

Lipids and chlorophyll in bleached and recovering *Montipora capitata* from Hawaii: An experimental approach

Lisa J. RODRIGUES* and Andréa G. GROTTOLO

Department of Earth & Environmental Science, University of Pennsylvania, 240 South 33rd Street, Philadelphia, PA 19104-6316

*Corresponding author: L.J. Rodrigues

FAX: 215-898-0964, e-mail: rodrigul@sas.upenn.edu

Abstract During bleaching, zooxanthellae and/or chlorophyll concentrations decline resulting in a decrease in photosynthesis and consequently, the amount of photosynthetically fixed carbon translocated to the coral host. Corals may have to rely on stored energy reserves, including lipids for their source of fixed carbon to survive and ultimately recover from bleaching events. Bleached corals are expected to have depleted lipid levels following a bleaching event, however, *Montipora capitata* experienced no change in total lipids three months after a natural bleaching in 1998 (Grottoli et al. 2004). In September 2003, to further understand lipid dynamics during bleaching and recovery, fragments of *M. capitata* were experimentally bleached in outdoor flow-through tanks by raising the seawater temperature 3°C above ambient to 30°C. Additional fragments from the same parent colonies were maintained at ambient seawater temperatures (27°C) in separate tanks as controls. After one month in the tanks, a subset was frozen and the remaining fragments were placed back on the reef for *in situ* recovery. Both control and experimental fragments were analyzed for chlorophyll *a* and lipid concentrations immediately after, 1.5 months and 4 months after bleaching. Immediately after bleaching *M. capitata* fragments were visibly bleached with significantly lower chlorophyll *a* and lipid concentrations relative to controls. By 1.5 months, lipid concentrations had increased to 71% of control values, despite chlorophyll *a* decreasing to less than 4% of control values during the same time period. Our experimental study shows that *M. capitata* is able to recover lipid reserves prior to recovering chlorophyll concentrations, a result that is directly opposite to past observations. Our study provides further evidence that to survive bleaching events *M. capitata* may rely on sources other than photosynthesis for fixed carbon.

Key Words bleaching, energy reserves, recovery, lipids, chlorophyll, photosynthetically-fixed carbon

Introduction

In healthy corals, photosynthetically-fixed carbon is translocated from the endosymbiotic zooxanthellae to the coral host, providing up to 100% of its daily metabolic

energy requirements (eg. Muscatine and Cernichiaro 1969; Patton and Burris 1983; Muscatine et al. 1984). Any excess is stored in the host tissue as lipids (Muscatine and Cernichiaro 1969; Patton et al. 1977; Battey and Patton 1984) and represents a significant energy reserve in corals (Edmunds and Spencer Davies 1986; Harland et al. 1993). Under physiologically stressful conditions, corals lose their endosymbiotic zooxanthellae and/or their photosynthetic pigments causing the colony to appear pale or white. This is referred to as bleaching, which under natural conditions is primarily caused by elevated seawater temperatures (Gleason and Wellington 1993; Glynn 1996; Brown 1997; Wilkinson 2000) and/or increased ultraviolet radiation (Gleason and Wellington 1993; Glynn 1996; Brown 1997; Wilkinson 2000).

The physiological mechanisms underlying bleaching, and in particular, variability in bleaching (Fisk and Done 1985; Oliver 1985; Ghiold and Smith 1990; Edmunds 1994; Grottoli-Everett and Kuffner 1995; Marshall and Baird 2000) are poorly understood. To date, much of the research has focused on genetic variation among the *Symbiodinium* zooxanthellae type to account for this variation in bleaching susceptibility (eg. Rowan et al. 1997; LaJeunesse 2001; Toller et al. 2001). Fewer studies have examined the effect of bleaching on the host. In bleached corals, decreases in zooxanthellae densities and/or chlorophyll *a* levels result in a net decrease in photosynthesis (Porter et al. 1989; Lesser 1997). Thus the amount of photosynthetically-fixed carbon energy translocated to the coral host is expected to also decrease and bleached corals may have to rely on stored energy reserves. A decrease in lipids over time has been shown in artificially shaded *Porites compressa* (Stimson 1987) and in naturally bleached Caribbean *Montastrea annularis* and *Agaricia lamarcki*, where total tissue biomass decreased (Porter et al. 1989; Fitt et al. 1993; Fitt et al. 2000). However, Grottoli et al. (2004) observed that three months after a natural bleaching event, *P. compressa* corals depleted their total lipid stores while *Montipora capitata* corals maintained them. These results suggest that bleached *M. capitata* may be reducing their metabolic rate and demand for stored energy, increasing heterotrophy, or some combination of both. Does *M. capitata* consume lipids during a

bleaching event? If so, at what time during recovery do lipid concentrations return to normal, pre-bleaching levels? To address these questions, we simulated a temperature-induced bleaching event in outdoor flow-through tanks and compared chlorophyll *a* and total lipids in temperature treated *M. capitata* fragments to untreated control fragments at three time intervals: at 0, 1.5, and 4 months of recovery from a month-long bleaching event.

Materials and Methods

Study Site

Kaneohe Bay is on the windward side of Oahu, Hawaii and is 12.7 km long x 4.3 km wide (Bathen 1968). Mean summer/fall temperatures (June to October) average $27 \pm 1^\circ\text{C}$ and winter/spring temperatures (November to May) average $24.5 \pm 1.5^\circ\text{C}$ (data from Hawaii Institute of Marine Biology weather station). Corals from this study were collected from the Point Reef (Coconut Island), Kaneohe Bay, Hawaii ($21^\circ26.18'\text{N}$; $157^\circ47.56'\text{W}$) (Fig. 1).

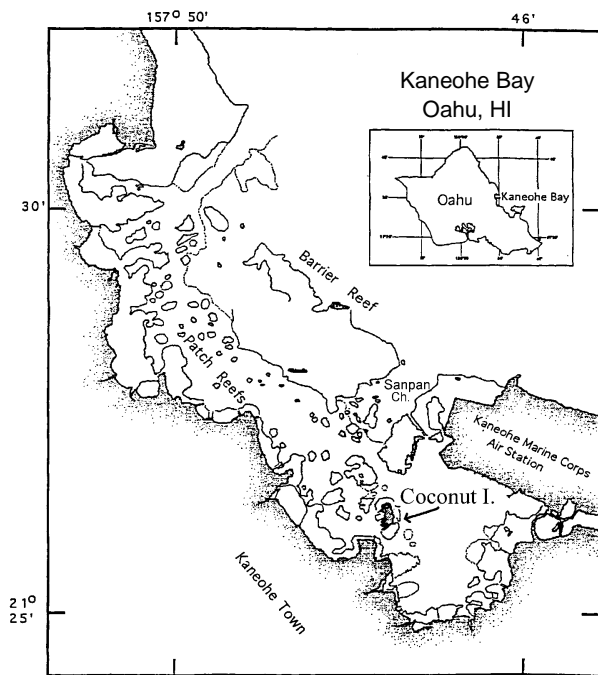


Fig. 1. Map of Kaneohe Bay, Oahu, HI. Arrow is indicating Coconut Island, the location of the Hawaii Institute of Marine Biology and the field site for this study.

Coral cover on the reef slope approaches 100%, extending from the surface to 8.5 m depth, consisting mainly of *Montipora capitata* Dana 1864 and *Porites compressa*. In addition, there are some colonies of *Pocillopora damicornis* and the solitary coral, *Fungia scutaria*, both found at shallower depths. *M. capitata* is a dark to medium brown coral, often observed to have beige to white tips. Its form ranges from plating (typically found at deeper depths) to branching (typically found at shallower depths) with both forms sometimes expressed in a single colony. All fragments of *M.*

capitata collected for this study were of the branching form.

Experimental Design

In late August 2003, twelve large, healthy colonies of *Montipora capitata* were identified at 2 m depth and seven fragments were collected from each colony for a total of 84 fragments. One fragment from each colony was immediately analyzed to determine initial chlorophyll *a* and total lipid concentrations (see below). The remaining six fragments were randomly assigned to both a temperature (ambient control or 30°C) and recovery treatment (0, 1.5, or 4 months after bleaching). On 4 September 2003, the 30°C treatment fragments were randomly placed in one of four 30°C treatment tanks, and the control fragments were randomly placed in one of four ambient control tanks for a one-month period. The 30°C tanks were each fitted with three Aquarium Pharmaceuticals Rena Cal 200 wt heaters. An Onset Corporation temperature logger monitored the seawater temperature of each tank every hour throughout the month-long period. The mean hourly temperature of the four ambient tanks for the one-month period was 26.8°C , while the mean hourly temperature of the four treatment tanks during the same time period was 29.9°C (Fig. 2). All tanks were covered with neutral density mesh to mimic PAR light levels at 2 m depth. The inflow pipe of each tank was fitted with a $50 \mu\text{m}$ -filter. To minimize tank effects, coral fragments were rotated between tanks within each treatment every week, so that by the end of the month-long period, each coral had been in each of their respective treatment tanks once. To minimize positional effects, corals were rotated within each tank daily.

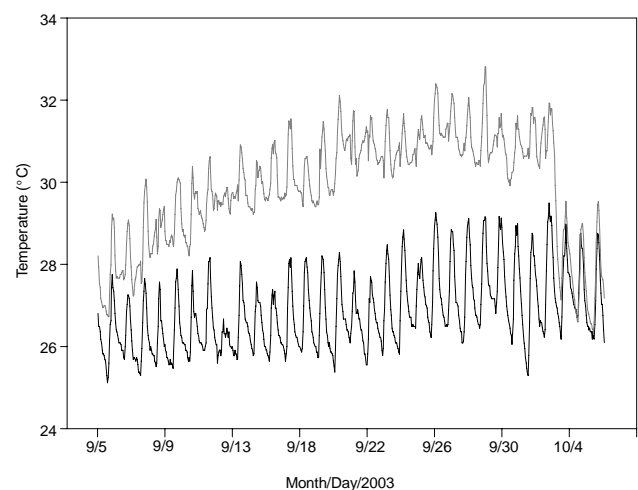


Fig. 2. Mean hourly temperature of four ambient tanks (black line) and four increased temperature tanks (gray line) from 4 September 2003 to 7 October 2003 obtained from Onset Corporation temperature loggers placed in each tank. Aquarium heaters in the increased temperature tanks were gradually turned off on 4 October 2003.

On 4 October 2003, those fragments assigned to the 0 month recovery group were immediately frozen. All remaining fragments were placed on the reef at 2 m depth for *in situ* recovery. At 1.5 months (16 November 2003) and 4 months (2 February 2004) of recovery, the respective coral fragments were collected and immediately frozen at -80°C. All frozen fragments were transported to the Department of Earth and Environmental Science, University of Pennsylvania, Philadelphia, PA for laboratory analyses.

Laboratory Analyses

All physiological variables were measured on ground whole coral samples and standardized to ash-free dry tissue weight according to methods described in Grottoli et al. (2004). Normalization to tissue biomass is more robust than normalization to coral surface area because the penetration thickness of the coral tissue into the skeleton can vary among different colonies (Edmunds and Gates 2002). In addition, the surface of *M. capitata* is highly irregular, making any measurement of surface area inaccurate.

Chlorophyll *a* and total lipid concentrations were measured on two separate branch tips from each coral fragment. Chlorophyll *a* was extracted from ground whole coral samples (tissue plus skeleton) in 100% acetone according to Jeffrey and Humphrey (1975). The chlorophyll *a* concentration was used as a quantitative measure of bleaching, irrespective of numbers of zooxanthellae. Total lipids were extracted from ground whole coral samples in a 2:1 chloroform:methanol solution, washed in 0.88% KCl, and the extract was then dried under grade 5.0 N₂ gas.

Statistical Analyses

A two-way ANOVA was used to test for significant treatment and recovery interval effects in chlorophyll *a* and total lipid concentrations. *A posteriori* Tukey tests were used to determine which means significantly differed from each other. The use of replicate genotypes across temperature treatments and recovery times reduced the overall variation between treatments. For both chlorophyll *a* and lipid concentrations, data were normally distributed. JMP 5.1 Statistical Software was used for all statistical analyses. A $p < 0.05$ was considered significant.

Results

At the start of this study, all fragments of *Montipora capitata* were dark brown in color. Immediately following temperature-induced bleaching, stressed fragments were white in color, at 1.5 months of recovery, they were pale to light brown in color, and by 4 months of recovery, they were light brown to brown in color. At all times during the experiment, the control fragments were dark brown in color.

Forty-nine samples were analyzed for chlorophyll *a* concentrations. The plot of the residual versus the predicted chlorophyll values indicated that the data were normally distributed and a two-way ANOVA was used to

test for differences between mean values. Chlorophyll *a* concentrations were significantly lower in the 30°C corals (bleached) than in the ambient temperature control (non-bleached) corals at all times during recovery in *M. capitata* (Table 1; Fig. 3a,c). Tukey tests revealed that immediately after bleaching, chlorophyll *a* levels had decreased significantly to 22% of control levels. After 1.5 months of recovery, chlorophyll levels had dropped further to less than 4% of control values, before showing signs of recovery at 4 months of recovery (increased to 48% of control values). Chlorophyll *a* levels in bleached fragments after 4 months of recovery were still significantly lower than the control fragments at the same time, indicating that *M. capitata* had not fully recovered their levels of chlorophyll by that time.

Table 1. Results of a two-way ANOVA comparing control and bleached fragments of *Montipora capitata* mean chlorophyll *a* and total lipid concentrations at 0, 1.5, and 4 months of recovery. F=F-statistic, *df*=degrees of freedom, P=probability.

| | F | <i>df</i> | P |
|----------------------|--------|-----------|---------|
| Chlorophyll <i>a</i> | 35.654 | 48 | <0.0001 |
| Total Lipids | 5.9601 | 57 | 0.0002 |

Fifty-eight samples were analyzed for total lipid concentrations. The plot of the residual versus the predicted lipid values indicated that the data were normally distributed. A two-way ANOVA was used to test for differences between mean values. Total lipid concentrations were significantly lower in bleached than non-bleached corals immediately after bleaching but were not significantly different from the controls after 1.5 and 4 months of recovery (Table 1, Fig. 3b, d). Tukey tests revealed that immediately following bleaching, total lipid concentrations had decreased significantly to 60% of control levels. By 1.5 months of recovery, lipids had begun to increase in bleached fragments, representing 71.5% of control concentrations. By 4 months of recovery, lipid concentrations of temperature treated fragments were not statistically distinguishable from control fragments.

Discussion

Previous studies have shown that *Montipora capitata* does not experience a change in lipid concentrations when experimentally bleached with light and ultraviolet radiation for two weeks (Grottoli-Everett 1995) or three months after a natural temperature-induced bleaching event (Grottoli et al. 2004). These results are contrary to the hypothesis that stored lipid reserves should decrease during bleaching as photosynthetically-fixed carbon decreases. To further investigate if and when lipids are consumed by *M. capitata* during bleaching and recovery, we measured the chlorophyll *a* concentration and total lipid concentration of experimentally bleached control fragments before, immediately after, 1.5, and 4 months after bleaching.

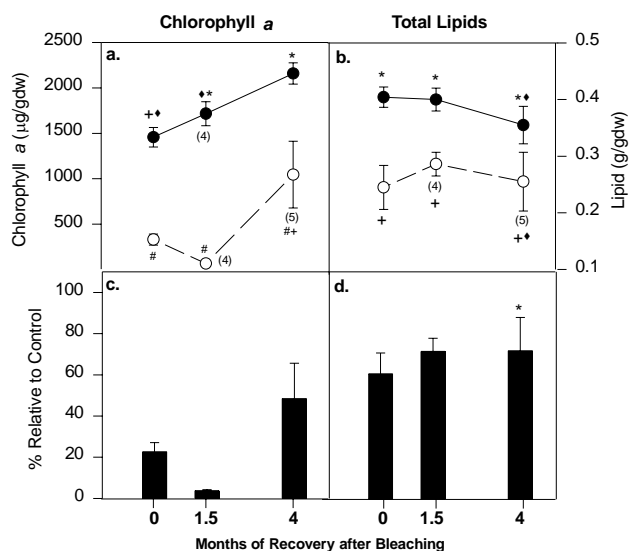


Fig 3. a-d. Mean (a) chlorophyll *a* and (b) total lipid concentrations of *Montipora capitata* control fragments (filled circles) and bleached fragments (open circles) at 0, 1.5, and 4 months of recovery. The percentage of mean (c) chlorophyll *a* and (d) total lipids in bleached fragments relative to control fragments at each time interval after bleaching. In panels (a) and (b) symbols (*, +, #, ♦) indicate significant differences between means by *a posteriori* Tukey tests. In panels (c) and (d) symbols (*) indicate where recovery has occurred and bleached fragments are not significantly different from control fragments. Sample size for each mean is 12 unless provided in parentheses. All means are shown \pm 1 SE. gdw=grams dry weight of whole coral tissue (host tissue + algal symbionts + lipid). Statistical analyses in Table 1.

Here, chlorophyll *a* concentrations decreased in *M. capitata* experimentally exposed to elevated seawater temperatures for one month relative to control fragments immediately after bleaching. This result is consistent with other studies that followed natural bleaching events (Porter et al. 1989; Fitt et al. 1993; Warner et al. 1996; Ambarasari et al. 1997; Fitt et al. 2000; D'Croz and Maté 2001; Hueerkamp et al. 2001; Grottoli et al. 2004). *M. capitata* continued to lose chlorophyll during the first 1.5 months of recovery, despite being exposed to ambient seawater temperatures. By 4 months of recovery, bleached fragments had slightly increased concentrations of chlorophyll, but complete recovery of chlorophyll had not yet been attained. Our results for chlorophyll *a* during the recovery periods are consistent with observations of *Montastraea annularis* from the Caribbean, which experienced no real increase in chlorophyll concentrations after 5 and 10 months of recovery following a natural bleaching event (Fitt et al. 1993).

Bleached *M. capitata* fragments had significantly lower lipid concentrations than non-bleached fragments after one month of exposure to elevated seawater temperatures. A decrease in lipid biomass of *M. capitata* immediately following the bleaching event is consistent

with findings for Caribbean corals showing that tissue biomass, total carbon, total lipid, and total nitrogen all decreased in bleached *M. annularis* (Porter et al. 1989; Szman and Gassman 1990; Fitt et al. 1993). However, our study is the first to experimentally pinpoint that lipid concentrations had completely recovered by 4 months after a bleaching event, without a similar recovery in chlorophyll *a* concentrations (Fig. 3). Although *M. capitata* initially consumed a fraction of its lipid reserves immediately following bleaching, it recovered its entire lipid reserves before recovering its level of chlorophyll *a*. Our results following an experimental bleaching event are consistent with and confirm the findings of Grottoli et al. (2004) who observed no significant difference in the lipids of completely bleached, partially bleached, or non-bleached *M. capitata* at 3 months after a natural bleaching event. Grottoli-Everett (1995) also did not measure a difference in the total lipids of *M. capitata* after 2 weeks of exposure to increased solar radiation, despite measuring a decrease in chlorophyll *a* levels.

Four possible mechanisms as proposed by Grottoli et al. (2004) may be responsible for the observed lack of lipid consumption by *M. capitata*, despite being visibly bleached. First, *M. capitata* has been reported to have a proportionately low respiration rate (Coles and Jokiel 1977), allowing bleached colonies to better conserve energy reserves, including lipids, compared to other species. Maintaining a higher photosynthesis to respiration ratio during elevated seawater temperatures has been shown to contribute to bleaching resistance in some species (Coles and Jokiel 1977) and may make those species more likely to survive the bleaching event.

Second, *M. capitata* may be able to utilize other stored energy reserves (eg. protein and carbohydrates) preferentially to lipid reserves. Specific energy reserves have only been assessed in bleached and non-bleached *M. annularis*, *Agaricia lamarcki* (Porter et al. 1989) and *Montastraea franksi* (Fitt et al. 1993). In *M. annularis* and *A. lamarcki*, total lipids, protein and carbohydrates were depleted by 39-73% after 5 months of recovery, indicating that all three reserves may be utilized while bleaching. In *M. franksi*, glycerol, free fatty acids, and protein were not depleted after 3 weeks of recovery from bleaching.

Third, *M. capitata* may be increasing its rate of heterotrophy during bleaching. Scleractinian corals are believed to be primarily autotrophic, with more than 97% of photosynthetically-fixed carbon translocated from the zooxanthellae to the coral host, providing the animal with up to 100% of its daily metabolic energy requirements (eg.: Muscatine et al. 1981; Falkowski et al. 1984; Muscatine et al. 1984; Spencer Davies 1984; Harland et al. 1991; Falkowski et al. 1993). However, corals have been shown to feed on a range of plankton types (Porter 1978; Sebens et al. 1996; Palardy et al. in press) and heterotrophy has been shown to increase and compensate for reduced photosynthesis in highly turbid environments (Anthony and Fabricius 2000) and in deep compared to shallow environments (Palardy et al. in review-a). Furthermore, in *Stylophora pistillata*, corals

experimentally grown in a dark environment ingested twice as much carbon as those grown in a light environment (Ferrier-Pages et al. 1998). During bleaching, the reduction in photosynthesis (Porter et al. 1989; Lesser 1997) may result in increased heterotrophy in some corals, including *M. capitata*, and may contribute to the faster recovery of lipid than chlorophyll *a* concentrations that we observed in our present study.

Finally, *M. capitata* may have begun to recover and rebuild lipid reserves by the time the Grottoli et al. (2004) samples were collected. The results of our present study provide experimental evidence that this is likely to be true. *M. capitata* does consume lipid reserves immediately after bleaching, but is able to recover them by 4 months after the event (this study), and as early as 3 months after bleaching (Grottoli et al. 2004), despite having low levels of chlorophyll *a*. Previous studies suggest that chlorophyll *a* levels and algal symbiont concentrations recover within a couple months to a year after bleaching (Jokiel and Coles 1990; Fitt et al. 1993, 2000) and that tissue biomass and energy reserves take longer, more than a year, to return to pre-bleaching levels even if chlorophyll *a* and algal symbiont levels are normal (Fitt et al. 1993, 2000). Our experimental study shows the direct opposite of these past observations, that *M. capitata* is able to recover lipid reserves prior to recovering chlorophyll concentrations.

Overall, the present study provides experimental evidence that *M. capitata* consumes lipid reserves immediately after bleaching events, but is able to recover them despite a reduction in nutritional input from their symbiotic zooxanthellae. Several mechanisms requiring further study may be responsible including, a decrease in metabolic rate and requirement for stored energy reserves, a preferential use of protein and/or carbohydrate reserves, an increase in the rate of heterotrophy or some combination of all three.

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