LETTERS

Heterotrophic plasticity and resilience in bleached corals

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Mass coral bleaching events caused by elevated seawater temperatures[1,2] have resulted in extensive coral mortality throughout the tropics over the past few decades[3,4]. With continued global warming, bleaching events are predicted to increase in frequency and severity, causing up to 60% coral mortality globally within the next few decades[4–6]. Although some corals are able to recover and to survive bleaching[7,8], the mechanisms underlying such resilience are poorly understood. Here we show that the coral host has a significant role in recovery and resilience. Bleached and recovering *Montipora capitata* (branching) corals met more than 100% of their daily metabolic energy requirements by markedly increasing their feeding rates and CHAR (per cent contribution of heterotrophically acquired carbon to daily animal respiration), whereas *Porites compressa* (branching) and *Porites lobata* (mounding) corals did not. These findings suggest that coral species with high-CHAR capability during bleaching and recovery, irrespective of morphology, will be more resilient to bleaching events over the long term, could become the dominant coral species on reefs, and may help to safeguard affected reefs from potential local and global extinction.

Coral reefs provide essential goods and services to maritime tropical nations[9] and are the most diverse marine ecosystems on the planet. Unfortunately, reefs are seriously declining because of global warming[3,4]. At elevated seawater temperatures, scleractinian corals lose their endosymbiotic dinoflagellates (zooxanthellae), which renders the colony pale or white in colour, giving it a bleached appearance and often resulting in death. 'Susceptibility' of corals to bleaching has been explained primarily by coral morphology[7,8] and zooxanthellae type or density[10–13]. However, coral 'recovery' from bleaching events cannot be satisfactorily explained by these two factors. The role of the coral polyp itself (that is, the host) in recovery from bleaching has been studied only indirectly in a few studies[14–16] and represents a relatively unexplored source of potential resilience in corals.

In the absence of their zooxanthellae, which can provide the coral animal with up to 100% of its daily metabolic energy (DME) requirements[17], bleached and recovering corals must rely on alternative sources of fixed carbon to meet their DME needs. Stored energy reserves and heterotrophy (that is, feeding) are two such alternative sources. Whereas some coral species markedly deplete their energy reserves during bleaching[14–16], others do not[15]. However, the potential for heterotrophy as a significant source of fixed carbon for bleached and recovering corals has not been previously evaluated. Because energy reserves are a limited resource, species that can significantly increase their heterotrophic input of fixed carbon during bleaching and recovery should have an ecological advantage for long-term survival.

We considered that corals can meet their DME requirements during bleaching and recovery by consuming existing energy reserves, by switching from acquiring fixed carbon primarily photoautotrophically to primarily heterotrophically, or by a combination of both. These hypotheses could be tested only with combined tank and field experiments. Branches from healthy *Porites compressa* and *Montipora capitata* coral colonies from Kaneohe Bay, Hawaii, were bleached in outdoor, flow-through, filtered-seawater tanks by exposing them to elevated temperatures (30 °C treatment, no zooplankton). An equal number of coral branches were kept in similar tanks at ambient seawater temperature as controls (27 °C, no zooplankton). After 30 d, half of the treatment and control branches were collected for analyses and the remaining branches were returned to the reef to recover *in situ* at ambient seawater temperatures (27 °C) and zooplankton concentrations.

In *P. compressa*, branches in the 30 °C treatment tanks bleached white and then regained some colour (pale brown) after 6 weeks of recovery. This colour change was reflected in the chlorophyll *a* (Chl *a*) concentrations (Fig. 1a) and photosynthetic rates (Fig. 1b), which decreased significantly during bleaching and had begun to recover (Fig. 1a) or had completely recovered (Fig. 1b) after 6 weeks, respectively. Total energy reserves (Fig. 1c) and total biomass (Fig. 1d) decreased significantly during bleaching, and continued to decrease during recovery. Thus, in the absence of photosynthetically and heterotrophically derived fixed carbon, *P. compressa* depleted its energy reserves significantly during bleaching. During recovery, this species continued to deplete its energy reserves, despite an increase in Chl *a* and photosynthesis and the presence of zooplankton. These findings are consistent with observations of lower Chl *a* and total lipid concentrations in bleached *P. compressa* after a natural bleaching event on the same reef in 1996 (ref. 15). Overall, these results support the hypothesis that bleached and recovering *P. compressa* corals meet their DME requirements by consuming existing energy reserves, and are largely dependant on significant inputs of zooxanthellae-derived photosynthetic carbon to recover those reserves.

In *M. capitata*, branches in the 30 °C treatment tanks bleached white and remained bleached after 6 weeks of recovery. Consistent with these observations, Chl *a* and photosynthetic rates markedly decreased during bleaching and continued to decrease during 6 weeks of recovery by a total of 97% and 90%, respectively (Fig. 1e, f). Total energy reserves (Fig. 1g) and total biomass (Fig. 1h) decreased significantly during bleaching by 39% and 34%, respectively, but were fully replenished after 6 weeks of recovery. Thus, in the absence of photosynthetically and heterotrophically derived fixed carbon, *M. capitata* significantly depleted its energy reserves and total biomass during bleaching. Once exposed to naturally available zooplankton on the reef, however, total energy reserves and total biomass were fully replenished within 6 weeks despite persistently low Chl *a* and photosynthetic rates. These results are consistent with previous findings showing that total lipids do not differ between

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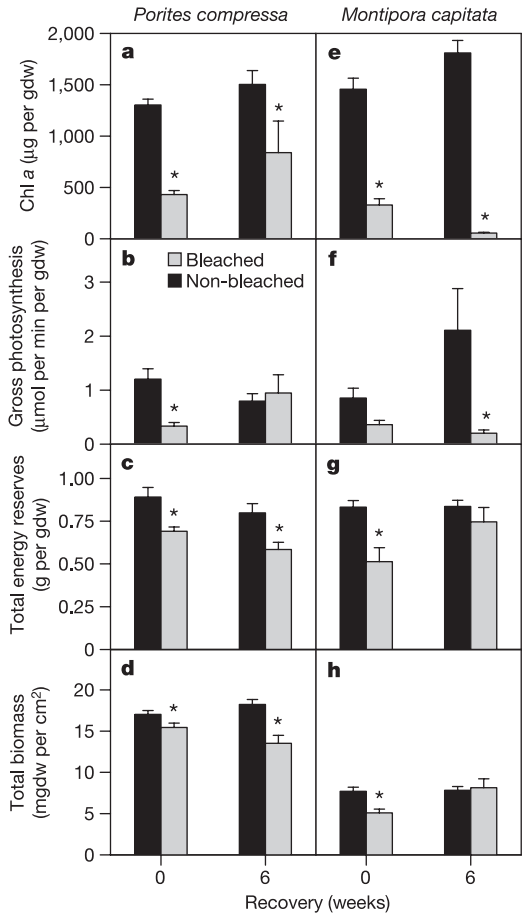

Figure 1 | Coral bleaching and recovery. Shown are Chl *a* content (**a**, **e**), gross photosynthesis (**b**, **f**), total energy reserves (**c**, **g**) and total biomass (**d**, **h**) in bleached (grey bars) and non-bleached control (black bars) *P. compressa* (**a**–**d**) and *M. capitata* (**e**–**h**) corals after 0 and 6 weeks of recovery. Data are the mean ± s.e.m. ($n = 4$–12). Significant differences (asterisks) between averages within each recovery interval were determined by *a posteriori* tests. gdw, grams of ash-free dry weight (AFDW); mgdw, milligrams of AFDW. Additional statistical results are given in the Supplementary Information.

bleached and non-bleached corals of this species after a natural bleaching event[15]. Collectively, these results suggest that when zooplankton are available, bleached and recovering *M. capitata* corals may acquire large quantities of fixed carbon heterotrophically in excess of DME needs and, unlike *P. compressa*, are not dependant on symbiotic photosynthesis to recover energy reserves.

To quantify the amount of fixed carbon acquired heterotrophically in recovering *P. compressa* and *M. capitata*, a feeding experiment was conducted on bleached and non-bleached branches of each species, and on fragments of an additional species, *P. lobata* (mounding coral). For each species, feeding rates under natural conditions on the reef were determined, the daily heterotrophic carbon input (H_C) was calculated, and the CHAR (per cent contribution of heterotrophically acquired carbon to daily animal respiration (R_C)) for each coral was calculated as:

$$\mathrm{CHAR} = \frac{H_C}{R_C} \times 100\% \qquad (1)$$

CHAR is thus the percentage of a coral's DME demand that can be met through heterotrophy alone, assuming that all of the carbon in zooplankton is biologically available. These assumptions are analogous to those for CZAR (per cent contribution of zooxanthellae-acquired carbon to daily animal respiration)[17], which was also calculated.

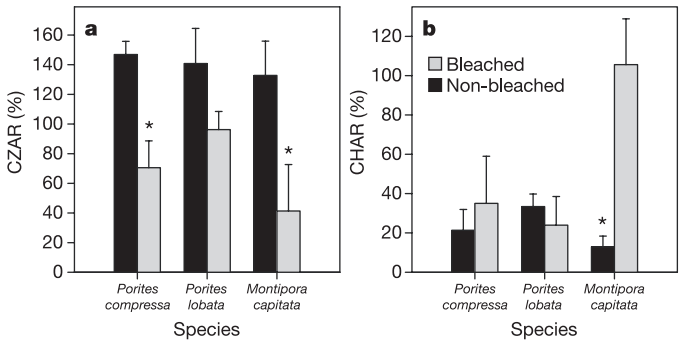

Figure 2 | Heterotrophically and photoautotrophically acquired carbon. **a**, Average per cent contribution of zooxanthellae-acquired carbon to daily animal respiration (CZAR). **b**, Average per cent contribution of heterotrophically acquired carbon to daily animal respiration (CHAR). Shown are the mean ± s.e.m. values in bleached (grey bars) and non-bleached control (black bars) *P. compressa*, *P. lobata* and *M. capitata* after 2 weeks of recovery. Significant differences (asterisks) between bleached and non-bleached corals of each species were determined by Student's *t*-test.

All three coral species had CZAR values >100% when non-bleached (controls) and <100% when bleached, decreasing by an average of 50% (Fig. 2a). Despite this reduction in photosynthetically derived carbon, feeding rates for *P. compressa* and *P. lobata* did not differ between bleached and non-bleached corals (Table 1). As a result, CHAR calculations show that for both of these species, only 21–35% of their DME demand was met heterotrophically, irrespective of bleaching status (Fig. 2b). Thus, measured decreases in the total energy reserves and biomass in bleached *P. compressa* (Fig. 1c, d) are independent of feeding rates. Therefore, with markedly diminished CZAR values *P. compressa* consumes its finite energy reserves during recovery from bleaching. Although energy reserve data are unavailable for *P. lobata* corals from Hawaii, the low-CHAR capability of bleached *P. lobata* coupled with weakened CZAR (Fig. 2a) values suggests that, like *P. compressa*, this species would also consume part or all of its energy reserves during bleaching and recovery.

In marked contrast to the two *Porites* corals, feeding rates were more than fivefold higher in bleached versus non-bleached *M. capitata* (Table 1). As a result, bleached *M. capitata* corals met their whole DME demands (average CHAR = 105%) from heterotrophy alone (Fig. 2b), more than compensating for the significantly reduced CZAR values (Fig. 2a) and enabling them to replenish their energy reserves once zooplankton was available. Non-bleached corals of this species showed the opposite pattern: low-CHAR and high-CZAR values (Fig. 2). Collectively, these findings support a previously unrecognized strategy for corals to meet metabolic demand and to maintain energy reserves and biomass, whereby some species shift from a primarily photoautotrophic to a primarily heterotrophic carbon-acquiring mode during bleaching and recovery.

The two CHAR strategies observed in bleached and recovering corals are predicted to affect coral physiology in two significant ways. First, the production of gametes (which are lipid-rich) and spawning are typically reduced or absent in corals for up to two years after a bleaching event[4,18,19]. With depleted energy reserves and total biomass, *P. compressa* may require a prolonged recovery period before successfully spawning after bleaching. By contrast, the high energy-reserve content and total biomass of recovering *M. capitata* would facilitate uninterrupted gamete production and spawning, regardless of bleaching status. Thus, as bleaching events increase in frequency, low-CHAR corals such as *P. compressa* may not have sufficient time to replenish their energy reserves between events, resulting in lower reproductive output and selection against low-CHAR species. Second, the ability of *P. compressa* and *P. lobata* to sustain their energy demand

Table 1 | *In situ* average natural feeding rates of corals in this study

Species	Average feeding rate*		*t*	*P*
	Bleached (treatment)	Non-bleached (control)		
Porites compressa	10.9 (7.3)	12.8 (6.0)	0.20	>0.5
Montipora capitata	32.6 (4.7)	5.7 (2.3)	5.61	<0.001
Porites lobata	20.6 (10.4)	18.8 (2.9)	0.17	>0.5

*The average feeding rate (±1 s.e.m.) is the number of zooplankton caught per gram of coral AFDW per hour. Statistical results are from Student's *t*-tests for each species; feeding rates were considered significantly different at $P \leq 0.05$.

while bleached and recovering is limited by their stored energy reserves. By contrast, bleached *M. capitata* colonies should theoretically be able to sustain their DME demand indefinitely, provided zooplankton is available. During prolonged bleaching events, low-CHAR corals such as *Porites* are thus predicted to be more susceptible to mortality than high-CHAR corals such as *M. capitata*.

These findings show that energy reserves and heterotrophic capability of the coral host have a key and previously unassessed role in coral resilience to bleaching. Under future situations of increasing frequency and duration of bleaching events[3,4,6], we predict that coral species with high-CHAR capability will have an ecological advantage over low-CHAR species. Although a thick tissue layer or mounding morphology has been associated with recovery from past bleaching events[7,8], neither feature will necessarily provide sufficient energy reserves to sustain coral DME demand and reproductive output during future bleaching events and recovery. Thus, over the coming decades, coral reefs may experience a shift in coral species composition towards those with high-CHAR capability, independent of coral morphology.

METHODS

Chl *a*, photosynthesis, respiration, energy reserves and biomass. Eight branches from 12 healthy colonies of *P. compressa* and *M. capitata* (branching form) were collected at a 2-m depth in Kaneohe Bay, Hawaii (21° 26.18′ N; 157° 47.56′ W), in August 2003 and placed in eight outdoor flow-through seawater tanks at the Hawaii Institute of Marine Biology. The tanks were shaded with screens to simulate photosynthetically active radiation levels at a 2-m depth, and the seawater was filtered to exclude zooplankton >50 μm. On 4 September 2003, the seawater temperature was raised in four tanks by aquarium heaters (mean ± s.e.m. temperature, 30.06 ± 0.21 °C); the other four tanks were kept at ambient seawater temperature as controls (26.80 ± 0.09 °C). The corals in the 30 °C tanks gradually bleached. On 4 October 2003, photosynthesis and day and night respiration of the bleached and non-bleached control corals were measured at 30 °C and 27 °C, respectively, as described[20], and standardized to ash-free dry weight (AFDW). One branch per colony, per treatment and per species was collected and frozen at −80 °C. The remaining branches were placed back on the reef at a 2-m depth for 6 weeks of recovery (mean ± s.e.m. reef temperature, 26.86 ± 0.15 °C; range, 24.5–28.2 °C). On 16 November 2003, photosynthesis and respiration were measured at ambient seawater temperature, and an additional branch from each colony, species and treatment was collected and frozen at −80 °C. All remaining branches were left on the reef as part of a separate experiment.

Chlorophyll *a* (ref. 21), carbohydrates[22] and proteins[23] were measured as described. Total lipid extractions were modified from ref. 15. Total energy reserves were calculated as the sum of total lipids, carbohydrates and soluble proteins per gram of AFDW. Total AFDW biomass was standardized to surface area. Four-way analysis of variance (ANOVA) was used to test for significant species, genotype, treatment and recovery interval effects in Chl *a*, photosynthesis, total energy reserves and total biomass with SAS software[24] (Supplementary Table 1). Because all of the coral branches were reared under the exact same conditions except temperature during the first month, differences between bleached and control corals for any of the measured variables were due to the month-long temperature treatment alone, independent of natural seasonal variation.

CHAR and CZAR. Two fragments from five healthy *P. compressa* and *M. capitata* (branching form) and *P. lobata* (mounding form) colonies were collected on 26 May 2004, bleached or not bleached (control) in tanks for 25 d, and allowed to recover on the reef *in situ* for 2 weeks as described above. Each day from 6 to 10 July 2004, a pair of bleached and control coral fragments of each species were starved *in situ* for 8 h in isolation chambers[25], and then allowed to feed on ambient zooplankton for 1 h beginning 1 h after sunset. Corals were then collected and preserved in 10% formalin, and 250 polyps of each fragment were dissected as described[25].

Feeding rate (F_R) was calculated as the number of zooplankton caught per hour per coral fragment, standardized to coral AFDW. The proportionate contribution of individual zooplankton taxa to the coral diet (P_i) was determined on additional coral fragments as described[25]. Average P_i did not differ between bleached and non-bleached controls of any species (multivariate analysis of variance, $P = 0.827$). The average AFDW of individual zooplankton of each taxa (M_i) and the natural abundance of each taxa were determined from nightly plankton tows. The average per cent carbon of zooplankton (C_z) in the 200–400-μm size fraction (the size corresponding to most zooplankton eaten; refs 25, 26, and J.E.P., L.J.R. and A.G.G., unpublished data) and of bulk zooplankton samples was 31% and 35%, respectively.

Daily heterotrophic carbon input (H_C) was calculated by the equation:

$$H_C = 8F_R C_z \sum_{\text{taxa}=1}^{n} M_i P_i \quad (2)$$

where C_z was conservatively set to 30%. H_C was calculated assuming 8 h of feeding per night[27], which is a conservative estimate because *P. compressa* and *M. capitata* keep their tentacles extended continuously day and night, and the contribution of microzooplankton (<50 μm) and dissolved organic matter to the coral diet, which can be significant[28], was not measured. Average day and night respiration rates were converted to total daily grams of carbon respired per gram of AFDW (R_C), assuming a mole-to-mole relationship of O_2 consumed to CO_2 produced during respiration. CHAR for bleached and non-bleached control corals of each species was then calculated by equation (1). The standard error of CHAR is the propagated error from the H_C and R_C calculations.

CZAR (adopted from ref. 17) was calculated by equation (3):

$$\text{CZAR} = \frac{P_C}{R_C} \times 100\% \quad (3)$$

where total daily grams of photosynthetically fixed carbon per gram of AFDW (P_C) was calculated as the sum of net photosynthetically fixed carbon plus respired carbon during the day assuming a mole-to-mole relationship of CO_2 consumed (produced) to O_2 produced (consumed) during photosynthesis (respiration).

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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