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RESEARCH ARTICLE

In Situ Coral Nurseries Serve as Genetic Repositories for Coral Reef Restoration after an Extreme Cold-Water Event

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Abstract

During an unusual cold-water event in January 2010, reefs along the Florida Reef Tract suffered extensive coral mortality, especially in shallow reef habitats in close proximity to shore and with connections to coastal bays. The threatened staghorn coral, *Acropora cervicornis*, is the focus of propagation and restoration activities in Florida and one of the species that exhibited high susceptibility to low temperatures. Complete mortality of wild staghorn colonies was documented at 42.9% of donor sites surveyed after the cold event. Remarkably, 72.7% of sites with complete *A. cervicornis* mortality had fragments surviving within in situ coral nurseries. Thus, coral nurseries served as repositories for genetic material that would have otherwise been completely lost from donor sites. The location of the coral nurseries at deeper habitats and distanced from shallow nearshore habitats that experienced extreme temperature conditions buffered the impacts of the cold-water event and preserved essential local genotypes for future *Acropora* restoration activities.

Key words: ***Acropora*, coral nurseries, coral restoration, Florida, mortality, thermal stress.**

Introduction

Historically, the Florida Reef Tract has experienced significant episodic cold-water events that caused mass coral mortality (Roberts et al. 1982; Burns 1985). For example, in 1977 and 1981, when temperatures dropped below 16°C, an accepted low thermal threshold for hermatypic zooxanthellate Caribbean corals (Mayor 1915), reefs in the Florida Keys and the Dry Tortugas experienced extensive coral mortality and fish kills (Walker et al. 1982; Bohnsack 1983). During these and other cold-water events, the staghorn coral, *Acropora cervicornis*, was found to be particularly susceptible to low temperatures and experienced extensive mortality (Shinn 1966; Davis 1982). While these events are not common, they can have dramatic and long-lasting effects on coral communities. Similar episodic events have occurred worldwide, with cold-water bleaching observed in Curaçao, Bonaire (Kobluk & Lysenko 1994; Bak et al. 2005), and the Great Barrier Reef (Hoegh-Guldberg et al. 2005), and coral mortality observed after exposure to extreme low temperatures in Bermuda (Verrill 1902), the Persian Gulf (Shinn 1976; Coles & Fadlallah 1991), and Taiwan (Hsieh et al. 2008). In January 2010, the Florida Reef Tract experienced a cold-water anomaly with temperatures below 16°C recorded for up to 14 days (Lirman et al. 2011). In this study, we evaluated the effects of this unusual but significant low-temperature event on the survivorship of wild colonies and nursery-reared fragments of the threatened Caribbean coral *A. cervicornis* and document the significant role of coral nurseries as repositories of genetic material during extreme climatic events.

Caribbean acroporid populations have declined drastically throughout their range, with declines of up to 95% (Jaap et al. 1988; Porter & Meier 1992). This decline has prompted *Acropora* propagation and restoration efforts to contribute to its natural recovery and removal from the threatened status achieved in 2006 (Bowden-Kerby et al. 2005; Hogarth 2006). As part of *Acropora* restoration efforts in Florida, USA, small fragments (<10 cm) from healthy colonies were collected and propagated within in situ nurseries located from Broward

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County to the Lower Florida Keys (Herlan & Lirman 2008; Lirman et al. 2010). In this study, we document the impacts of the 2010 cold-water event on populations of *A. cervicornis* along the Florida Reef Tract by examining the survivorship of both donor populations and fragments maintained within in situ coral nurseries. Moreover, we hypothesized that: (1) populations of *A. cervicornis* located in shallow habitats close to shore would be exposed to lower temperatures and higher thermal variation during the 2010 cold-water event compared to deeper, offshore locations; and (2) that mortality of *A. cervicornis* would be related to temperature minima and duration of exposure to low temperatures.

Methods

In situ *Acropora cervicornis* nurseries have been established in Broward County, Biscayne National Park (North and South), Upper Keys, Middle Keys, and Lower Keys (Big Pine Key and Looe Key), Florida (Fig. 1). In each region, *A. cervicornis* fragments were collected from healthy donor colonies from inshore (mean distance to shore $= 2,888 \pm 2,021$ m; mean depth $= 3.9 \pm 1.4$ m), mid-channel (mean distance to shore $= 5,503 \pm 1,503$ m; mean depth $= 4.9 \pm 1.2$ m), and offshore (mean distance to shore $= 8,240 \pm 1,203$ m; mean depth $= 5.1 \pm 1.1$ m) shelf zones, and placed within nurseries using cement platforms or line nurseries (Fig. 1). Water temperatures were recorded using HOBO loggers at each nursery and all reef zones (Fig. 1). In the Middle Keys, temperature data were not collected with HOBO loggers as part of this study. However, for comparison with other areas, sea temperature data recorded by SEAKEYS CMAN stations at Long Key (inshore) and Sombrero Reef (offshore) were included. It must be noted that the Long Key CMAN station is located in Florida Bay and does not fully represent a true inshore reef environment. Visual surveys of *A. cervicornis* colonies at all donor sites and nursery

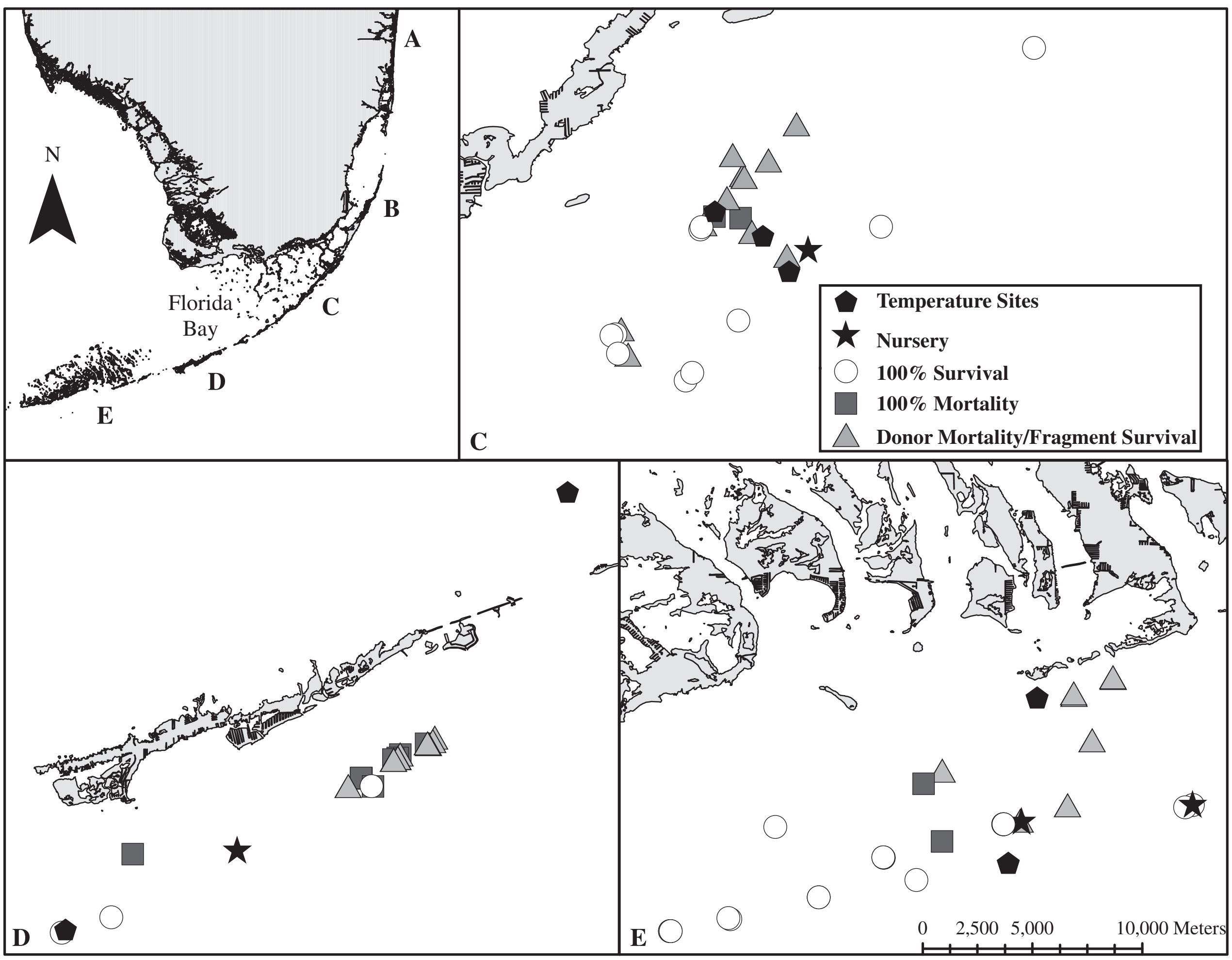

Figure 1. Location of coral nurseries (black stars), temperature monitoring sites (black pentagons), and *Acropora cervicornis* donor sites in Broward County (A), Biscayne National Park (B), the Upper Keys (C), the Middle Keys (D), and the Lower Keys (E). Sites in Broward County and Biscayne National Park are not included within expanded boxes due to limited *A. cervicornis* mortality in response to the cold-water event. Sites with 100% survival of all donor colonies (white circles), 100% mortality of all *A. cervicornis* donor colonies and nursery fragments (gray squares), and mortality of all *A. cervicornis* donor colonies with fragment survival in the nursery (gray triangles) are represented.

locations were conducted in November and December, 2009, prior to the cold-water event, and between 19 January 2010 and 9 February 2010, after the event, to document mortality patterns. Differences in percent mortality of donor colonies along cross-shelf gradients were compared within regions with Chi-square tests.

Results

During the January 2010 cold-water event, water temperatures remained above 16°C at the Broward County coral nursery and at inner, middle, and outer reef zones (Table 1; Figs. 2 & 3). In Biscayne National Park, temperatures remained above the thermal threshold at both coral nurseries and the offshore reef zone but dropped below 16°C in the inshore and mid-channel zones for 7 and 4 days, respectively. In the Upper Keys, the nursery and all three reef zones experienced temperatures below the thermal threshold. Inshore, mid-channel, and offshore zones were below 16°C for 7, 4, and 1 days, respectively. At the Upper Keys nursery, temperatures were below 16°C for 4 days. In the Middle Keys, inshore temperatures dropped as low as 8.7°C and remained below 16°C for 14 days. Offshore habitats in the Middle Keys did not go below the thermal threshold during the cold-water anomaly. The mid-channel Middle Keys nursery was exposed to temperatures as low as 12.8°C and remained below 16°C for 5 days. In the Lower Keys, temperatures at inshore habitats fell to 12.3°C and remained below 16°C for up to 5 days, while the offshore habitats remained above the thermal threshold during the cold-water event. Temperatures at the mid-channel Lower Keys nursery dropped below 16°C for 4 days.

The mortality of both donor colonies and nursery fragments was directly related to the temperature patterns documented. From Broward County to the Lower Keys, a total of 105 reefs (67 inshore, 23 mid-channel, 15 offshore) were used as donor sites (Fig. 1). Complete mortality of all *Acropora cervicornis* colonies, including donor colonies, occurred at 45 (42.9% of all sites) donor sites. All of the sites that experienced coral mortality were located south of Broward County and Biscayne National Park in the Florida Keys where temperatures dropped below the 16°C threshold. Temperature-related mortality patterns were also documented based on the shelf position and depth. Significantly higher mortality of *A. cervicornis* colonies occurred at inshore (49.3% of all inshore sites) and mid-channel (43.5%) sites compared to offshore (6.7%) sites ($\chi^2 = 9.374$, degrees of freedom $[df] = 2$, $p = 0.009$). Of the 45 sites that had complete *A. cervicornis* mortality, 32 (71.1%) sites had surviving coral fragments within the nurseries, including fragments from 24 inshore, 8 mid-channel, and 1 offshore sites. Sites with 100% *A. cervicornis* mortality in the Florida Keys were located closer to tidal passages (mean distance $= 6{,}585 \pm 1{,}484$ m) than sites with surviving colonies (mean distance $= 9{,}004 \pm 2{,}666$ m), indicating a direct relationship with proximity to tidal flow from Florida Bay.

In Broward County, where temperatures never reached the lower thermal threshold, no *A. cervicornis* mortality was observed at the 27 inshore donor sites or the coral nursery. In Biscayne National Park, no *A. cervicornis* mortality was recorded at the four donor sites (one inshore and three mid-channel) or the mid-channel nurseries, but mortality occurred for *A. cervicornis* colonies at one inshore (58.2% mortality of

Table 1. Minimum temperatures recorded at inshore, mid-channel, offshore reef zones, and nursery sites along the Florida Reef Tract during the 2010 cold-water event.

Region	*Year Established*	*Reef Zone*	*Min Temp (°C)*	*Distance to Shore (m)*	*Depth (m)*	*Number of Days at or Below 16°C*
Broward County		Inner Reef	21.6	985	6.1	0
		Middle Reef	22.0	1,623	12.2	0
		Outer Reef	22.1	2,145	18.3	0
	2007	Nursery (Inshore)	19.9	392	5.2	0
Biscayne National Park		Inshore	12.8	4,976	1.5	7
		Mid-channel	13.9	6,165	3.6	4*
		Offshore	20.6	9,799	13.3	0
	2009	North Nursery (Mid-channel)	17.6	5,592	5.8	0
	2007	South Nursery (Mid-channel)	16.0	7,310	5.8	3*
Upper Keys		Inshore	11.3	4,551	3.6	7
		Mid-channel	12.0	6,136	6.1	4*
		Offshore	15.9	8,163	13.0	1
	2001	Nursery (Offshore)	13.5	10,832	10.6	4*
Middle Keys		Inshore	8.7	4,506	3.0	14*
	2009	Nursery (Mid-channel)	12.8	5,680	7.3	5*
		Offshore	19.0	6,880	3.0	0
Lower Keys		Inshore	12.3	827	3.7	5*
	2007	Nursery (Mid-channel)	13.2	6,407	8.2	4*
	2009	Offshore	18.7	7,621	7.8	0

Days marked with an asterisk (*) indicate consecutive days below 16°C. Mean distance to shore and mean depth of each reef zone and year of nursery establishment are included.

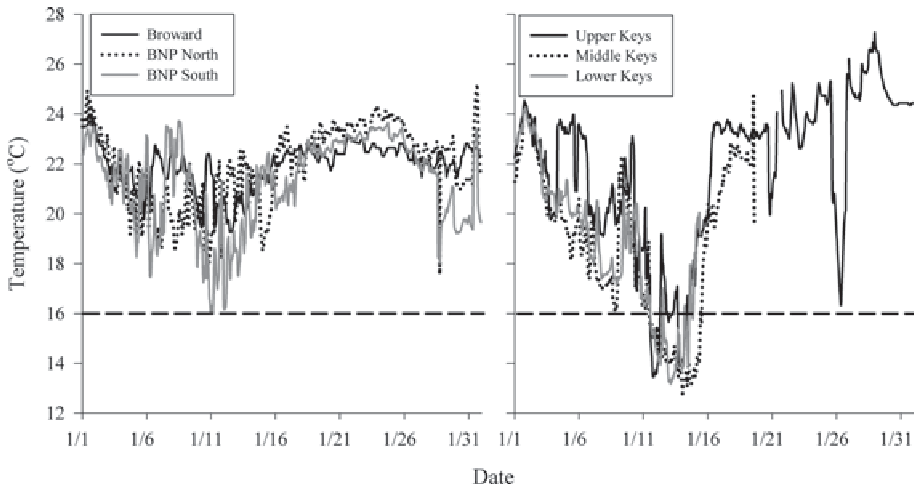

Figure 2. Hourly sea temperatures at Broward County and Biscayne National Park (BNP) and the Upper Keys, Middle Keys, and Lower Keys nursery locations during the January 2010 cold-water event. The dashed black line delineates the lower thermal tolerance (16°C) of Caribbean hermatypic zooxanthellate corals.

colonies) and one mid-channel (40.0% mortality of colonies) site surveyed as part of a separate project.

In the Upper Keys, 25 donor sites were surveyed after the cold-water event. Complete mortality of *A. cervicornis* colonies occurred at 13 sites (52.0% of Upper Keys sites) including 8 inshore, 4 mid-channel, and 1 offshore sites ($\chi^2 = 3.098$, $df = 2$, $p = 0.212$) (Fig. 1). While mortality was prevalent in donor sites in the Upper Keys, 11 of these 13 donor sites (84.6%) had fragments surviving within the coral nursery (Fig. 4). A difference in fragment survival related to the propagation methods used within the Upper Keys nursery was observed, with approximately 30% mortality of fragments on cement platforms and only 0.7% mortality (1 out of 150 fragments) of fragments hung from line nurseries.

In the Middle Keys, fragments collected from 26 donor sites were propagated in both the Upper Keys and the Middle Keys nurseries. Complete mortality of *A. cervicornis* colonies occurred at 22 donor sites (84.6% of Middle Keys sites; Fig. 1). Twenty-one of 22 inshore sites (95.5%) in the Middle Keys experienced 100% mortality of all *A. cervicornis* compared to only 1 of 2 mid-channel sites, and 0 of 2 offshore sites (Fig. 4). These spatial patterns were significantly different ($\chi^2 = 14.826$, $df = 2$, $p = 0.0006$). The coral nursery in the Middle Keys was the only nursery that experienced 100% mortality of all fragments. At the Upper Keys nursery, 13 of 16 Middle Keys inshore donor sites (81.3%) had surviving fragments within the nursery.

In the Lower Keys, 23 donor sites were surveyed after the cold-water event. Ten sites (43.5% of Lower Keys sites) experienced 100% mortality of all *A. cervicornis*, including four inshore sites and six mid-channel sites (Fig. 1). No mortality was observed at any of the eight offshore sites in the Lower Keys. Again, spatial patterns of decreasing mortality with increasing distance from shore were statistically significant ($\chi^2 = 11.902$, $df = 2$, $p = 0.003$). Of the 10 sites with 100% *A. cervicornis* mortality, 8 sites (4 inshore and 4 mid-channel) had surviving fragments within the coral nurseries (Fig. 4). While there was no mortality of coral fragments located in the offshore nursery, there was 82.6% mortality of fragments located in the mid-channel nursery.

Discussion

The 2010 cold-water anomaly caused the sea temperatures of the Florida Keys to drop well below coral mortality thresholds for extended periods of time. Extreme cold temperatures were especially concentrated in nearshore, shallow environments where the mortality of *Acropora cervicornis* colonies was significantly higher compared to deeper habitats. In fact, many reefs located in the Upper, Middle, and Lower Florida Keys suffered total *A. cervicornis* mortality during the cold-water anomaly. Patterns of *A. cervicornis* mortality were directly related to depth, cross-shelf, and latitudinal position, with significantly higher mortality recorded at inshore and mid-channel sites. Mortality patterns were also associated with the number of days that temperatures were below 16°C, the documented low-temperature threshold for Caribbean hermatypic zooxanthellate corals (Mayor 1915). Remarkably, a large proportion of coral fragments collected from donor colonies prior to the cold-water event survived within in situ coral nurseries. Nurseries were typically located in mid-channel and offshore reef zones that did not experience temperatures less than 16°C. These nurseries now house the only surviving coral tissue from many reefs where 100% *A. cervicornis* mortality occurred. Therefore, these coral nurseries served as repositories for genetic material lost from donor reefs following this acute disturbance and provide a sustainable local stock from which to enhance *Acropora* populations to these reefs. This is of particular importance because many suggest that restoration activities should only use tissue from local sources to maintain the valuable genetic structure of

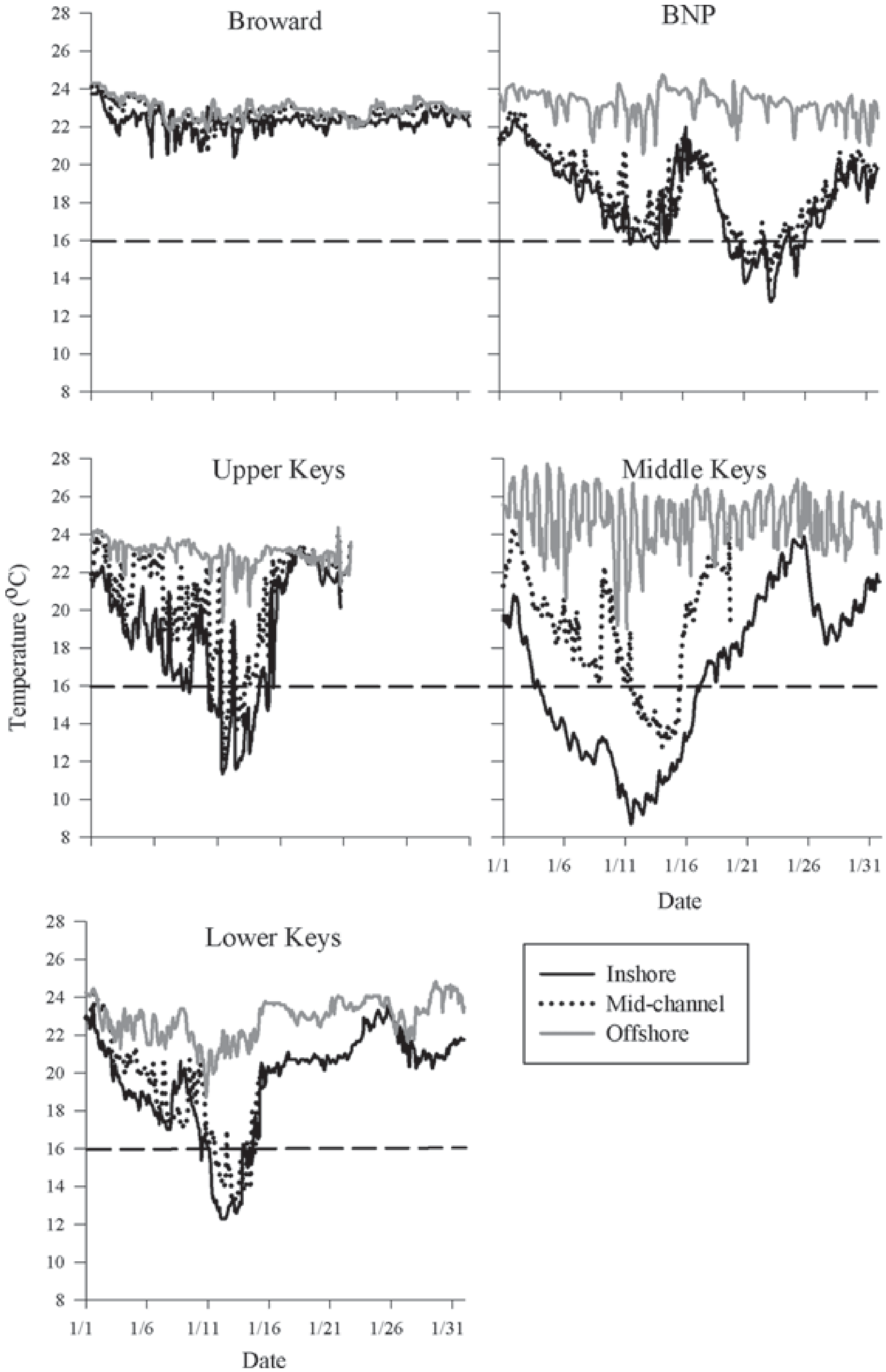

Figure 3. Hourly sea temperatures recorded in Broward County, Biscayne National Park, Upper Keys, Middle Keys, and Lower Keys at inshore (solid black line), mid-channel (dotted black line), and offshore (solid gray line) shelf zones during the January 2010 cold-water event. The dashed black line delineates the lower thermal tolerance (16°C) of Caribbean hermatypic zooxanthellate corals.

endemic threatened or endangered populations (Fant et al. 2008; Shearer et al. 2009).

During the 2010 cold-water anomaly, *Acropora* mortality was higher within inshore and mid-channel sites compared to deeper offshore habitats, and these spatial patterns were correlated with temperature minima and duration of exposure to cold temperatures (Lirman et al. 2011). Similar patterns of coral mortality were directly related to site location in the Florida Keys during the 1977 cold-water event (Roberts et al. 1982; Walker et al. 1982). Sites closer to the tidal passages

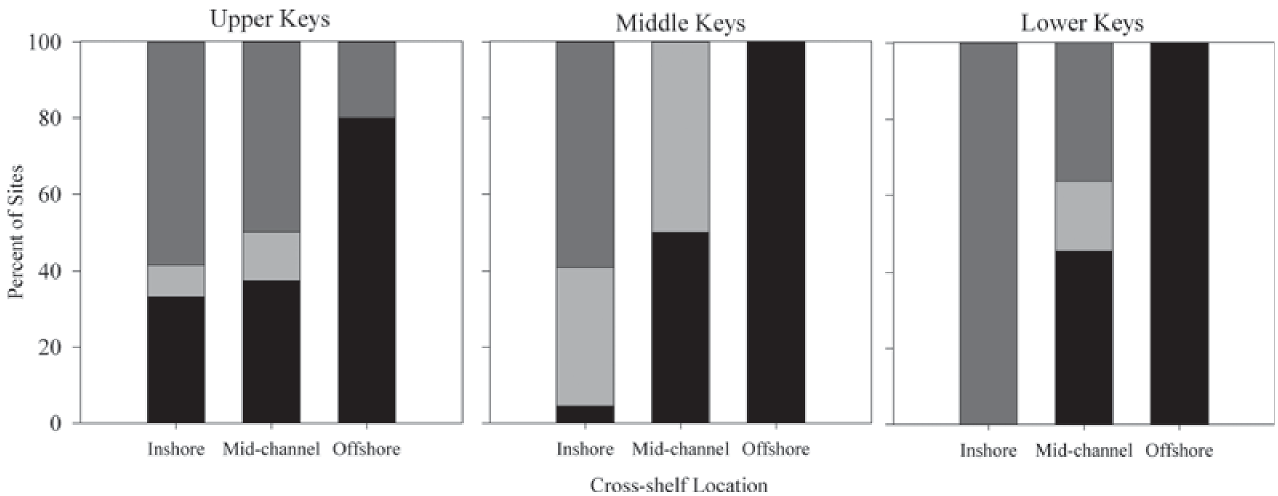

Figure 4. Percentage of sites in the Upper Keys, Middle Keys, and Lower Keys with complete survival of *A. cervicornis* colonies and nursery fragments (black bars), complete mortality of donor colonies and nursery fragments (light gray bars), and mortality of donor colonies with surviving nursery fragments (dark gray bars) at inshore, mid-channel, and offshore reef zones.

that connect the Florida shelf to shallow coastal lagoons, such as Florida Bay, experienced both lower temperatures due to the flow of cold water from the bay and higher *Acropora* mortality than sites further from these influences, a pattern that was previously documented for staghorn corals by Shinn (1966). In addition, mortality of *A. cervicornis* colonies and nursery fragments was restricted to the Florida Keys where sites were exposed to colder temperatures for longer duration as opposed to northern sites in Broward County and Biscayne National Park. These patterns suggest that nursery location strongly influenced the survival of coral fragments during the 2010 cold-water event. Nurseries placed in mid-channel-to-offshore locations may be protected from thermal anomalies by increasing the distance from sources of cold and warm water like Florida Bay or other shallow coastal lagoons and reducing temperature variability often seen at shallow inshore locations. Therefore, the spatially concentrated impacts documented in this study strongly suggest using multiple nursery sites within a region to mitigate the potentially devastating impacts of localized disturbance events such as thermal anomalies, storm damage, or ship groundings.

Fragment survival varied between two nurseries in this study likely due to small differences in nursery depth and location, as evidenced by the different fate of fragments collected from the same donor colony locations. Five donor sites used to populate both the Upper Keys and Middle Keys nurseries experienced 100% mortality of *A. cervicornis* populations. While all corresponding fragments died in the Middle Keys nursery, fragments from four of the five donor sites survived in the Upper Keys nursery. The Middle Keys nursery (7.3 m depth) experienced temperatures below the thermal threshold of 16°C for up to 5 days and diurnal temperatures did not go above 16°C for three of those days. However, the deeper Upper Keys nursery (10.6 m depth) was exposed to temperatures below 16°C for up to 4 days, but diurnal temperatures were above 16°C on all 4 days. Hence, dividing fragments into several nurseries within and among regions would be a productive strategy for reducing the risk of coral mortality during disturbance events. The strategic deployment of coral nurseries in areas with reduced risk (i.e. deeper, further away from habitats with wide fluctuations or stressful environmental conditions) may follow guidelines similar to those proposed for the targeted deployment of Marine Protected Areas (MPAs) in areas or habitats that boost coral resistance and resilience during and after large-scale disturbance events (Mumby & Steneck 2008).

Nursery design can also influence the survival of coral fragments, as minimal mortality was recorded for coral fragments suspended from mid-water line nurseries in the Upper Keys compared with approximately 30% mortality of fragments on cinderblock platforms secured to the benthos. Temperature stratification with depth is common in Florida and other regions with cooler temperatures observed near the substrate and warmer temperatures within the water column (Leichter et al. 2006). In the Lower Keys nursery, temperature differences of up to 4.4°C are typical throughout the year with cooler temperatures observed at the bottom of the line nursery (13.2 m depth) and warmer temperatures near mid-water lines (approximately 3 m) indicating the potential for even more severe thermoclines to exist during extreme thermal anomalies (E. Bartels 2010, Mote Marine Laboratory, Summerland Key, Florida, unpublished data). Therefore, propagating coral fragments using different methods within nurseries may mitigate thermal stress, minimize associated mortality, and contribute to the success of propagation efforts.

The field of in situ coral propagation is fairly new and methods are rapidly evolving to produce large numbers of coral fragments at reduced costs (e.g. Shafir et al. 2006). While coral propagation efforts will always pale in comparison with the scale of natural recovery or a good recruitment event, targeted propagation and restoration efforts can still have a considerable impact on the localized recovery or restoration of damaged coral reefs (Edwards 2010). The ultimate goal of *A. cervicornis* nurseries is clearly not to recover this species through propagation, but to grow sufficient amounts of healthy coral tissue for use in the targeted restoration of degraded coral reefs while exerting minimal impact on existing wild *A. cervicornis* populations (Lirman et al. 2010). Coral nurseries can be extremely productive (Soong & Chen 2003; Rinkevich 2005; Shafir et al. 2006) and can also contribute to preserving and enhancing the local genotypic diversity of depleted coral populations. This is a key consideration for the restoration of *Acropora* populations, particularly those within Florida and the western Caribbean that presently exhibit limited genetic diversity (Baums et al. 2005; Vollmer & Palumbi 2007). Reduced genetic diversity may also hinder sexual reproduction and thereby reduce the ability of scleractinian corals to naturally recover from mortality events (Hunter 1993; Baums et al. 2006; Williams et al. 2008). Thus, preserving and propagating genotypes from local sources within coral nurseries will provide a larger living gene bank for use in restoration activities similar to genetic stock preserved in captive breeding programs, parks, and zoos (Wildt 1992), thereby facilitating successful sexual reproduction and promoting the enhancement of *Acropora* populations.

This study demonstrates that coral nurseries served as a repository for genetic material following the 2010 cold-water event that significantly affected wild *A. cervicornis* populations in the Florida Reef Tract. Survival of coral fragments within the coral nurseries will provide essential genetic material to restock local reefs affected during the event and highlights the importance of coral nurseries to the overall survival of this threatened Caribbean species. In the face of climate change and the increasing likelihood of acute thermal disturbances (Donner et al. 2005; Hoegh-Guldberg et al. 2007; Manzello 2010), we suggest that reef managers design management and conservation efforts around the ability of coral nurseries to provide a sustainable source of coral colonies for future restoration activities.

Implications for Practice

- Coral reef management, restoration and conservation efforts should include the use of coral nurseries to propagate a sustainable stock of healthy and genetically diverse corals for population enhancement of threatened and endangered species.
- Coral nurseries can be extremely productive and can preserve local genotypic diversity of depleted coral populations during extreme weather events.
- Site selection for coral nurseries and potential restoration sites is paramount for mitigating the impacts of localized acute disturbances. Habitats with reduced risk (i.e. areas buffered from wide temperature fluctuations or other extreme environmental conditions) and multiple propagation methodologies should be utilized to increase the success of coral propagation and survival.

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