Thermal stress exposure, bleaching response, and mortality in the threatened coral *Acropora palmata*

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ABSTRACT

Demographic data for Elkhorn coral, *Acropora palmata,* and in situ water temperature data from seven upper Florida Keys (USA) reefs revealed three warm thermal stress events between 2010 and 2016. During a mild bleaching event in 2011, up to 59% of colonies bleached, but no mortality resulted. In both 2014 and 2015, severe and unprecedented bleaching was observed with up to 100% of colonies bleached. *A. palmata* live tissue cover declined by one-third following the 2014–2015 events. Colony mortality of mildly- and non-bleached colonies did not differ but increased significantly with more severe bleaching. Increased bleaching prevalence corresponded to maximum daily average water temperatures above 31.3 °C. However, the cumulative days with daily average exceeding 31.0 °C provided a better predictor of bleaching response. The bleaching response of surviving colonies in 2015 was not consistent with acclimatization as most individual colonies bleached at least as badly as in 2014.

1. Introduction

Coral bleaching events have devastating effects on the entire coral reef ecosystem (Graham et al., 2008). For corals, thermal stress results in the expulsion of their zooxanthellae, dinoflagellates of the genus *Symbiodinium*, leaving the coral tissue pale or bleached. Bleached corals experience severe physiological stress including oxidative stress and starvation. Furthermore, if zooxanthellae are not restored, the coral tissue will eventually die. Even after apparent recovery, corals may be functionally impaired for up to several years, having compromised reproduction (Levitan et al., 2014) and increased susceptibility to disease (Miller et al., 2009; Muller et al., 2008; Pinzon et al., 2014; Ritchie, 2006; Rogers and Muller, 2012). Coral taxa vary widely in both the level of thermal exposure that leads to bleaching (i.e., tolerance) as well as the severity of their bleaching response. With the global warming trend continuing unabated, thermal stress events are expectedly increasing in frequency (van Hooidonk et al., 2015). The varied responses of different coral taxa to this bleaching stress will shape the future of coral reefs. Other environmental factors (Brown, 1997; Carilli et al., 2009; Wooldridge, 2009) and past exposure to thermal stress have profound influence on the response to thermal stress at both individual and community levels, further complicating the ability to predict future

outcomes (Hughes et al., 2017; van Woesik et al., 2011).

Acroporid corals historically functioned as foundational reef-builders on Atlantic reefs, providing complex reef structure through their fast growing branching morphology (e.g., Adey, 1978). The functional loss of these species is a major factor contributing to negative shifts in carbonate budgets throughout the region (Perry et al., 2015) as well as losses in habitat complexity (Alvarez-Filip et al., 2009). In spite of this foundational role, little documentation exists of *Acropora palmata*'s response to or consequences from thermal stress. Most of what is known about *in situ* bleaching response and consequences for *Acropora* spp. is based on the many species native to the Indo-Pacific, which are generally reported to be among the most highly susceptible genera to warming (Marshall and Baird, 2000; McClanahan et al., 2007). However, more recent reports show high variability within this genus (Guest et al., 2012). Mass bleaching events in the Caribbean have only been well documented in the past 30 years, after *A. palmata* began its precipitous decline in abundance. Prior to 2005, large-scale Caribbean bleaching events occurred in 1982/83, 1987/88 and 1997/98 (Causey, 2008; Eakin et al., 2010). Relatively few reports of *A. palmata* bleaching during these earlier events exist, which likely indicates that *A. palmata* colonies bleached less than neighboring coral species (Goreau, 1990; Jaap et al., 1979; Manzello et al., 2007; McField, 1999; Wilkinson,

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1998; Williams and Bunkley-Williams, 1990). Consequently, this species has been considered generally less susceptible to bleaching, in terms of both temperature threshold and recovery. Nonetheless, *A. palmata* bleaching has been reported in more recent thermal stress events. During the 2005 wide-scale Caribbean bleaching event, *A. palmata* in the USVI was reported bleached for the first time (Lundgren and Hillis-Starr, 2008; Muller et al., 2008; Rogers and Muller, 2012; Wilkinson and Souter, 2008). During this event, an estimated 15–65% (Lundgren and Hillis-Starr, 2008; Muller et al., 2008) of *A. palmata* colonies in the USVI were affected by bleaching, and bleached colonies that survived were found to be more vulnerable to disease-associated mortality (Muller et al., 2008). Additionally, in Puerto Rico, *A. palmata* colonies severely bleached during both the 2005 (García-Sais et al., 2008) and 2010 (Ricaurte et al., 2016) thermal stress events.

Some coral communities show evidence of increased tolerance of thermal stress following previous exposure, either to a single thermal stress event (Baker, 2001; Guest et al., 2012; Maynard et al., 2008) or to a history of greater thermal variability (Carilli et al., 2012; Thompson and van Woesik, 2009). Increased tolerance at the community level can be driven by selection among coral species, where more susceptible species succumb leaving more heat-tolerant species to dominate (e.g., Loya et al., 2001). Within a species, heat-tolerant genets may survive better than other heat-sensitive genets (e.g., Sampayo et al., 2008). On an individual colony level, increased thermal tolerance often results from shifts to more heat-resistant zooxanthellae clades (Baker, 2004; Baker et al., 2004; Jones et al., 2008; Kemp et al., 2014; Silverstein et al., 2015). Berkelmans and van Oppen (2006) demonstrated that acclimatization of *Acropora millepora* could occur when the host shuffled its symbiont type from C to D, which conferred an increased thermal tolerance of 1–1.5 °C. In contrast, *A. palmata*, particularly in the Florida Keys, shows remarkable fidelity in hosting a single *Symbiodinium* clade, A3 (Thornhill et al., 2006), and most often, each colony will host only a single genotype of clade A3 (Baums et al., 2014; Parkinson et al., 2015). *Symbiodinium* clade A3 is known to have photoprotective characteristics (Reynolds et al., 2008); thus, *A. palmata* switching to a different zooxanthellae clade may invoke tradeoffs between heat susceptibility and light susceptibility. This is particularly relevant because *A. palmata* is a shallow habitat specialist. At present, substantive zooxanthellae shuffling in *A. palmata* has not been documented.

The aim of this study was to characterize the bleaching response of the threatened coral, *A. palmata,* to repeated thermal stress events on upper Florida Keys reefs. First, we evaluate spatial and temporal patterns in bleaching response among *A. palmata* populations at seven reef sites and over six years. Second, we characterize thermal stress exposure constituting bleaching thresholds for *A. palmata* by analyzing the relationship between temperature and colony-based bleaching observations. Finally, we evaluate the bleaching response at the colony-level, specifically, whether genotype or prior thermal stress exposure affects the bleaching response or fate of colonies.

2. Materials and methods

2.1. Data collection

Seven-meter radius plots were established on the upper Florida Keys reef tract at sites ranging from 2 to 7 m in depth in 2004 and 2010. In spring 2010, all *A. palmata* colonies in each plot were identified and genotyped as reported in Williams et al. (2014). Here we analyzed observations starting in spring 2010 at which time there were 23 plots among seven reef sites (Fig. S1; three plots at each site except four at each of Elbow and Carysfort). In spring 2010 and 2011 and each fall from 2011 to 2015, 'full plot surveys' were conducted during which all attached live *A. palmata* colonies in each plot were measured (length, width and height) and the percent live tissue cover was visually estimated (see Williams and Miller, 2012 for more detailed methods). A subset of colonies in each plot was randomly selected and tagged for

more frequent 'colony condition surveys' three times per year (winter, spring and fall); in plots with fewer than 12 live colonies, all were tagged. When one of the tagged colonies died it was replaced by a randomly selected colony identified during the next full plot survey unless no additional live colonies remained in the plot.

At each colony condition survey, the tagged colonies were measured for size and percent live was visually estimated. A colony 'live area index' (Colony LAI) was calculated for each colony based on its average dimension squared and the resulting area adjusted for the percent live tissue cover (Williams and Miller, 2012). Plot LAI was calculated by summing the Colony LAI for all colonies found in each plot during a full plot survey. For each tagged colony, bleaching severity was scored on a scale of 0 to 5 with '0' indicating that tissue color was within "normal range" and '5' indicating all live tissue appeared completely white. All measurements and bleaching severity scores were assessed by a single observer (DEW) and cross-checked for consistency among sites and years by reference to colony photographs taken at each survey. Bleaching prevalence for each reef was calculated as the proportion of tagged colonies on a reef (pooled from all plots) with a bleaching score ranked greater than zero during the fall survey. Bleaching severity for a reef was calculated by averaging the bleaching scores recorded during the fall survey for each living tagged colony (including those scored as normal or zero) on a reef.

Water temperature loggers (Onset HOBO Pendant®) were deployed in a shaded position within one plot at each reef (Miller and Williams, 2016). The sensors logged temperature every 30 min, and a daily average (DailyAvg) temperature was calculated for each 24 h day at each reef. The maximum of this daily average (MaxDailyAvg) observed between June and October was determined for each site and year where complete data were available (Table 1a). To evaluate cumulative heat stress, the number of days between June and October in which the daily average exceeded 30.5 °C, 30.8 °C, 31.0 °C and 31.3 °C were tallied for each reef (Table 1b). These candidate cumulative stress temperatures were selected to span the temperature threshold identified in Manzello et al. (2007) as the best predictor for coral bleaching in the Florida Keys (30.5 °C), and the MaxDailyAvg temp we observed as a threshold (31.3 °C) of elevated bleaching in the focal population of this study.

2.2. Analyses

To analyze bleaching response among sites and years we used

Table 1
Temperature exposure observed between June and October from 2010 to 2016 at each monitored reef in the upper Florida Keys, expressed as (a) in situ maximum of the daily average water temperatures and (b) number of days in which the *in situ* daily average water temperature was at least 31.0 °C.

Reef	2010	2011	2012	2013	2014	2015	2016
(a) Maximum of daily average water temperature							
Carysfort Reef	31.2	31.4	30.6	30.2	≥ 31.4*	31.5	30.9
Grecian Rocks	**	31.8	30.6	30.5	31.7	31.6	31.0
Key Largo Dry Rocks	31.0	31.8	30.6	30.4	31.8	31.7	31.1
French Reef	30.7	31.3	30.4	30.2	**	31.5	30.9
Molasses Reef	30.6	31.4	30.5	30.1	**	31.5	30.7
Sand Island	31.0	31.2	30.3	30.2	31.6	31.4	30.8
Elbow Reef	30.8	31.2	30.4	30.1	31.4	31.5	30.7
(b) Days ≥ 31.0 °C							
Carysfort Reef	3	14	0	0	32*	34	0
Grecian Rocks	**	22	0	0	32	38	1
Key Largo Dry Rocks	0	16	0	0	31	44	2
French Reef	0	11	0	0	**	39	0
Molasses Reef	0	13	0	0	**	29	0
Sand Island	0	10	0	0	22	25	0
Elbow Reef	0	11	0	0	19	25	0

* Gap in temperature data between Aug. 7 and Sep. 16, day count interpolated based on similar sites.

** Logger not recovered.