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NOTE

Bleached *Porites compressa* and *Montipora capitata* corals catabolize δ^{13}C-enriched lipids

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Abstract Corals rely on stored energy reserves (i.e., lipids, carbohydrates, and protein) to survive bleaching events. To better understand the physiological implications of coral bleaching on lipid catabolism and/or synthesis, we measured the δ^{13}C of coral total lipids ($\delta^{13}C_{TL}$) in experimentally bleached (treatment) and non-bleached (control) *Porites compressa* and *Montipora capitata* corals immediately after bleaching and after 1.5 and 4 months of recovery on the reef. Overall $\delta^{13}C_{TL}$ values in treatment corals were significantly lower than in control corals because of a 1.9 and 3.4‰ decrease in $\delta^{13}C_{TL}$ immediately after bleaching in *P. compressa* and *M. capitata*, respectively. The decrease in $\delta^{13}C_{TL}$ coincided with decreases in total lipid concentration, indicating that corals catabolized δ^{13}C-enriched lipids. Since storage lipids are primarily depleted during bleaching, we hypothesize that they are isotopically enriched relative to other lipid classes. This work further helps clarify our understanding of changes to coral metabolism and biogeochemistry when bleached and helps elucidate how lipid classes may influence recovery from bleaching and ultimately coral survival.

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Introduction

Coral bleaching events are believed to be primarily caused by increased seawater temperatures and/or solar radiation that result in a reduction in endosymbiotic zooxanthellae and/or photosynthetic pigments giving the colony a white or "bleached" appearance (Brown 1997; Hoegh-Guldberg 1999). When the coral colony is healthy, photosynthetically fixed carbon from zooxanthellae can provide the coral host with up to 100% of its daily metabolic energy requirements (i.e., Muscatine et al. 1981; Edmunds and Spencer Davies 1986; Grottoli et al. 2006). Excess fixed carbon is stored in the host tissue as lipids (Muscatine and Cernichiari 1969; Patton et al. 1977; Battey and Patton 1984), representing an important energy reserve (Edmunds and Spencer Davies 1986; Rodrigues and Grottoli 2007). Seasonal variability in total lipid concentration is often related to rates of photosynthesis and light intensity (Stimson 1987). Total lipid concentrations decline in some (Porter et al. 1989; Fitt et al. 1993; Yamashiro et al. 2005; Rodrigues and Grottoli 2007; Anthony et al. 2009), but not all species, when zooxanthellae and/or chlorophyll *a* concentrations are low in bleached corals (Grottoli et al. 2004; Rodrigues and Grottoli 2007; Fitt et al. 2009). Lipid recovery following bleaching can occur in as little as 4 months in Hawaiian corals due to increased photosynthesis and/or increased heterotrophy (Rodrigues and Grottoli 2006, 2007). Here, we examined the total lipid δ^{13}C ($\delta^{13}C_{TL}$) values in Hawaiian *Porites compressa* and *Montipora capitata* corals to gain insight into lipid catabolism during bleaching and lipid acquisition and/or synthesis

during recovery. This is the first study to examine $\delta^{13}C_{TL}$ values in both bleached and non-bleached corals.

Materials and methods

A detailed description of the tank design can be found in Rodrigues and Grottoli (2006). Briefly, in late August 2003, six fragments were collected from each of twelve large, healthy colonies (~2 m diameter) of branching *P. compressa* and branching *M. capitata* (=*Montipora verrucosa*) at 2 m depth from the Point Reef (Coconut Island), Kaneohe Bay, Hawaii (21°26.18′N; 157°47.56′W). The fragments were randomly placed into one of eight flow-through tanks with 50-μm filtered seawater. On September 4, 2003, the seawater temperature in four tanks was raised gradually over ten days and maintained at 30.1°C ± 1.2 (1 SD) for 1 month (treatment) to mimic the timing, temperature, and duration of a natural bleaching event that occurred in the same location (Jokiel and Brown 2004). Seawater temperature was unaltered in the remaining four tanks and averaged 26.8°C ± 0.9 (1 SD) (control) during the same period. Within the treatment and control tanks, one fragment from each colony was randomly assigned to 0, 1.5, or 4 months of recovery. On October 4, 2003, the heaters were turned off and the 0-month recovery fragments were collected and frozen at −80°C. All remaining treatment and control fragments were returned to the reef at 2 m depth to recover in situ. At 1.5 months (16 November 2003) and 4 months (2 February 2004), the respective, pre-assigned coral fragments were recollected, frozen, and stored at −80°C until their analysis.

Total lipids were extracted from ground whole coral samples as reported in Rodrigues and Grottoli (2007), resuspended in 5 ml of 100% chloroform, and stored at −80°C. In preparation for isotopic analysis, each available lipid extract was dried completely at 50°C under ultra-high-purity N_2 gas, resuspended in 300 μl of 100% chloroform, and a few crystals of n-hexane-cleaned sodium sulfate salt were added to remove any water. A 250–600 μg subsample was then transferred directly to pre-weighed tin capsules and dried down at 50°C under ultra-high-purity N_2 gas to a constant weight. Each sample was combusted in a Costech elemental analyzer (EA) and the resulting CO_2 gas was automatically analyzed for $\delta^{13}C$ with a Finnigan Delta IV stable isotope ratio mass spectrometer via a Finnigan ConFlow III open-split interface. $\delta^{13}C_{TL}$ values were reported relative to Vienna Peedee Belemnite Limestone Standard (V-PDB) ($\delta^{13}C$ = per mil deviation of the ratio of stable carbon isotopes ^{13}C:^{12}C relative to V-PDB). Repeated measurements of the USGS24 standard ($n = 23$) had a standard deviation of ±0.05‰.

Most lipid samples used for isotope analysis were extracted between November 2003 and July 2004 and stored at −80°C until analyzed. To test for the possible effects of sample storage on the $\delta^{13}C$ value, new lipid samples were extracted according to the methods described above between October 2008 and December 2009 from 14 of the original −80°C frozen whole coral samples. Paired *t* test comparison showed no significant storage effect on $\delta^{13}C_{TL}$ for either *P. compressa* ($n = 9$, $P > 0.05$) or *M. capitata* ($n = 5$, $P > 0.2$).

All data for each species were tested for normality using the Kolmogorov–Smirnow test and found to be normal. Significant differences in $\delta^{13}C_{TL}$ between treatment and control corals of each species were determined using a three-way ANOVA with temperature (treatment vs. control) and recovery (0, 1.5, or 4 months) being fixed effects and genotype being a random effect. Probabilities less than 0.05 were considered significant. When main terms or interactions were significant, post hoc Tukey tests were conducted. Power was not high enough to include both species in a single ANOVA, necessitating that each species be analyzed separately.

Results and discussion

At 0 months of recovery, the treatment fragments of both species appeared pale or white (i.e., bleached) due to significant decreases in chlorophyll *a* in both species, significant decreases in zooxanthellae concentrations in *P. compressa*, and decreases in the Chl *a* per zooxanthellae cell in *M. capitata* (Table 2) (Rodrigues and Grottoli 2007; Rodrigues et al. 2008a). After 4 months of recovery, *P. compressa* was dark brown and not visually different from controls, while treatment *M. capitata* were still visually paler than the controls (Rodrigues and Grottoli 2007). A complete record of the coral appearance, Chlorophyll *a*, total lipid, protein, carbohydrates, biomass, energy reserves, mortality rates, lipid class composition, calcification rates, carbon and nitrogen isotopic composition of the host, zooxanthellae, and skeleton, algal fluorescence, photosynthesis, and respirations rates at 0, 1.5, and 4 months of recovery for each species in this experiment are presented elsewhere (Rodrigues and Grottoli 2006, 2007; Rodrigues et al. 2008a, b). This paper focuses on the total lipid $\delta^{13}C$ ($\delta^{13}C_{TL}$).

The $\delta^{13}C_{TL}$ values significantly differed among all recovery intervals in *P. compressa* indicating that there is natural seasonal variation in $\delta^{13}C_{TL}$ in this species (Table 1; Fig. 1). Since *P. compressa* is known to be primarily photoautotrophic (Grottoli et al. 2006; Palardy et al. 2008), decreases in light intensity during the winter months of this study may have resulted in observed seasonal variation that was not observed in $\delta^{13}C_{TL}$ of *M. capitata*. Nevertheless, we can evaluate the effect of bleaching

Table 1 Results of three-way ANOVAs for coral lipid $\delta^{13}C_{TL}$

Species	Effect	df	SS	F	P
Porites compressa					
	T	1	5.546	9.98	**0.004**
	R	2	19.029	17.12	**<0.001**
	T × R	2	8.338	7.50	**0.003**
	G	9	16.227	3.24	**0.010**
Montipora capitata					
	T	1	13.356	6.03	**0.024**
	R	2	2.210	0.50	0.615
	T × R	2	4.744	1.07	0.363
	G	11	30.990	1.27	0.311

The overall model was significant for *Porites compressa* ($F = 6.89$, $P < 0.0001$) and *Montipora capitata* (model $F = 2.09$, $P = 0.0629$)

Significant effects are in bold

T temperature, *R* recovery interval, *G* genotype, *df* degrees of freedom, *SS* sum of squares of the effect

independent of seasonal effects by comparing treatment to control $\delta^{13}C_{TL}$ at each recovery interval (see Rodrigues and Grottoli 2006, 2007 for details). While one genotype of *P. compressa* was significantly different from all of the others and was the source of the significant genotype effect for this species (Table 1), it does not interfere with the overall interpretation of the data.

Overall, the $\delta^{13}C_{TL}$ values were significantly lower in treatment corals than in control corals by 0.52‰ in *P. compressa* and 1.70‰ in *M. capitata* (Table 1; Fig. 1). This decrease was driven by dramatic decreases in $\delta^{13}C_{TL}$ of 1.9 and 3.4‰ in bleached *P. compressa* and *M. capitata* corals, respectively, after 0 months of recovery (Fig. 1) that coincided with a 33 and 39% decreases in total lipid concentration, respectively (Table 2) (Rodrigues and Grottoli 2007), and dramatic decreases of 56% and 82% in the storage lipid triacylglycerol, respectively (Table 2), and moderate decreases of 36 and 35% in phospholipids, respectively (Table 2) (i.e., a structural lipid) (Rodrigues et al. 2008b). These results indicate that corals catabolize $\delta^{13}C$-enriched lipids when bleached and suggest that storage lipids are isotopically enriched relative to other lipid classes. The only other study to report $\delta^{13}C_{TL}$ values in scleractinian corals showed that $\delta^{13}C_{TL}$ in *Stylophora pistillata* and *Favia favus* corals decreased by 6–10‰ along a 60 m depth gradient in the Red Sea and that animal host lipid $\delta^{13}C$ values were consistently 0.5–2.5‰ lighter than zooxanthellae lipid $\delta^{13}C$ values throughout the depth gradient (Alamaru et al. 2009). Thus, there are three possible factors contributing to the decrease in $\delta^{13}C_{TL}$ in bleached *P. compressa* and *M. capitata*.

First, lipid loses due to algal endosymbiont expulsion could account for some or all of the initial 1.9‰ decrease in *P. compressa* $\delta^{13}C_{TL}$ where zooxanthellae concentrations decreased by a factor of 7 at 0 months of recovery (Table 2) (Rodrigues and Grottoli 2007). However, $\delta^{13}C_{TL}$ no longer differed between treatment and control corals at 1.5 and 4 months in *P. compressa*, even though endosymbiont concentrations remained low at those times (Table 2) (Rodrigues and Grottoli 2007). Furthermore, *M. capitata* experienced no endosymbiont loses during bleaching (Table 2) (Rodrigues and Grottoli 2007) and still experienced dramatic decreases in $\delta^{13}C_{TL}$. Therefore, lipid loses due to algal endosymbiont expulsion have minimal to no effect on $\delta^{13}C_{TL}$ throughout recovery.

Second, rates of coral photosynthesis rates may be altering the $\delta^{13}C_{TL}$ values. If photosynthetically fixed carbon is the primary source of carbon for lipids in corals

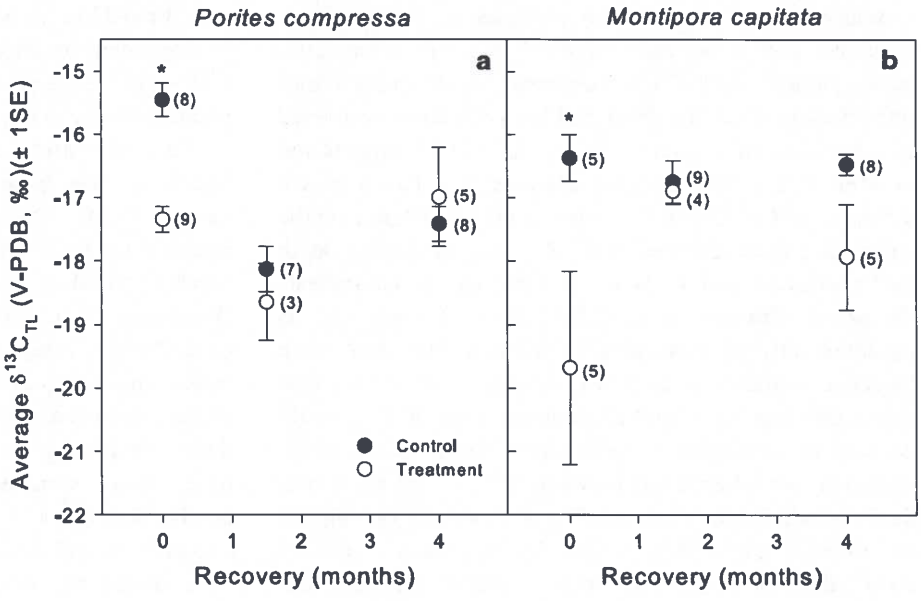

Fig. 1 Average $\delta^{13}C$ of coral total lipids ($\delta^{13}C_{TL}$) (±1 SE) for treatment (i.e., bleached) and control (i.e., non-bleached) Hawaiian **a** *Porites compressa* and **b** *Montipora capitata* corals after 0, 1.5, and 4 months of recovery. Sample size of each average indicated in *brackets*. Significant differences between means at a given recovery interval indicated with an *asterisk*

Table 2 Previously published data of total lipids, triacylglycerol, phospholipids, zooxanthellae, rates of photosynthesis, and host tissue and zooxanthellae $\delta^{13}C$ at 0, 1.5, and 4 months after bleaching for control and treatment corals of *Porites compressa* and *Montipora capitata*

Recovery (months)		*Porites compressa*			*Montipora capitata*		
		0	1.5	4	0	1.5	4
Total lipids[a] (g/gdw)	Control	0.31 ± 0.02*	0.25 ± 0.03*	0.20 ± 0.02	0.40 ± 0.06*	0.40 ± 0.07*	0.36 ± 0.11*
	Treatment	0.21 ± 0.02	0.16 ± 0.03	0.17 ± 0.03	0.25 ± 0.03	0.26 ± 0.12	0.26 ± 0.12
Triacylglycerol[b] (mg/gdw)	Control	35.04 ± 7.86*	29.73 ± 4.67*	7.39 ± 1.45	17.66 ± 7.98*	6.91 ± 3.53	1.73 ± 1.73
	Treatment	15.35 ± 7.95	3.48 ± 1.78	10.07 ± 7.28	3.26 ± 0.64	1.06 ± 1.06	6.06 ± 3.44
Phospholipids[b] (mg/gdw)	Control	24.03 ± 4.68	45.74 ± 5.37*	23.75 ± 3.20	40.81 ± 2.63*	47.65 ± 7.53*	31.63 ± 0.32*
	Treatment	15.36 ± 3.55	18.86 ± 5.42	19.92 ± 4.58	26.52 ± 13.80	28.98 ± 6.78	68.66 ± 13.44
Chlorophyll *a*[a] (µg/gdw)	Control	1303.7 ± 122.5*	1505.7 ± 166.7*	199.1 ± 122.5	1457.6 ± 122.5*	1815.5 ± 226.9*	2158.5 ± 122.5*
	Treatment	431.0 ± 122.5	841.2 ± 166.7	1953.6 ± 166.3	329.9 ± 122.5	115.3 ± 226.9	801.9 ± 201.5
Zooxanthellae[a] ($\times 10^6$/gdw)	Control	3.40 ± 0.64*	1.40 ± 0.58*	2.01 ± 0.58*	2.95 ± 0.54	1.56 ± 0.42	4.07 ± 0.39
	Treatment	0.49 ± 0.64	0.15 ± 0.58	0.13 ± 0.58	2.99 ± 0.55	1.02 ± 0.45	3.61 ± 0.42
Chl *a*/zoox[c] (ng/cell)	Control	0.75 ± 0.28	1.29 ± 0.32*	1.21 ± 0.30*	0.52 ± 0.18	0.78 ± 0.11	0.46 ± 0.14
	Treatment	0.97 ± 0.17	12.79 ± 5.04	10.34 ± 0.76	0.14 ± 0.08	0.06 ± 0.08	0.41 ± 0.19
Gross P[a] (µmol/min/gdw)	Control	1.20 ± 0.19*	0.80 ± 0.14	1.11 ± 0.35	0.85 ± 0.36	2.12 ± 0.77*	1.11 ± 0.13
	Treatment	0.40 ± 0.09	0.95 ± 0.34	1.08 ± 0.35	0.36 ± 0.08	0.21 ± 0.06	1.04 ± 0.33
Host tissue[d] $\delta^{13}C$ (‰)	Control	−15.88 ± 0.42	−16.29 ± 0.54	−16.36 ± 0.39	−15.02 ± 0.42	−15.77 ± 0.53*	−15.87 ± 0.47
	Treatment	−16.44 ± 0.47	−16.70 ± 0.42	−16.47 ± 0.42	−15.12 ± 0.47	−17.53 ± 0.47	−15.72 ± 0.47
Zooxanthellae[d] $\delta^{13}C$ (‰)	Control	−15.78 ± 0.47	−16.64 ± 0.47	−16.13 ± 0.47	−15.14 ± 0.47*	−16.20 ± 0.47	−16.20 ± 0.47
	Treatment	−16.70 ± 0.39	−16.52 ± 0.42	−15.94 ± 0.42	−16.56 ± 0.42	−16.95 ± 0.42	−16.13 ± 0.41

All data are means ± 1 standard error. * indicates significant differences at $P \leq 0.05$ between control and treatment samples for each analysis within a species and recovery month. *Zoox* zooxanthellae, *P* photosynthesis

[a] Originally published in Rodrigues and Grottoli (2007)

[b] Originally published in Rodrigues et al. (2008b)

[c] Originally published in Rodrigues et al. (2008a)

[d] Originally published in Rodrigues and Grottoli (2006)

(and assuming that lipids are being catabolized at a slower rate than they are being synthesized), decreases in photosynthesis would result in an increase in isotopic fractionation and a decrease in $\delta^{13}C_{TL}$. In *P. compressa*, photosynthesis and $\delta^{13}C_{TL}$ decreased in treatment corals immediately after bleaching and both variables recovered at 1.5 months of recovery (Fig. 1; Table 2) (Rodrigues and Grottoli 2007). This positive relationship between photosynthesis and $\delta^{13}C_{TL}$ in *P. compressa* is consistent with the steady decrease observed in $\delta^{13}C_{TL}$ with increasing depth in *S. pistillata* and *F. favus* as light and photosynthesis decreased (Alamaru et al. 2009). Since *P. compressa* is predominantly photoautotrophic when healthy and when bleached (Grottoli et al. 2006; Palardy et al. 2008), it is reasonable that total lipid concentration and $\delta^{13}C_{TL}$ could be largely controlled by photosynthesis in this species. However, no relationship between $\delta^{13}C_{TL}$ and photosynthesis exists for *M. capitata* (Fig. 1; Table 2) (Rodrigues and Grottoli 2007). Recent work by Hughes et al. (2010) shows that for both *P. compressa* and *M. capitata*, the carbon used for tissue building is heterotrophically, not photoautotrophically, derived. Any new lipid synthesis would most likely come from heterotrophic carbon and not be dependent on photosynthesis rates. Therefore, depleted $\delta^{13}C_{TL}$ in treatment corals are not likely due to reduced photosynthesis in either species.

Third, the decrease in $\delta^{13}C_{TL}$ immediately following bleaching may have been driven by the catabolism of storage lipids. Decreases in storage lipids have been reported for eight species of naturally bleached Japanese corals (Yamashiro et al. 2005) and for both experimentally (Rodrigues et al. 2008b) and naturally bleached (Grottoli et al. 2004) *P. compressa* and *M. capitata* corals. If storage lipids are isotopically more enriched than other lipid classes, then the catabolism of storage lipids would produce isotopically depleted $\delta^{13}C_{TL}$ values. Since not all lipid classes were equally catabolized in our bleached corals (Rodrigues et al. 2008b), differences in the $\delta^{13}C$ composition and catabolism rate of each lipid class could have driven the overall decrease in the $\delta^{13}C_{TL}$ value.

Furthermore, after 4 months of recovery, $\delta^{13}C_{TL}$ values no longer differed between treatment and control *P. compressa* corals (Fig. 1a), which coincided with the recovery of total lipid concentrations and lipid classes in this species (Rodrigues and Grottoli 2007; Rodrigues et al. 2008b). While total lipids concentrations had also fully recovered after 4 months of recovery in *M. capitata* (Rodrigues and Grottoli 2007), the non-significant but quite noticeable decrease in $\delta^{13}C_{TL}$ values in treatment corals compared with the controls (Fig. 1b) was coupled with significant increases in structural lipids (i.e., phospholipids and sterols) and free fatty acids (Rodrigues et al. 2008b). Dramatic increases in heterotrophically derived carbon in the diet of bleached *M. capitata* (Grottoli et al. 2006; Palardy et al. 2008) are the logical sources for the sterols (Rodrigues et al. 2008b). Such a hypothesis is consistent with recent findings showing that heterotrophic carbon is used for tissue building during recovery (Hughes et al. 2010) and with the general knowledge that phospholipids and sterols are critical to cell wall architecture and function.

Unfortunately, there are no published $\delta^{13}C$ values for lipid classes in corals, or any other anthozoans for that matter, and the existing literature on the free fatty acid $\delta^{13}C$ values of corals and other marine organisms (i.e., Duan et al. 2004; Bachok et al. 2006; Treignier et al. 2009) does not shed light on lipid class $\delta^{13}C$. In addition, the relationship between total lipid concentration (Rodrigues and Grottoli 2007) and $\delta^{13}C_{TL}$ (this study) is not linear because the $\delta^{13}C_{TL}$ value integrates the weighted isotopic composition of all lipid classes together independent of total lipid concentration. Therefore, the $\delta^{13}C$ analysis of coral lipid classes is needed to confirm our hypothesis that storage lipids are isotopically enriched relative to other lipid classes and drive the overall decrease in total lipid $\delta^{13}C$ values in bleached corals. This would help clarify our understanding of changes to coral metabolism and biogeochemistry when bleached and help elucidate how lipid classes may influence recovery from bleaching and ultimately coral survival.

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