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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

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

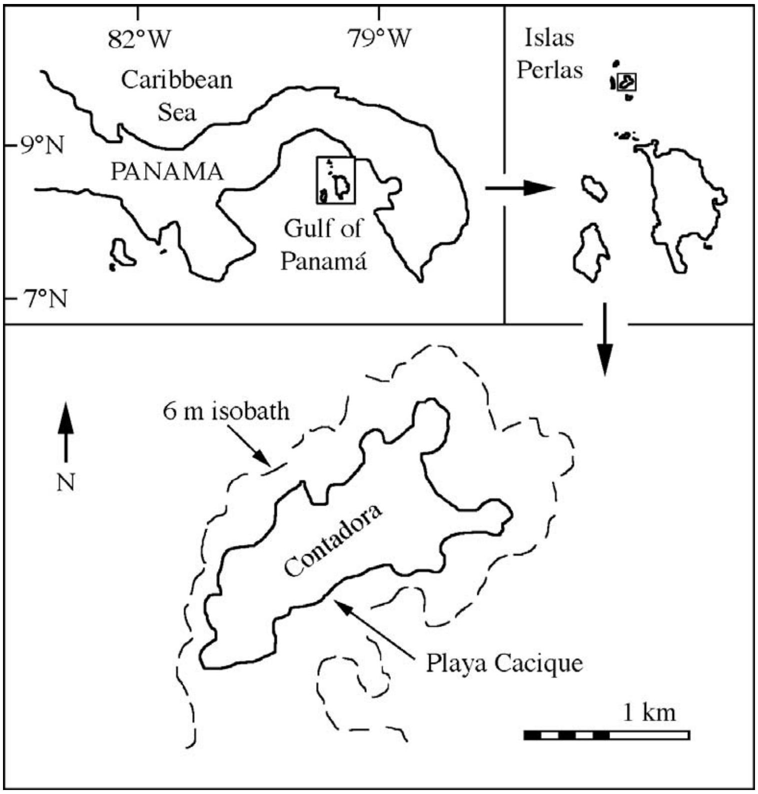

Fig. 1. Isla Contadora, Gulf of Panamá, Panamá (8°37′N, 79°02′W) (modified from Wellington, 1982). The dashed line indicates the 6-m isobath.

were allowed to feed for 1 h according to the following experimental design. In one chamber, coral fragments were fed high concentrations of natural zooplankton concentrated with 50 μm Nitex mesh (see Palardy et al., 2005 for collection details), serving as a control for variation in zooplankton abundance caused by factors such as light intensity or tidal height that vary over the lunar cycle. A single experimental chamber containing all species was used each night to minimize error in supplying each enclosure with identical concentrations of zooplankton. In a second chamber, coral fragments remained unfed, serving as a control for the effectiveness of the isolation chambers. The isolation chamber covers were removed from the remaining two chambers and these fragments were exposed to ambient flow and zooplankton concentrations. The collection of the coral fragments, and the identification of number and types of zooplankton captured were executed according to Palardy et al. (2005) with the exception that 250 polyps were dissected in each coral fragment exposed to ambient flow and zooplankton concentrations. Ambient flow was oscillatory and ranged between 10 and 20 cm/s throughout all feeding periods, with in-chamber velocities approximately 50% of ambient velocities (according to methods reported by Sebens et al., 1998). Additional details regarding the flow in the chambers is presented in Palardy et al. (2005).

Each night, while the corals were feeding, two vertical plankton tows from 6 m to mean sea level were taken using a 0.5-m diameter plankton net with 50 μm mesh within 5 m of the experimental site. Although these tows are not completely accurate representations of the zooplankton community immediately above the coral feeding surfaces, they provide a reasonable estimate of the zooplankton community immediately adjacent to where the experiment was conducted. It is likely that many of these plankters would be transported across the actively feeding coral tentacles by flow. The plankton collected by one tow were preserved in formalin as a bulk sample, while plankton from the other tow were passed through a columnar sieve, with 1000 μm, 400 μm, 200 μm, 100 μm and 50 μm filters. Each size fraction was individually preserved in a 10% formalin solution, and the total number and taxon of captured plankton recorded and standardized to zooplankton per m^3.

2.3. Statistics

All data were tested for normality using a Shapiro–Wilk test. A fully factorial two-way model I ANOVA tested the effects of species and lunar cycle on coral feeding rates per cm^2, for corals exposed to either natural or enhanced zooplankton concentrations over the lunar cycle. One-way model I ANOVAs were used to test changes in zooplankton concentrations over the 10 March–2 April (March) lunar cycle. Within all lunar cycle effects, a posteriori Tukey–Kramer HSD test determined changes in feeding rates or zooplankton concentrations by lunar quarter. To assess changes in captured zooplankton assemblages by species and lunar phase, absolute zooplankton capture values per 250 polyps were converted into proportional capture values per fragment, and tested with a fully factorial model I MANOVA with an orthogonalized contrast M-matrix. To test differences between available and captured zooplankton taxa, proportions of zooplankton captured by all species were compared against proportionate prey availability in a zooplankton sample with a two-sample T^2 test. To test the response of feeding rates to ambient zooplankton concentrations, regressions of feeding rate against zooplankton per m^3 was performed for each species. All null hypotheses were rejected for $p \leq 0.05$.

3. Results

Total zooplankton concentration did not change significantly ($p = 0.214$) over the March lunar cycle (Fig. 2). The concentration of zooplankton in the 200–400 µm size fraction, however, did vary significantly over this lunar cycle ($p < 0.001$), with concentrations in the 3rd quarter significantly lower than during all other lunar phases (Fig. 2). Concentrations of this 200–400 µm size fraction varied significantly (ANOVA, $p < 0.0001$) by as much as 350%, from an average of 110.3 plankters m^{-3} during the third quarter of the lunar cycle to an average of 385.7 plankters m^{-3} during the full moon (Fig. 2). Concentrations of zooplankton in the 400–1000 µm, 100–200 µm, and 50–100 µm did not change significantly over the lunar cycle (ANOVA, 400–1000 µm, $p = 0.55$, 100–200 µm, $p = 0.15$ and 50–100 µm, $p = 0.07$, respectively).

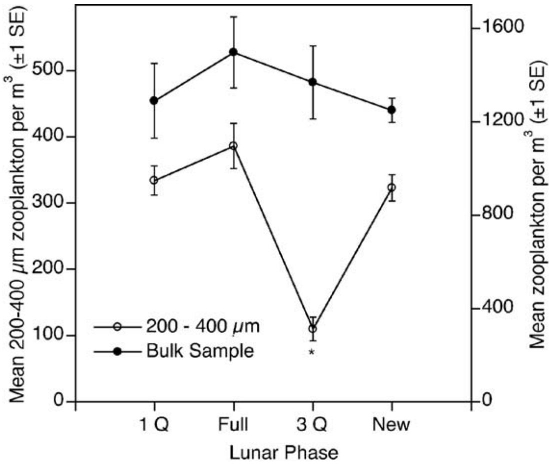

Fig. 2. Average number of 200–400 µm (± 1 S.E.) and bulk zooplankton (± 1 S.E.) per m^3 in the water column over the 10 March–2 April 2003 lunar cycle ($n = 3$ per average). Significant differences among lunar phases are indicated with *.

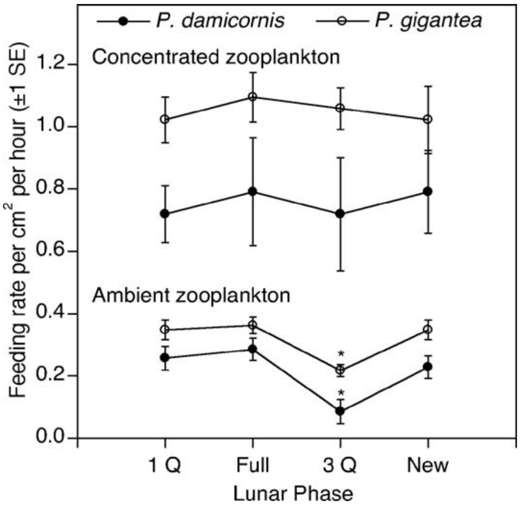

Fig. 3. Average zooplankton captures per cm^2 per hour for fragments of *P. gigantea* and *P. damicornis* exposed to enhanced and ambient zooplankton concentrations ($n = 6$ per average) at 1 m depth over the 10 March–2 April 2003 lunar cycle. Significant differences among lunar phases are indicated with *.

Unfed control corals ate less than 1% and 5% the number of zooplankton that fed corals and corals exposed to ambient zooplankton did, respectively. As such, the coral isolation chambers were effective at restricting zooplankton capture during feeding trials. Given this low rate, unfed control fragments were excluded from statistical analysis.

In corals fed concentrated zooplankton, feeding rates per cm^2 averaged 45% higher in *P. gigantea* (average ± S.E.: 16.9 ± 0.51 polyps cm^{-2}) than in *P. dami-*

Table 1

Results of a fully factorial two-way model I ANOVA on experimentally fed fragments, and fragments exposed to ambient flow and zooplankton. Main effects are species and lunar phase

Source	Fed			Ambient zooplankton		
	df	F ratio	Prob > *F*	*df*	F ratio	Prob > *F*
Model	7	20.04	<0.01	7	21.03	<0.01
Species	1	139.50	<0.01	1	123.21	<0.01
Lunar phase	3	0.17	0.92	3	6.56	<0.01
Species × lunar phase	3	0.09	0.96	3	1.44	0.24

df = degrees of freedom.

Table 2
Captured zooplankton assemblage: results of the Hotelling–Lawley trace statistic of a fully factorial three-way model I MANOVA assessing the proportionate contribution of zooplankton taxa to feeding rate, with species and lunar phase as main effects

Source	Value	Approximate *F*	*df*	Prob > *F*
Model	1.61	1.58	172	0.03
Species	0.18	1.30	36	0.29
Lunar phase	1.17	2.71	104	<0.01
Species × lunar phase	0.26	0.59	104	0.88

df = degrees of freedom. $P<0.05$ indicates a significant difference in the captured zooplankton assemblage.

cornis (33.4 ± 1.22 polyps cm^{-2}) (Fig. 3, Table 1). Within each species, average feeding rates for corals fed concentrated zooplankton did not significantly differ over the March lunar cycle (Fig. 3, Table 1). Relative differences in feeding rates between species did not differ significantly across feeding regimes (*t*-test, $p=0.69$) (Fig. 3).

For corals exposed to ambient flow and zooplankton concentrations, feeding rates were significantly higher in *P. gigantea* than in *P. damicornis*, by an average of 65% (Table 1, Fig. 3). Feeding rates for both species varied significantly over the lunar cycle, with rates during the 1st quarter, full moon, and new moon being significantly higher than rates during the 3rd quarter of the lunar cycle (Table 1, Fig. 3). For *P. gigantea* and *P. damicornis*, average feeding rates during the 3rd quarter were 39% and 50% lower, respectively, than during the remainder of the lunar cycle (Fig. 3). The non-significant interaction term (Table 1) indicates that the relative capture rates between the species did not vary over the lunar cycle.

Under ambient zooplankton feeding conditions, captured zooplankton communities did not differ significantly between species (Table 2). As such, the data were pooled in further analyses. The community of captured zooplankton did, however, vary significantly over the lunar cycle (Table 2, Fig. 4). In all lunar

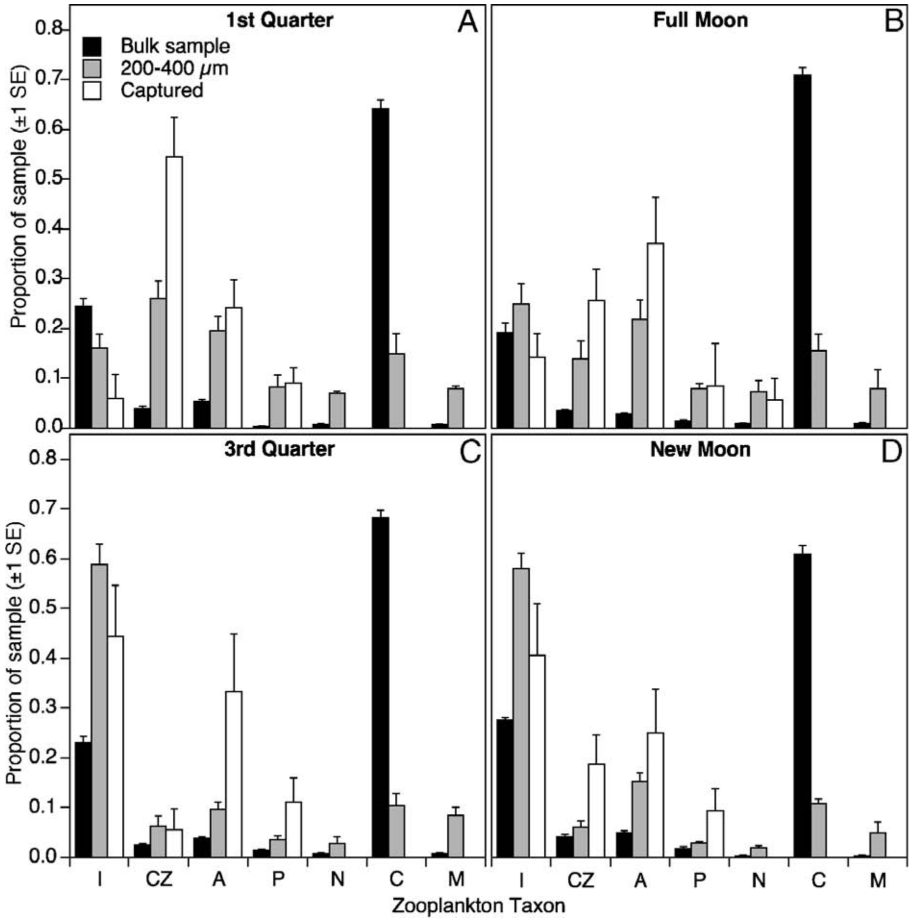

Fig. 4. Proportion of zooplankton availability by taxonomic grouping within bulk and 200–400 μm size classes ($n\geq3$), and proportion of captured zooplankton by corals ($n\geq6$) for all species, as a proportion of the total sample (+1 S.E.) over all sampling dates. Zooplankton taxa (left to right): I = isopod, CZ = crab zoeae, A = amphipod, P = polychaete, N = nematode, C = copepod, M = mysid.

Table 3
Assemblages of available zooplankton and captured zooplankton. Results of a two-sample T^2 test

Lunar phase	*F* ratio	*df*	Prob>*F*
1st quarter	26.83	6, 7	<0.01
Full moon	26.83	6, 7	<0.01
3rd quarter	25.33	6, 7	<0.01
New moon	26.67	6, 7	<0.01

$P<0.05$ indicates a significant difference between zooplankton assemblages available and captured. *df* is degrees of freedom. The first number in the *df* entry is degrees of freedom in the numerator, the second, degrees of freedom in the denominator.

phases, isopods, amphipods, and crab zoeae accounted for a minimum of 75% of zooplankton captures. The relative importance of each of these taxa, however, varied greatly. For example, crab zoea accounted for 8.3 ± 9.6% of captures during the 3rd quarter, but 47.4 ± 6.0% during the 1st quarter (Fig. 4).

Additionally, throughout the lunar cycle, a significant difference existed between the ambient and captured zooplankton assemblages (Table 3, Fig. 4). Despite accounting for a minimum of 61% of individuals in the zooplankton community, no copepods were captured by any corals (Fig. 4). This may be contrasted with crab zoea and amphipods, which were regularly highly over-represented in coral captures (Fig. 4).

Feeding rates of corals exposed to ambient levels of zooplankton were not related to variation in total zooplankton concentrations (*P. gigantea*: $r^2=0.18, p=0.12$; *P. damicornis*: $r^2=0.20, p=0.09$). A regression of feeding rate against zooplankton concentration in the 200–400 μm size class, however, indicates that 67.5% ($p<0.01$) and 74.9% ($p<0.01$) of the variation in feeding rates of *P. gigantea* and *P. damicornis*, respectively, may be explained by changes in 200–400 μm zooplankton concentrations (Fig. 5).

4. Discussion

Here, we examine the feeding rates of two eastern Pacific scleractinian corals on ambient zooplankton concentrations in situ and show that feeding rates are driven by concentrations of zooplankton in the 200–400 μm size class.

Due to logistical problems, feeding rates were standardized to zooplankton captures per cm^2 of skeletal area per hour. Although not ideal (Edmunds and Gates, 2002), standardizing to skeletal surface area is consistent with many previously published results, and enables the comparison of our results with many in the literature.

Feeding rates cm^{-2} were significantly higher in *P. gigantea* (mounding, 3.0 mm polyps) than in *P. damicornis* (branching, 1.0 mm polyps) in all cases (Table 1, Fig. 3). This result is consistent with prior direct observation (Palardy et al., 2005) for these coral species at this site. In addition to higher feeding rates, the polyps of *P. gigantea* were observed to remain expanded throughout the day. As such, it is possible that this species is even more reliant upon heterotrophic input

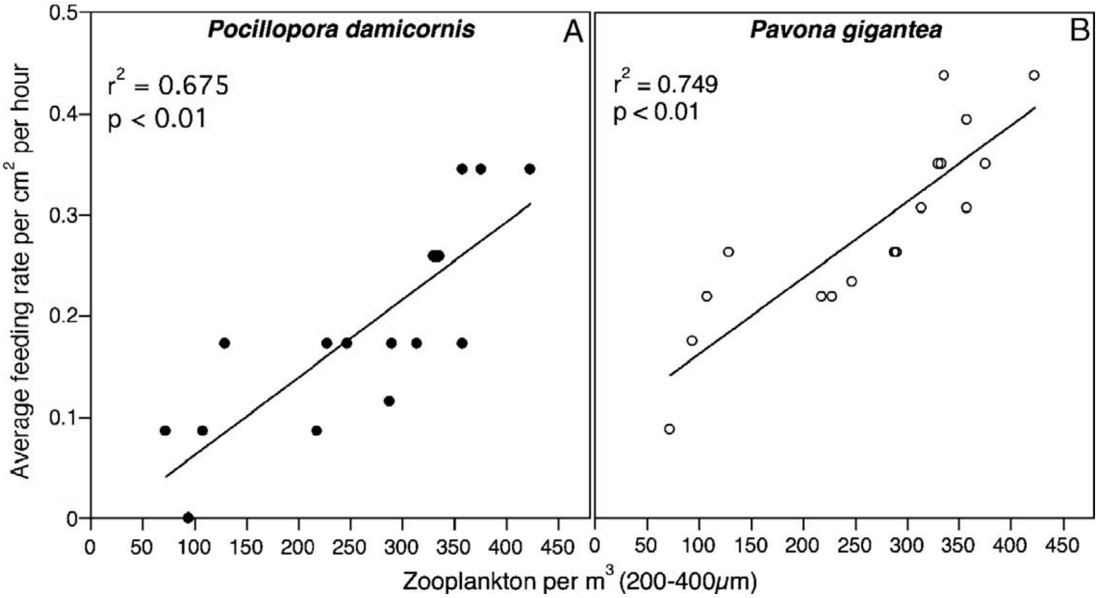

Fig. 5. Regression of average feeding rate per cm^2 for fragments of *P. gigantea* ($y=7.5\times10^{-3}x+8.7\times10^{-2}$) and *P. damicornis* ($y=7.7\times10^{-3}x-1.4\times10^{-2}$) exposed to ambient zooplankton against 200–400 μm zooplankton per m^3.

to fulfil its daily carbon requirements than *P. damicornis*. Although feeding rates were higher in *P. gigantea* than in *P. damicornis* when exposed to ambient zooplankton concentrations, the assemblage of captured zooplankton did not differ significantly between species (Table 2, Fig. 3). That is, the relative proportion of zooplankton taxa contributing to the coral diet was similar for both species. This result is in agreement with prior studies that have shown that the ability to capture a wide range of zooplankton taxa is not related to polyp size (Sebens et al., 1996; Palardy et al., 2005). The results, however, do not discount the possibility that colony morphology may play a significant role in determining the heterotrophic–phototrophic requirements of a coral (Porter, 1976). However, to truly determine if patterns of coral morphology govern feeding, measurements of the relative contribution of heterotrophy to the coral's daily metabolic requirements at ambient zooplankton concentrations are necessary. Such data do not yet exist in the literature.

Relative differences in feeding rates between the corals *P. gigantea* and *P. damicornis* were not significantly different when exposed to either ambient or concentrated zooplankton (Fig. 3). As in previous studies (Sebens et al., 1996; Ferrier-Pagès et al., 2003), a positive relationship between feeding rate and zooplankton concentration was observed, and scaled equivalently with zooplankton concentration regardless of coral morphology. As such, *qualitative* conclusions drawn from experiments using enhanced natural zooplankton concentrations to determine feeding rates (e.g. Johnson and Sebens, 1993; Sebens et al., 1996, 1998; Ferrier-Pagès et al., 2003; Palardy et al., 2005) are applicable to natural in situ feeding rates on ambient zooplankton concentrations, as shown in this study.

Feeding rates for both species varied significantly over the lunar cycle (Table 1, Fig. 3) and were strongly correlated with zooplankton concentrations in the 200–400 μm size class when exposed to ambient zooplankton (Fig. 5). This is in contrast to feeding rates in control corals, where feeding rates of neither *P. gigantea* nor *P. damicornis* varied over the lunar cycle when fed uniformly concentrated zooplankton concentrations (Table 1, Fig. 3). As feeding rates in fed control fragments did not vary, cues associated with the lunar cycle, such as moonlight and tidal variation (which may vary significantly throughout a night's feeding, due to cloud cover, the variable timing of moonrise, and tidal cycles) do not have a direct effect on coral feeding rates. Instead, variations in coral feeding rates observed over the lunar cycle in treatment corals are indirect and driven by changes in zooplankton concentrations in the 200–400 μm size range. Thus, coral feeding rates may be cyclic in many locations, as zooplankton concentrations often follow a pattern linked to the lunar cycle (i.e. Jacoby and Greenwood, 1989; Hernández-León et al., 2001; Hernández-Leon et al., 2002; Heidelberg et al., 2004).

Since heterotrophic intake of zooplankton can vary by as much as 50% over the lunar cycle, corals must cope with major changes to fixed carbon and nutrient inputs over relatively short timescales. Accordingly, multiple types of heterotrophic inputs, including zooplankton, detritus, and bacteria, may be necessary to maintain maximal coral growth. In cases where multiple sources of heterotrophic input cannot compensate for reduced zooplankton capture, average growth rates of skeleton and tissue may be reduced (Wellington, 1982; Ferrier-Pagès et al., 2003).

Changes in feeding rates in corals exposed to ambient zooplankton concentrations were not correlated to changes in overall plankton concentrations, but were significantly correlated with zooplankton concentrations in the 200–400 μm size fraction (Fig. 5). Additional results by Palardy et al. (2005) further suggest that both *P. damicornis* (1.0 mm diameter polyps) and *P. gigantea* (3.0 mm diameter polyps) preferentially feed on 200–400 μm sized zooplankton even though they have a 3-fold difference in their polyp sizes. These results indicate a strong feeding bias towards zooplankton <400 μm, a result in direct opposition to previous studies on Caribbean corals (Sebens et al., 1996), where less than 10% of zooplankton captures by *Madracis mirabilis* (5 mm diameter polyps) and *Montastrea cavernosa* (10 mm diameter polyps) were <500 μm (Sebens et al., 1996). In this study, no plankton larger than approximately 600 μm were observed in the gut of any dissected polyp, and none larger than 3000 μm observed in ambient zooplankton. Therefore: (1) zooplankton community compositions may affect heterotrophic intake in corals at different sites, (2) broad categories of small polyped corals (1–3 mm diameter) may prefer small zooplankton compared to larger polyped corals (5–10 mm diameter) which prefer larger zooplankton, and/or (3) the size of captured zooplankton relative to polyp size may differ between Caribbean and eastern Pacific corals.

Over the lunar cycle, the proportional contribution of zooplankton taxa to the coral diet varied significantly (Table 2, Fig. 4), suggesting that coral feeding rates are associated with zooplankton composition. Variations in life cycles may significantly affect the zooplankton concentration in the 200–400 μm size fraction. As zooplankton concentrations of this size fraction account for 67–75% of the variance in feeding rates (Fig. 5), variations in zooplankton life cycles between taxa are likely to have a measurable impact on the zooplankton assemblages eaten by corals. In Panamá, the quantity of crab zoea, isopods and amphipods varied significantly over the lunar cycle (Fig. 4), a pattern which may be related to their reproductive cycles.

A significant difference between available zooplankton prey items and captured items was observed in this study (Table 3, Fig. 4). The zooplankton taxa most commonly captured in relation to their abundance, crab zoea, polychaetes, and amphipods (Fig. 4), also have poor swimming abilities. Extremely large (mysids, >2000 μm) or small (copepods, ~200 μm) prey items and faster swimming taxa such as isopods, were captured rarely with respect to their relative abundance (Fig. 4). As such, it is likely that coral feeding rates not only depend upon zooplankton size, but also upon its species composition. This result is consistent with results from the same species and location in 5-day periods in February and May 2003, where captures of isopods, amphipods, and crab zoea accounted for an average of 79% of the coral diet, varying little across species, depth, and temperature (Palardy et al., 2005). Sebens et al. (1996) and Heidelberg et al. (1997) have hypothesized that variable predation avoidance techniques accounted for the difference between prey availability and capture. This hypothesis is supported by our data: for all coral species, disproportionate numbers of small and/or slow prey items were captured, while large and highly evasive zooplankton taxa were rarely, if ever, captured.

Coral feeding rates in this study did not change significantly when zooplankton concentrations were experimentally held constant throughout the lunar cycle. However, under in situ conditions where zooplankton concentrations naturally varied, coral feeding rates varied by as much as 40% over the lunar cycle, and were highly correlated with zooplankton concentrations in the 200–400 μm size fraction. As such, corals must cope with major swings in sources of fixed carbon and nutrients over relatively short timescales.

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