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Effect of naturally changing zooplankton concentrations on feeding rates of two coral species in the Eastern Pacific

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Abstract

Zooplankton concentrations are known to vary by as much as an order of magnitude over a lunar cycle. Here, we conducted an experiment to determine the effect of ambient zooplankton concentrations over a lunar cycle on feeding rates of the corals *Pavona gigantea* (Verrill) (mounding coral, 3.0 mm diameter polyps) and *Pocillopora damicornis* (Linnaeus) (branching coral, 1.0 mm diameter polyps) in situ on a shallow reef at Isla Contadora, Gulf of Panamá (Pacific), Panamá. Coral fragments exposed to either enhanced or ambient zooplankton concentrations were allowed to feed for 1 h, collected, and their gut contents dissected. The number of zooplankton captured was counted, feeding rates calculated per cm^2, and the species composition of captured zooplankton assemblages determined. Although both species captured the same zooplankton assemblage, feeding rates were always significantly higher for *P. gigantea* than for *P. damicornis*. Under ambient flow and zooplankton concentrations, feeding rates were highly correlated with zooplankton concentration in the 200–400 μm size class. Under constantly enhanced zooplankton concentrations in the control fragments, feeding rates did not vary significantly over the lunar cycle. As such, coral feeding rates vary not as a result of lunar phase per se, but with changes in zooplankton abundance over the lunar cycle. Coral feeding rates are directly proportional to ambient zooplankton concentrations and may vary by as much as 50% over a lunar cycle, suggesting that corals must cope with major swings in sources of fixed carbon and nutrients over relatively short timescales.

Keywords: Coral; Feeding; Heterotrophy; Lunar cycle; Zooplankton concentration

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1. Introduction

Although found in tropical oligotrophic waters, coral reefs are characterized by high rates of productivity (Furnas, 1992; Sorokin, 1995). It is generally accepted that fixed carbon translocated to the coral host from endosymbiotic zooxanthellae represents the primary source of energy for scleractinian corals, supplying the coral host with up to 100% of its daily metabolic demands (Falkowski et al., 1984; Muscatine et al., 1985; Edmunds and Davies, 1986). However, although 100% of a coral's energetic demands may be met through photosynthesis alone, corals may exude up to half of that carbon as mucus (Crossland et al., 1980; Davies, 1984; Crossland, 1987; Wild et al., 2004). In addition to photosynthetic inputs, corals have been observed to use multiple heterotrophic inputs as food sources, including

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particulate organic matter (Rosenfeld et al., 1999; Anthony, 2000; Anthony and Fabricius, 2000), bacteria (Sorokin, 1973, 1991; Ferrier-Pagès et al., 1998), and zooplankton (e.g. Johnson and Sebens, 1993; Sebens et al., 1996; Helmuth et al., 1997; Ferrier-Pagès et al., 2003; Sebens et al., 2003; Palardy et al., 2005).

In addition to fixed carbon, zooplankton are thought to provide corals with nutrients such as nitrogen and phosphorus that are not supplied by zooxanthellae (Muscatine and Porter, 1977; Szmant-Froelich and Pilson, 1980; Lewis, 1992; Risk et al., 1994; Titlyanov et al., 2000; Fitt and Cook, 2001; Titlyanov et al., 2001). It is believed that heterotrophic inputs are necessary for maximal coral growth (Wellington, 1982; Miller, 1995; Houlbrèque et al., 2003), with isotopic evidence indicating that as much as 66% of the fixed carbon in coral skeletons can come from these inputs (Grottoli and Wellington, 1999).

Although several studies have measured coral feeding rates on concentrated natural zooplankton under field conditions (Johnson and Sebens, 1993; Sebens et al., 1996, 1998; Palardy et al., 2005), coral feeding rates under natural conditions and zooplankton concentrations have not been directly examined. Ingestion rates are better understood on other coelenterates such as anemonies and hydroids (e.g. Lasker, 1981; Sebens and Koehl, 1984; Lewis, 1992; Coma et al., 1994; Ribes et al., 1998; Lin et al., 2002), for which annual variations in feeding rates have been investigated (Ribes et al., 1999).

Under controlled experimental conditions, coral feeding rates have been shown to increase with zooplankton (Sebens et al., 1996; Ferrier-Pagès et al., 2003) and brine shrimp (Grottoli, 2002) concentrations. Furthermore, many studies have observed a significant lunar cycle in zooplankton concentrations with ambient concentrations varying by as much as an order of magnitude (e.g. Alldredge and King, 1980; Tarling et al., 1999; Heidelberg et al., 2004). Consequently, we expect that coral feeding rates would reflect these natural fluctuations in zooplankton concentrations over the lunar cycle.

Only one known study has investigated feeding rates of Caribbean corals (Porter, 1974) and one of Hawaiian corals (Johannes and Tepley, 1974), in situ at natural zooplankton concentrations and flow regimes. To our knowledge, no studies investigating the effects of either temporal variation or natural zooplankton concentrations on feeding rates in situ have been performed. Here, we examined the relationships between feeding rates and zooplankton concentrations in situ, in the eastern Pacific, on a patch reef at Isla Contadora, Gulf of Panamá, Panamá. The feeding rate at ambient zooplankton concentrations of *Pavona gigantea* (mounding colony morphology, 3.0 mm diameter polyps) and *Pocillopora damicornis* (branching colony morphology, 1.0 mm diameter polyps) were observed at each lunar phase in March–May 2003. To control for possible effects of the lunar cycle unrelated to zooplankton concentrations, the feeding rates of *P. gigantea* and *P. damicornis* were observed when fed uniform concentrations of concentrated zooplankton throughout. For each species in each feeding regime, numbers and taxonomy of captured zooplankton were used to evaluate the hypotheses that coral feeding rates vary with changes in natural zooplankton concentrations that occur over the course of the lunar cycle.

2. Methods

2.1. Study site

The experiment was carried out on a patch reef located at Playa Cacique, on the southern coast of Isla Contadora in the Perlas Archipelago, Gulf of Panamá, Pacific Ocean (8°37′N, 79°02′W) (Fig. 1). Detailed oceanographic conditions of the Gulf of Panamá and reef layout of the Perlas Archipelago are described in D'Croz and Robertson (1997) and Glynn and Maté (1997), respectively.

2.2. Experiment

Feeding rates in *P. gigantea* and *P. damicornis* were measured in the evenings at each phase of the lunar cycle from 10 March to 10 May 2003. Maximum variation in water temperature over all feeding nights was 2.3°C (Optic StowAway, Onset Corp.). For each coral species, one fragment was collected from 48 separate colonies at 1–3 m depth below mean low tide at least 2 weeks prior to experimentation and allowed to acclimate. Each collected fragment was cemented to a 5 cm × 5 cm Plexiglas plate using Splash Zone compound and attached to the substrate at 1 m depth below mean low tide. Only corals that appeared healthy (normal coloration and expanded polyps) were used in experimentation. Testing occurred on three nights of each phase of the lunar cycle. At noon for each of these periods, 10–12 March and 9–10 May (1st quarter), 17–19 March and 16 April (full moon), 23–25 March and 23 April (3rd quarter), 31 March – 2 April and 1 May (new moon), four coral isolation chambers were fastened to the substrate at 1 m and one fragment of each species was placed inside each isolation chamber for a minimum of 7 h to allow them to digest any previously captured zooplankton. For chamber details, see Palardy et al. (2005). During nautical twilight, corals