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Long-term recovery of Caribbean corals from bleaching

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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 ($\delta^{13}C_h$, $\delta^{15}N_h$) and endosymbiotic algal fractions ($\delta^{13}C_e$, $\delta^{15}N_e$) 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 finding 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

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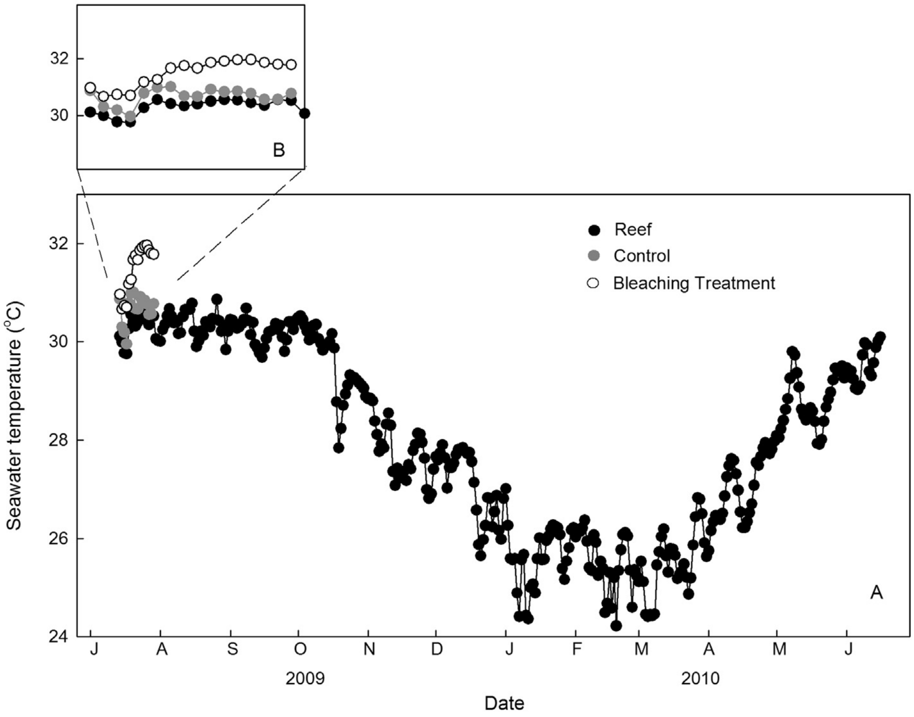

Fig. 1. Average daily seawater temperature profile (A) throughout the study. Inset box shows details of average daily temperature profiles of the treatment and control tanks during (B) the experiment. Months are indicated by their first letter. Modified from Grottoli et al. (2014).

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-Gottlib 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 ($\delta^{13}C$) 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 ($\delta^{15}N$) 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, $\delta^{13}C$ and $\delta^{15}N$ 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

Puerto Morelos, Mexico at depths ranging from 3 to 8 m, and were acclimated to outdoor, flow-through tanks for five days and then each fragment was buoyantly weighed according to methods by Jokiel et al. (1978). Each fragment was individually placed onto a plastic tile for identification and visibly healing with live tissue starting to grow over the exposed skeleton. On 14 July 2009, half of the fragments from each colony and species were placed into one of five treatment tanks (31.48 ± 0.20 °C) (bleached treatment fragments) and the other half of the fragments were placed into one of five control tanks that received ambient reef seawater (30.66 ± 0.24 °C) (non-bleached fragments) (Fig. 1). The maximum monthly mean (MMM) sea surface temperature (SST) during the warmest months of August and September is 29.0 °C at this site with a bleaching threshold of 30.0 °C (MMM + 1 °C, NOAA Coral Reef Watch Virtual Station Version 2, Yucatan Peninsula, Mexico). After 15 days, all tanks were returned to ambient temperatures. Thus, treatment corals were exposed to estimated heat stress levels of 3 to 4-degree heat weeks (DHW) relative to the control corals. This is similar to heat stress levels measured during the 1998 bleaching event in the Caribbean (Eakin et al., 2010). Furthermore, this area had experienced zero and one DHW in 2007 and 2008, respectively, suggesting these corals had not experience a previous bleaching event stress in the immediate years prior to this experiment (NOAA Coral Reef Watch, 2000).

On the 15th day of the experiment, one treatment and one control fragment pair from each colony of each species was collected, their appearance recorded, buoyantly weighed, and then immediately frozen at −80 °C. The appearance of each fragment was scored prior to freezing according to methods modified from Rodrigues and Grottoli (2007). In brief, coral were assigned one of the following designations based on their appearance: 1- non-bleached fragments were dark brown in color and completely covered by living tissue, 2- partially bleached fragments were either entirely pale (but not white) or some of the tissue was bleached and some healthy, and completely covered by living tissue, 3- bleached fragments were 100% white in color or > 50% white and the rest pale, and completely covered by living tissue, 4- partially dead non-bleached fragments were partially covered by filamentous or encrusting algae (or both), and partially covered by patches of living tissue that was brown in color, 5- partially dead bleached fragments were partially covered by filamentous or encrusting algae (or both), and partially covered by patches of living tissue that were pale in color, 6- dead fragments were completely covered by filamentous or encrusting algae (or both), with no living tissue remaining.

The remaining treatment and control fragments were placed back on the back reef at 4.9 m depth and approximately 1.5 km from shore (20°52.8150 N, 86°50.9890 W) to recover in situ (Fig. 1), with zooplankton densities averaging 365 zooplankton > 55 μm per liter (Levas et al., 2015). After 1.5 (22 September 2010) and 11 months on the reef (13 June 2010), one treatment and control pair of fragments from each colony and species were collected, their appearance scored, buoyantly weighed, cut in half, and each piece frozen at −80 °C. One half of each fragment was shipped to The Ohio State University for the following analyses: total soluble lipid, soluble animal protein, soluble animal carbohydrate, tissue biomass, the natural δ^{13}C and δ^{15}N of the animal and endosymbiont fraction. The other half of each fragment was shipped to the University of Delaware for endosymbiont concentration analysis.

2.2. Endosymbiont concentrations, energy reserves, and calcification

Endosymbiont concentrations were measured per Warner et al. (2006). Total soluble lipid, soluble animal protein, and soluble animal carbohydrate concentrations were each measured on a 1 cm^2 coral plug from each fragment. Each measurement was made on whole coral samples (skeleton + animal tissue + endosymbiont), ground with a mortar and pestle, and normalized to total ash-free dry tissue biomass of the organic fraction (animal tissue + endosymbiont). Total soluble lipids were extracted using methods described in Rodrigues and Grottoli (2007), while soluble animal carbohydrate and protein concentrations were measured using the methods modified from Dubois et al. (1956) and Smith et al. (1985), respectively, as described in Rodrigues and Grottoli (2007). Calcification was determined using the buoyant weight technique (Jokiel et al., 1978) and normalized to surface areas of each fragment obtained using the foil technique (Marsh, 1970). Calcification is reported as mg calcium carbonate produced per day per cm^2. Therefore, any differences between treatment and control fragment rates are independent of colony size.

2.3. Stable isotopic analyses

A full description of these methods is given in Hughes et al. (2010). In summary, coral fragments were airbrushed to remove all tissue from the skeleton. The tissue and endosymbionts were separated by centrifugation and filtered onto prebaked (450 °C for six hours) GF/F filters. Animal host tissue and endosymbiont fraction δ^{15}N values ($\delta^{15}N_h$ and $\delta^{15}N_e$, respectively) were reported relative to air (δ^{15}N = per mil deviation of the ratio of stable nitrogen isotopes ^{15}N:^{14}N relative to air). Repeated measurements of internal standards (n = 60) had a standard deviation of ± 0.07‰ for organic δ^{13}C and ± 0.14‰ for organic δ^{15}N. Animal host and endosymbiont δ^{13}C values ($\delta^{13}C_h$ and $\delta^{13}C_e$, respectively) were determined using a Costech Elemental Analyzer where the resulting CO_2 gases were analyzed for δ^{13}C with a ThermoFisher Delta IV stable isotope ratio mass spectrometer (IRMS) via a Conflo II interface. $\delta^{13}C_h$ and $\delta^{13}C_e$ values were reported relative to Vienna Peedee Belemnite Limestone standard (VPDB) (δ^{13}C = per mil deviation of the ratio of stable C isotopes ^{13}C:^{12}C relative to VPDB). The difference between $\delta^{13}C_h$ and $\delta^{13}C_e$ (i.e., $\delta^{13}C_h$ - $\delta^{13}C_e$) was calculated to assess if there were any changes in the proportionate contribution of photoautotrophically and heterotrophically acquired C sensu Rodrigues and Grottoli (2006).

2.4. Statistical analyses

A multivariate one-way analysis of similarity (ANOSIM) was used to test for significant differences between treatment and controls at each time interval for each species. A SIMPER analysis was conducted to determine which physiological variables contributed most to the observed differences at each time interval. In addition, a two-way ANOSIM was used to test for overall significant differences among species and treatments. Non-parametric multidimensional scaling (NMDS) was used to graphically represent relationships between species and treatment in multidimensional space. In order to prevent bias from including all isotopic variables, only $\delta^{13}C_h$ - $\delta^{13}C_e$ and $\delta^{15}N_e$ were included in the above mentioned multivariate analyses along with endosymbiont concentrations, lipid, protein, carbohydrate, and calcification.

Univariate three-way analysis of variance (ANOVA) was then used to test the effect of temperature, time, and colony on endosymbiont concentrations, total soluble lipid, soluble animal protein, soluble animal carbohydrate, calcification rate, $\delta^{13}C_h$, $\delta^{13}C_e$, $\delta^{13}C_h$ - $\delta^{13}C_e$, $\delta^{15}N_h$, and $\delta^{15}N_e$ values for each species separately. Temperature was a fixed effect with two levels (treatment and control), time on the reef was a fixed effect with 3 levels (0, 1.5, and 11 months), and colony was a random effect. All data were tested for normal distribution using a Shapiro-Wilk's test of the residuals for each variable. Any data sets that were non-normal were transformed using the natural log to achieve normality, which was subsequently used in the ANOVA. A posteriori slice tests were used to determine if treatment and control averages significantly differed from each other within each time interval. Since all fragments were exposed to identical conditions except temperature during the tank portion of the experiment, any differences in the measured variables between treatment and control fragments were due to the temperature effects alone, independent of natural seasonal variation. A particular variable was deemed to be fully recovered when the treatment coral values no longer significantly differed, or were greater, than the controls. A coral species was deemed to be fully recovered when all of the treatment variables no longer differed or were greater than the corresponding controls.

3. Results

Treatment fragments of all species were visibly paler or bleached relative to the controls immediately after bleaching (Fig. S1, S2), though a larger percentage of *O. faveolata* corals experienced some level of bleaching compared to the other two species (S2). After 1.5 months on the reef, treatment fragments continued to show some paling and bleaching (Fig. S2), and control *O. faveolata* were slightly pale due to a mild bleaching event in the late summer of 2009 (Fig. S1). After 11 months on the reef, all corals visually appeared recovered (pers. observation) (Fig. S1). Only one treatment fragment of *O. faveolata* and *P. astreoides* died by the end of the study.

3.1. Multivariate analyses

Control and treatment fragments significantly differed within each species at the end of the tank treatment (i.e., 0 months on the reef) (Table 1, Fig. S3). For all three species, endosymbiont concentration alone accounted for 23–28% of the variation between treatment and control corals (Table 1, Fig. S3). After 1.5 months on the reef, treatment and controls no longer differed from each other overall (Table 1, Fig. S3). Over the entire 11 months of the study, all three species significantly differed from each other with *P. divaricata* being the most different from the other two species (Table 2, Fig. S3).

3.2. Physiology

3.2.1. P. divaricata

Treatment *P. divaricata* endosymbiont cell density decreased to 55% of control fragment values initially, but had fully recovered after 1.5 months on the reef (Table 3; Fig. 2A). In addition, treatment *P. divaricata* had 35% lower lipid concentrations after 1.5 months on the reef but had fully recovered by 11 months (Table 3; Fig. 2B). Protein and carbohydrate concentrations did not differ between treatment and controls at any point during the experiment (Table 3, Fig. 2C, D). Calcification rates significantly decreased by 24% initially in treatment corals compared to controls, and had fully recovered after 1.5 months on the reef (Table 3; Fig. 2E).

3.2.2. P. astreoides

Treatment *P. astreoides* endosymbiont concentrations decreased to 54% of control fragment values initially, but recovered after 1.5 months on the reef (Table 3; Fig. 2F). Despite reduced endosymbiont concentrations, there were no significant differences in lipids, proteins, or carbohydrates between treatment and control *P. astreoides* fragments at any time during the study (Table 3; Fig. 2G-I). Finally, treatment coral fragments initially had 36% lower calcification rates than controls, but had fully recovered after 1.5 months on the reef (Table 3; Fig. 2J).

Table 2
Results of a two-way ANOSIMs where the factors were treatment (Global *R*-statistic: 0.008; *p-value*: 0.254) and species (Global -statistic: 0.412; *p-value*: 0.001) with all pairwise tests among species. Significant *p*-values ($p \leq 0.05$) are highlighted in bold.

Species Pairwise Tests	*R*-statistic	*p-value*
Porites divaricata and *Porites astreoides*	0.485	0.010
Porites divaricata and *Orbicella faveolata*	0.540	0.010
Porites astreoides and *Orbicella faveolata*	0.248	0.010

3.2.3. O. faveolata

Endosymbiont concentrations in treatment fragments initially decreased by 70% compared to that of controls and had fully recovered after 1.5 months on the reef (Table 3; Fig. 2K). Despite significant decreases in the average endosymbiont concentrations, lipid, protein, and carbohydrate concentrations did not significantly differ between treatment and control fragments at any time (Table 3; Fig. 2L-N). In contrast, calcification rates in treatment corals declined by 61% relative to controls after 1.5 months on the reef and had fully recovered by 11 months (Table 3; Fig. 2O).

3.3. Stable isotopes

3.3.1. P. divaricata

$\delta^{13}C_h$ values did not differ between treatment and control fragments during the experiment (Table 4; Fig. 3A), while $\delta^{13}C_e$ was significantly lighter in treatment fragments than in controls after 1.5 months on the reef and significantly heavier after 11 on the reef (Table 4; Fig. 3B). The average difference between animal host and endosymbiont $\delta^{13}C$ did not differ between treatment and control fragments over the first 1.5 months on the reef; however treatment values were significantly lighter than control values after 11 months on the reef (Table 4; Fig. 3C). $\delta^{15}N_h$ and $\delta^{15}N_e$ values did not significantly differ between treatment and control *P. divaricata* corals at any time during the study (Table 4; Fig. 3D, E).

3.3.2. P. astreoides

$\delta^{13}C_h$, $\delta^{13}C_e$, $\delta^{13}C_h$ - $\delta^{13}C_e$, and $\delta^{15}N_h$ of treatment and control corals did not differ from each other at any time during the study (Table 2; Fig. 3F-I). However, $\delta^{15}N_e$ of treatment corals was 0.43‰

Table 1
Results of a one-way ANOSIM (Global R Statistic: 0.477; *p-value*: 0.001) with all pairwise tests among species, time intervals, and treatments.

Pairwise Test	*R*-statistic	*p-value*	SIMPER variable (percent contribution)
Porites divaricata			
0 months	0.237	0.0190	$\delta^{15}N_e$ (29), endosymbiont (27.9), calcification (17.1)
1.5 months	0.023	0.3060	lipid (44.5), calcification (20.8), $\delta^{15}N_e$ (12.6)
11 months	−0.187	0.8810	carbohydrate (33.1), protein (19.66), $\delta^{15}N_e$ (19.4)
Porites astreoides			
0 months	0.150	0.0160	calcification (32.2), endosymbiont (23.1), $\delta^{13}C_h$ - $\delta^{13}C_e$ (22.5)
1.5 months	0.078	0.1240	$\delta^{15}N_e$ (35.7), protein (18.5), calcification (12.3)
11 months	−0.066	0.8350	protein (25.4), $\delta^{15}N_e$ (19.5), lipid (18.7)
Orbicella faveolata			
0 months	0.202	0.0220	$\delta^{13}C_h$ - $\delta^{13}C_e$ (36.6), endosymbiont (26.7), protein (17.6)
1.5 months	0.001	0.3920	$\delta^{15}N_e$ (27), endosymbiont (26.7), protein (17.6)
11 months	0.046	0.2020	calcification (27.9), protein (26.3), endosymbiont (20.1)

Shown are only the pairwise test between treatment and controls within each species at each time interval. In addition, the percent contribution of each variable to the average dissimilarity of each pairwise test by SIMPER analysis is given in parentheses. Significant *p*-values ($p \leq 0.05$) are highlighted in bold.

Table 3
Results of three-way ANOVAs for chlorophyll *a* (Chl *a*), lipid, protein, carbohydrate concentrations, and calcification rates of *Porites divaricata*, *Porites astreoides*, and *Orbicella faveolata*.

Variable	Effect	df	SS	*F*-statistic	*p-value*
P. divaricata					
Endosymbiont	Model	13,50	2.4×10^{12}	2.71	< 0.0087
	T	1	3.6×10^{11}	5.19	0.0286
	R	2	2.8×10^{11}	2.02	0.1464
	C	8	7.9×10^{11}	1.41	02233
	T × R	2	8.9×10^{11}	6.33	0.0043
Lipids	Model	13, 46	124,482,637	1.93	0.0631
	T	1	23,666,691	4.90	0.0338
	R	2	9,635,915	1.00	0.3795
	C	8	5,698,794	1.18	0.3401
	T × R	2	18,874,920	3.91	0.0299
Protein	Model	13, 46	16,802,126	7.86	< 0.0001
	T	1	1123.01	0.01	0.9346
	R	2	11,244,830	34.21	< 0.0001
	C	8	5,561,895	4.23	0.0014
	T × R	2	114,604	0.35	0.7082
Carbohydrates	Model	13, 46	3,405,299	2.01	0.0526
	T	1	1602.43	0.01	0.5798
	R	2	144,577	0.55	0.5798
	C	8	3,224,058	3.09	0.0103
	T × R	2	91,908	0.35	0.7057
Calcification	Model	13, 48	5.17	5.88	< 0.0001
	T	1	0.0703	1.04	0.3150
	R	2	2.9006	21.34	< 0.0001
	C	8	1.5735	2.91	0.0135
	T × R	2	0.3340	2.47	0.0994
P. astreoides					
Endosymbiont	Model	13,53	9.9×10^{12}	10.68	< 0.0001
	T	1	9.8×10^{11}	13.74	0.0006
	R	2	4.9×10^{12}	34.61	< 0.0001
	C	8	1.7×10^{12}	2.97	0.0105
	T × R	2	2.3×10^{12}	16.06	< 0.0001
Lipids	Model	13, 53	40,320,168	1.32	0.2399
	T	1	2,709,974	1.16	0.2885
	R	2	1,734,778	0.37	0.6928
	C	8	35,727,128	1.91	0.0859
	T × R	2	148,287	0.03	0.9689
Protein	Model	13, 53	5,725,228	0.85	0.6048
	T	1	367,198	0.71	0.4040
	R	2	1,330,574	1.29	0.2868
	C	8	3,375,054	0.82	0.5919
	T × R	2	652,402	0.63	0.5368
Carbohydrates	Model	13, 53	1,558,382	1.37	0.2180
	T	1	71,916	0.82	0.3707
	R	2	38,544	0.22	0.8037
	C	8	1,145,364	1.63	0.1463
	T × R	2	302,557	1.72	0.1912
Calcification	Model	13, 52	0.00010	2.99	0.0041
	T	1	0.00002	8.53	0.0058
	R	2	0.00003	5.58	0.0074
	C	8	0.00003	1.80	0.1066
	T × R	2	0.00001	1.93	0.1581
O. faveolata					
Endosymbiont	Model	13,52	6.6×10^{12}	4.22	0.0003
	T	1	3.9×10^{12}	3.24	0.0796
	R	2	1.3×10^{12}	5.61	0.0074
	C	8	2.1×10^{12}	2.19	0.0501
	T × R	2	2.4×10^{12}	10.05	0.0003
Lipids	Model	13, 52	142,803,092	2.65	0.0094
	T	1	822,603	0.20	0.6585
	R	2	108,296,029	13.06	< 0.0001
	C	8	31,457,730	0.95	0.4892
	T × R	2	2,226,419	0.27	0.7659
Protein	Model	13, 51	18,917,773	2.07	0.0411
	T	1	401,532	0.57	0.4548
	R	2	7,166,258	5.09	0.0110
	C	8	10,395,552	1.85	0.0985
	T × R	2	768,499	0.55	0.5839
Carbohydrates	Model	13, 51	147,724	1.50	0.1615
	T	1	4383.29	0.58	0.4512
	R	2	76,829	5.08	0.0111
	C	8	61,811	1.02	0.4368
	T × R	2	554.69	0.04	0.9640
Calcification	Model	13, 52	0.4451	1.97	0.0513
	T	1	0.0063	0.37	0.5487
	R	2	0.0119	0.34	0.7117
	C	8	0.3931	0.89	0.4176
	T × R	2	0.0310	2.83	0.0142

The effect of temperature (T) was fixed and fully crossed with two levels (control, treatment). Time (R) was fixed and fully crossed with 3 levels (0, 1.5, and 11 months). Colony (C) was a random effect with 9 levels. Significant *p*-values ($p \leq 0.05$) are highlighted in bold.
df, degrees of freedom; SS, sum of squares of the effect.

more enriched than controls initially and had recovered after 1.5 months on the reef (Table 4; Fig. 3J).

3.3.3. *O. faveolata*

$\delta^{13}C_h$, $\delta^{13}C_e$, $\delta^{13}C_h$ - $\delta^{13}C_e$ and $\delta^{15}N_h$ of treatment corals never differed from control corals at any point throughout the study (Table 4, Fig. 3K-N). At the same time, treatment coral $\delta^{15}N_e$ values were 0.5‰ heavier on average than the $\delta^{15}N_e$ values of controls at 1.5 months on the reef, but did not differ after 11 months on the reef (Table 4; Fig. 3O).

4. Discussion

Despite all treatment corals having significantly reduced endosymbiont concentrations and calcification at some point during the first 1.5 months on the reef (Fig. 2), all physiological variables in treatment corals of all three species had recovered by 11 months on the reef. Reduced endosymbiont density and calcification in all three species immediately after bleaching is consistent with that observed during natural (Fitt et al., 1993; Fitt et al., 1989; Grottoli et al., 2004; Porter et al., 1989) and experimentally induced bleaching (Grottoli et al., 2014; Hueerkamp et al., 2001; Rodrigues and Grottoli, 2007).

4.1. *P. divaricata*

Although *P. divaricata* are capable of taking up dissolved organic carbon (DOC) when bleached, this source of fixed C is insufficient to completely compensate for lost photosynthetically derived C (Grottoli et al., 2014; Levas et al., 2015). Instead, treatment *P. divaricata* catabolized energy reserves and decreased calcification (Fig. 2A, E), while at the same time failed to increase zooplankton feeding and the percent of contribution of heterotrophy to respiration (CHAR) (Levas et al., 2015; Grottoli et al., 2014). However, the subsequent enrichment of $\delta^{13}C_e$ in *P. divaricata* at 11 months suggests that photosynthesis rates had recovered (Fig. 3B). This is corroborated by measurements of *P. divaricata* absorptance, a measure of productivity, which did not differ between treatment and control fragments after 11 months on the reef (Aschaffenburg, 2012). The significantly lower $\delta^{13}C_h$ - $\delta^{13}C_e$ values in treatment *P. divaricata* at 11 months on the reef further indicate that the proportion of heterotrophic C to coral tissues was greater in treatment than in control corals almost a year later. This is consistent with findings by Hughes and Grottoli (2013) where assimilated heterotrophic C overcompensation persisted for at least 11 months following bleaching in *P. compressa* corals in Hawaii. Thus, both branching *Porites* species studied to date exhibit heterotrophic overcompensating during long-term recovery from bleaching. Heterotrophic overcompensation could indicate that the treatment corals have not yet fully recovered or that a switch to enhanced incorporation of heterotrophic carbon is an

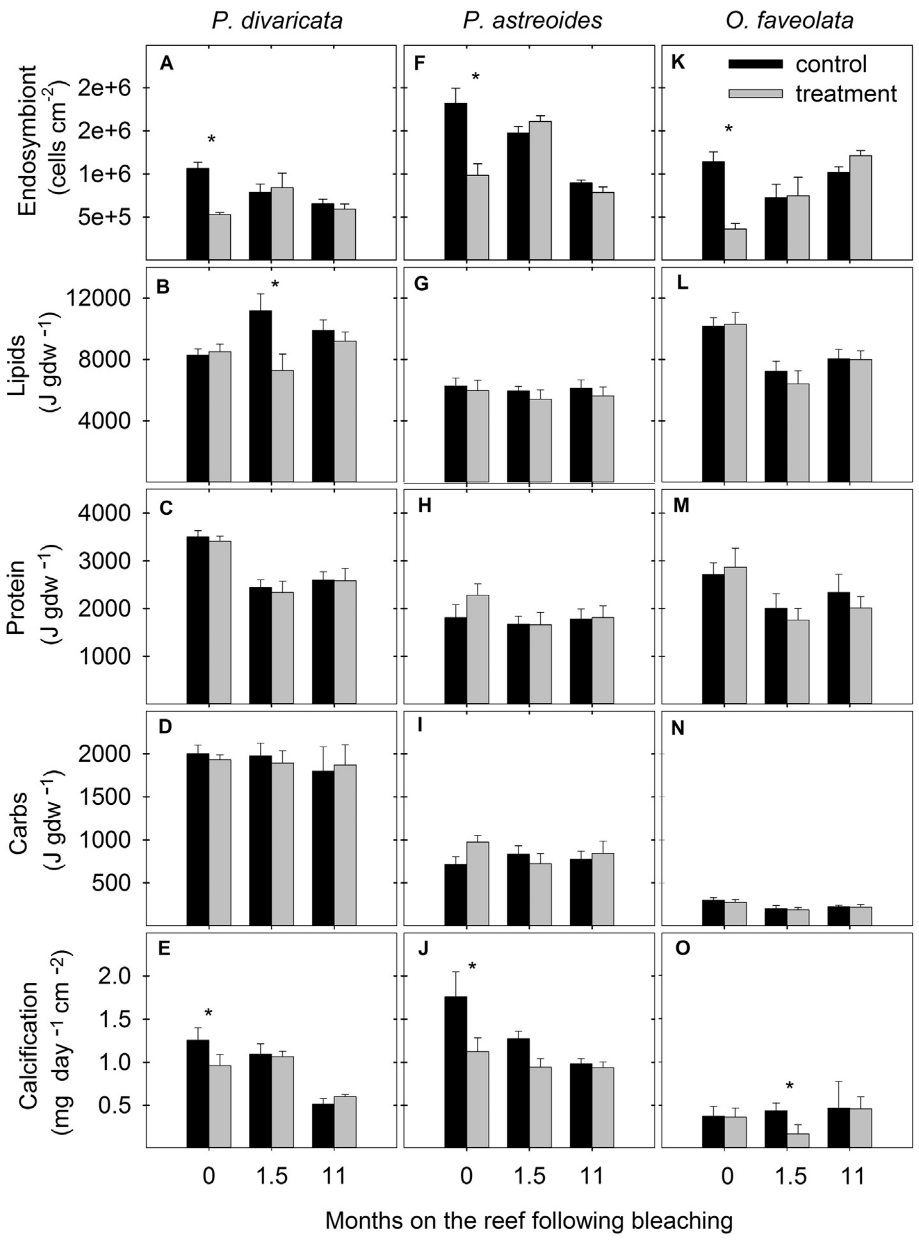

Fig. 2. Physiological response of bleached treatment and control corals. Average (A, F, K) endosymbiont, (B, G, L) lipids, (C, H, M) protein, (D, I, N) carbohydrates (carbs), and (E, J, O) calcification rates in controls (black bars) and treatment (grey bars) *Porites divaricata*, *Porites astreoides*, and *Orbicella faveolata* after 0, 1.5, and 11 months on the reef. All averages are standardized to grams of ash-free dry tissue weight (gdw) or to surface area (cm^2) and are shown ± 1SE. Symbols (*) indicate significant difference at $p \leq 0.05$ between means within a species and time interval by a posteriori least-squares mean slice tests. Sample sizes range between 7 and 9. Accompanying ANOVA results are in Table 3.

acclimatization strategy that imparts a strategic advantage during a bleaching event the next year (Hughes and Grottoli, 2013). Given that *P. divaricata* was the most resilient to repeated bleaching (Grottoli et al., 2014; Schoepf et al., 2015), this suggests that heterotrophic compensation in this species is an acclimatization strategy making this species a long-term winner.

4.2. *P. astreoides*

Corresponding with significant initial losses of endosymbiotic algal cells, treatment *P. astreoides* also had reduced calcification rates (Fig. 2J). Yet work published in two companion papers has shown that through a combination of reduced respiration rates, increased heterotrophic feeding on zooplankton and DOC, treatment *P. astreoides* were able meet well over 100% of their metabolic demand (i.e., Percent contribution of total carbon to animal respiration (CTAR)) (Grottoli et al., 2014; Levas et al., 2015). The negative effect of thermal bleaching on coral calcification rates has been well documented (Abramovitch-Gottlib et al., 2002; Goreau and Macfarlane, 1990; Jokiel and Coles, 1977; Leder et al., 1991; Rodrigues and Grottoli, 2006; Suzuki et al., 2003). Since calcification in corals is tightly coupled to photosynthesis (Hughes et al., 2010), bleached *P. astreoides* may be unable to maintain calcification due to reduced photosynthesis even when CTAR is maintained. This is consistent with the knowledge that heterotrophically derived C does not contribute to calcification in bleached Hawaiian corals but is essential to maintaining or building energy reserves (Hughes et al., 2010). Our findings indicate that this is also true in the Caribbean coral *P. astreoides* as well.

In the past decades, *P. astreoides* has increased in abundance throughout the Caribbean, with most studies attributing this to its high temperature tolerance (Warner et al., 2006) and ability to survive disturbance better than other coral (Darling et al., 2012; Green et al., 2008). Here, we corroborate the findings from previous studies and demonstrate that the underlying physiological mechanisms responsible for *P. astreoides* resilience to single bleaching events are two-fold. The first mechanism is the continuation of high feeding rates and an increase in DOC uptake, and maintenance of CZAR despite lower *Symbiodinium* density and photosynthesis rates immediately after bleaching (Aschaffenburg, 2012; Grottoli et al., 2014; Levas et al., 2015). Such physiological adaptations most likely facilitated the maintenance of

Table 4

Results of three-way ANOVAs for $\delta^{15}N_h$, $\delta^{15}N_e$, $\delta^{13}C_h$, $\delta^{13}C_e$, $\delta^{13}C_h$-$\delta^{13}C_e$, $\delta^{13}C_s$, and $\delta^{18}O_s$ of *Porites divaricata, Porites astreoides*, and *Orbicella faveolata*.

Variable	Effect	df	SS	*F*-statistic	*p-value*
P. divaricata					
$\delta^{13}C_h$	Model	33, 46	31.0495	8.59	< 0.0001
	T	1	0.0057	0.02	0.8860
	R	2	12.3394	22.20	< 0.0001
	C	8	15.6230	7.03	< 0.0001
	T × R	2	1.3152	2.37	0.1096
$\delta^{13}C_e$	Model	13, 45	22.5428	5.84	< 0.0001
	T	1	0.1918	0.65	0.4275
	R	2	3.0825	5.19	0.0112
	C	8	15.6395	6.58	< 0.0001
	T × R	2	3.6576	6.16	0.0055
$\delta^{13}C_h$ - $\delta^{13}C_e$	Model	13, 45	5.3577	3.91	0.0008
	T	1	0.3650	3.46	0.0720
	R	2	4.0100	19.02	< 0.0001
	C	8	0.8750	1.04	0.4294
	T × R	2	0.9815	4.66	0.0168
$\delta^{15}N_h$	Model	13, 44	10.5318	2.20	0.0357
	T	1	0.0463	0.13	0.7252
	R	2	5.1850	7.04	0.0030
	C	8	4.7444	1.61	0.1623
	T × R	2	0.9763	1.33	0.2804
$\delta^{15}N_e$	Model	13, 45	15.0675	3.54	0.0018
	T	1	0.1884	0.58	0.4535
	R	2	9.3337	14.26	< 0.0001
	G	8	4.4690	1.71	0.1349
	T × R	2	0.7169	1.10	0.3466
P. astreoides					
$\delta^{13}C_h$	Model	13, 53	0.0003	1.48	0.1669
	T	1	0.0000	0.03	0.8608
	R	2	0.0000	0.12	0.8863
	C	8	0.0002	1.63	0.1470
	T × R	2	0.0001	2.98	0.0623
$\delta^{13}C_e$	Model	13, 52	0.0007	2.78	0.0068
	T	1	0.0000	0.38	0.5391
	R	2	0.0001	4.95	0.0121
	C	8	0.0004	2.52	0.0260
	T × R	2	0.0001	2.79	0.0740
$\delta^{13}C_h$ - $\delta^{13}C_e$	Model	13, 51	25.79	3.23	0.0024
	T	1	0.0580	0.09	0.7604
	R	2	8.0151	6.52	0.0037
	C	8	12.8688	2.62	0.0219
	T × R	2	3.7904	3.08	0.0575
$\delta^{15}N_h$	Model	13, 53	20.00	1.78	0.0819
	T	1	0.0885	0.10	0.7508
	R	2	14.7324	8.50	0.0008
	C	8	2.6519	0.38	0.9236
	T × R	2	2.5325	1.46	0.2440
$\delta^{15}N_e$	Model	13, 52	14.38	5.55	< 0.0001
	T	1	0.6442	3.23	0.0801
	R	2	8.8026	22.06	< 0.0001
	C	8	4.5851	2.87	0.0130
	T × R	2	0.3991	1.00	0.3769
O. faveolata					
$\delta^{13}C_h$	Model	13, 51	0.0006	2.63	0.0102
	T	1	0.0000	0.05	0.8241
	R	2	0.0000	2.47	0.0979
	C	8	0.0004	3.67	0.0031
	T × R	2	0.0000	0.24	0.7911
$\delta^{13}C_e$	Model	13, 51	0.0006	1.67	0.1080
	T	1	0.0000	0.28	0.5977
	R	2	0.0004	6.86	0.0029
	C	8	0.0002	0.84	0.5742
	T × R	2	0.0000	0.57	0.5711
$\delta^{13}C_h$ - $\delta^{13}C_e$	Model	13, 51	9.4838	2.54	0.0127
	T	1	0.2439	0.85	0.3625
	R	2	3.2388	5.64	0.0072
	C	8	5.8545	2.55	0.0250
	T × R	2	0.0818	0.14	0.8676
$\delta^{15}N_h$	Model	13, 51	10.9561	1.70	0.0999
	T	1	0.0006	0.00	0.9720
	R	2	1.7087	1.73	0.1913
	C	8	8.8208	2.23	0.0465
	T × R	2	0.4728	0.48	0.6236
$\delta^{15}N_e$	Model	13, 51	16.1407	4.68	< 0.0001
	T	1	0.8550	3.23	0.0805
	R	2	5.4807	10.34	0.0003
	C	8	8.8135	4.16	0.0012
	T x R	2	0.8529	1.61	0.2135

The effect of temperature (T) was fixed and fully crossed with two levels (control, treatment). Time (R) was fixed and fully crossed with 3 levels (0, 1.5, and 11 months). Colony (C) was a random effect with 9 levels. Significant p-values ($p \le 0.05$) are highlighted in bold.
df, degrees of freedom; SS, sum of squares of the effect.

energy reserves and rapid recovery of calcification rates (Fig. 2), as high heterotrophic inputs in bleached corals have been shown to be an important factor in bleaching resilience (Anthony et al., 2009; Grottoli et al., 2006; Palardy et al., 2008) and in thermal tolerance under ocean acidification conditions (Schoepf et al., 2013). Pulse-chase isotope labeling of dissolved inorganic nitrogen (DIN) has shown the endosymbiont takes up DIN directly from the seawater (Tanaka et al., 2015). Thus, the increased $\delta^{15}N_e$ values within treatment *P. astreoides* during the first 1.5 months on the reef are suggestive of DIN incorporation by the endosymbiont with the potential translocation to the host. The increase in $\delta^{15}N_e$ in bleached *P. astreoides* and *O. faveolata* suggests an uptake of DIN and a second possible mechanism for cellular repair and growth of the endosymbiont. Thus, heterotrophic plasticity, maintenance of CZAR, and DIN uptake by the *Symbiodinium* cells provides *P. astreoiodes* with the combination of traits that make it very tolerant of bleaching. However, under annual bleaching conditions, *P. astreoides* is not able to increase feeding rates, change *Symbiodinium* populations, nor fully recover after a year on the reef (Schoepf et al., 2015; Grottoli et al., 2014). Therefore, *P. astreoides* is considered a winner under single heat stress events as it is well adapted to tolerate these events when they are more than a year apart, which could account for its current increase in abundance on Caribbean reefs. However, once bleaching events become annual occurrences, it is predicted that *P. astreoides* will decrease in abundance thus making it a loser under future climate scenarios.

4.3. *O. faveolata*

Treatment *O. faveolata* maintained energy reserves throughout the study (Fig. 2L-N) despite initial decreases in endosymbiont concentrations and declines in calcification rates (Fig. 2K, O). A similar pattern was observed in another mounding coral, the bleaching resilient Hawaiian coral *Porites lobata* (Levas et al., 2013). *Porites lobata* bleaching resilience has been attributed to harboring a thermally tolerant species of *Symbiodinium* (C15) combined with large tissue biomass and the ability to utilize large amounts of heterotrophic sources of C to buffer itself against fixed C losses from low photosynthesis during bleaching (Levas et al., 2013). Initially, treatment *O. faveolata* harbored thermally sensitive species of *Symbiodinium*, C7 and B17 (Grottoli et al., 2014). However, after 1.5 and 11 months on the reef 35 and 50%, respectively, of *O. faveolata* treatment fragments were dominated by the thermally tolerant *Symbiodinium* D1a (Grottoli et al., 2014; McGinley, 2012). Cunning et al. (2015) has also shown similar results for *O. faveolata*, where the proportion of clade D1a endosymbiont increases due to thermal stress. Coinciding with the endosymbiont switch and possibly facilitated by a greater proportion of D1a, the $\delta^{15}N_e$ increased after 1.5 months on the reef suggesting endosymbiont facilitated uptake of DIN in *O. faveolata* similar to *P. astreoides* after 0 months on the reef. In

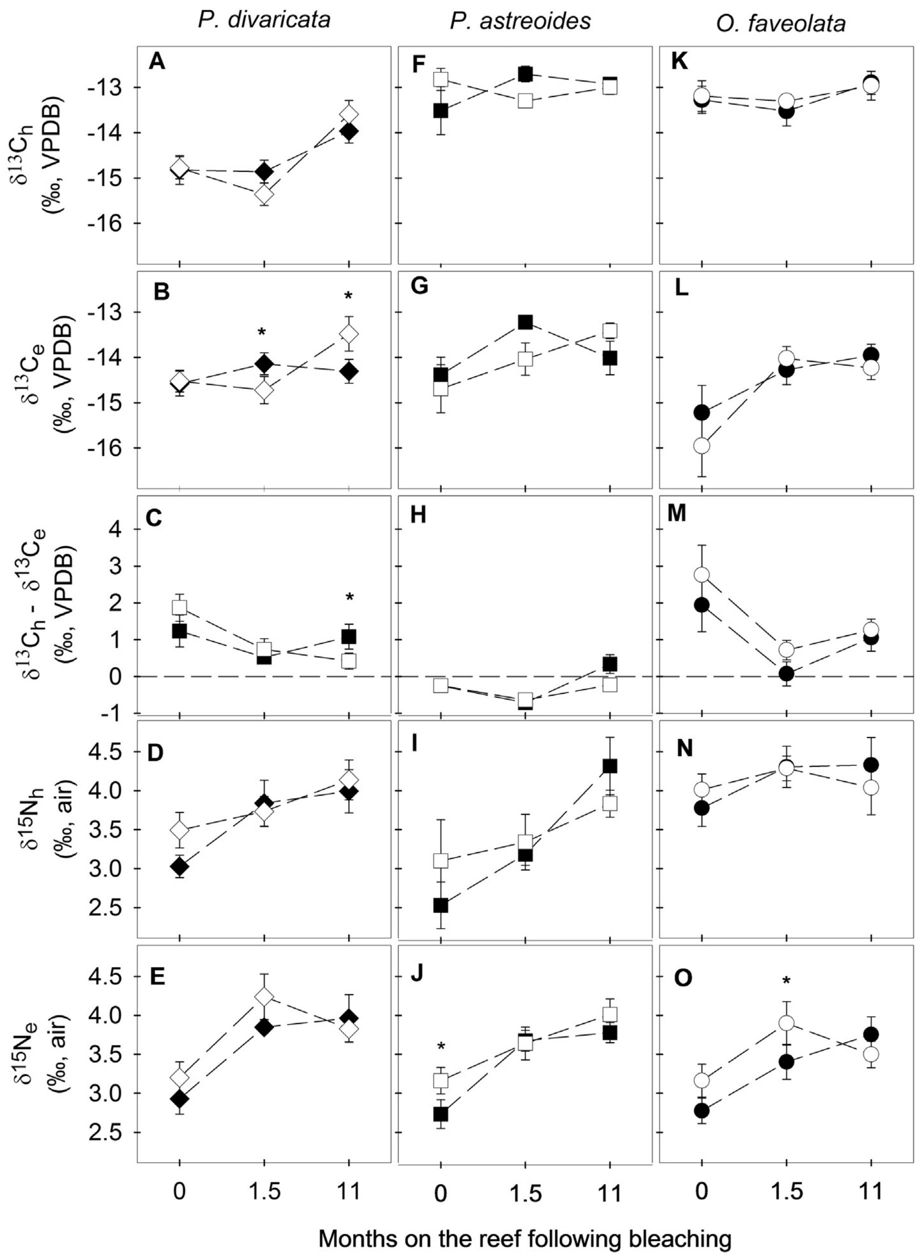

Fig. 3. Stable carbon and nitrogen isotopic values of bleached treatment and control corals. Average (A, F, K) stable carbon isotopic ($\delta^{13}C_h$) values of the animal host, (B, G, L) endosymbiont fractions ($\delta^{13}C_e$), (C, H, M) $\delta^{13}C_{h\text{-}e}$, (D, I, N) stable nitrogen isotopic ($\delta^{15}N_h$) of the animal host, and (E, J, O) endosymbiont fractions ($\delta^{15}N_e$) in *Porites divaricata* (diamond), *Porites astreoides* (square), and *Orbicella faveolata* (circle) corals after 0, 1.5, and 11 months on the reef. For $\delta^{13}C_{h\text{-}e}$, heterotrophic C is preferentially incorporated into tissues when the difference is < 0, whereas photosynthetic C is preferentially incorporated when the difference is greater than or equal to 0. All averages are ± 1SE. Symbols (*) indicate significant differences at $p \leq 0.05$ between control (filled symbols) and treatment (open symbols) averages within a species and time interval by a posteriori least-squares mean slice tests. Sample sizes range between 7 and 9. Accompanying ANOVA results are in Table 4.

addition to endosymbiont swithching, bleached *O. faveolata* are capable of taking up and utilizing DOC as a fixed carbon source (Levas et al., 2015) thereby facilitating the maintenance of energy reserves. Thus, *O. faveolata*'s resilience to bleaching is attributed to its ability to shuffle its *Symbiodinium* type to a thermally tolerant one and to compensate for at least some of the C losses from low photosynthesis by increasing its heterotrophic uptake of DOC. In the case of both the mounding corals *P. lobata* and *O. faveolata,* heterotrophy and thermally tolerant *Symbiodinium* types underlie their bleaching resilience making them the overall winner in response to mild bleaching events. This further corroborates findings by Loya et al. (2001) and van Woesik et al. (2011) who show mounding species tend to survive bleaching events in greater number than branching species of coral.

4.4. Long-term recovery from bleaching

Porites divaricata exhibited negative responses to bleaching initially (i.e., catabolism of lipids, decreases in calcification) and failed to increase feeding to compensate for photosynthesis losses, yet recovered all but one ($\delta^{13}C_h$ - $\delta^{13}C_e$) of the measured variables within 11 months (Figs. 2, 3) (Grottoli et al., 2014; Levas et al., 2015). *Porites astreoides* exhibited two adaptive traits (i.e., increased feeding and increased nitrogen uptake by endosymbionts to facilitate their recovery) in response to bleaching and had fully recovered within 1.5 months (Figs. 2, 3) (Grottoli et al., 2014; Levas et al., 2015). The difference in response strategies to bleaching between these corals may be why the percent cover of *P. astreoides* has increased over the past few decades in the Caribbean (Green et al., 2008). Although previous studies have shown *O. faveolata* to be susceptible to bleaching and tissue biomass decreases (Fitt et al., 2000; Thornhill et al., 2011), the current results indicate that *O. faveolata* fully recovers within a year (Figs. 2, 3) and may be more resilient than previously thought. Through a combination of host characteristics that include the utilization of DOC as a fixed carbon source coupled with increased proportions of thermally tolerant endosymbionts (Grottoli et al., 2014; Levas et al., 2015), *O. faveolata* is able to maintain its energy reserves when bleached and recover calcification rates within a year (Fig. 2). This is consistent with observations of low mortality rates in *O. faveolata* colonies following natural

Table 5

Months after bleaching when response variables no longer significantly differed between treatment (i.e., bleached) and control corals from the Caribbean *Porites divaricata* (*P. d.*), *Porites astreoides* (*P. a.*), and *Orbicella faveolata* (*O. f.*), and Pacific *Montipora capitata* (*M. c.*), *Porites compressa* (*P. c.*), and *Porites lobata* (*P. l.*).

Variable	Ocean Basin					
	Caribbean			*Pacific*		
	P. d.	*P. a.*	*O. f.*	*M. c.*	*P.c.*	*P. l.*
Symbiont density (cells cm^{-2})	1.5[a]	1.5[a]	1.5[a]	-[f]	8[f]	-[b]
Calcification (mg day^{-1} cm^{-2})	1.5[a]	1.5[a]	11[a]	8[c]	> 8[c]	> 1.5[b]
Lipids (J gdw^{-1})	11	–	–	4[f]	4[a]	-[b]
Proteins (J gdw^{-1})	–	–	–	1.5[f]	8[f]	-[b]
Carbohydrates (J gdw^{-1})	–	–	–	1.5[f]	8[f]	-[b]
$\delta^{13}C_{h\text{-}e}$ (‰)	> 11	–	–	4[c]	-[c]	-[b]
$\delta^{15}N_e$ (‰)	–	1.5	11	4	4[c]	1[b]
Symbiont Change	-[d]	-[d]	Yes[d]	Yes[e]	-[e]	-[e]
Full recovery by month	> 11	1.5	11	8	> 8	> 1.5

The symbol '-' denotes no statistically significant difference between treatment and control corals at any time and ' > 11' or ' > 8' indicates that bleached corals had not recovered by 11 months for Caribbean corals or by 8 months for the Pacific corals when those studies ended, respectively. Updated from Schoepf et al. (2015) with new data from this study.

[a] Schoepf et al., 2015.

[b] Levas et al., 2013.

[c] Rodrigues and Grottoli, 2006.

[d] Grottoli et al., 2014.

[e] Stat et al., 2013.

[f] Rodrigues and Grottoli, 2007.

bleaching events (Manzello et al., 2015).

Yet, are the patterns observed in the Caribbean applicable in other ocean basins? The only other directly comparable long-term experimentally controlled bleaching studies to this one were conducted on Hawaiian corals (Grottoli et al., 2006; Levas et al., 2013; Rodrigues and Grottoli, 2006, 2007). A broader comparison of the long-term recovery of six species of coral (*P. divaricata, P. astreoides, O. faveolata, Montipora capitata, Porites compressa* and *Porites lobata*) in two ocean basins (Caribbean and central Pacific) reveals several interesting findings. First, irrespective of species or basin, each coral species suffered significant declines in calcification in response to bleaching, but not all recovered calcification rates within 8 months (Table 5). This corroborates previous research showing the overall negative impact of bleaching on coral calcification (Abramovitch-Gottlib et al., 2002; Goreau and Macfarlane, 1990; Jokiel and Coles, 1977; Leder et al., 1991; Rodrigues and Grottoli, 2006; Suzuki et al., 2003) and makes apparent that long-term recovery is highly variable among species. Furthermore, it is evident that initial declines in CZAR following bleaching (Table 6) are not necessarily a predictor of which species will most likely recover calcification rates.

The initial bleaching response of corals and how they manage their carbon budgets play an integral role in both short- and long-term recovery (Grottoli et al., 2006; Grottoli et al., 2014; Levas et al., 2015; Schoepf et al., 2015). For instance, ***M. capitata*** in the Pacific and ***P. astreoides*** in the Caribbean increase their feeding rates in response to bleaching (Table 6) and subsequently recover faster than non-heterotrophically plastic species (Table 5). However, corals such as *P. divaricata, O. faveolata,* and *P. compressa* that do not increase their feeding rates in response to bleaching, suffer noticeable declines in their overall carbon budgets (i.e., CTAR) (Table 6) and take the longest to recover compared to their heterotrophically plastic counterparts (Table 5). *Porites lobata* is interesting in that despite no increase in feeding rates in response to bleaching, it had the highest baseline feeding irrespective of bleaching status (Palardy et al., 2008). We hypothesize that the high baseline feeding rates provide stability to the *P. lobata* carbon budget and imparts resistance to the short and long-term impacts of bleaching (Table 6). Irrespective of the basin, bleached corals that can either increase feeding rates in response to bleaching or have high baseline high feeding rates are capable of maintaining their carbon budgets (Table 6) and recover more quickly from bleaching events. However, direct comparisons of bleaching response of corals from different basins should be interpreted with caution due to differences in the amount of heat stress placed on the treatment corals from each study. For example, the corals used in the Hawaiian experiment were subjected to a maximum of 20 DHW compared to the 3–4 DHW exposure to the corals studied here.

Overall, this study suggests that all three species of Caribbean corals are resilient to a mild bleaching event, as all three fully recovered within a year. However, this interpretation assumes that the response of these species to single bleaching events is indicative of their responses to repeat bleaching stress – a bleaching frequency that has already been observed and is expected to increase during this century – and does not take into account the possible interactive effects of ocean acidification and temperature on coral resilience. Where bleaching events are not annual, our data show that coral like *P. astreoides* will survive and increase in abundance over the coming decades. Yet, once bleaching events become annual occurrences, it is *P. divaricata* and *O. faveolata*

Table 6

Changes in carbon budget parameters in bleached Caribbean corals Porites divaricata (P. d.), Porites astreoides (P. a.), and Orbicella faveolata (O. f.), and the Pacific corals *Montipora capitata* (M. c.), *Porites compressa* (P. c.), and *Porites lobata* (P. l.) relative to non-bleached controls.

Variable	Basin					
	Caribbean			*Pacific*		
	P. d.	*P. a.*	*O. f.*	*M. c.*	*P. c.*	*P. l.*
Feeding Rate[a,b]	No change	Increase*	No change	Increase	No change	No change
CHAR[b,c,d]	No change	No change	No change	Increase	No change	No change
CZAR[b,c,d]	Decline	No change	Decline	Decline	Decline	No change
CTAR[b,c]	Decline	No change	Decline	Increase	Decline	No change
Overall Carbon Budget Bleaching Response	Decline	Improved*	Decline	Improved	Decline	No change

All changes are statistically significant (except where noted with an *, which indicates a noticeable increase or decline trend that was not statistically significant). The overall carbon budget in bleached corals declined if at least one parameter declined and all others did not change, improved if at least one parameter increased while the others did not change, or if CTAR increased. CZAR = Percent contribution of zooxanthellae derived carbon to animal respiration, CHAR = Percent contribution of heterotrophy to animal respiration, CTAR = Percent contribution of total carbon to animal respiration.

[a] Levas et al., 2015.

[b] Grottoli et al., 2006.

[c] Palardy et al., 2008.

[d] Grottoli et al., 2014.

that are more likely to persist and *P. asteroides* to decrease in abundance (Grottoli et al., 2014; Schoepf et al., 2015).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2018.06.003.

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