Coral Reefs
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REPORT

Can heterotrophic uptake of dissolved organic carbon and zooplankton mitigate carbon budget deficits in annually bleached corals?

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Abstract Annual coral bleaching events due to increasing sea surface temperatures are predicted to occur globally by the mid-century and as early as 2025 in the Caribbean, and severely impact coral reefs. We hypothesize that heterotrophic carbon (C) in the form of zooplankton and dissolved organic carbon (DOC) is a significant source of C to bleached corals. Thus, the ability to utilize multiple pools of fixed carbon and/or increase the amount of fixed carbon acquired from one or more pools of fixed carbon (defined here as heterotrophic plasticity) could underlie coral acclimatization and persistence under future ocean-warming scenarios. Here, three species of Caribbean coral—*Porites divaricata*, *P. astreoides*, and *Orbicella faveolata*—were experimentally bleached for 2.5 weeks in two successive years and allowed to recover in the field. Zooplankton feeding was assessed after single and repeat bleaching, while DOC fluxes and the contribution of DOC to the total C budget were determined after single bleaching, 11 months on the reef, and repeat bleaching. Zooplankton was a large C source for *P. astreoides,* but only following single bleaching. DOC was a source of C for single-bleached corals and accounted for 11–36 % of daily metabolic demand ($CHAR_{DOC}$), but represented a net loss of C in repeat-bleached corals. In repeat-bleached corals, DOC loss exacerbated the negative C budgets in all three species. Thus, the capacity for heterotrophic plasticity in corals is compromised under annual bleaching, and heterotrophic uptake of DOC and zooplankton does not mitigate C budget deficits in annually bleached corals. Overall, these findings suggest that some Caribbean corals may be more susceptible to repeat bleaching than to single bleaching due to a lack of heterotrophic plasticity, and coral persistence under increasing bleaching frequency may ultimately depend on other factors such as energy reserves and symbiont shuffling.

Keywords Coral · Zooplankton · DOC · Bleached · Annual · Heterotrophy

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Introduction

Coral reefs are threatened globally due to mass bleaching events that are already causing coral reef decline worldwide (Wilkinson 2008). Bleaching events are expected to increase in frequency and intensity in the coming decades

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(Hoegh-Guldberg 1999; Donner et al. 2007; Frieler et al. 2013). At the current rate of greenhouse gas emissions and warming sea surface temperatures (SSTs), models predict that reefs globally will experience annual bleaching events by 2040, with parts of the Caribbean potentially experiencing annual bleaching events as soon as 2025 (van Hooidonk et al. 2015).

At sustained elevated SSTs, corals lose their endosymbiotic algae (*Symbiodinium* spp.) rendering them pale white or bleached (Jokiel and Coles 1990; Glynn 1996; Brown 1997; Hoegh-Guldberg 1999; D'Croz et al. 2001). While healthy scleractinian corals can obtain up to 100 % of their daily metabolic demand from the translocated photosynthate of their endosymbiotic algae, dramatic decreases in photosynthesis in single-bleached and some repeat-bleached corals can lead to coral carbon (C) budget deficits of up to 80 % (Muscatine et al. 1981; Falkowski et al. 1993; Grottoli et al. 2006; Palardy et al. 2008; Tremblay et al. 2012; Grottoli et al. 2014). To recover from bleaching, corals may rely on a combination of alternative sources of fixed carbon such as energy reserves and/or increased heterotrophy in conjunction with recovery of photosynthesis.

In addition to autotrophically acquired C, both healthy and stressed corals can obtain up to 150 % of fixed carbon from the ingestion of zooplankton (Grottoli et al. 2006; Palardy et al. 2008; Anthony et al. 2009; Houlbreque and Ferrier-Pages 2009; Grottoli et al. 2014), pico- and nanoplankton (Tremblay et al. 2012), non-living sedimentary and particulate organic matter (Anthony 1999, 2000; Ferrier-Pages et al. 2011; Leal et al. 2014), and dissolved organic matter (Tremblay et al. 2012). For example, singly bleached corals *Montipora capitata* and *Porites astreoides* increase their zooplankton consumption and can meet more than 100 % of their metabolic demand (heterotrophically plastic), thus replenishing or maintaining energy reserves during bleaching events (Grottoli et al. 2006; Rodrigues and Grottoli 2007; Palardy et al. 2008; Grottoli et al. 2014). Even in corals that do not increase their heterotrophic organic C intake when bleached, such as *P. lobata* and *P. compressa*, heterotrophically acquired zooplankton C still represents a significant component (25 and 40 %, respectively) of their total fixed C budgets (Grottoli et al. 2006; Palardy et al. 2008). However, for the Caribbean corals *P. divaricata* and *Orbicella faveolata*, zooplankton heterotrophy represents <4 % of their total fixed C budgets, irrespective of bleaching status or bleaching frequency (Grottoli et al. 2014). Thus, zooplankton heterotrophy is highly species specific and varies based on single versus sequential annual bleaching. However, little is known about Caribbean coral preferences for zooplankton size and species. If bleached Caribbean corals selectively capture a specific group and/or size of zooplankton similar to Hawaiian corals (Palardy et al. 2008), changes in zooplankton communities could potentially have drastic effects on bleached coral recovery.

In recent years, dissolved organic carbon (DOC) has been increasingly recognized as another source of fixed carbon for corals and may play an important role in coral resistance to bleaching. Healthy corals are typically net producers of DOC (Haas et al. 2010; Naumann et al. 2010, 2012; Levas et al. 2015) via the release of mucus and/or dissolved organic materials that account for losses of 5–45 % of photosynthetically fixed C (Crossland et al. 1980; Edmunds and Davies 1986; Crossland 1987; Bythell 1988; Ferrier-Pages et al. 1998; Tanaka et al. 2009), although DOC can be utilized by some corals (Naumann et al. 2010; Tremblay et al. 2012). However, temperature stress and bleaching may at times influence coral net DOC fluxes. For example, Haas et al. (2010) observed greater DOC losses from temperature-stressed coral, while Niggl et al. (2009) and Levas et al. (2015) found no differences in DOC fluxes between temperature-stressed and control corals.

DOC uptake could help mitigate or offset the loss of autotrophic C during bleaching events in Caribbean corals, which could experience annual bleaching by 2025 (van Hooidonk et al. 2015). However, such heterotrophic plasticity could potentially be influenced by the frequency of bleaching events as seen with zooplankton heterotrophy in bleached *P. astreoides* (Grottoli et al. 2014). To test these hypotheses, we quantified the proportion of coral organic C budgets derived from DOC fluxes and compared it with those derived from symbiont photosynthesis and zooplankton feeding from Grottoli et al. (2014) in singly bleached, repeat-bleached, and non-bleached control fragments of three ecologically important species of Caribbean corals. Understanding and quantifying changes in the various components of carbon budgets for singly and repeatedly bleached corals are essential for determining potential coral resilience to predict future increases in SST.

Materials and methods

Coral collection, acclimation, experimental design, and procedures used in this study have been largely described previously by Grottoli et al. (2014). Briefly, fragments of *Porites divaricata*, *P. astreoides*, and *Orbicella faveolata* were collected from the reefs near Puerto Morelos, Mexico, from July 4 to 9, 2009 (Electronic Supplementary Material, ESM, Table S1). After 5-d acclimation (July 14, 2009), half of the fragments from each colony and species were placed into tanks where the temperature was slowly increased over 5 d (to 31.5 ± 0.20 °C) (single bleaching treatment) and the other half of the fragments were kept in ambient control tanks (30.66 ± 0.24 °C) (Fig. 1a). On July

29, 2009, after 15 d, the heaters in the treatment tanks were turned off, and one-third of the bleached and control fragments were collected and immediately frozen. The other fragments were transplanted back to the reef at 4.9 m depth (20°52.815′N, 86°50.989′W). After 11 months on the reef (June 20, 2010), one treatment and control fragment from each colony of each species was collected and DOC fluxes were measured from June 20 to 26, 2010, according to methods described below (Fig. 1a).

On July 22, 2010, the bleaching experiment was repeated with the remaining treatment corals from the previous year exposed to elevated temperatures again (31.6 ± 0.24 °C) (repeat bleaching treatment), while the control fragments from 2009 were maintained at ambient temperature (30.4 ± 0.23 °C). At the end of 17 d (7 August 2010), heaters were turned off. DOC fluxes were measured August 5–10, 2010, and all the fragments were placed back on the reef. Feeding rates were quantified a week later, on August 15 and 17, 2010 (see below), according to Palardy et al. (2008).

The feeding fragment samples from the single bleaching experiment done in 2009 were inadvertently discarded (Grottoli et al. 2014). Thus, in order to obtain DOC fluxes and feeding rates, and calculate a total carbon budget, a second single bleaching experiment was conducted from June 28, 2010, to July 15, 2010. Two new coral fragments from nine different parent colonies from the same location of *P. divaricata, P. astreoides,* and *O. faveolata* (Fig. 1b) were collected and are referred to as redo corals. Half of the corals were exposed to elevated temperatures (31.24 ± 0.21 °C), and the other fragments remained at ambient control temperatures (29.47 ± 0.22 °C). After 17 d (July 15, 2010), heaters were turned off and DOC fluxes were measured from July 13 to 18, 2010. All coral fragments were transplanted to the reef for 1 week, and then, feeding rates were determined in situ according to Palardy et al. (2008) (see below). Since these corals had not yet had the opportunity to recover except for 1 week on the reef, they are referred to as singly bleached corals. Differences between discarded samples and these corals should be minimal as these corals were collected from the same populations of corals as the initial single and repeat bleaching experiments and were subjected to similar temperature regimes. Thus, differences between single and repeat-bleached corals are most likely due to differences in experimental thermal history (Grottoli et al. 2014).

Coral feeding measurements

On July 27, 2010, four clear 50-L polypropylene plastic chambers with 50-µm Nitex screen windows were placed over half of the redo corals for 12 h during the day. The Nitex screen windows allowed for sufficient flow but prevented zooplankton from entering the chambers (Palardy et al. 2005), enabling the corals to fully empty their guts. One hour after dusk, the chambers were removed and the coral fragments were allowed to feed on the natural assemblage of zooplankton and seston on the reef. After 1 h of feeding, the fragments were collected and fixed in formalin to prevent digestion of ingested zooplankton. On July 29, 2010, this procedure was repeated with the remainder of the single-bleached and control fragments. Within 48 h, all or 150 polyps (whichever came first) of the coral fragments were dissected (Palardy et al. 2005) under a dissecting microscope (20 to 100× power) by probing with a dissection needle and subsequent scraping of the skeleton to expose any remaining zooplankton (Palardy et al. 2008). Prey larger than 50 µm were visible, and only plankton inside the polyp were counted. The number of zooplankton eaten per polyp as well as the prey taxon and

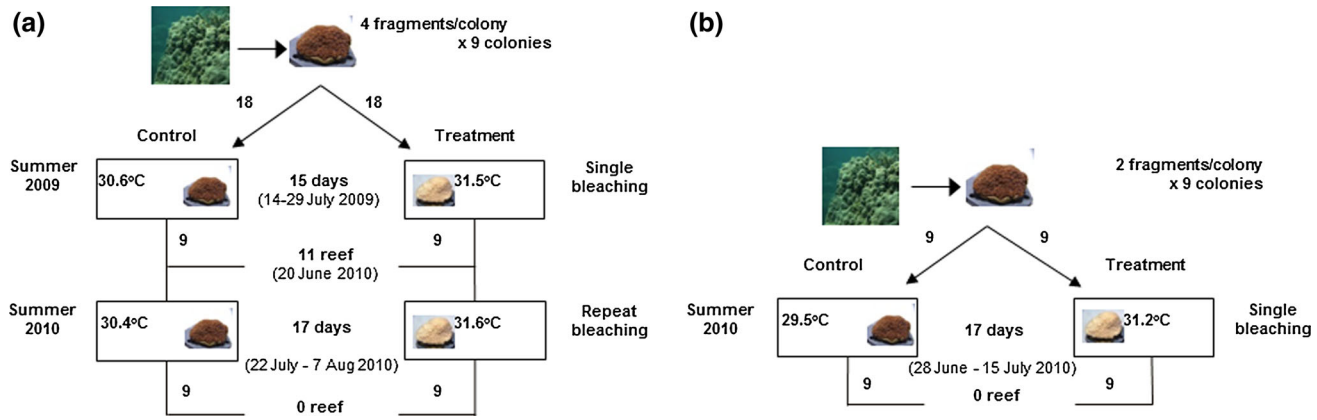

Fig. 1 Experimental design for **a** the single and repeat bleaching experiment of 2009–2010 for *Porites divaricata*, *P. astreoides*, and *Orbicella faveolata* and **b** the single bleaching experiment of 2010 for *O. faveolata*. Days = number of days corals were in the tanks, reef = number of months corals were on the reef, feed = coral fragments used for feeding measurements, and numbers indicate number of fragments collected. Diagram modified from Grottoli et al. (2014)

size was recorded. Size was determined using a stage micrometer. If a consumed plankter could not be identified, it was classified as unidentified, but size was measured. Feeding rates were standardized to grams ash-free dry weight of each coral fragment (plankton captured h^{-1} g^{-1} dw). On August 13 and 17, 2010, the same procedure was repeated to measure feeding rates of repeat-bleached and control corals.

Each night, while the corals were feeding, at least two vertical plankton tows from 4 m depth to the surface were taken using a 0.5-m-diameter plankton net with 50-µm mesh. The tows were performed within 10 m of the experimental site and passed through a columnar sieve with 800-, 400-, 150-, and 50-µm filters and preserved in 10 % formalin. These size-fractioned samples were sorted and counted in broad taxonomic groups (ostracods, shrimp, eggs, isopods, snails, Cumacea, amphipods, polychaetes, crab zoea, and unidentifiable).

DOC flux experiments

DOC fluxes were measured outdoors using the respective treatment water (i.e., bleached corals received elevated temperature, while the controls received ambient water) under the same light used in the experiment in submerged closed-top UV-transparent acrylic chambers according to Levas et al. (2015). Briefly, two sets of incubations were conducted between 1000 and 1600 h and between 2000 and 0200 h over 6 d at each time point. One chamber contained no coral fragment and served as a control. It took 3 d to complete the incubations for the bleached fragments (1 d per species) and an additional 3 d to complete the incubations for the non-bleached control fragments (1 d per species).

Immediately after all chambers were sealed, two 1-L seawater samples were taken from the flow-through tank inflow, representing the background initial seawater DOC concentrations. After 1.5 h of incubation, each chamber lid and coral fragment were removed and the seawater from each chamber was collected into individual 1-L polycarbonate brown bottles pre-cleaned with 10 % trace metal-grade HCl and placed on ice. One 30-mL seawater aliquot was taken for DOC analysis from each brown bottle. Duplicate 30-mL seawater aliquots were taken from the control chamber. A duplicate 30-mL aliquot was randomly collected from one of the coral chambers. The procedure was identical for the second set of incubations.

Seawater samples were kept frozen at −20 °C until analysis by high-temperature catalytic oxidation (HTCO) using a Shimadzu TOC 5050 in the Aquatic Biogeochemistry Laboratory at The Ohio State University according to Levas et al. (2015). The standard deviation of replicate measurements of a glucose standard was ±4 % ($n = 100$).

For each set of incubations, the average of the initial DOC concentrations was corrected for potential micro-heterotrophic and microautotrophic biases by subtracting the average of the control DOC concentrations from the same incubation set. The DOC flux for each fragment was calculated as the difference between the measured DOC concentration and the corrected initial DOC concentration for its incubation set and standardized to the fragment surface area as determined by the foil technique (Marsh 1970). Negative fluxes indicated a net uptake of DOC, whereas positive fluxes indicated a net release of DOC into the incubation chambers.

Contribution of DOC to coral respiration

The percent contribution of zooxanthellae (*Symbiodinium* spp.) to animal respiration (CZAR, Muscatine et al. 1981), contribution of zooplankton heterotrophy to animal respiration ($CHAR_{ZOO}$, Grottoli et al. 2006), and the total acquired fixed carbon (CTAR, sum of CZAR and $CHAR_{ZOO}$) for the same fragments used in this study were calculated as in Grottoli et al. (2014). In this study, the percent contribution of DOC to heterotrophy was also calculated ($CHAR_{DOC}$, Levas et al. 2015) relative to respiration and a new comprehensive total carbon budget (i.e., CTAR) was calculated as the sum of CZAR, $CHAR_{ZOO}$, and $CHAR_{DOC}$.

$CHAR_{DOC}$ for each fragment was calculated as the sum of daytime and nighttime DOC fluxes in µg C standardized to grams ash-free dry weight hr^{-1} (DOC_f), divided by the µg C lost via the sum of daytime and nighttime respiration hr^{-1} (R_c), assuming a mole-to-mole relationship of O_2 consumed to CO_2 produced during respiration (sensu Grottoli et al. 2006). Thus, $CHAR_{DOC}$ was calculated as:

$$\mathrm{CHAR_{DOC}} = \frac{DOC_f}{R_c} \times 100\,\% \quad (1)$$

Therefore, $CHAR_{DOC}$ is the percent of a coral's respiration that can be met or lost through DOC uptake or release. Negative $CHAR_{DOC}$ values indicate a net loss of DOC relative to respiratory demand, and positive $CHAR_{DOC}$ values indicate a net gain of DOC relative to respiratory demand.

Statistical analyses

To determine whether zooplankton capture differed by size and bleaching status, all zooplankton captured were converted into relative contributions by taxon and size class. These relative contributions were tested for differences across species and bleaching status using a factorial

MANOVA. No differences in the composition of zooplankton taxa or size were found among species or bleaching status for either year (ESM Table S2). Therefore, data were pooled among experimental treatments and analyzed with one-way ANOVAs and Tukey tests to determine whether the proportion of captured zooplankton varied among size classes and taxa.

Data for coral feeding rates, DOC flux measurements, the $CHAR_{DOC}$, and CTAR estimates were non-normal, and variances were heterogeneous. Therefore, the effects of treatment (treatment, control) and time (0 and 11 months recovery during single bleaching and 0 months for repeat bleaching) on feeding rates, DOC fluxes, $CHAR_{DOC}$, and CTAR between treatment and control corals of each species at each time point were analyzed using the nonparametric Kruskal–Wallis test using SAS version 9.2. Values of $p \leq 0.05$ were considered significant.

Nonparametric two-way analysis of similarity (ANOSIM) was used to test for significant species (*P. divaricata, P. astreoides, O. faveolata*) or bleaching event (single vs repeat) effects in total DOC and CTAR. Since total DOC encompasses both day and night DOC fluxes (see Fig. 4), the individual day and night DOC flux values were not used in the analysis. Since combining total DOC and CTAR did not change the results of the ANOSIM, we do not include those analyses here. Similarly, CTAR is comprised of several other measurements (see Fig. 5) that were not included in the ANOSIM for the same reason. ANOSIM analyses were done using Primer6.

Results

Feeding

Overall feeding rates did not differ between treatment and control corals of *P. divaricata*, *P. astreoides*, or *O. faveolata* after single or repeat bleaching (Fig. 2). However, *P. astreoides* feeding rates were higher than those of *P. divaricata* and *O. faveolata* (Fig. 2).

At the same time, the size and the relative abundances of zooplankton taxa captured by corals did not differ significantly by coral species or bleaching status in either year (ESM Table S2a). Therefore, all feeding data were pooled for each year to create an average assemblage composition of zooplankton captured by size and taxa (ESM Table S2b). Almost all (95 %) captured zooplankton were larger than >400 µm yet constituted <20 % of zooplankton availability on the reef (Fig. 3; ESM Fig S2). Between 28 and 69 % of captured zooplankton were polychaetes, crab zoea, or unknown, even though these plankton represent <1.5 % of available zooplankton on the reef. Copepods represented one of the most frequently captured zooplankton types, yet their proportionate contribution to the zooplankton assemblage captured by corals is still lower than their availability on the reef. Approximately 82 % of the zooplankton captured by singly bleached corals, in order of most to least captured, was unidentifiable zooplankton, crab zoea, polychaetes, and copepods (Fig. 3c). However, in repeat-bleached corals, 89 % of the coral diet, in order of most to least captured, consisted of copepods, crab zoea, snails, and polychaetes (Fig. 3d).

DOC fluxes

Single and repeat bleaching had no significant effect on daytime or nighttime DOC fluxes of *P. divaricata* compared to controls (Fig. 4a, b). Overall, the net 24-h DOC fluxes were negative in both singly bleached and control corals due to the strong negative fluxes measured at night (Fig. 4c). Net 24-h DOC fluxes were positive for both treatment and control corals in the rest of the study due to consistently neutral or positive day and night fluxes (Fig. 4c).

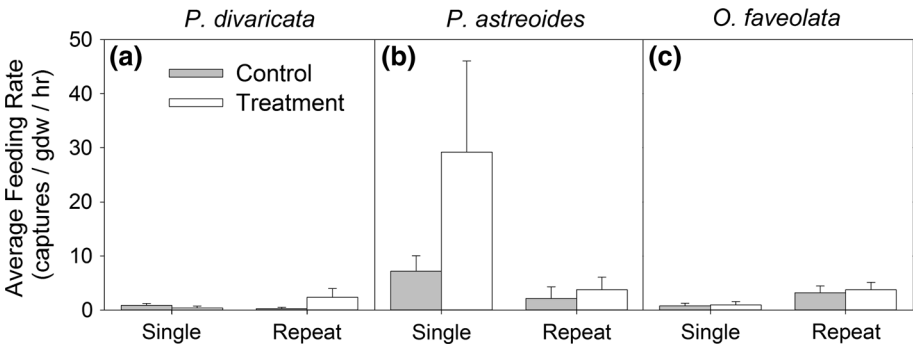

Fig. 2 Average feeding rate (±SE) of coral fragments in control (*gray bars*) and bleached treatments (*white bars*) after single and repeat bleaching of **a** *Porites divaricata*, **b** *Porites astreoides*, and **c** *Orbicella faveolata*. Values are standardized to coral fragment grams dry weight per hour. Sample size for each average was 8 or 9. No significant differences were detected between treatment and control average pairs using Kruskal–Wallis tests

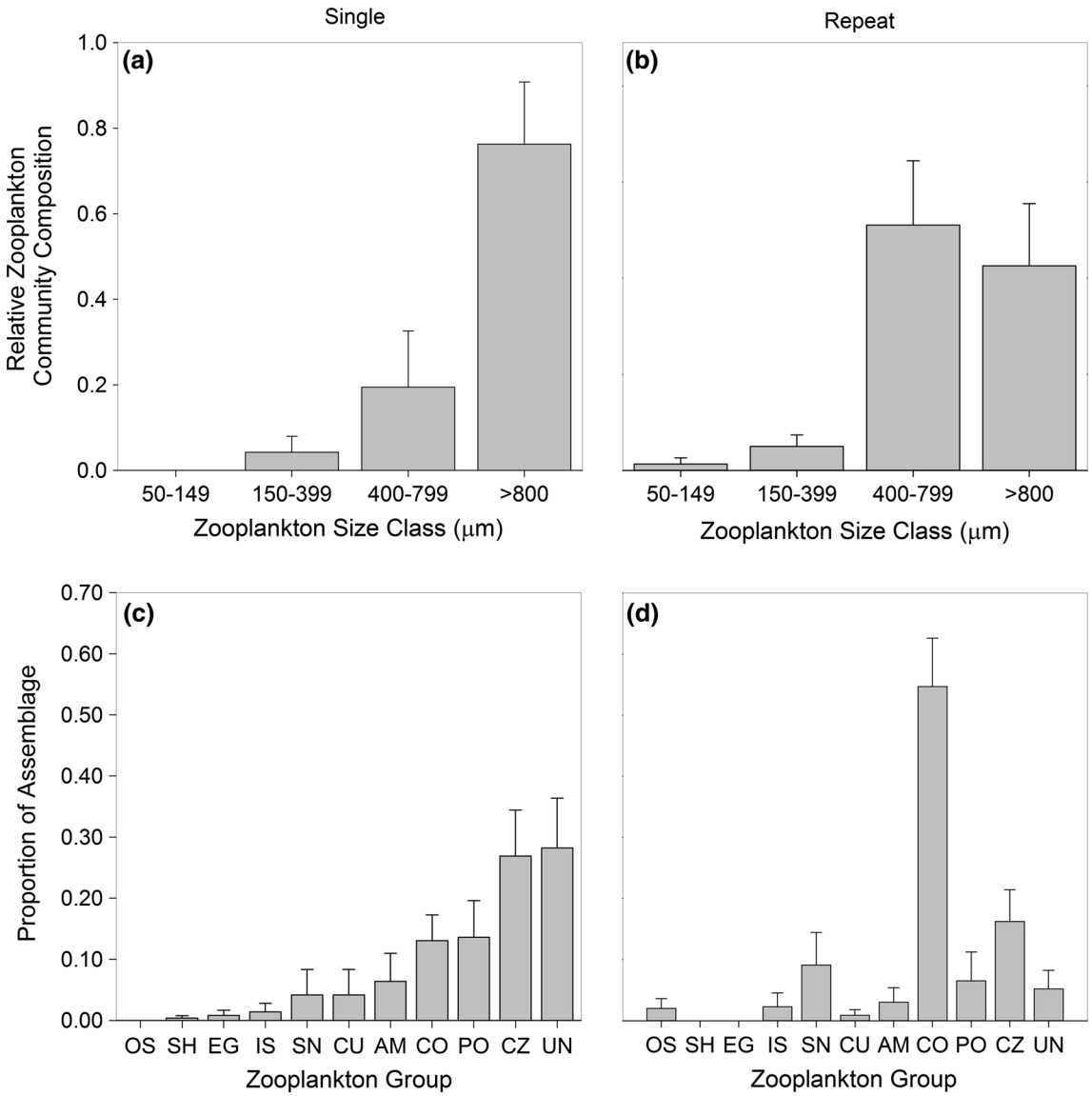

Fig. 3 Average proportion (± SE) of (**a**, **b**) size and (**c**, **d**) composition of zooplankton assemblage captured by corals exposed to ambient concentrations of zooplankton in (**a**, **c**) single- and (**b**, **d**) repeat-bleached corals. Zooplankton groups: UN = unidentified, CZ = crab zoea, PO = polychaetes, CO = copepods, AM = amphipods, CU = Cumacea, SN = snails, IS = isopods, EG = eggs, SH = shrimp, OS = ostracods

Singly bleached *P. astreoides* had lower daytime DOC fluxes than controls; this suppression of DOC flux persisted after 11 months on the reef (Fig. 4d). In contrast, repeat bleaching had no significant effect on daytime DOC fluxes. At night, DOC fluxes did not differ between treatment and control corals after single bleaching and 11 months on the reef, but repeat-bleached corals had greater DOC fluxes than controls (Fig. 4e). Integrated over 24 h, treated *P. astreoides* took up DOC when singly bleached, but released DOC after 11 months on the reef and immediately after repeat bleaching (Fig. 4f). Net 24-h fluxes of the control corals were positive throughout the study (Fig. 4f).

Like *P. astreoides*, singly bleached *O. faveolata* fragments had lower daytime DOC fluxes than controls (Fig. 4g). Nighttime DOC fluxes only differed between treatment and control corals after 11 months on the reef (Fig. 4h). Integrated over 24 h, treated *O. faveolata* had negative DOC fluxes when singly bleached, but the controls had positive fluxes (Fig. 4i). As with *P. divaricata* and *P. astreoides,* net 24-h DOC fluxes did not differ between repeat-bleached and control *O. faveolata* corals and were positive (Fig. 4a–i).

Total DOC fluxes did not differ between species and only mildly differed between single and repeat bleaching

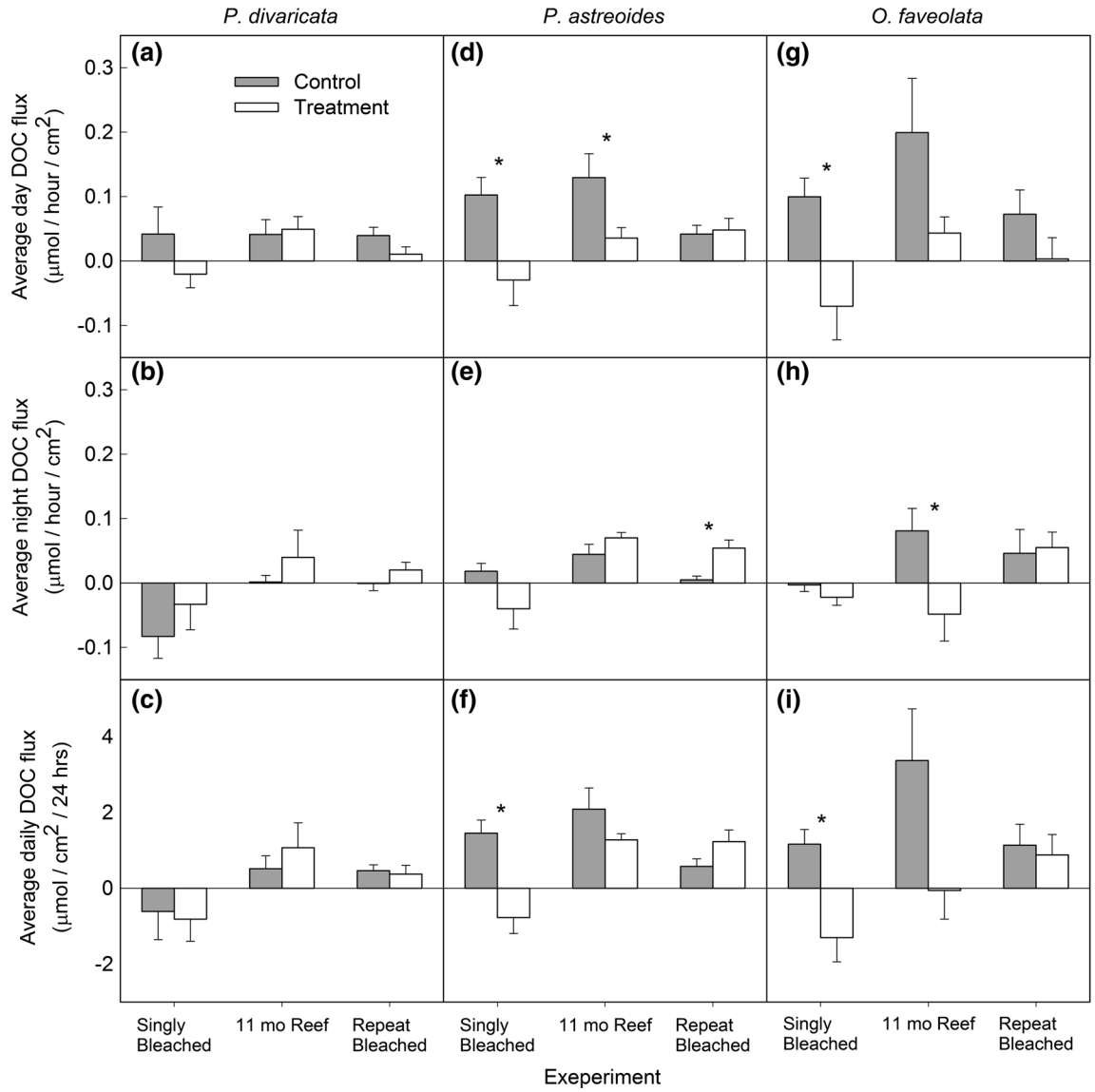

Fig. 4 Average DOC fluxes (±SE) during **a**, **d**, **g** daytime, **b**, **e**, **h** nighttime, and **c**, **f**, **i** diurnal for control (*gray bars*) and treatment (*white bars*) *Porites divaricata* (**a**, **b**, **c**), *Porites astreoides* (**d**, **e**, **f**), and *Orbicella faveolata* (**g**, **h**, **i**) after single bleaching, 11 months on the reef, and repeat bleaching. All averages are standardized to coral surface area and time. Negative fluxes indicate uptake, while positive fluxes are release of DOC. For each species, asterisks indicate significant differences at $p \leq 0.05$ between treatment means within a time interval using Kruskal–Wallis tests. Sample sizes for each average ranged from 5 to 9

events (two-way ANOSIM; species: $R = 0.027$, $p = 0.082$; bleaching events: $R = 0.062$, $p = 0.01$).

Percent contribution of DOC and zooplankton to coral respiration

Singly bleached *P. divaricata*, *P. astreoides*, and *O. faveolata* met 35, 10, and 16 % of their daily metabolic demand from DOC uptake, respectively, but control corals lost 1–10 % of their total fixed carbon through DOC release (Fig. 5a–c). However, only singly bleached *O. faveolata* had significantly greater $CHAR_{DOC}$ than the controls (Fig. 5c). As previously shown in Grottoli et al. (2014), zooplankton contributed <15 % of total metabolic demand in *P. divaricata* and *O. faveolata* irrespective of bleaching at any time (Fig. 5d, f). However, zooplankton feeding contributed dramatically to metabolic demand in the controls (50 %) and treatment corals (140 %) following single bleaching of *P. astreoides* (Fig. 5e). While the contribution of zooplankton feeding to CTAR has already been documented (Grottoli et al. 2014) (Fig. 5g–i), the addition of $CHAR_{DOC}$ to CTAR from Grottoli et al. (2014) resulted in a net increase in total CTAR in singly bleached corals and a slight decrease in their respective controls (Fig. 5g–i).

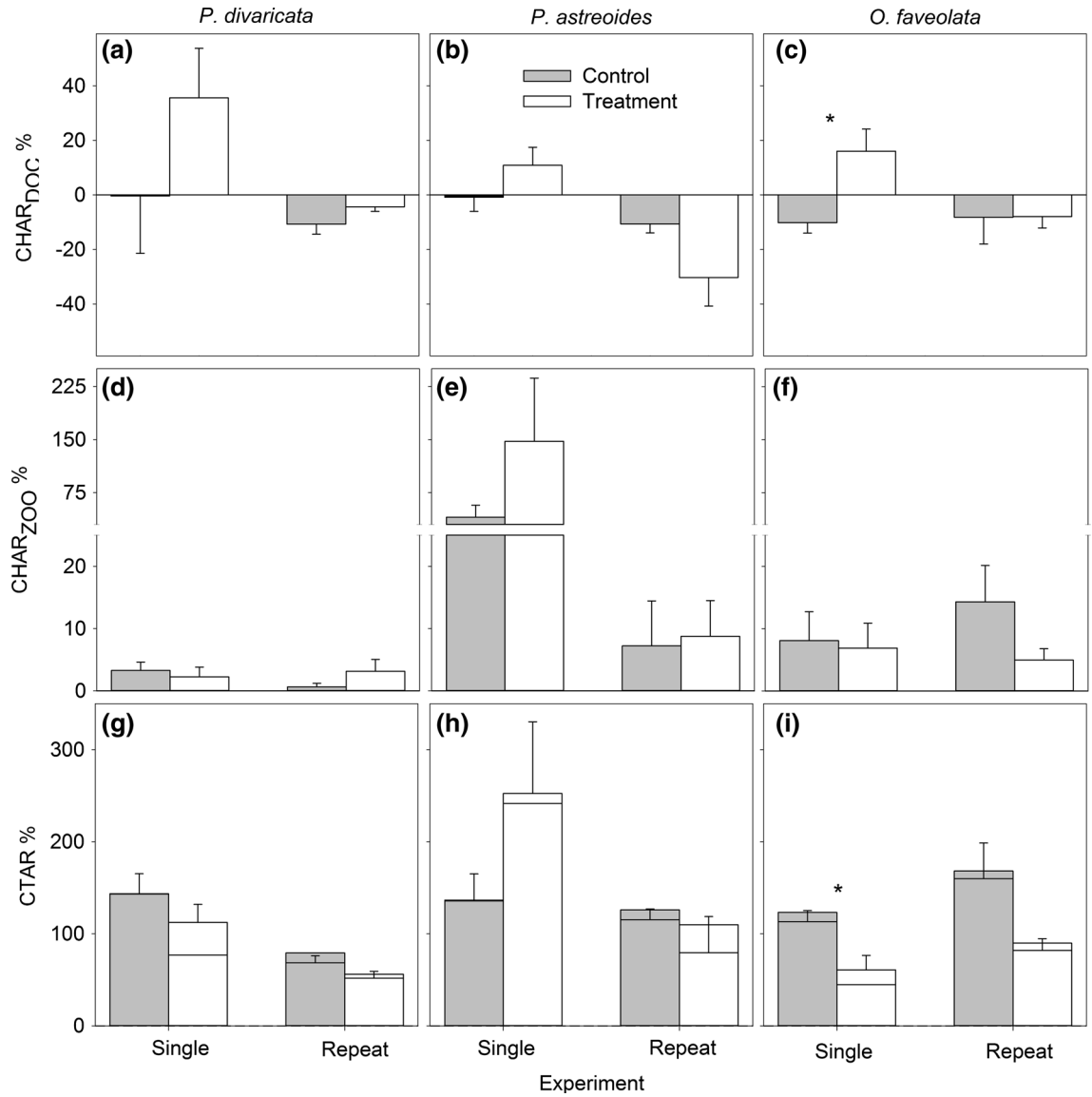

Fig. 5 Average (±SE) **a**, **b**, **c** $CHAR_{DOC}$, **d**, **e**, **f** $CHAR_{ZOO}$, and **g**, **h**, **i** CTAR in control (*gray bars*) and treatment (*white bars*) for *Porites divaricata* (**a**, **d**, **g**), *Porites astreoides* (**b**, **e**, **h**), and *Orbicella faveolata* (**c**, **f**, **i**) after single and repeat bleaching. $CHAR_{ZOO}$ values from Grottoli et al. (2014). For CTAR graphs (**g**, **h**, **i**), lines without *error bars* represent CTAR values from Grottoli et al. (2014) without $CHAR_{DOC}$ values. For each species, asterisks indicate significant differences at $p \leq 0.05$ between treatment means within a time interval using Kruskal–Wallis tests

When repeat-bleached, treatment corals lost 4–30 % of their metabolic C and control corals lost 8–10 % of their metabolic C as DOC (Fig. 5g–i). Therefore, the addition of $CHAR_{DOC}$ to CTAR from Grottoli et al. (2014) resulted in a net 5–25 % decline in the CTAR of repeat-bleached corals and a net 5–10 % decline in the CTAR of control corals.

CTAR significantly differed between species and bleaching events (two-way ANOSIM; species: $R = 0.048$, $p = 0.014$; bleaching events: $R = 0.041$, $p = 0.032$). Pairwise tests within ANOSIM revealed that *P. divaricata* had lower overall CTAR values than either *P. astreoides* ($R = 0.066$, $p = 0.014$) or *O. faveolata* ($R = 0.071$, $p = 0.015$).

Discussion

Previous studies have established that some thermally stressed corals are capable of utilizing zooplankton heterotrophy and DOC to meet metabolic demand and recover more quickly Grottoli et al. (2006, 2014). However, this is the first study to quantify the relative contribution of each pathway to the C budget of bleached corals

and assess whether this heterotrophic plasticity was affected by increased frequency of bleaching events.

Coral feeding

Similar to *Montipora capitata* in Hawaii (Grottoli et al. 2006; Palardy et al. 2008), *P. astreoides* could completely meet its metabolic demand from zooplankton heterotrophy when initially bleached (Grottoli et al. 2014). However, neither singly bleached *P. divaricata* nor *O. faveolata* exhibited any heterotrophic plasticity (Fig. 2a, c), and they could not meet their metabolic demand after single bleaching (Grottoli et al. 2014). Interestingly, none of the species studied here were able to increase their feeding rates (Fig. 2), nor meet their metabolic demand following repeat bleaching (Grottoli et al. 2014). This suggests that for *P. astreoides*, the cumulative impact of multiple bleaching events inhibits zooplankton heterotrophy and corroborates previous findings by Grottoli et al. (2014) that acclimatization and/or resilience to multiple bleaching events is independent of zooplankton heterotrophy for all three species.

Uniformity in zooplankton size and community composition captured among coral species within each year, irrespective of bleaching status, is consistent with findings from previous studies where the size and taxa of zooplankton captured were the same regardless of coral species, polyp size, morphology, and depth (Sebens et al. 1996; Palardy et al. 2005, 2006, 2008). As with other Caribbean corals (Sebens et al. 1996), the vast majority of zooplankton captured in this study were relatively large (>400 μm) and consisted of crab zoea, polychaetes, and copepods or were unidentified. Our data show that all three species of coral were selectively feeding on copepods, crab zoea, and polychaetes >400 μm independently of their abundance on the reef (Fig. 3; ESM Fig. S2). This contrasts with Pacific corals where ~70 % of the zooplankton captured were much smaller (<400 μm) and primarily amphipods, crab zoea, isopods, and larval shrimp (Palardy et al. 2006, 2008). Thus, the size and preferred taxa of zooplankton captured by corals appear to differ between Pacific and Caribbean species.

Some studies suggest that climate change will reduce zooplankton population abundances (Tada et al. 2003; Piontkovski and Castellani 2009). This may ultimately decrease the potential resilience of corals that increase their heterotrophic subsidies in response to a single bleaching event such as *P. astreoides* (this study) and *M. capitata* (Grottoli et al. 2006; Palardy et al. 2008). However, since none of the Caribbean species studied here displayed any heterotrophic plasticity following repeat bleaching (Fig. 2) and zooplankton represented <9 % of daily metabolic demand when corals were repeat-bleached (Grottoli et al. 2014) (Fig. 5d–f), any long-term changes in reef zooplankton abundance may have little to no effect on coral resilience to repeated bleaching stress.

Daily DOC fluxes

Throughout the study, non-bleached control *P. astreoides* and *O. faveolata* released DOC (Fig. 4f, i), consistent with findings from most previous studies of healthy non-bleached coral DOC fluxes (Crossland 1987; Wild et al. 2004, 2005, 2008, 2010a, b; Tanaka et al. 2008, 2009; Haas et al. 2010; Naumann et al. 2010; Levas et al. 2015). At the same time, non-bleached control *P. divaricata* took up DOC after the single bleaching event (Fig. 4c), just as did healthy *Pocillopora* sp., *Fungia sp.*, and *Stylophora pistillata* (Naumann et al. 2010; Tremblay et al. 2012). However, similar to *P. astreoides* and *O. faveolata*, non-bleached control *P. divaricata* released DOC during the remainder of the study (Fig. 4c). These findings further show that while DOC typically represents a loss of C from healthy corals, it can sometimes also be a source of C.

When singly bleached, all three species in this study took up DOC (Fig. 4c, f, i). While this is consistent with DOC uptake observed for bleached *P. lobata* (Levas et al. 2013), it contrasts with other findings of DOC release for bleached *Acropora* sp., *Porites* spp., and *S. pistillata* (Niggl et al. 2009; Haas et al. 2010). Naumann et al. (2010) inferred that DOC uptake in non-bleached corals was the result of heterotrophic microbial activity at the coral surface and not due to active uptake by the coral host. Conversely, Haas et al. (2010) hypothesized that DOC uptake in one species of stressed *Manicinia* was the result of active DOC ingestion by the coral in direct response to temperature stress. The plasticity of DOC flux observed in all three species in this study suggests that some species of bleached corals do take up DOC as a source of fixed C. The ability of singly bleached *P. divaricata*, *P. astreoides*, and *O. faveolata* to utilize DOC as a fixed C source could provide these corals with a significant advantage over species that are incapable of doing so when bleached.

After 11 months on the reef, singly bleached *P. astreoides* had recovered its DOC fluxes and released DOC (Fig. 4f). *Porites divaricata* DOC fluxes never differed from controls, indicating that DOC fluxes were not sensitive to bleaching in this species. However, both bleached and non-bleached *P. divaricata* displayed a seasonal pattern in their DOC fluxes that had not been previously observed—both had negative DOC flux in late summer (after single bleaching) and positive flux 11 months later in late spring/early summer (Fig. 4c). Only one species of healthy coral has shown significant seasonal differences in the magnitude of DOC release (Naumann et al. 2010), but with no change in the direction of DOC flux. These

findings suggest that DOC fluxes in these Caribbean corals are not only highly species specific and affected by seasonality, but also driven by the bleaching status of the coral.

Although all singly bleached corals took up DOC, all repeat-bleached corals released DOC to the same extent as the control corals (Fig. 4c, f, i). This suggests that repeat bleaching altered the capacity of corals to utilize DOC as a fixed C source. Thus, it appears that repeat-bleached corals are unable to obtain supplemental heterotrophic nutrition from either DOC (Fig. 4) or zooplankton feeding (Fig. 2), making them even more dependent on either energy reserves (Anthony et al. 2009; Grottoli et al. 2014) or shifts in *Symbiodinium* type (Thornhill et al. 2006; LaJeunesse et al. 2009; Grottoli et al. 2014) to survive annual bleaching events.

Contribution of DOC to animal respiration ($CHAR_{DOC}$)

Single bleaching

When singly bleached, *P. divaricata, P. astreoides*, and *O. faveolata* were able to supplement their C budget by taking up DOC as a source of heterotrophic C (Fig. 5a–c). With the large addition of $CHAR_{DOC}$, the overall CTAR budget for singly bleached *P. divaricata* was >100 % and no longer significantly different from non-bleached controls corals as was the case without $CHAR_{DOC}$ in Grottoli et al. (2014) (Fig. 5g). Other studies have shown that some species of corals are capable of taking up DOC when bleached or thermally stressed (Haas et al. 2010; Levas et al. 2013). Thus, DOC uptake can serve as a critical mechanism for some species to maintain their C budgets when singly bleached and to promote recovery from bleaching.

In contrast, the significant increase in zooplankton feeding (Fig. 2b) in singly bleached *P. astreoides* accounted for more than 140 % of its total C budget (Grottoli et al. 2014) (Fig. 5d), and the additional 10 % from $CHAR_{DOC}$ served to further magnify its C budget surplus (Fig. 5g). This large CTAR surplus most likely played a role in the rapid recovery of this coral from single bleaching (Grottoli et al. 2014). Similar dramatic increases in zooplankton feeding have also been observed in singly bleached Hawaiian *M. capitata* and resulted in CTAR < 100 % (Grottoli et al. 2006; Palardy et al. 2008) accompanied by rapid recovery of energy reserves, and maintenance of normal spawning rates the year following bleaching (Cox 2007). Therefore, increased zooplankton feeding is a strong mechanism for some species to maintain their C budgets when singly bleached and to promote recovery from bleaching.

Finally, singly bleached *O. faveolata* had low feeding rates (Fig. 3c) and were not able to make up for the C budget deficit through feeding on zooplankton (Fig. 5f) nor by taking up DOC as a fixed C source (Fig. 5c, i). Even were this species to gain a potential 8 % more CHAR from eating pico- and nano-plankton (Tremblay et al. 2012) or other sources such as sediment organic matter and particulate organic matter that were not measured here and may play a vital role in coral heterotrophy, it would not be sufficient additional heterotrophic C to bring its CTAR up to 100 % and meet daily metabolic demand. Of the three species, *O. faveolata* was also the only species that did not recover calcification rates and had increased levels of the *Symbiodinium trenchii* (ITS-type D1a) within 6 weeks following single bleaching (Grottoli et al. 2014). Thus, heterotrophy by *O. faveolata* cannot compensate for reduced CTAR due to dramatic decreases in photosynthesis during single bleaching (Grottoli et al. 2014). As such, prolonged periods of a deficient C budget could put this species at particular risk during long bleaching events.

Irrespective of the total C obtained by singly bleached corals, DOC represents a significant source of fixed carbon to these corals (Fig. 5a–c). $CHAR_{DOC}$ values ranged from 11 to 36 % and represented a greater source of heterotrophic carbon to singly bleached *P. divaricata* and *O. faveolata* than did zooplankton feeding (Fig. 5d–f). Alterations to the quantity, composition, and quality of coral reef DOC pools by climate change, as predicted by Brocke et al. (2015), could impact those corals that rely on DOC as a C source when singly bleached.

Repeat bleaching

Interestingly, all three species of corals lost DOC when repeat-bleached; $CHAR_{DOC}$ losses were greatest in *P. astreoides* and least in *P. divaricata* (Fig. 4c, f, i). These DOC loses exacerbated the C limitation already caused by significant declines in photosynthesis (Grottoli et al. 2014) and resulted in a decline in the CTAR of all three species. None of the repeat-bleached corals were able to meet metabolic demand (CTAR < 100 %) (Fig. 5g–i). Declines in CTAR values most likely contributed to the dramatic declines in energy reserves and calcification in both repeat-bleached *P. astreoides* and *O. faveolata* (Grottoli et al. 2014). Even though *P. divaricata* had the lowest CTAR values of all three species, the values did not differ between repeat-bleached and control fragments (Fig. 5g). In addition, this species had lower chlorophyll *a* levels after repeat bleaching (Schoepf et al. 2014) but was otherwise unaffected and maintained its endosymbiont density, high levels of energy reserves, and calcification rates (Grottoli et al. 2014), suggesting that *P. divaricata* obtained additional fixed C from a source that was not quantified in this study (possibly particulate organic carbon <50 μm). Coupled with the shuffling of its *Symbiodinium* (Grottoli et al.

2014) and the smallest $CHAR_{DOC}$ losses of all three species, *P. divaricata* appears to have several physiological traits that facilitate acclimatization to repeated bleaching stress. However, prolonged periods of a C deficiency could put species like *P. astreoides* and *O. faveolata* at particular risk of death in the future if bleaching events occur annually and are longer in duration. Overall, these findings add to the growing body of evidence that annual bleaching may lead to a decline in both *P. astreoides* and *O. faveolata* abundance, but that corals like *P. divaricata* could rapidly acclimatize and persist. While previous studies have suggested that some corals can acclimatize to bleaching events separated by several years (Maynard et al. 2008; Middlebrook et al. 2008; Bellantuono et al. 2012; Guest et al. 2012; McClanahan and Muthiga 2014), they have not shed light on coral responses to annual bleaching. This study is the first to show that at least one Caribbean coral could rapidly acclimate to annual bleaching, but that other species may be at risk of significant decline in the face of annual bleaching stress.

Implications

Our findings showed that DOC and zooplankton can represent significant sources of organic C for some bleached and healthy Caribbean corals. However, the proportionate contribution of DOC and zooplankton varied with bleaching status, bleaching frequency, seasons, and among species. While DOC was a critical source of organic C for singly bleached *P. divaricata* and zooplankton for singly bleached *P. astreoides*, neither contributed meaningfully to the C budget of repeat-bleached corals in any of the three species. In fact, DOC losses resulted in an increased C deficiency for repeat-bleached corals rather than mitigating resource limitation. This suggests that the capacity for heterotrophic plasticity (i.e., DOC uptake and zooplankton feeding) in corals is compromised under annual bleaching stress and that any climate change-driven changes in the quality or quantity of reef seawater DOC or zooplankton (Tada et al. 2003; Piontkovski and Castellani 2009; Brocke et al. 2015) are therefore not likely to have an impact on coral resilience to annual bleaching. This is in direct contrast to single isolated bleaching events where both DOC and zooplankton feeding can be vital to maintaining coral C budgets and promoting recovery (Grottoli et al. 2006, 2014; Palardy et al. 2008; Levas et al. 2013). Instead, other physiological variables such as energy reserves (Rodrigues and Grottoli 2007; Anthony et al. 2009; Grottoli et al. 2014) and *Symbiodinium* shuffling (Thornhill et al. 2006; LaJeunesse et al. 2009; Grottoli et al. 2014) are more likely to dictate which species or populations of species are expected to survive and persist in a future with annual bleaching.

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