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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 plankters 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.

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 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).

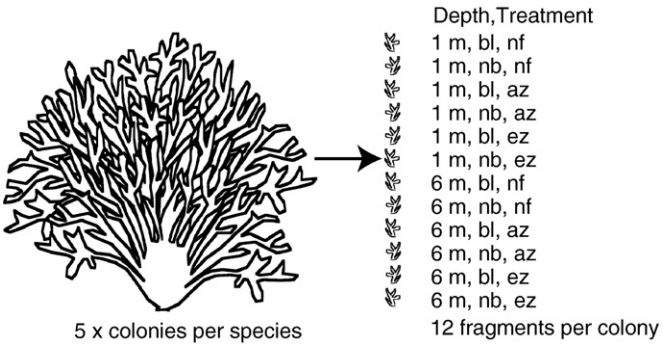

Fig. 1. Schematic representation of the experimental design. Treatments: bl=bleached, nb=non-bleached, nf=not fed, az=ambient zooplankton, ez=enhanced zooplankton.

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