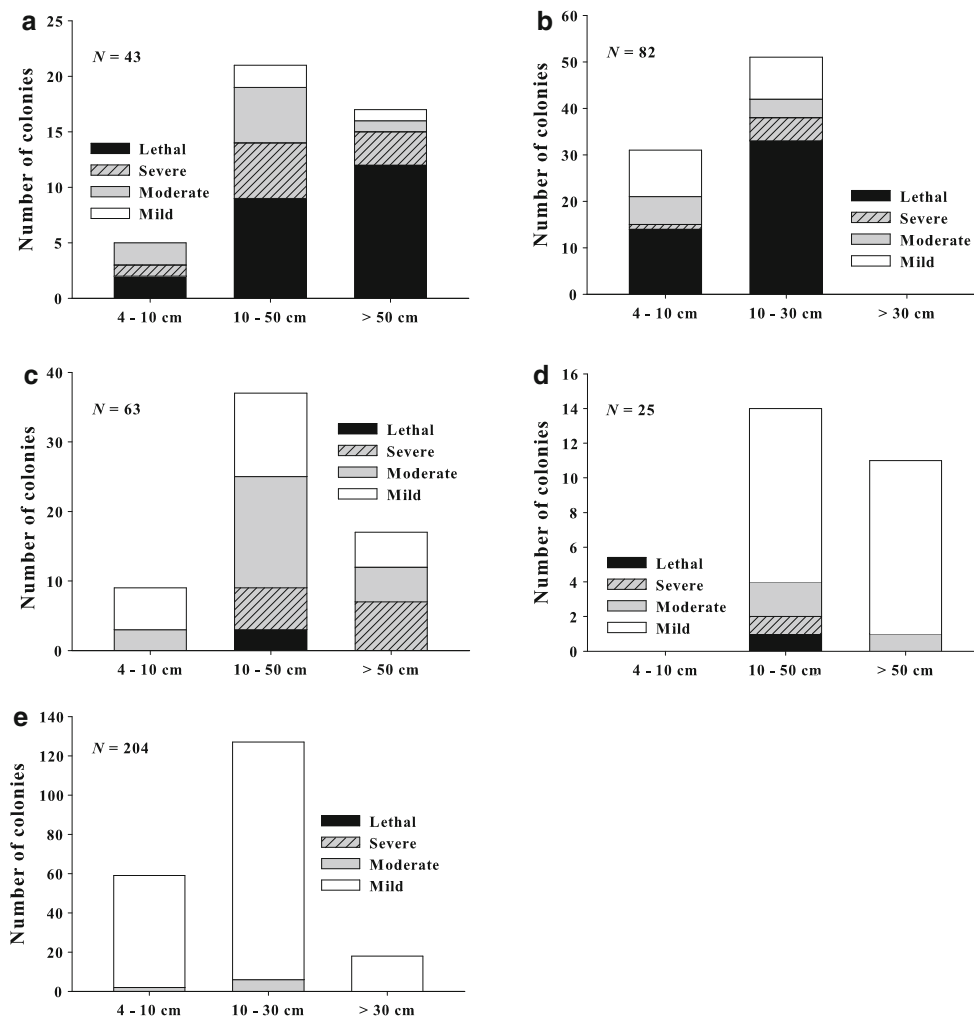


Fig. 4 The number of colonies categorized with mild (<10%), moderate (10–50%), severe (51–90%), and lethal (>90%) partial mortality in each size class (I, II, and III) for five scleractinian species during the 2010 cold-water event as determined by demographic

surveys. The total number of colonies is given for each species. **a** *Montastraea annularis* complex, **b** *Porites astreoides*, **c** *M. cavernosa*, **d** *Colpophyllia natans*, **e** *Siderastrea siderea*

et al. 1982). The severity of the 2010 event may also be demonstrated by comparing temperatures at the Florida Bay observing stations in 1977, 1981, and 2010. The minimum temperatures reached in 1981 and 2010 were the same (8.7°C), but the duration of temperatures $\leq 16^\circ\text{C}$ in 2010 was more than double that in 1981 (316 h vs. 156 h; Table 1). The number of hours $\leq 16^\circ\text{C}$ was also less in 1977 (192 h) than in 2010 (316 h), and the minimum temperature recorded, 12.9°C, was nearly 2°C higher in 1977.

Prior accounts of cold-water-induced mortality focused primarily on scleractinian corals (Voss 1973; Porter et al. 1982; Walker et al. 1982; Lirman et al. 2011); only one study describes cold-induced mortality in octocorals, and that only briefly (Roberts et al. 1982). In the current study, changes in percent cover show that the entire reef assemblage was affected, with octocorals suffering the greatest reduction in cover, decreasing to nearly half their 2009

values. Octocoral tolerances to hypothermic stress have been described for several species and range from 13 to 17.5°C (Goldberg 1973). Although cover of individual octocoral species was not estimated, field observations confirmed that encrusting (e.g., *Erythropodium caribaeorum*), branching (e.g., *Plexaura* spp., *Pseudoplexaura* spp., *Pseudopterogorgia* spp., *Eunicea* spp.), and flabellate (e.g., *Gorgonia ventalina*) growth forms were all affected. Affected octocoral colonies exhibited acute and rapid tissue necrosis, with no incidence of disease or bleaching occurring prior to mortality. Tissue was observed “sloughing” off colony axes and would readily detach from the colony if lightly touched, a process similar to that described during a warm-water mortality event in The Bahamas in 1998 (Lasker 2005).

Less is known about the cold-water thermal tolerances of tropical sponges; however, some tropical Atlantic

sponge species can occur at latitudes at which annual water temperatures drop below 12°C (Freeman et al. 2007; Ruzicka and Gleason 2008). Cover of sponges declined significantly, though not as much as the cover of stony corals and octocorals, partly because the sites that were most exposed to cold water had low sponge cover beforehand.

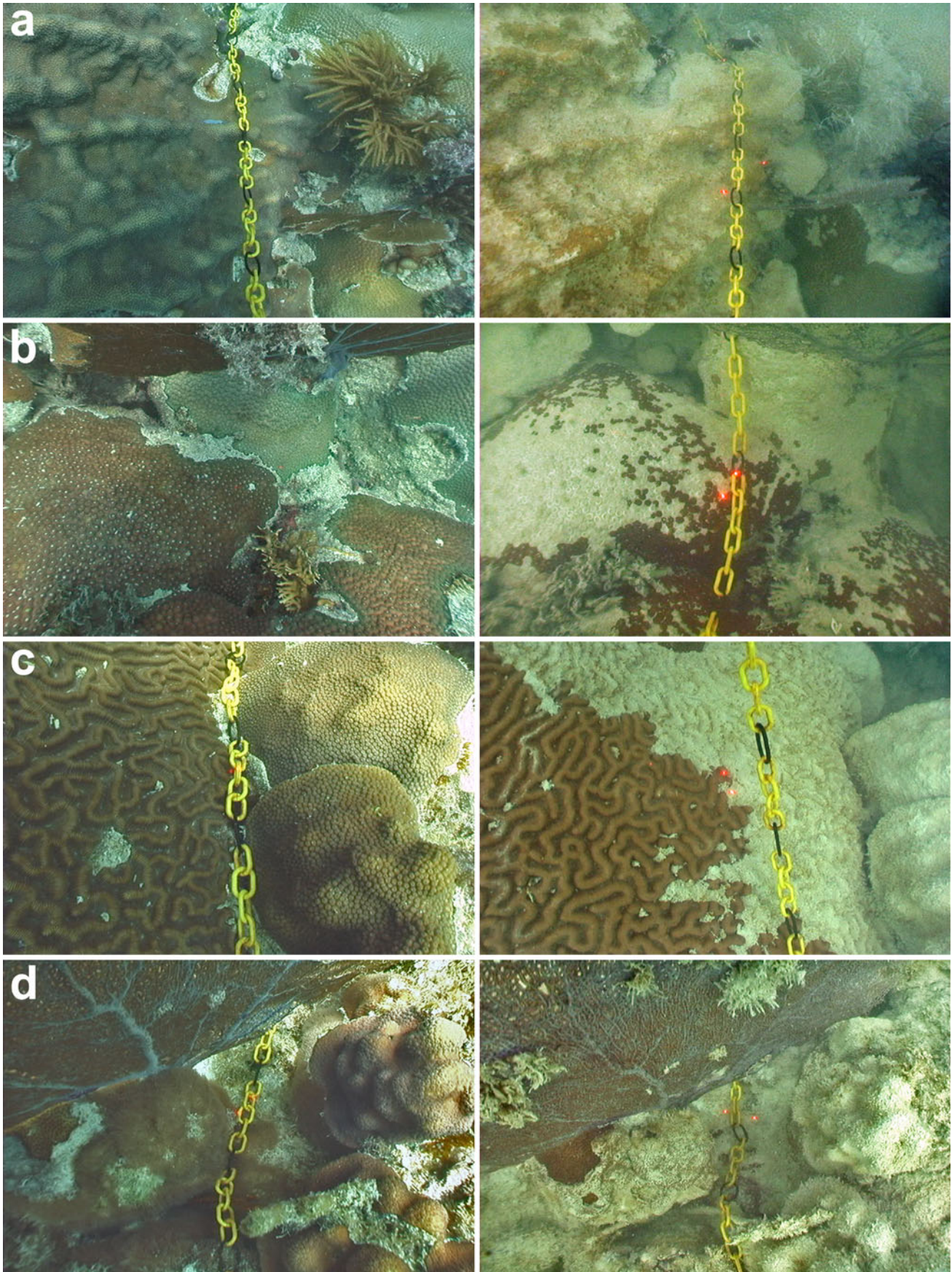
The changes in scleractinian cover were a product of coral community composition, species-specific thermal tolerances, and the severity of cold-water exposure at each site. Although scleractinian mortality was observed across all sites, the declines were greatest at the two sites that endured the longest exposure to lethal temperatures, Burr Patch and Dustan Rocks. The significant decline in coral cover at Burr Patch and Dustan Rocks was also directly tied to the high cover values of *M. annularis* complex at these two sites (Table 2). *Montastraea annularis* complex cover exceeded 6% at both sites in summer 2009, whereas the cover of this species at West Turtle Shoal and Thor Patch was $\leq 0.5\%$. At both Burr Patch and Dustan Rocks, the cover of *M. annularis* complex was reduced by $>85\%$ following the mortality event (Table 2). The drastic reduction in cover is directly linked to the high incidence of lethal and severe levels of mortality observed on the largest *M. annularis* complex colonies. An alarming 88% percent of colonies in the largest size class suffered lethal or severe mortality (Fig. 4a). Likewise, *P. astreoides* was nearly extirpated at Burr Patch and Dustan Rocks. Across the four survey sites, 57% of all colonies (spanning all size classes for *P. astreoides*) suffered lethal mortality (Fig. 4e). The lower tolerance of *M. annularis* complex and *P. astreoides* to cold-water-induced stress has been described before (Mayor 1914; Voss 1973; Roberts et al. 1982) and contributed heavily to the overall reduction in coral cover reported here (Table 2). The cover of *M. cavernosa* also significantly declined but was attributed to a higher rates of partial, rather than lethal mortality (Fig. 4b). Patches of surviving *M. cavernosa* tissue were small and highly fragmented, often consisting of only a single or very few polyps (Fig. 5). Corals with larger polyps, such as *M. cavernosa*, are believed to have physiological advantages over corals with smaller polyps during stress events (Porter 1976; Rogers 1979, 1990; Lasker 1980), which may explain why lethal mortality was less common for *M. cavernosa* than for *M. annularis* complex and *P. astreoides*.

Colpophyllia natans and *S. siderea* were the most tolerant of cold-water stress among the five species examined in detail. A significant change in cover was not detected for *C. natans*, and *S. siderea* cover increased between summer 2009 and February 2010. The increase in *S. siderea* cover is more likely an artifact of the image analysis and the result of mortality to other organisms than an increase in growth or population size of *S. siderea*. The

Fig. 5 Images of mortality from video transects in summer 2009 prior to mortality (left) and in winter 2010 following mortality (right). **a** Mortality of *Montastraea annularis* complex (left) and a branching octocoral with surviving *M. cavernosa* tissue (right) at Dustan Rocks. **b** Mortality of *M. cavernosa* with surviving tissue isolates and polyps at Dustan Rocks. **c** Partial mortality of *Colpophyllia natans* and whole colony mortality of *M. annularis* complex at Burr Patch. **d** Whole colony mortality of *Erythropodium caribaeorum* and *M. annularis* complex at Burr Patch

mortality of large, branching octocorals and the removal of macroalgae most likely increased the probability of a random point landing on an *S. siderea* colony that may have been obscured in the 2009 images. This idea is also supported by the result that marginal increases in *S. siderea* cover were evident across all study sites (Table 2). The ability of *S. siderea* to survive during periodic cold-water events is consistent with its broad geographic range, which implies a greater tolerance of extreme low temperatures. *Siderastrea siderea* is found in a variety of habitats that experience annual water temperatures well below 14°C, including rock outcroppings off the coast of North Carolina (Macintyre and Pilkey 1969) and carbonate ledges in the Gulf of Mexico (Colella et al. 2008). Additionally, early temperature experiments by Mayor (1914) showed that this species and its congener, *S. radians*, are two of Florida's most cold-water tolerant scleractinian species.

The results presented here are consistent with Lirman et al. (2011). Both studies portray catastrophic mortality on patch reefs in the middle and upper Keys with the most adverse affects occurring at sites that had the longest exposure to lethal temperatures. These findings are concerning for multiple reasons. Patch reefs possess the highest stony coral cover of any reef environment in the Florida Keys and have been resistant to numerous stressors in recent decades (Lirman and Fong 2007; Ruzicka et al. 2010). For example, following the mass bleaching associated with the 1997/98 El Niño, CREMP documented a nearly 40% reduction in scleractinian cover in the Florida Keys; however, most of the mortality was relegated to shallow and deep forereef environments, leaving patch reefs relatively unaffected (Sommerfield et al. 2008). Two of the sites assessed in this study, Dustan Rocks and West Turtle Shoal, in addition to four other patch reefs, represented six of only 10 sites monitored by CREMP (34 total) that have not exhibited a declining trend in coral cover since 1996 (Ruzicka et al. 2010). Corals on patch reefs are subjected to large variations in annual temperatures compared to corals on offshore bank reefs where temperatures are regulated by oceanic currents. This regular exposure to a wide range of temperatures over long periods of time is believed to have increased their tolerance to temperature fluctuations (Soto et al. 2011). Despite this increased tolerance, the temperature minima reached during January



2010 greatly exceeded those normally experienced by patch reef corals and resulted in considerable mortality.

The mortality of *M. annularis* complex described here also suggests that the January 2010 winter event was one of the most severe on record. The presence of large, healthy colonies of *M. annularis* complex at some patch reefs in the middle and upper Keys prior to 2010 suggests that they survived extreme cold-water fluctuations in the last century (Lirman and Fong 2007; Ruzicka et al. 2010). However, it is also possible that *M. annularis* complex were better suited to endure previous cold-water disturbances. Recent declines have been reported for *M. annularis* complex throughout much of the Caribbean and have been linked to a suite of acute and chronic stressors (Hughes and Tanner 2000; Rogers and Miller 2006; Edmunds and Elahi 2007). It is plausible that the cumulative effect of multiple stressors documented in the Florida Keys (Lirman 2001; Patterson et al. 2002; Lipp et al. 2002; Lapointe et al. 2004; Lirman and Fong 2007; Donahue et al. 2008; Wagner et al. 2010) has inhibited the ability of *M. annularis* complex to persist through major disturbances like the one described herein.

At reefs like Burr Patch and Dustan Rocks, *M. annularis* complex will be noticeably absent in the future. Instead, the coral communities at reefs like these will be characterized by faster growing and highly reproductive corals like *P. astreoides* and corals that have demonstrated the ability to withstand numerous stressors (e.g., *S. siderea*). CREMP has not documented recovery of *M. annularis* complex on patch reefs located north of the Florida Keys in the decade following a harmful algal bloom that decimated the population (Hu et al. 2003; Somerfield et al. 2008, Ruzicka et al. 2010). At Burr Patch and Dustan Rocks, any recovery of *M. annularis* complex will require decades, if not longer, because the high rates of lethal and severe mortality left only small surviving tissue fragments (Fig. 4a) and *M. annularis* complex has been undergoing widespread recruitment failure over the last quarter century (Keller and Donahue 2006; Edmunds and Elahi 2007).

Acute disturbances that cause widespread coral mortality can often result in temporary or permanent changes in community structure (Hughes 1994; Norström et al. 2009). A proliferation of macroalgae is most commonly associated with this change (Hughes 1994; Rogers and Miller 2006; Norström et al. 2009), but elevated levels of macroalgal cover have not been sustained on Florida Keys reefs following catastrophic disturbances (Maliao et al. 2008; Somerfield et al. 2008; Ruzicka et al. 2010). Sponges and octocorals are important components of the benthic assemblage on Florida Keys reefs and can rival or outnumber stony corals in abundance (Schmahl 1991; Miller et al. 2009). Prior to 2010, octocoral cover exceeded the cover of stony corals at three of the four patch reefs

(Table 2). Although mortality rates were high for octocorals, octocorals have demonstrated a marked resilience following two periods of major disturbance in the Florida Keys (e.g., 1997/1998 El Niño and 2004/2005 hurricane seasons) and cover has rebounded twice (Ruzicka et al. 2010). Multiple studies on Caribbean reefs have indicated that sponges can also become the most abundant taxa following major perturbations (Aronson et al. 2002; Weil et al. 2002). Given the large octocoral and sponge assemblages at these sites prior to the mortality event and their ability to recover following disturbances, we anticipate that any temporary or permanent change in community structure would involve these taxa.

Temperature has long been recognized as a proximate control of coral reef formation and community structure in the Florida Keys (Vaughan 1919), and this study provides quantitative evidence that, as hypothesized by Ginsburg and Shinn (1964, 1994), inimical waters are important in structuring nearshore coral communities in the Florida Keys. Our results expand upon previous observations (Roberts et al. 1982; Walker et al. 1982; Lirman et al. 2011) that periodic extreme cold weather fluctuations can result in catastrophic mortality on nearshore patch reefs in the Florida Keys. Although cold-water-induced mortalities have been described before, the record-breaking weather of January 2010 and concordant mortality at formerly healthy patch reefs suggest that this event was one of the most severe in the last century. The catastrophic mortality described herein and by Lirman et al. (2011) is particularly concerning because patch reefs in the Florida Keys had previously survived numerous stressors that were deleterious to corals in other habitats. Our findings corroborate those reported by Lirman et al. (2011) and when compared with descriptions of previous cold-water mortalities on Florida coral reefs strongly suggest the 2010 event was likely the worst on record.

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