The importance of zooplankton to the daily metabolic carbon requirements of healthy and bleached corals at two depths

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ABSTRACT

Bleached and non-bleached fragments of three species of Hawaiian corals were exposed to enhanced and ambient concentrations of zooplankton at 1 and 6 m depth to determine the contribution of zooplankton to the coral's daily carbon budget. The size and taxonomic grouping were recorded for every zooplankton captured and the relative input of zooplankton of different size classes was determined. The contribution of heterotrophy to animal respiration (CHAR) was calculated using an improved method that included the proportionate contribution of zooplankton from all size classes. Results show that the proportionate effects of species, depth and bleaching treatments on coral feeding rates were not significantly different between ambient and enhanced zooplankton concentrations. Corals captured the same size and assemblage of zooplankton under all evaluated conditions, and preferentially captured planters smaller than 400 μm. Feeding rates of *Porites lobata* increased with depth regardless of bleaching status. Feeding rates of *Porites compressa* increased with depth in non-bleached corals, but not in bleached corals. Within depth, feeding rates of bleached *Montipora capitata* increased, *P. compressa* decreased and *P. lobata* remained unchanged relative to non-bleached fragments. Therefore, the feeding response of corals to the same disturbance may vary considerably. Calculated CHAR values show that heterotrophic carbon from zooplankton plays a much larger role in the daily carbon budget of corals than previously estimated, accounting for 46% of some coral species' daily metabolic carbon requirements when healthy and 147% when bleached. Thus, heterotrophically acquired carbon made an important contribution to the daily carbon budget of corals under all experimental conditions. These results suggest that the relative importance of autotrophic and heterotrophic carbon to a coral's energetic needs is mediated by a coral's bleaching status and environment, and should be considered on a continuum, from 100% photoautotrophy to 100% heterotrophy.

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1. Introduction

Although healthy corals acquire fixed carbon from both heterotrophic and autotrophic sources, it is generally accepted that the majority of the carbon utilized by healthy corals is fixed by photosynthetic zooxanthellae (Muscatine and Porter, 1977; Grottoli and Wellington, 1999; Lesser et al., 2000; Houlbrèque et al., 2003). Since zooxanthellae cannot provide nitrogen, phosphorous, or many other nutrients (Titlyanov et al., 2000; Fitt and Cook, 2001), the coral host must replenish these through heterotrophic means.

Corals are known to have multiple heterotrophic inputs, including particulate organic matter (Rosenfeld et al., 1999; Anthony, 2000), bacteria (Sorokin, 1973; Ferrier-Pagès et al., 1998), and zooplankton (e.g., Yonge and Nicholls, 1931; Coles, 1969; Johnson and Sebens, 1993). In addition to providing nutrients, heterotrophically acquired carbon

may provide a substantial portion of a corals energetic demands when conditions are suboptimal for zooxanthellae photosynthesis. For example, increased heterotrophic intake has been observed in turbid water conditions (Anthony and Fabricius, 2000) and at increasing depths (Grottoli and Wellington, 1999; Palardy et al., 2005) for healthy corals. Additionally, some corals have been observed to increase heterotrophic intake while bleached (Grottoli et al., 2006).

Although several field studies have measured feeding rates on both enhanced (Sebens et al., 1996, 1998; Palardy et al., 2005) and ambient (Johannes and Tepley, 1974; Porter, 1974; Palardy et al., 2006) concentrations of natural zooplankton, only one has directly measured the importance of heterotrophic carbon acquisition to coral fixed carbon requirements (i.e., the contribution of heterotrophy to animal respiration; CHAR) under field conditions, and then only at a single depth (Grottoli et al., 2006). Three broad questions that remain unaddressed are: 1) How does the taxonomy and size of captured zooplankton change with depth and bleaching status? 2) What are the effects of artificially manipulated zooplankton availability on feeding patterns? And 3) Given that initial calculations by Grottoli et al. (2006)

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were limited to the 200-400 μm size class of zooplankton, resulting in a conservative estimate of CHAR, what is the total CHAR value when all size classes are included?

With elevated seawater temperatures corals may lose their dinoflagellate symbionts (e.g., Hoegh-Guldberg and Smith, 1989; Glynn and D'Croz, 1990; Hoegh-Guldberg, 1999). This breakdown of the positive interaction between alga and invertebrate renders the host pale or white in coloration, or bleached. Under bleached conditions, the amount of photosynthetically fixed carbon available to the host is reduced (e.g., Grottoli et al., 2006). To maintain metabolic demand during bleaching events, some coral species have been observed to consume stored energy reserves (Porter et al., 1989; Grottoli et al., 2004, 2006; Rodrigues and Grottoli, 2007), or increase heterotrophic intake (Grottoli et al., 2006). The general importance of heterotrophic intake to bleached corals, however, remains poorly understood.

Here, the effects of weakening (i.e., reduced photosynthetic input with increasing depth) and full breakdown (i.e., bleaching) of the coral-algal positive interaction on feeding rates, the size structure and community composition of plankton captured by, and CHAR values for *Montipora capitata*, *Porites compressa* and *Porites lobata* coral species was examined. Specifically, the following hypotheses were evaluated: 1) The size and taxonomy of captured zooplankton does not change with depth or bleaching. 2) Relative feeding rates of corals under different experimental conditions do not change with changing zooplankton concentrations. 3) At increasing depths or when bleached, corals increase heterotrophic input. Additionally, using detailed information about the assemblage of captured zooplankton, the contribution of heterotrophic intake to animal respiration (CHAR) was calculated to obtain an accurate estimate of the importance of zooplankton to coral fixed carbon requirements.

2. Methods

2.1. Study site and natural history

The experiment was carried out on three coral species at the Hawaii Institute of Marine Biology (HIMB), on Coconut Island, Kaneohe Bay, Hawaii, USA. Kaneohe Bay is a eutrophic tropical bay on the windward side of the island of Oahu, Hawaii. The rice coral, *M. capitata*, occurs in branching and plating coral morphologies (all fragments in this study were branching) with 0.8 mm polyps, ranging from dark to medium brown color and commonly observed to have beige to white tips. As its common name suggests, the finger coral, *P. compressa*, is a finger-like coral with 1.2 mm diameter polyps, ranging in color from yellow-brown to dark brown. The lobed coral, *P. lobata*, is a massive coral with polyps 1.3 mm in diameter that ranges in color from pale brown to green.

2.2. Experimental design

On 25-26 May 2004, five large, non-bleached colonies (genotypes) of *M. capitata* and *P. compressa* were identified at 2 m depth on the Point Reef of Coconut Island in Kaneohe Bay, HI, USA. Five large, non-bleached colonies (genotypes) of *P. lobata* were collected at 5 m depth on the outer reef of Kaneohe Bay. Twelve fragments were collected from each colony of each species for a total of 180 coral fragments (Fig. 1). Colonies were spaced a minimum of 2 m apart and chosen randomly. Since 45 colonies of *P. compressa* sampled on a nearby reef contained 43 genotypes (Hunter, 1993), we considered all colonies to have unique genotypes. Fragments were cemented to labeled 5 cm×5 cm Plexiglas plates using Splash Zone compound and placed in two outdoor flow-through tanks at HIMB. All tanks were covered with neutral density mesh to mimic photosynthetically active radiation (PAR) levels at 2 m depth. Incoming seawater was filtered to exclude zooplankton >50 μm. For 26 days (from 28 May 2004 to 23

Depth, Treatment
1 m, bl, nf
1 m, nb, nf
1 m, bl, az
1 m, nb, az
1 m, bl, ez
1 m, nb, ez
6 m, bl, nf
6 m, nb, nf
6 m, bl, az
6 m, nb, az
6 m, bl, ez
6 m, nb, ez

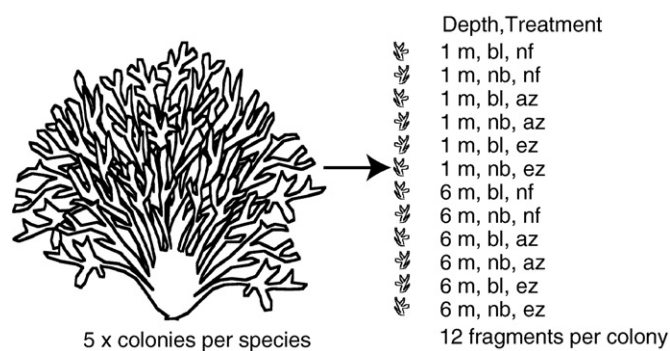5 x colonies per species   12 fragments per colony

Fig. 1. Schematic representation of the experimental design. Treatments: bl=bleached, nb=non-bleached, nf=not fed, az=ambient zooplankton, ez=enhanced zooplankton.

June 2004), seawater temperature in one tank was raised with aquarium heaters by ~2.5 °C above ambient to mimic a natural bleaching event (temperature 30.0±1.3 °C, average±SD), while the other tank (control treatment) remained at ambient seawater temperature (26.7±1.1 °C). At the end of an identical tank experiment in 2003, zooxanthellae concentrations in bleached *P. compressa* decreased to 14% of control levels but did not change significantly in *M. capitata* (Rodrigues and Grottoli, 2007). However, Chlorophyll *a* concentrations in bleached fragments of *M. capitata* decreased to 23% of control levels (Rodrigues and Grottoli, 2007).

On 23 June 2004, all of the coral fragments in the bleaching treatment were visibly bleached (i.e., completely white), while the control corals remained non-bleached (i.e., dark brown in color). Six control and six bleached fragments of each genotype were placed on the reef at 1 and 6 m depth (Fig. 1) for a minimum of 14 days to acclimate to natural environmental conditions (i.e., temperature and depth). Although the difference between treatment depths is not large, light attenuation within Kaneohe Bay is rapid. As such, corals at 6 m receive less than 42% of the photosynthetically active radiation received by corals at 1 m (Jokiel et al., 1997).

At noon for five consecutive days, 6-10 July 2004, three coral isolation chambers (described in Palardy et al., 2005) were fastened to the substrate at each of 1 and 6 m depth. Since flow has a strong effect on zooplankton capture rates (Johnson and Sebens, 1993; Sebens et al., 1998), chambers were oriented perpendicular to water flow. Ambient flow on the reef was unidirectional and low (<10 cm/s across all sampling periods). Flow rates within the feeding chambers were observed to be approximately 50% that of ambient flow rates.

Each day, a single genotype of each species was selected for experimentation (Fig. 1). Two randomly selected fragments (one non-bleached, one bleached) of each species were placed inside each feeding chamber. A single experimental chamber was used for bleached and non-bleached sample pairs to minimize error in supplying these chambers with identical concentrations of zooplankton. Thus, although strictly non-independent in analysis (Hurlbert, 1984), enclosing bleached and non-bleached samples in the same chamber reduced experimental error. Additionally, since the number of plankters captured by any coral fragment was several orders of magnitude smaller than the number of plankters introduced into the chamber, the samples can be considered biologically independent.

One hour after sunset, at each depth, the 'enhanced zooplankton' chamber was injected with >5×ambient concentrations of natural zooplankton that were concentrated using 50 μm nitex mesh (details in Palardy et al., 2005), the 'ambient zooplankton' chamber had its cover removed, allowing the coral fragments to feed on ambient concentrations of zooplankton at ambient flow, and the 'control' chamber was injected with seawater. All corals were visually inspected to ensure that the coral tentacles were expanded, then allowed to feed for 60 min. Coelenteron contents of 100 polyps each from the enhanced zooplankton and control chambers and 250 polyps

from the ambient zooplankton chambers were dissected under a dissecting microscope (20 to 100x power) by probing with a dissecting needle then scraping the skeleton to expose any remaining zooplankters. Prey larger than 50 μm were visible and generally identifiable. Since zooplankton were concentrated using 50 μm mesh, and because of the difficulty observing all zooplankton of this size captured, the contribution of microzooplankton (i.e., <50 μm) was not assessed. The number, size class (50-100 μm, 100-200 μm, 200-400 μm, 400-1000 μm, and >1000 μm) and taxonomy of zooplankton captured was recorded according to Palardy et al. (2005, 2006). Since it is considered to be more appropriate when comparing coral species of different morphologies (Edmunds and Gates, 2002), feeding rates were standardized to coral ash-free dry tissue mass (AFDTM).

Each night, while the corals were feeding, a vertical plankton tow from 6 m to the surface was taken using a 0.5-m diameter plankton net with 50 μm mesh. These plankton, collected within 10 m of the experimental site, were then passed through a columnar sieve, with 1000 μm, 400 μm, 200 μm, 100 μm and 50 μm filters, and preserved in a 10% formalin solution. These size-fractionated samples were later sorted and counted according to broad taxonomic groups (i.e., isopods, amphipods, copepods, crab zoeae, polychaetes, shrimp, and unidentifiable). Although not completely accurate representations of the zooplankton community immediately above the coral feeding surfaces, these tows provide a reasonable estimate of the local zooplankton community.

Using plankton capture data plankton tows, a maximum-likelihood estimator (Chesson, 1978) of Manly's measure of preference (Manly et al., 1972) was used to test whether particular sizes or taxa of prey were over-represented in the coral diet. The index was calculated for all size classes (m=5) and identified taxa (m=6) according to the formula:

$$\alpha_i = \frac{r_i/n_i}{\sum\limits_{j=1}^{m} r_j/n_j} , i = 1, \dots, m \tag{1}$$

where r_i is the proportion of plankton of type i captured by the coral (determined by the dissection of corals exposed to ambient plankton and flow), n_i is the proportion of plankton of type i available for capture (determined by plankton tows), and j refers to values of i. The value α_i represents the proportion of zooplankton of type i that would be captured if all food types were available in equal quantities. Observed values of α_i were tested against expected values that assumed no capture preference (i.e., $\alpha_i = 1/m$).

To determine per-plankter AFDTM for all size classes and taxa, size-fractionated samples from plankton tows were sorted into taxonomic groups (as above), rinsed in deionized water, dried at 60 °C for a minimum of 48 hours, and weighed in pre-burned aluminum pans to the nearest 1 μg. These pans were then burned at 450 °C for 6 hours, and re-weighed. Per-plankter AFDTM is the difference in mass between measurements, divided by the number of plankton in the sample. For 2 taxa, per-plankter AFDTM was not available in the 50-100 μm size class. Missing values were estimated with a log-linear least-squares model that assumed constant allometric growth among size classes (i.e., the scaling exponent did not change with zooplankton size). The estimate produced by this model was then reduced by 25% to ensure a conservative estimate of heterotrophically acquired carbon.

Using the per-plankter AFDTM values and observed size and taxon specific feeding rates of corals exposed to ambient flow and plankton, the contribution of heterotrophically acquired carbon to animal respiration (CHAR) (Grottoli et al., 2006) was calculated. Since the capture of plankters >1000 μm was rare and disproportionately increased CHAR estimates, these captures were counted as captures in the 400 – 1000 μm size class to ensure a conservative calculation. CHAR was calculated for shallow fragments of all coral species using the respiration rates for each species reported in Rodrigues and Grottoli (2007).

2.3. Statistics

2.3.1. Size and taxonomy of captured zooplankton

Zooplankton captured by coral fragments exposed to ambient flow and zooplankton were converted into proportions by taxon and size. These proportional assemblage data were arcsine-square root transformed and tested for differences across species, depth and bleaching treatment with factorial MANOVA. No differences in the composition of zooplankton captures by either taxon or size were found among species, depths or bleaching treatments. Thus, data were pooled among experimental treatments, and the data analyzed with one-way ANOVAs and Tukey tests to determine if the proportion of captured zooplankton varied among size classes and taxa.

These pooled data were also used to calculate feeding preferences for each zooplankton taxa and size according to Manly et al.'s (1972) measure of preference. Hotelling T^2 tests were used to test for differences among size classes and taxa. Where significance was found, t-tests corrected for multiple comparisons (Benjamini and Hochberg, 1995) were used to determine capture preference with respect to plankton size and taxa.

2.3.2. Feeding rates

A t-test determined that the feeding rate of unfed control corals was not significantly different from 0. As such, these data were not used in further analysis, and capture rates of experimental fragments were not adjusted to compensate for prior feeding. Partially-nested four-way mixed-model ANOVAs on Box-Cox power transformed data tested the effects of species, genotype (nested within species), depth and bleaching and all interactions of the main factors on coral feeding rates per gram AFDTM when exposed to enhanced and ambient concentrations of natural zooplankton. Genotype effects were not significant (p>0.35), and the data were therefore re-analyzed as factorial three-way mixed-model ANOVAs. A factorial two-way mixed-model ANOVA tested the effects of species and bleaching on CHAR of corals from 1 m depth. Within effects of all ANOVAs, a posteriori Tukey tests were used to determine pairwise differences. Where pairwise differences of >25% were not found to be significant, power analyses were conducted to determine the minimum detectable effect size (MDES).

To test if the direction and relative magnitude of changes in feeding rates were similar among species, depth and bleaching between corals fed enhanced and ambient concentrations of zooplankton, feeding rates for all treatments were standardized within species to shallow, non-bleached fragments. These data were transformed with a Box-Cox power transformation and used to test for effects of species, depth, bleaching, and feeding treatment with a factorial 4-way mixed-model ANOVA.

In all statistical models, depth, bleaching and feeding treatments were considered fixed effects while species was considered a random effect. Following transformation where applicable, residuals for feeding rates, captured assemblage and size classes were normally distributed according to the plots of the residuals versus predicted values for each variable. All analyses were conducted in R version 2.5.1 (R Development Core Team, 2007), and all null hypotheses were rejected for p≤0.05.

3. Results

3.1. Unfed controls

A total of two zooplankton, both largely digested and unidentifiable, were found in the coelenterons of unfed control coral polyps, less

Table 1
Factorial MANOVA assessing the effects of coral species, depth and bleaching status on the composition of captured zooplankton by size and taxa

Source	Zooplankton Size			Zooplankton Taxa		
	DF	V	p	DF	V	p
Species	10, 86	0.169	0.39	8, 92	0.923	0.52
Depth	5, 42	0.077	0.49	4, 45	1.521	0.20
Bleaching	5, 42	0.072	0.52	4, 45	1.179	0.34
Species*Depth	10, 86	0.056	0.95	8, 92	1.447	0.17
Species*Bleaching	10, 86	0.166	0.41	8, 92	1.043	0.41
Depth*Bleaching	5, 42	0.204	0.08	4, 45	0.923	0.48
Species*Depth*Bleaching	10, 86	0.142	0.54	8, 92	0.908	0.53

Data are from corals exposed to ambient flow and zooplankton concentrations. V is the value of Pillai's trace statistic, DF is degrees of freedom.

than 1% of that eaten by experimentally fed corals, and not significantly different from 0 (t-test, 57 df, p=0.15). Therefore, the coral isolation chambers were effective at excluding ambient zooplankton, and fed corals ate only zooplankton provided for them.

3.2. Size and taxa of captured zooplankton

The size of zooplankton captured when exposed to ambient flow and zooplankton concentrations did not significantly differ by species, depth, or bleaching (Table 1). As such, all data were pooled. The size of captured zooplankton was overwhelmingly dominated by plankters <400 μm (Fig. 2a). Plankters 200-400 μm, 100-200 μm and 50-100 μm accounted for 57%, 21% and 12% respectively, of all captures (Fig. 2a).

Proportional assemblages of zooplankton taxa captured did not significantly differ by species, depth, or bleaching status (Table 1). As such, all data were pooled to create an average assemblage of captured zooplankton by taxa (Fig. 2b). The captured assemblage was dominated by amphipods, crab zoeae and shrimp nauplii, accounting for 33%, 31% and 27% of all captured zooplankton, respectively (Fig. 2b).

Preference values for both plankton size class (Hotelling T^2=507.4, 5,4 DF, p<0.01) and taxon (Hotelling T^2=369.4, 6,4 DF, p<0.01) were found to be significant. Univariate analyses revealed that corals captured significantly more plankton between 100 μm and 400 μm and significantly less plankton greater than 400 μm than expected under the null hypothesis of no size preference (Fig. 2c, Table 2). Analyses also determined that significantly fewer isopods and copepods, and significantly more amphipods, crab zoeae and shrimp were captured than expected under the null hypothesis of no taxon preference (Fig. 2d, Table 2).

3.3. Feeding rates: enhanced zooplankton

Within species, feeding rates in non-bleached corals did not significantly change with depth in *M. capitata*, but increased by 69% and 44% in *P. compressa* and *P. lobata*, respectively (Tukey test, Fig. 3a, b). In bleached corals, feeding rates of *M. capitata* and *P. compressa* did not change with depth, while feeding rates in bleached *P. lobata* were 39%
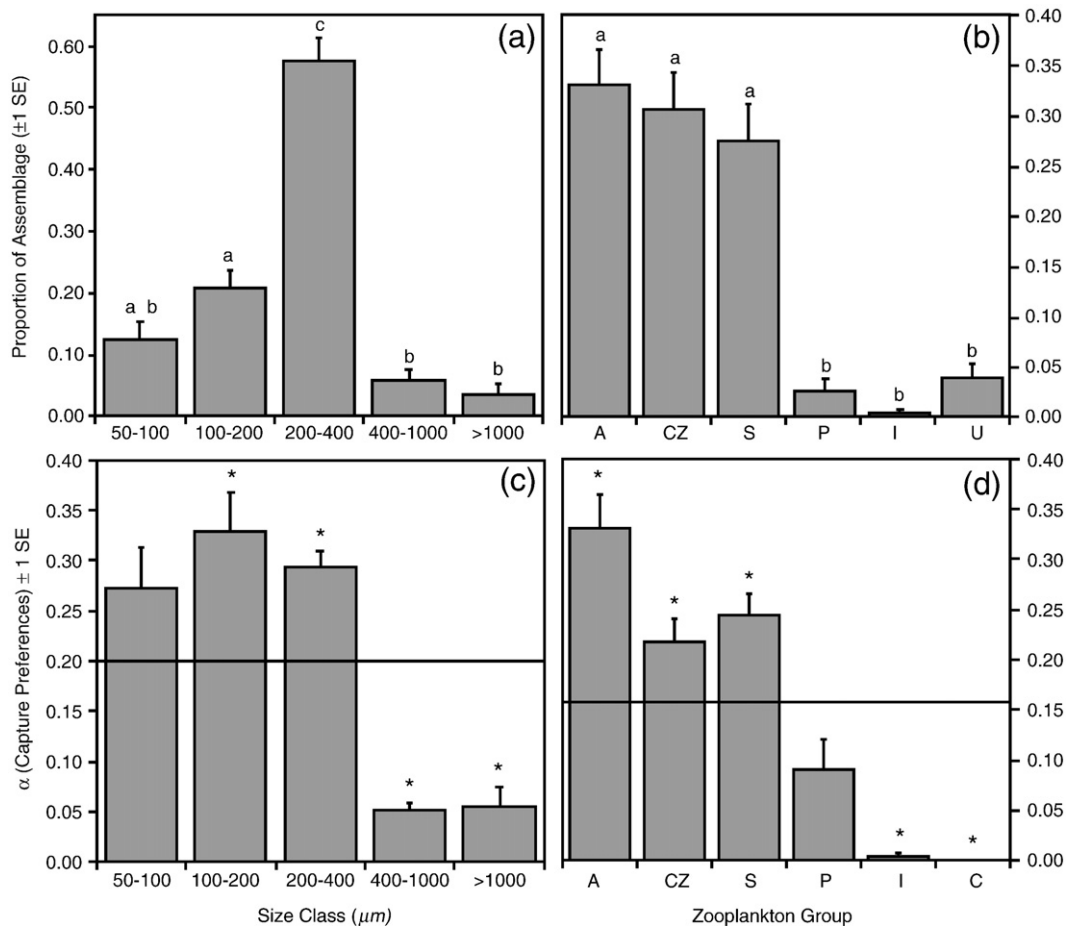

Fig. 2. Size and taxonomy of zooplankton assemblage captured by corals exposed to ambient concentrations of zooplankton. (a) Size of captured zooplankton. (b) Taxa of captured zooplankton. (c) Capture preference by zooplankton size. (d) Capture preference by zooplankton taxa. In all panels, values are averages±1 standard error pooled across all coral species. Zooplankton groups: A=amphipods, CZ=crab zoeae, S=shrimp, P=polychaetes, I=isopods, U=unidentified, C=copepods. Letters above bars (a, b) indicate significant differences in capture proportion among taxa and size classes (Tukey tests, p<0.05, n=60). Horizontal lines (c, d) indicate values expected under the null hypothesis of no preference. * indicates significant differences from the null hypothesis (t-tests, p<0.05, n=60).

Table 2
T-tests assessing coral preferences for zooplankton by size and taxa

Size Class	t	DF	P	Taxon	t	DF	P
50-100	1.74	4	0.16	**Amphipods**	4.87	4	**0.02**
100-200	3.39	4	**0.03**	**Isopod**	-45.25	4	**<0.01**
200-400	5.85	4	**0.01**	**Crab zoea**	3.11	4	**0.04**
400-1000	-19.62	4	**<0.01**	Polychaete	-2.32	4	0.08
>1000	-7.30	4	**<0.01**	**Shrimp**	3.72	4	**0.03**

Captures were pooled among species and depth treatments of coral fragments exposed to ambient zooplankton and flow. t is the value of the t statistic, DF is degrees of freedom. P-values were corrected for multiple comparisons according to Benjamini and Hochberg (1995). Bold type indicates p<0.05.

greater in corals at 6 m than at 1 m (Tukey tests, Fig. 3a, b). Overall, feeding rates differed between bleached and non-bleached corals, with *M. capitata*<*P. compressa*<*P. lobata* in non-bleached corals, and *P. compressa*<*M. capitata*<*P. lobata* in bleached corals (Tukey tests, Fig. 3a, b). Bleached fragments of *M. capitata* fed 148% and 291% more than non-bleached fragments at 1 m and 6 m, respectively (Tukey test, Fig. 3a, b). Conversely, bleached fragments of *P. compressa* fed 54% and 69% less than non-bleached fragments, at 1 and 6 m, respectively (Fig. 3a, b). Feeding rates among bleached and non-bleached fragments of *P. lobata* did not differ at either depth (Tukey test, Fig. 3a, b).

3.4. Feeding rates: ambient zooplankton

Within fragments exposed to ambient zooplankton concentrations, statistical inference on absolute differences in feeding rates was restricted by considerably higher variance than observed in similar experiments (Palardy et al., 2006) used in power analyses to design the experiment. However, the direction and proportionate effect size of species, bleaching, and depth treatments on feeding rates were not statistically significantly different between zooplankton concentrations (i.e. enhanced or ambient) (Table 4; p>0.15 for all factors containing 'Zooplankton Concentration'). In other words, the concentration of zooplankton had no significant effect on the proportionate effects of species, depth, or bleaching.

Within *M. capitata*, and *P. compressa*, feeding rates in non-bleached corals did not change with depth. For *P. lobata,* changes in observed average feeding rates for non-bleached corals were not significantly different between depths (observed change 45%, power 0.13, Minimum Detectable Effect Size (MDES) 57% change) (Fig. 3c, d, Table 5). In bleached corals, average feeding rates of *M. capitata* and *P. compressa* did not change with depth. For bleached *P. lobata*, changes in observed average feeding rates were not significantly different between depths (observed change 42%, power 0.08, MDES 61% change) (Fig. 3, c,d, Table 5). Relative to feeding rates in non-bleached fragments at 1 and 6 m, bleached fragments of *M. capitata* fed 338% and 319% more,
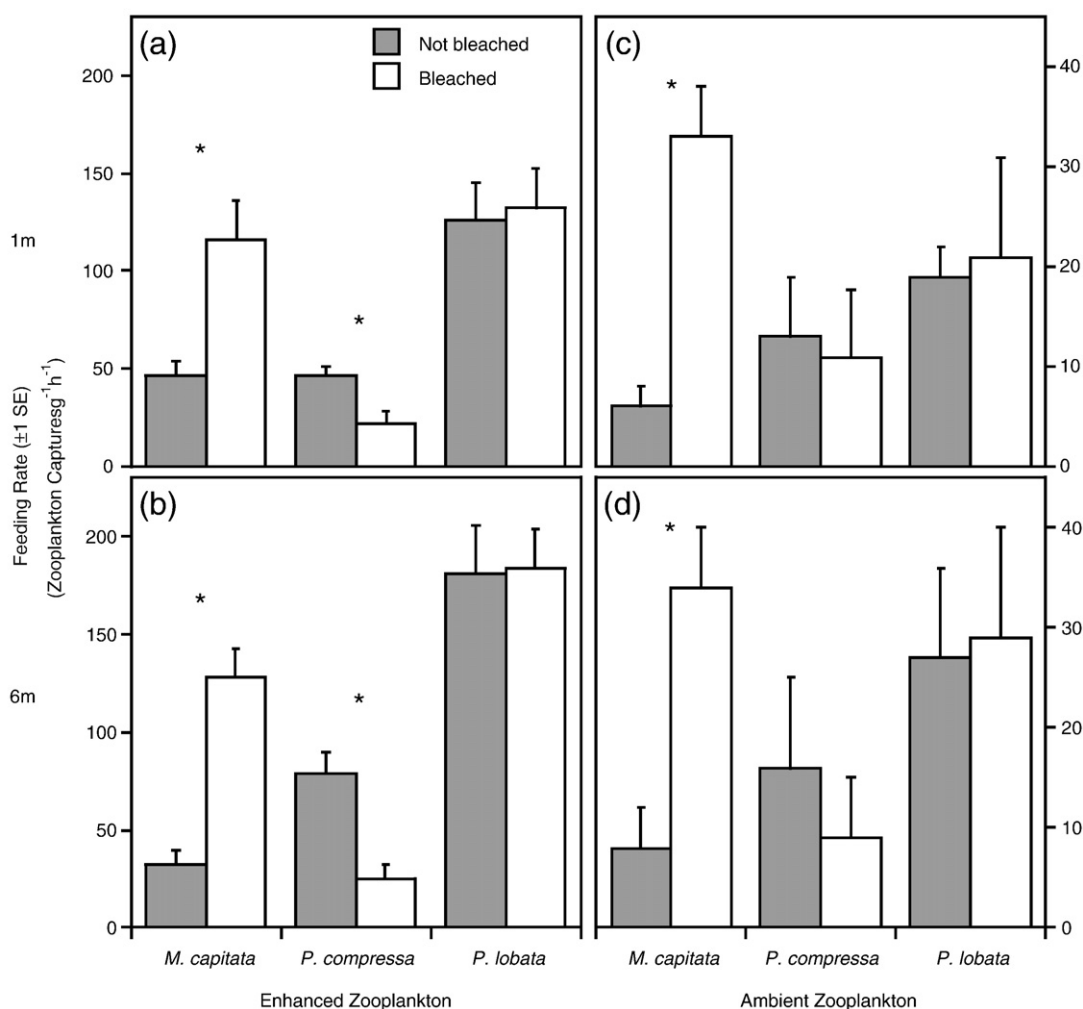

Fig. 3. Average feeding rate per gram ash free dry tissue mass (AFDTM) per hour+1 standard error for *Montipora capitata*, *Porites compressa* and *Porites lobata* fed enhanced zooplankton at (a) 1 m and (b) 6 m, and fed ambient zooplankton at (c) 1 m and (d) 6 m. Sample size is 5 in each case. * indicates significant differences between bleached and non-bleached corals within species and depth treatments (Tukey tests, p<0.05). Significant differences were also detected between corals fed enhanced zooplankton at 1 and 6 m within species and bleaching treatments as follows: non-bleached *P. compressa* 1 m<6 m, non-bleached *P. lobata* 1 m<6 m, and bleached *P. lobata* 1 m<6 m (Tukey tests, p<0.05).

respectively (Fig. 3, c,d, Tukey tests, p<0.05). For *P. compressa*, observed changes in feeding rates for bleached and non-bleached fragments were not statistically significantly different (bleached: observed change 25%, power 0.06, MDES 79% change. Non-bleached: observed change 50%, power 0.08, MDES 71%) (Fig. 3, c,d, Table 5). Feeding rates of *P. lobata* did not change at either depth when bleached (Fig. 3, c, d).

Feeding rates show statistically significant differences among species exposed to ambient levels of zooplankton with non-bleached *M. capitata*<*P. compressa*<*P. lobata* and bleached *P. compressa*<*P. lobata*<*M. capitata*, leading to a statistically significant species by bleaching interaction effect (Table 3, Fig. 3).

3.5. Contribution of heterotrophy to animal respiration (CHAR)

When accounting for zooplankton captures of all size classes, CHAR for all coral species were much higher than the estimates of Grottoli et al. (2006) (Fig. 4). For non-bleached fragments of *M. capitata*, heterotrophy accounted for 18% of daily metabolic carbon (DMC) requirements, significantly less than for bleached fragments, wherein heterotrophy accounted for 147% of DMC (Fig. 4, Table 6). For *P. compressa* and *P. lobata*, CHAR did not significantly differ between bleached and non-bleached fragments (Fig. 4, Table 6). On average, heterotrophic intake accounted for 39% and 40% of DMC in *P. compressa* and *P. lobata*, respectively (Fig. 4).

4. Discussion

4.1. Size and taxonomy of captured zooplankton

Since the assemblage and size of zooplankton captured did not change with species, bleaching, or depth, differences in feeding rates among species were not due to innate abilities to capture a more diverse assemblage or different size classes of zooplankton. This result is consistent with those obtained by Sebens et al. (1996) and Palardy et al. (2005, 2006) where size and taxonomy of zooplankton captured by corals from the same site were not different, despite differences in polyp size, depth, and overall coral morphology. Instead, changes in feeding effort were likely responsible for changes in capture rate with depth (Palardy et al., 2005; this study) and bleaching (Fig. 3).

There was a strong bias among corals to capture relatively small zooplankton, with fewer than 10% of all captures >400 μm (Fig. 2a). Likewise, the concentration of planters in the 200-400 μm size class explained greater than 65% of the variance in feeding rates of *Pocillopora damicornis* and *Pavona gigantea* in the Gulf of Panamà (Palardy et al., 2006). In addition to size class, the assemblage of captured zooplankton observed in this study (Fig. 2b) was similar to the community captured by the corals *P. damicornis*, *P. gigantea*, and *Pavona clavus* in Panamà. Amphipods, crab zoeae, and shrimp nauplii accounted for >90% of all captures in Hawaiian (Fig. 2b), and >80% in
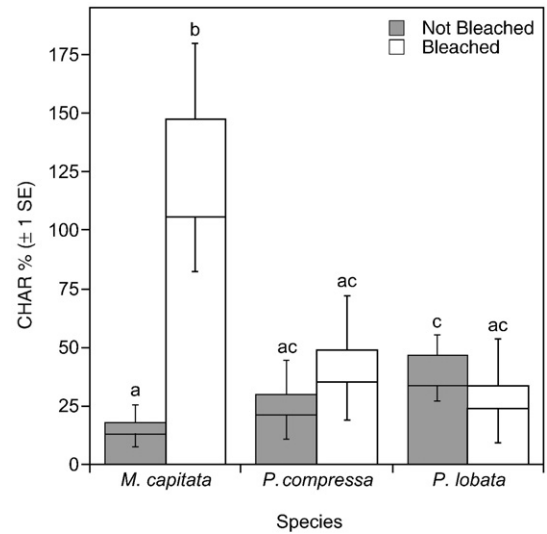

Fig. 4. Contribution of heterotrophically acquired carbon to animal respiration (CHAR)±1 standard error for *Montipora capitata*, *Porites compressa* and *Porites lobata*. Internal bars assume all plankton captured were 200 - 400 μm (Grottoli et al., 2006), external bars reflect all observed capture sizes (this study). Letters above the error bars indicate significant differences among means as determined by a posteriori Tukey tests.

Panamanian corals (Palardy et al., 2005). In each location, these taxa were observed to have relatively poor swimming abilities and were over-represented in captured assemblages when compared to net tows (Palardy et al., 2005; Fig. 2c). Together, these observations suggest that corals, including those with much larger polyps (Sebens et al., 1996), are unable to capture considerable numbers of highly motile taxa such as copepods (Fig. 2d), typically the most abundant group of zooplankton on coral reefs (Heidelberg et al., 2004).

4.2. Feeding rates

The direction and proportionate effect size of coral species, depth, and bleaching treatments, were not statistically different under ambient and enhanced zooplankton concentrations in Hawaii (Table 4). Additionally, the magnitude of depth effects were similar to the results of experiments conducted in Panama (Palardy et al., 2006). This suggests that qualitative conclusions based on data from

Table 3
Mixed model ANOVA assessing the effects of species (random effect), depth and bleaching status (fixed effects) on feeding rates per gram dry weight coral tissue

Source	DF	Enhanced		Ambient	
		SS	p	SS	p
Species	2	89636.90	**<0.01**	1579.61	**0.04**
Depth	1	3877.70	0.28	132.28	0.41
Bleaching	1	1249.41	0.82	632.94	0.52
Species×Depth	2	3508.81	0.08	252.91	0.57
Species×Bleaching	2	35271.00	**<0.01**	2161.97	**0.01**
Depth×Bleaching	1	2.08	0.96	0.61	0.65
Species×Depth×Bleaching	2	1583.63	0.30	4.50	0.99
Residual	46	29548.70		10058.07	

Coral fragments were exposed to ambient or enhanced concentrations of natural zooplankton. Bold type indicates p<0.05. DF is degrees of freedom, SS is sum of squares.

Table 4
A mixed model ANOVA assessing the effects of species (random effect), depth, bleaching status, and zooplankton concentration (ZC) (i.e. ambient or enhanced concentrations) (fixed effects) on feeding rates standardized within species to shallow, non-bleached fragments

Source	DF	SS	F	P
Species	2	7.82	7.95	**<0.01**
Depth	1	0.61	1.49	0.35
Bleaching	1	0.55	0.07	0.82
Zooplankton Concentration (ZC)	1	0.82	5.29	0.15
Species×Depth	2	0.82	0.83	0.44
Species×Bleaching	2	16.67	16.95	**<0.01**
Species×ZC	2	0.31	0.32	0.73
Depth×Bleaching	1	0.00	0.03	0.88
Depth×ZC	1	0.37	1.64	0.33
Bleaching×ZC	1	0.01	0.02	0.90
Species×Depth×ZC	2	0.45	0.46	0.63
Species×Depth×Bleaching	2	0.67	0.68	0.51
Species×Bleaching×ZC	2	0.96	0.98	0.38
Depth×Bleaching×ZC	1	0.14	3.11	0.22
Species×Depth×Bleaching×ZC	2	0.09	0.09	0.91
Residual	91	44.75		

The data were Box-Cox power transformed to meet the assumptions of ANOVA. Bold type indicates p<0.05. DF is degrees of freedom, SS is sum of squares.

Table 5
Results of a mixed model ANOVA assessing the effects of species (random effect) and bleaching status (fixed effect) on CHAR

Source	SS	DF	F	P
Species	22247.32	2	0.41	0.71
Bleaching	28931.83	1	1.06	0.41
Species×Bleaching	54216.90	2	7.84	**<0.01**
Residual	174007.53	28		

Bold type indicates p<0.05. DF is degrees of freedom, SS is sum of squares.

the enhanced zooplankton treatment should be valid for corals exposed to ambient zooplankton concentrations.

For five pairwise comparisons of coral fragments feeding on ambient zooplankton, observed changes in feeding rates ≥25% were not statistically significantly different (Fig. 3). The same comparisons, for coral fragments feeding on enhanced zooplankton concentrations were all statistically significant, and displayed similar proportionate changes (Table 4). Moreover, the magnitude of the observed difference for each pairwise comparison was similar to independently reported responses from direct (Palardy et al., 2005, 2006) or indirect (Grottoli and Wellington, 1999; Rodrigues and Grottoli, 2006) measures of heterotrophic response to depth or bleaching. As such, though they were not statistically significantly different, it is likely that the changes observed between these pairwise comparisons (Table 5) are biologically relevant.

Therefore, given the low power and high variance of results of corals feeding on ambient zooplankton concentrations, experiments designed to investigate effects of environmental or morphological factors on feeding rates should use experimentally enhanced zooplankton concentrations to minimize dissection time and increase sample size. However, experiments designed to assess energy or carbon budgets, absolute feeding rates and/or CHAR (Grottoli et al., 2006), must allow corals to feed under natural conditions, despite requiring larger sample sizes to achieve suitable statistical power.

Coral feeding rates of non-bleached *P. compressa* and *P. lobata* increased with increasing depth (Fig. 3a, b; Tukey tests) despite feeding on the same community and size class of zooplankton (Table 1). This indicates that many shallow corals do not maximize heterotrophic intake when healthy. Instead, the results further suggest the plasticity of feeding rates (Anthony, 2000; Anthony and Fabricius, 2000; Grottoli, 2002; Palardy et al., 2005), and support the hypothesis that feeding rates increase with depth to compensate for a reduction in photosynthetically derived carbon (Porter, 1976; Muscatine et al., 1989; Grottoli and Wellington, 1999; Palardy et al., 2005). Since there was no change in the captured zooplankton assemblage with depth, increased feeding rates do not result from changes in feeding technique or ability, but likely in changes in feeding effort.

Coral feeding rates also varied when bleached (Fig. 3). The >140% increase in feeding rates in bleached *M. capitata* suggests that this species is capable of dramatic trophic plasticity under stress. It also implies that coral reef conservation plans should encompass the ecosystem as a whole and consider the impact of plankton population densities on coral survival. With the expected increase in frequency and intensity of bleaching events (e.g., Hoegh-Guldberg, 1999; Donner et al., 2007), the fate of coral species such as *M. capitata* that rely on increased heterotrophic input when bleached will depend on the health of the reef's plankton.

In contrast to the large increase in feeding rates in *M. capitata*, *P. compressa* fed an average of 46% less (across zooplankton concentrations) when bleached (Fig. 3). This observation is supported by stable isotope analysis, which indicates a decrease in the quantity of heterotrophic carbon obtained by bleached *P. compressa* (Rodrigues and Grottoli, 2006). Since *P. compressa* demonstrated heterotrophic plasticity with depth and captured similar sizes and assemblages of plankton when bleached and healthy, it is likely that the reduced

feeding levels of bleached *P. compressa* are the result of decreased feeding effort and not decreased feeding ability. This may indicate a substantial cost of feeding in *P. compressa* that is heightened under bleached conditions.

Unlike *M. capitata* and *P. compressa*, bleaching did not have an effect on feeding rates of *P. lobata* (Fig. 3). However, since *P. lobata* increased its feeding rate by an average of 30% with depth across zooplankton concentrations regardless of bleaching status, feeding effort appears to be independent of bleaching status.

Overall, it appears the mechanisms underlying the control of coral feeding effort differs between coral species, and can be influenced by depth (Palardy et al., 2005; this study), light levels (Anthony, 2000; Anthony and Fabricius, 2000), bleaching status (Grottoli et al., 2006; this study), or some combination of these factors (this study). Thus, changes in feeding effort may be related to metabolic need, the relative costs of the mechanics of zooplankton capture, or physiological changes (e.g., quantities of stored energy reserves), or some combination of all three, that vary with depth, seasonality, and bleaching.

When healthy, feeding rates at both depths (Fig. 3) and CHAR values (Grottoli et al., 2006; Fig. 4) were highest in the mounding coral *P. lobata* (low surface to volume (S/V) ratio), followed by the branching corals *P. compressa* (mid S/V), and *M. capitata* (high S/V). These observations are consistent with the results of stable isotopic analysis of *M. capitata* and *P. compressa* at the same field site (Rodrigues and Grottoli, 2006). As such, the importance of feeding to the intake of carbon in these corals appears to vary with the surface/volume (S/V) ratio (sensu Porter, 1976) when healthy. However, the dramatic increase in feeding rates (Fig. 3) and CHAR (Grottoli et al., 2006; Fig. 4) of bleached *M. capitata* clearly indicates that feeding rates are not driven by a coral colony's innate ability to capture plankton but its effort in doing so. In other words, some coral species are capable of increasing feeding rates when bleached because of increased feeding effort, irrespective of polyp size and/or colony morphology. These results are consistent with the plasticity in feeding rates observed for three other species of corals at two depths in the Gulf of Panama (Palardy et al., 2005).

Because of the tedious and labor intensive nature of obtaining capture rates by corals under ambient plankton concentrations, few data exist or have been published, and efforts have been made to develop stable isotope proxies for feeding (Felis et al., 1998; Grottoli and Wellington, 1999; Grottoli, 2002; Rodrigues and Grottoli, 2006). Since zooplankton are isotopically depleted relative to corals, increases in heterotrophic carbon should result in decreased coral and skeletal $\delta^{13}C$. The feeding rates observed across depths for each coral in the present study mirrors $\delta^{13}C$ data from these same species, at similar depths and at the same location (Grottoli, 1999). In light of these results, skeletal $\delta^{13}C$ appears to be a strong indicator of the relative contribution of heterotrophic carbon with depth in non-bleached corals. However in bleached corals, this relationship is more complex. Skeletal isotopic decreases were observed in moderately bleached corals (Grottoli et al., 2004) but not in severely bleached

Table 6
Absolute and relative carbon sources for *M. capitata*, *P. compressa* and *P. lobata*: the contribution of heterotrophy to animal respiration (CHAR), the contribution of zooxanthellae to animal respiration (CZAR), and the relative importance of carbon from heterotrophy (H %)

Species	Bleached?	CHAR	CZAR	H %
M. capitata	No	17.95	132.78	11.91
M. capitata	Yes	147.25	41.34	78.08
P. compressa	No	29.75	146.89	16.84
P. compressa	Yes	48.83	74.38	39.63
P. lobata	No	46.57	140.79	24.85
P. lobata	Yes	33.39	96.25	25.76

Values are averages for 1 m corals exposed to ambient flow and zooplankton. CZAR values are from Grottoli et al. (2006).

corals due to significantly decreased calcification rates (Rodrigues and Grottoli, 2006). Thus, skeletal δ¹³C can be used as a reliable indicator of coral feeding in healthy and moderately bleached corals where calcification rates are maintained, but not in severely bleached corals. In the case of severely bleached corals, direct measurements of coral feeding are the only reliable way to quantify feeding rates.

4.3. Heterotrophy and carbon inputs

By taking into account zooplankton captures from all size classes, CHAR for all coral species was much higher (39%) than initial, conservative estimates by Grottoli et al. (2006). These revised estimates are more comprehensive, enhance previous results, and further emphasize that heterotrophic carbon is a major source of carbon for both bleached and healthy corals. For example, zooplankton captured by healthy colonies of *P. compressa* and *P. lobata* provided over 30% and 47%, respectively, of daily metabolic carbon (DMC) requirements, without accounting for bacteria, particulate organic matter, or microzooplankton capture, which alone has been shown to account for over 8% of daily metabolic energy requirements in some coral species (Houlbrèque et al., 2004).

The use of CHAR at the fragment or colony scale may overlook the point-source nature of zooplankton capture. Variation in the number of plankton captured by each polyp will be great, and individual polyps will be limited by the ability of coral colonies to share resources. Thus, in addition to net heterotrophic intake, the ability to transfer nutrients among polyps is likely to be a major factor in successful long-term energy reserve maintenance. With bleaching events predicted to increase in both frequency and duration (Hoegh-Guldberg, 1999; Hughes et al., 2003; Donner et al., 2007), the ability to transfer nutrients between polyps may be placed under selection.

Because these experiments were not replicated across flow regimes, caution should be taken when generalizing these results. Flow effects the fundamental processes associated with CHAR, including rates of feeding (Johnson and Sebens, 1993; Sebens et al., 1998) and respiration (Bruno and Edmunds, 1998; Patterson et al., 1991; Sebens et al., 2003). Therefore, the importance of heterotrophy to carbon budgets may change across different flow regimes as corresponding feeding and metabolic rates are expected to change.

Zooxanthellae are known to provide >100% of DMC requirements for many non-bleached corals (Muscatine et al., 1984; Edmunds and Davies, 1989), including all three species examined in this paper (Grottoli et al., 2006). However, corals may exude over 40% of this photosynthetically derived carbon as mucus (Crossland et al., 1980; Wild et al., 2004). Additionally, photosynthetically acquired carbon appears to be consumed by cnidarians more rapidly and incorporated into fewer tissues than heterotrophic carbon (Bachar et al., 2007). As such, our data suggest that the importance of heterotrophy to corals is likely understated in the literature. Experiments that track the fate of both heterotrophic and autotrophic carbon in multiple coral species are required to determine if this is the case.

Since both CHAR (this study) and the contribution of zooxanthellae to animal respiration (CZAR; e.g., Muscatine et al., 1984; Edmunds and Davies, 1989; Grottoli et al., 2006) exhibit a great deal of variability across experimental treatments, total carbon budgets are likely to be variable in natural environments. Since feeding rates are observed to increase under conditions that minimize photosynthesis [including increased depth (Palardy et al., 2005; this study), turbidity (Anthony and Fabricius, 2000), and bleaching (Grottoli et al., 2006; this study)], energy and carbon budgets should incorporate both heterotrophic and autotrophic carbon inputs whenever possible.

To assess the importance of zooplankton heterotrophy to a coral's daily carbon demand, we determined the percentage of CHAR relative to the total carbon input (i.e., CHAR+CZAR) for bleached and non-bleached fragments of *M. capitata*, *P. compressa*, and *P. lobata* (H% in Table 6). On a scale from 0 to 100%, the percentage of carbon derived from heterotrophy varies with both CHAR and CZAR as environmental conditions change. Although these data indicate that zooxanthellae provide the majority of fixed carbon in healthy corals, they denote the importance of including heterotrophy in energy and carbon calculations for both bleached and non-bleached corals. Despite excluding micro-zooplankton, bacteria and particulate organic matter, and using very conservative CHAR calculations, the percent contribution of heterotrophy to coral total daily carbon intake ranged from 12-25% in non-bleached corals and from 25-78% in bleached corals. These results indicate that: (1) symbiotic corals should not be described simply as "primarily" autotrophic, even under non-bleached conditions, and (2) heterotrophy can be a more important source of carbon in bleached corals than photosynthetically derived carbon. As such, the relative importance of both autotrophic and heterotrophic carbon to a coral's energetic needs should be considered as a continuum, from 100% photoautotrophy to 100% heterotrophy.

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