



Long-term recovery of Caribbean corals from bleaching

Stephen Levas^{a,*}, Verena Schoepf^{a,1}, Mark E. Warner^b, Matthew Aschaffenburg^b, Justin Baumann^{a,2}, Andréa G. Grottoli^a

^a School of Earth Sciences, The Ohio State University, Columbus, OH 43210, USA

^b School of Marine Science and Policy, University of Delaware, Lewes, DE 19958, USA

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ABSTRACT

Mass coral bleaching events are increasing in frequency and intensity and are predicted to occur annually in the coming decades. However, it remains poorly understood how quickly Caribbean corals can recover from bleaching. To explore the responses to heat stress and subsequent recovery in Caribbean corals, three species (*Porites divaricata*, *Porites astreoides*, and *Orbicella faveolata*) were experimentally bleached in outdoor flow-through tanks for 15 days then allowed to recover on the reef for 1.5 and 11 months. At each interval on the reef, endosymbiont concentrations, energy reserves (i.e., total soluble lipid, soluble animal carbohydrate, soluble animal protein), calcification, and stable carbon and nitrogen isotope values of the animal host ($\delta^{13}\text{C}_h$, $\delta^{15}\text{N}_h$) and endosymbiotic algal fractions ($\delta^{13}\text{C}_e$, $\delta^{15}\text{N}_e$) were measured in treatment and control fragments of each species. Despite variations in bleaching recovery strategies among the coral species, all corals recovered within one year. Specifically, bleached *P. divaricata* catabolized lipids and decreased calcification in response to lower endosymbiont concentrations. In contrast, both *P. astreoides* and *O. faveolata* maintained energy reserves despite lower endosymbiont concentrations, yet both decreased calcification rates after bleaching. Overall, these findings indicate that these corals are capable of surviving and recovering from a mild bleaching event within one year. Though these findings indicate that *P. astreoides* and *O. faveolata* may be resilient through single isolated bleaching events under annual bleaching, many Caribbean coral reefs may still experience a decline over the coming decades.

1. Introduction

Coral reefs are threatened worldwide due to a combination of direct and indirect human impacts (Hoegh-Guldberg et al., 2007; Hoegh-Guldberg et al., 2012; Hughes et al., 2003). Periods of elevated sea surface temperatures are of primary concern as they can lead to mass coral bleaching events, whereby coral communities lose a significant proportion of their endosymbiotic algae (*Symbiodinium* spp.) (Brown, 1997; D'Croz et al., 2001; Glynn, 1996; Hoegh-Guldberg, 1999). Corals can have extremely different physiological responses to heat stress events: some corals bleach and die, others bleach and recover, and some do not visibly bleach at all (Fisk and Done, 1985; Marshall and Baird, 2000; Stimson et al., 2002). Variations in coral bleaching susceptibility are associated with both coral host and endosymbiont factors including the genetic type(s) of *Symbiodinium* (Baker, 2001; Baker et al., 2004; Grottoli et al., 2014; Rowan, 2004), algal density (Stimson et al., 2002),

coral morphology (Loya et al., 2001; Marshall and Baird, 2000), disease (Ravindran et al., 1999; Riegl, 2002), energy reserve or tissue biomass utilization (Anthony et al., 2009; Grottoli et al., 2014; Thornhill et al., 2011; Towle et al., 2015), and heterotrophic capabilities (Anthony et al., 2009; Ferrier-Pages et al., 2010; Grottoli et al., 2006; Grottoli et al., 2014; Levas et al., 2013; Towle et al., 2017).

Physiological studies have shown that healthy corals typically acquire the majority of their fixed C photosynthetically from their endosymbiotic algae and additional fixed C and N heterotrophically from the direct consumption of zooplankton and/or the uptake of dissolved organic and particular organic matter (Grottoli et al., 2006; Houlbreque and Ferrier-Pages, 2009; Levas et al., 2015; Levas et al., 2013; Muscatine et al., 1981; Tremblay et al., 2012). Fixed C is stored as energy reserves in the form of lipid, protein, and/or carbohydrate reserves (Battey and Patton, 1984; Porter et al., 1989; Rodrigues and Grottoli, 2007). However, when corals are bleached and photosynthesis

* Corresponding author at: Department of Geography, Geology, and Environmental Science, University of Wisconsin-Whitewater, Whitewater, WI 53190, USA.

E-mail address: levass@uwv.edu (S. Levas).

¹ Present address: ARC Centre of Excellence for Coral Reef Studies, School of Earth Sciences, and UWA Oceans Institute, The University of Western Australia, Crawley, WA 6009, Australia

² Present address: Department of Marine Sciences, University of North Carolina, Chapel Hill, NC 27599, USA

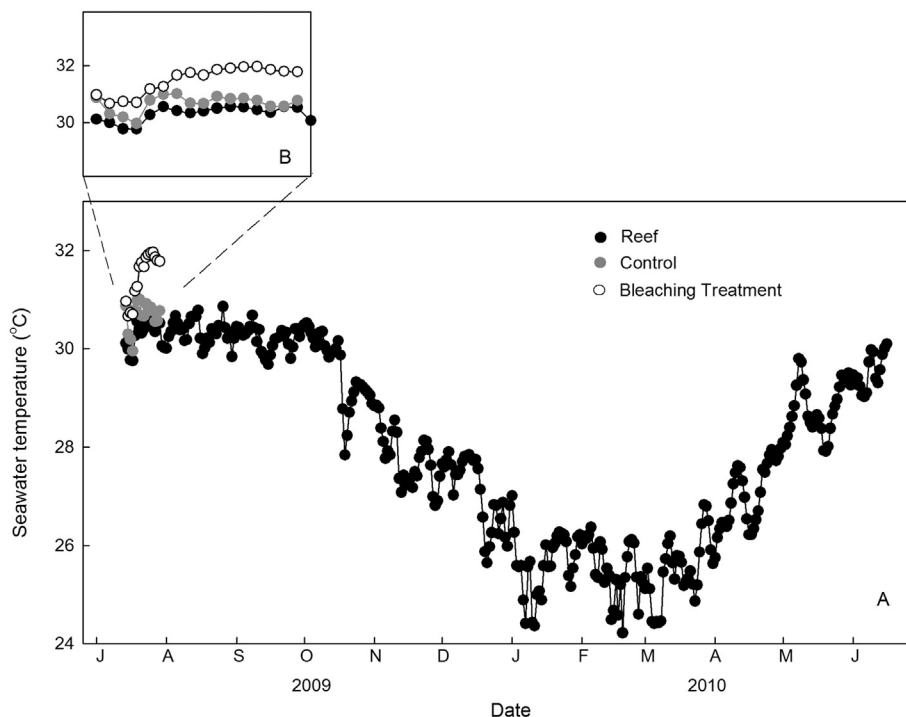


Fig. 1. Average daily seawater temperature profile (A) throughout the study. Inset box shows details of average daily temperature profiles of the treatment and control tanks during (B) the experiment. Months are indicated by their first letter. Modified from Grottoli et al. (2014).

is dramatically reduced (Fitt et al., 2000; Lesser, 1997; Porter et al., 1989; Rodrigues and Grottoli, 2007), resulting in a decrease in the amount of fixed C translocated to the coral host (Hughes et al., 2010), corals may depend on several alternative pathways to sustain themselves and recover, including: catabolize energy reserves (Fitt et al., 2000; Grottoli et al., 2006; Grottoli et al., 2014; Kenkel et al., 2013; Rodrigues and Grottoli, 2007; Schoepf et al., 2015), increase heterotrophic feeding (Anthony et al., 2009; Grottoli et al., 2006; Grottoli et al., 2014; Levas et al., 2015; Towle et al., 2017), decrease respiration (Borell et al., 2008), decrease calcification (Abramovitch-Gottlieb et al., 2002; Grottoli et al., 2014; Leder et al., 1991; Levas et al., 2013; Suzuki et al., 2003), and/or translocate carbon to the endosymbiotic algae to facilitate endosymbiont recovery (Hughes et al., 2010). For instance, the Caribbean coral *Porites astreoides* is able to meet at least 150% of metabolic demand and maintain energy reserves by increasing feeding immediately after bleaching (Grottoli et al., 2014; Levas et al., 2015), while *Porites divaricata* and *Orbicella faveolata* do not modify their feeding rates and must rely on a combination of energy reserves and endosymbiont switching and/or shuffling in the short-term presumably until endosymbiont populations recover (Grottoli et al., 2014; Levas et al., 2015). Previous studies have tracked similar coral species from the Caribbean throughout natural bleaching events and have shown low mortality rates (Fitt et al., 1989; Porter et al., 1989), with overall recovery of proteins and lipids within 14 months (Fitt et al., 1993). Yet, it remains unknown if these bleached corals fully recover their total energy reserves and calcification within the course of a year, which is especially pertinent given that the frequency of bleaching events are predicted to occur annually in the Caribbean by 2025 (van Hooidonk et al., 2015).

In addition to physiological research, biogeochemical studies have also enhanced our understanding of coral bleaching biology. For example, differences between the stable carbon isotopic signature ($\delta^{13}\text{C}$) of the coral host tissue and algal endosymbiont reflect changes in the proportionate contribution of heterotrophically and photoautotrophically derived C to coral tissues during recovery from bleaching (Rodrigues and Grottoli, 2006). The stable nitrogen isotopic

signatures ($\delta^{15}\text{N}$) of corals tracks the inorganic and organic sources of nitrogen to the coral holobiont (Heikoop et al., 2000; Hoegh-Guldberg et al., 2004; Rodrigues and Grottoli, 2006) and suggest that during bleaching recovery the endosymbionts take up inorganic nitrogen presumably to stimulate cell growth and recovery (Levas et al., 2013; Rodrigues and Grottoli, 2006; Schoepf et al., 2015).

Thus, traditional physiological measurements coupled with isotopic analyses can be powerful tools for understanding the underlying factors driving recovery from bleaching and why recovery rates can vary among species. To evaluate the long-term recovery patterns in Caribbean coral physiology and biogeochemistry following bleaching, we experimentally bleached *Porites divaricata*, *Porites astreoides*, and *Orbicella faveolata* with elevated seawater temperatures for 15 days in outdoor tanks and compared them to non-bleached control corals of the same colonies after 0, 1.5, and 11 months of in situ recovery. These three species have distinct morphologies, where *P. divaricata* is branching, *P. astreoides* is encrusting and mounding, and *O. faveolata* forms large mounding colonies that contribute substantially to the larger reef framework throughout the Caribbean. A large suite of variables including endosymbiont concentrations, total soluble lipid, soluble animal protein, soluble animal carbohydrate, calcification, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the animal host and endosymbiotic algae fractions were measured at each interval on the reef to track the bleaching and recovery response of *P. divaricata*, *P. astreoides*, and *O. faveolata*.

2. Methods

2.1. Coral collection and experimental design

Coral collection, acclimation, experimental design, temperature profiles, and procedures used in the present study have been largely described previously by Grottoli et al. (2014) and Schoepf et al. (2014). Briefly, in July 2009, nine separate colonies of each species at least 10 m apart to optimize chances corals were unique genotypes, were collected and separated into six different fragments for a total of 54 fragments per species. Coral colonies were collected from the reefs near

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