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Effects of upwelling, depth, morphology and polyp size on feeding in three species of Panamanian corals

James E. Palardy[1,2,*], Andréa G. Grottoli[2,3], Kathryn A. Matthews[2]

[1]Department of Ecology and Evolutionary Biology, Brown University, Box G-W, Brown University, Providence, Rhode Island 02912, USA

[2]Department of Earth and Environmental Science, University of Pennsylvania, 240 South 33rd Street, Philadelphia, Pennsylvania 19104, USA

[3]Department of Geological Sciences, Ohio State University, 125 South Oval Mall, Columbus, Ohio 43210, USA

ABSTRACT: We examined the effects of upwelling, depth, morphology and polyp size on coral feeding in 3 coral species in the eastern Pacific. Feeding rates and the species composition of zooplankton captured by these species were observed *in situ* on a shallow patch reef at Isla Contadora, Gulf of Panamá, in February (seawater temperature 20.7°C) and May (seawater temperature 28.5°C) 2003 at 1 and 6 m depths. Fragments of the corals *Pocillopora damicornis* (branching morphology, 1.0 mm diameter polyps), *Pavona clavus* (mounding morphology, 1.3 mm diameter polyps) and *Pavona gigantea* (mounding morphology, 3.0 mm diameter polyps) were collected at 3 m, transplanted to 1 and 6 m depth on the reef, placed inside feeding chambers, and exposed to high concentrations of natural zooplankton. After feeding, coral fragments were collected, the number and type of zooplankton within 100 polyps of each counted, and feeding rates calculated cm^{-2}. Feeding rates increased with increasing depth, were lower during periods of upwelling, and were higher in corals with mounding morphology than in those with branching morphology. Feeding rates cm^{-2} did not vary with polyp size. Assemblages of captured zooplankton did not change with upwelling, depth, morphology or polyp size. The proportionate contributions of poor-swimming and mid-sized (200 to 400 µm) zooplankton taxa eaten were over-represented relative to their abundance. When combined with prior studies, these results suggest that coral feeding rates are facultative and that feeding rates vary due to increased feeding effort and not necessarily due to increased colony morphology or polyp size.

KEY WORDS: Coral feeding · Upwelling · Zooplankton capture · Depth · Temperature

INTRODUCTION

Corals acquire fixed carbon from 2 main sources: (1) photosynthetically fixed carbon translocated to the coral host from endosymbiotic zooxanthellae, and (2) carbon obtained via the ingestion of plankton or other particles (heterotrophy). Although it is generally accepted that photoautotrophic processes represent the primary source of fixed carbon for corals (Muscatine & Porter 1977, Davies 1991, Grottoli & Wellington 1999, Lesser et al. 2000, Holbrèque et al. 2003), the relative contribution of heterotrophy to the scleractinian diet remains poorly understood.

Corals are known carnivores, and several studies have shown that many species of corals are active heterotrophs (Yonge & Nicholls 1931, Coles 1969, Wellington 1982, Sebens et al. 1996, Grottoli 2002, Holbrèque et al. 2003). Indeed, stable isotope analyses indicate that heterotrophy accounts for anywhere from 0 to 66% of the fixed carbon incorporated into coral skeletons (Muscatine et al. 1989, Grottoli & Wellington 1999). In addition to providing fixed carbon to the coral diet that is incorporated into both tissue and skeleton (Felis et al. 1998, Grottoli & Wellington 1999, Ferrier-Pagès et al. 2003), zooplankton are thought to provide corals with nutrients, such as phosphorus and nitrogen,

*Email: jpalardy@brown.edu

that are not supplied by zooxanthellae (Muscatine & Porter 1977, Risk et al. 1994, Fitt & Cook 2001).

In 1976, Porter proposed a model to predict the heterotrophic-phototrophic abilities of Caribbean corals based upon morphological characteristics. Under this model, (1) corals with large polyps and low surface:volume (S:V) ratios are ideally suited for plankton capture and are predicted to capture large quantities of zooplankton, (2) coral species with small polyps and a high S:V ratio are ideally shaped for light capture and less suited to zooplankton capture, and (3) feeding rates increase with increasing depth (Porter 1976). Because of the difficult nature of direct observation of coral feeding *in situ*, several indirect methods have been used to quantify prey intake and test Porter's model. The results, however, do not always agree with more recent direct observations of coral feeding.

Experiments by Wellington (1982) in Panamá showed that linear skeletal extension was greater in shaded massive corals (low S:V ratio) than in shaded branching corals (high S:V ratio), suggesting that low S:V ratio corals are more heterotrophic. Direct observations by Sebens et al. (1996, 1998), however, were contradictory, showing that branching corals in the Caribbean may capture more zooplankton per unit biomass than do mounding corals. Isotopic evidence demonstrated that within some mounding species, corals with large polyps rely more upon their heterotrophic abilities than those with small polyps over a variety of depths (Muscatine et al. 1989). Other isotopic observations of mounding species from shallow sites in Panamá show no difference in reliance upon heterotrophic input between congeners of differing polyp sizes (Grottoli & Wellington 1999). Additionally, direct observation of Caribbean corals has shown that small polyped corals capture more prey per unit biomass than do corals with much larger polyps (Sebens et al. 1996). Indirect experimental evidence based on skeletal extension (Wellington 1982), $\delta^{13}C$ (Muscatine et al. 1989, Grottoli & Wellington 1999) and oxygen flux (McCloskey & Muscatine 1984) indicates that species that are highly phototrophic in shallow water rely more upon heterotrophic inputs in deeper water. It is unknown, however, if the increased importance of heterotrophy to the coral diet is due to increased heterotrophic intake with depth, reduced light availability, or both.

Corals capture large amounts of both open-water and demersal zooplankton (Porter 1974, Ohlhorst 1982, Heidelberg et al. 2004). With few exceptions (Johnson & Sebens 1993, Sebens et al. 1998, Ferrier-Pagès et al. 2003), little is known about the feeding rates and diets of most corals on natural zooplankton. Additionally, due to the artificial nature of zooplankton species composition in many tank experiments, prey selection is poorly understood and is largely attributed to escape behavior of zooplankters, rather than differential feeding ability of coral species (Sebens et al. 1996). Factors such as light (Ferrier-Pagès et al. 1998, 2003, Titlyanov et al. 2000) and water flow (Helmuth & Sebens 1993, Johnson & Sebens 1993, Fabricius et al. 1995, Sebens 1997, Sebens et al. 1998, 2003) have well documented, significant effects on coral resource partitioning and particle capture ability, respectively.

Thermal conditions have long been recognized as exerting a limiting influence on coral reef development (Dana 1843, Glynn & Stewart 1973). As corals are often found in environments that approach their physiological limits, episodes of water temperatures above (Berkelmans & Oliver 1999, Fitt et al. 2001, Saxby et al. 2003) or below (Porter et al. 1982, Muscatine et al. 1991, Harriott & Banks 2002, Saxby et al. 2003) normal values are known to cause mass coral mortality and bleaching. Although the effects of upwelling on coral feeding are not well documented, it has been observed that cold water slows polyp contraction and may therefore limit heterotrophic intake (Johannes & Tepley 1974). As such, variations in coral feeding during periods of thermal stress may preclude, or enhance, coral survivability.

Despite the many publications on the topic, a direct, systematic experimental test of the effect of upwelling and depth on coral feeding under natural field conditions *in situ* has not been done to date. To directly test the relationships between feeding rates, upwelling and depth *in situ*, we fed concentrated natural zooplankton assemblages to 3 species of corals at 2 depths and at 2 different times of the year. We also considered the effect of morphology and polyp size on coral feeding and monitored the assemblage of zooplankton captured. The experiments were carried out at 1 and 6 m depths in the eastern Pacific at Isla Contadora, Gulf of Panamá, Panamá. *Pocillopora damicornis* (1.0 mm diameter polyps, high S:V) is a branching coral, while *Pavona gigantea* (3.0 mm diameter polyps, low S:V) and *Pavona clavus* (1.3 mm diameter polyps, low S:V) are both mounding corals. For each coral species, numbers and taxon of captured zooplankton were recorded and subjected to both univariate and multivariate tests to statistically evaluate the following hypotheses: (1) feeding rates are lower during periods of upwelling; (2) feeding rates increase with increasing depth; (3) the composition of captured zooplankton does not vary with upwelling; (4) the composition of captured zooplankton does not vary with depth; (5) coral feeding rate does not increase with increasing polyp size; (6) the composition of captured zooplankton varies with polyp size, (7) feeding rate increases as the S:V ratio of colony morphology decreases, and (8) the composition of captured zooplankton does not vary with the S:V

ratio of colony morphology. Thus, this study complements existing published work on the effect of morphology and polyp size on feeding rates from other locations and proxy records, and adds a direct test of upwelling and depth.

MATERIALS AND METHODS

In this study, the scleractinian corals *Pocillopora damicornis*, *Pavona clavus* and *Pavona gigantea* were fed concentrated natural zooplankton in submerged experimental enclosures *in situ* at 1 and 6 m below mean low tide from 9 to 13 February and 9 to 13 May 2003.

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). Due to migration of the intertropical convergence zone, the Gulf of Panamá experiences seasonal wind-driven upwelling, resulting in colder seawater temperatures (18 to 21°C), high salinity and nutrient concentrations, and low precipitation from December to April each year (Wellington & Dunbar 1995, D'Croz & Robertson 1997). From May to November, winds are weak and variable and upwelling is absent. Lower salinity and nutrient concentrations, warm seawater temperatures (27 to 30°C), and high levels of precipitation accompany this change (D'Croz & Robertson 1997). Detailed oceanographic conditions of the Gulf of Panamá and reef layout of the Perlas Archipelago are described in D'Croz & Robertson (1997) and Glynn & Maté (1997), respectively. Tides are semi-diurnal, with a mean spring range of 7.2 m (Wellington 1982).

Experiment. We collected a single fragment from 20 separate colonies, each a minimum of 5 m apart, of each species at 3 m depth below mean low tide on 25 and 26 January and on 20 and 21 April 2003. Fragments of *Pocillopora damicornis* and *Pavona gigantea* were collected on-site and *Pavona clavus* were collected at Punta Galéon (a site that is exposed to greater wave action, but otherwise has similar oceanographic conditions) on the northern coast of the island (Fig. 1) where they are present in abundance, and transported to Playa Cacique. Each collected fragment was cemented to a 5 × 5 cm Plexiglas plate using 2-part marine epoxy. We attached 10 fragments of each species to substrate at 1 and 6 m depth below mean low tide, and allowed them to acclimatize for a minimum of 14 d prior to experimentation. Only corals that appeared healthy (normal coloration and expanded polyps) were used in experimentation. *In situ* loggers at each depth (Optic StowAway, Onset) recorded temperature continuously during experimentation, with readings taken every 30 min.

At noon for 5 consecutive days, 9 to 13 February 2003 and 9 to 13 May, at both 1 and 6 m depths, 2 coral feeding chambers (Fig. 2) were fastened to the substrate; 1 chamber at each depth was used for experimentally fed fragments, 1 for unfed control fragments. We placed 1 randomly selected coral fragment of each species (each approximately 80 to 120 cm^3) inside each feeding chamber and allowed them to acclimate for a minimum of 7 h. A single experimental chamber (Fig. 2) containing all species was used to minimize error in supplying each enclosure

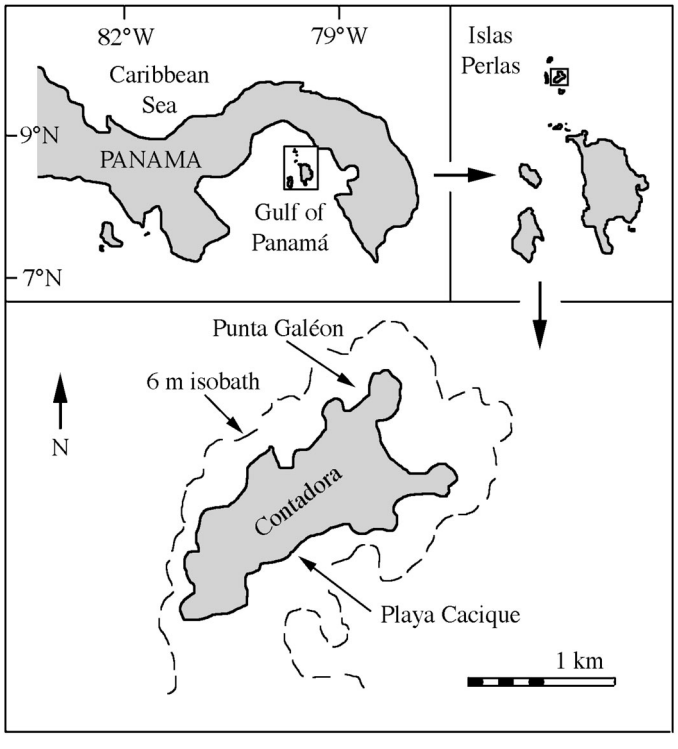

Fig. 1. Isla Contadora, Gulf of Panamá, Panamá (8° 37′ N, 79° 02′ W) (modified from Wellington 1982). Dashed line indicates 6 m isobath

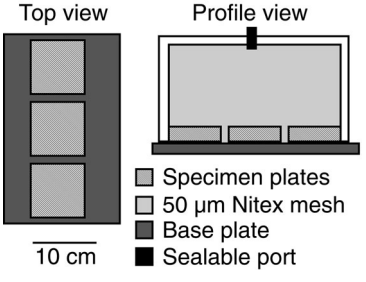

Fig. 2. Feeding chamber. Chamber profile is dominated by Nitex mesh side panels, maximizing water flow through chambers. In profile view, flow direction is away from reader

with identical concentrations of zooplankton. Coral feeding chambers consisted of a base plate with a transparent upper plastic container measuring approximately 32 × 18 × 12 cm, with 50 µm Nitex mesh side panels (Fig. 2). Each chamber had a sealable port in the upper right hand side through which plankton could be introduced to the chamber. Low flow is known to restrict zooplankton capture (Helmuth & Sebens 1993, Johnson & Sebens 1993, Fabricius et al. 1995, Sebens 1997, Sebens et al. 1998, 2003). Accordingly, the feeding chambers were oriented perpendicular to the flow, thereby maximizing flow through the mesh side-panels. Flow in the feeding chambers was oscillatory and observed to be approximately 50% that of ambient velocities (according to methods reported by Sebens et al. 1998), with in-chamber velocities ranging between 5 and 10 cm s^{-1} at both shallow and deep sites, during both cool upwelling and warm non-upwelling conditions.

Each evening during nautical twilight, when maximum vertical zooplankton migration rate is highest (Glynn 1973, Porter & Porter 1977, Ohlhorst 1982), zooplankton were collected in a large bucket with a dive light. Although plankter attraction to the light concentrates zooplankton without physical damage, it is unlikely that species composition is identical to ambient composition (Sebens et al. 1996, 1998). The trapped zooplankton were further concentrated by pouring the bucket sample through a 50 µm mesh. A subsample was preserved in a 10% formalin solution and the relative abundance of each broad taxonomic grouping was determined. Two 50 ml samples of the concentrated actively swimming plankters were then transferred to 60 ml syringes. At each depth, 1 coral isolator was injected with zooplankton through its sealable port using a randomly selected zooplankton-filled syringe. Thus, although the concentration of each syringe may not have been identical, the results are unbiased. The second isolator at each depth was injected with filtered seawater (50 µm) as a control. Following the injection, corals were visually inspected through the clear container wall to ensure that the coral tentacles were expanded and feeding, and allowed to feed for 60 min.

Upon completion of the feeding period, feeding chambers were immediately brought to the surface and drained of water to prevent the capture of additional plankton during transport to shore. Within minutes of retrieval, coral fragments were preserved in a 10% formalin solution to minimize digestion of captured zooplankton. Within 24 h, the entire gut content of a total of 100 polyps per coral fragment was examined by probing with a dissecting needle under a dissecting microscope (20 to 100× power), then scraping the skeleton to expose any remaining prey. Prey larger than 50 µm were clearly visible and generally identifiable. Total number and taxon of captured plankton were recorded. Only plankton clearly within the polyp were counted, and plankton attached to the outer surface of the coral were not counted. To calculate feeding rates as zooplankton captures cm^{-2} tissue area h^{-1}, an area of 2.5 cm^2 was delineated on 6 clean and dry coral fragments of each species using aluminium foil. Under a microscope, the number of polyps inside the delineated area were counted and averaged. Feeding rates cm^{-2} were calculated as:

$$\left(\frac{\#\,\text{polyps}}{\text{cm}^2}\right)\left(\frac{\#\,\text{zooplankton}}{\#\,\text{polyps}\times\text{h}}\right) = \frac{\#\,\text{zooplankton}}{\text{cm}^2\times\text{h}}$$

Statistics. Data were tested for normality using a Shapiro-Wilks test. Following a test of homogeneity of slopes among groups, the effects of upwelling, depth, polyp size, and morphology on feeding rates as well as feeding rates cm^{-2} were tested with a fully factorial Model I ANCOVA, with depth, species and upwelling as main effects and an unfed control as covariate. Within the species effect, contrast tests compared morphologies within polyp size, as well as polyp size within morphology. To test variation in the assemblage of captured zooplankton by depth, morphology and polyp size, absolute zooplankton capture values (100 $polyps^{-1}$ $fragment^{-1}$) were converted into proportional capture values $fragment^{-1}$, and tested with a fully factorial Model I MANOVA, a generalised linear model, multivariate analogue to ANOVA. To test variation between the assemblage of zooplankton captured by and the assemblage of zooplankton fed to each coral species, proportions of zooplankton captured by all species were compared against proportionate prey availability in a zooplankton sample with a 2-sample T^2 test. Multivariate analyses incorporated an orthogonalized contrast M-matrix. All null hypotheses were rejected at $\alpha = 0.05$.

RESULTS

Control and coral feeding chambers

A small amount of feeding was recorded for the unfed control fragments and was likely due to zooplankton that entered the coral isolation chambers during isolation of the corals from ambient zooplankton: unfed control corals consumed less than 5% of the amount of zooplankton consumed by fed corals, and means were adjusted accordingly according to this covariate. Thus, the coral isolation chambers were effective, and treatment corals ate only zooplankton that was provided for them experimentally.

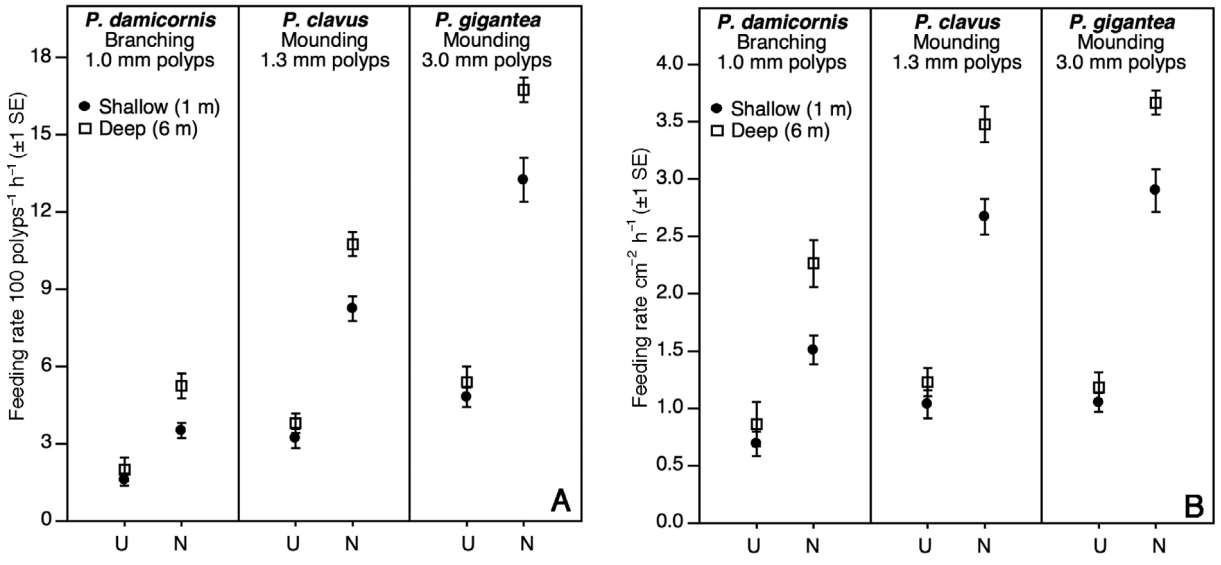

Fig. 3. *Pocillopora damicornis*, *Pavona clavus*, *Pavona gigantea*. (A) Average (±1 SE) feeding rate 100 polyps^{-1} h^{-1}; (B) average (±1 SE) feeding rate cm^{-2} h^{-1} for shallow and deep sites across all test days and feeding regimes. U: upwelling, seawater temperature 20.7°C, n = 5; N: non-upwelling, seawater temperature 28.5°C, n = 4. Significant differences occurred between all species, upwelling, depth, and upwelling × depth. Feeding rates were correlated with colony S:V (surface:volume) ratio (A,B) and with polyp size (A) (statistical analysis in Table 1)

Effect of upwelling on feeding rates

Feeding rates were significantly higher (average of 169%) during warm non-upwelling conditions, when seawater temperatures were on average 7.8°C warmer than during periods of upwelling (Fig. 3, Table 1). Additionally, the proportional difference in feeding rate between coral species between upwelling and non-upwelling conditions was significantly different (Table 1). In other words, feeding rates were 143, 171 and 194% higher during the warmer (non-upwelling) period than during the cooler (upwelling) period for *Pocillopora damicornis*, *Pavona clavus* and *Pavona gigantea*, respectively (Fig. 3).

Effect of depth on feeding rates

Feeding rates increased significantly with increasing depth by an average of 29.8% for all coral species (Table 1, Fig. 3). The increase in feeding rate with depth varied significantly as a function of upwelling. During cool upwelling conditions, feeding rates at 6 m depth were on average 18.7% higher than at 1 m, while during warmer non-upwelling conditions, feeding rates were 35% higher at 6 m than at 1 m depth.

Effect of colony morphology and polyp size on feeding

Feeding rates significantly differed between species (Fig. 3A, Table 1), with *Pavona gigantea* > *Pavona clavus* > *Pocillopora damicornis*. Feeding rate varied by an average of 250% within each depth and upwelling condition (Fig. 3A, Table 1). Between corals with small polyps (*P. clavus* and *P. damicornis*), feeding rates significantly increased, by a factor of 2, from branching to mounding morphology (Fig. 3A, Table 1).

Table 1. *Pocillopora damicornis*, *Pavona clavus* and *Pavona gigantea*. Results of fully factorial Model I ANCOVA on feeding rates 100 polyps^{-1} and cm^{-2}, with species, upwelling and depth as main effects, and unfed control as covariate. Assumption of homogeneity of slopes among groups was not rejected (p = 0.069). Data were normally distributed according to Shapiro-Wilks test for normality. $p < 0.05$ indicates significant difference in feeding rates h^{-1}

Source	Rate 100 polyps^{-1}			Rate cm^{-2}		
	df	*F*-ratio	p > *F*	df	*F*-ratio	p > *F*
Model	12	89.29	<0.01	12	48.20	<0.01
Species	2	209.11	<0.01	2	43.06	<0.01
Polyp size within morphology	1	−10.57	<0.01	1	−0.98	0.33
Morphology within polyp size	1	10.24	<0.01	1	7.47	<0.01
Upwelling	1	500.05	<0.01	1	418.77	<0.01
Depth	1	32.01	<0.01	1	31.60	<0.01
Species × Upwelling	2	60.96	<0.01	2	14.82	<0.01
Species × Depth	2	0.82	0.44	2	0.03	0.97
Upwelling × Depth	1	12.94	<0.01	1	12.85	<0.01
Species × Upwelling × Depth	2	0.60	0.55	2	0.01	0.99
Unfed control (covariate)	1	1.07	0.31	1	0.24	0.62

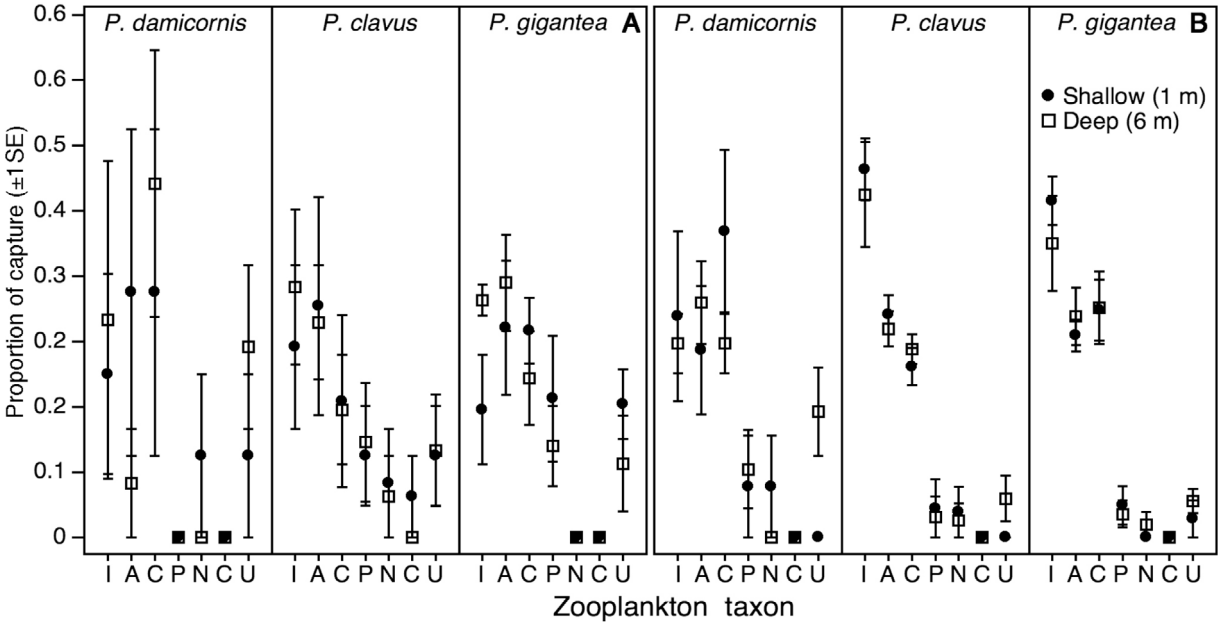

Fig. 4. *Pocillopora damicornis*, *Pavona clavus*, *Pavona gigantea.* Average (±1 SE) proportion of each zooplankton taxon captured 100 polyps^{-1} during (A) upwelling (seawater temperature 20.7°C, n = 5), and (B) non-upwelling (seawater temperature 28.5°C, n = 4) conditions for both shallow and deep sites across all test days. I: isopod; A: amphipod; C: crab zoea; P: polychaete; N: nematode; C: copepod; U: unidentified (statistical analysis in Table 2)

Within the mounding corals, feeding rates were significantly higher by an average of 45% in the large-polyped *Pavona gigantea* than in the smaller-polyped *P. clavus* (Fig. 3A, Table 1).

Feeding rates cm^{-2} differed significantly between species, with *Pavona gigantea* ≈ *Pavona clavus* > *Pocillopora damicornis* (Fig. 3B, Table 1). Feeding cm^{-2} did not differ with polyp size within the mounding morphology. Between corals with small polyps, zooplankton captures cm^{-2} increased significantly as the S:V ratio decreased: feeding cm^{-2} was 46% lower in branching (*P. damicornis*, high S:V) than in mounding (*P. clavus*, low S:V) corals (Fig. 3B, Table 1).

Effect of upwelling, depth, colony morphology and polyp size on prey selection

The assemblage of zooplankton captured did not significantly change with upwelling, depth, colony morphology or polyp size (Fig. 4). The majority of identified zooplankton captured by all 3 species of corals consisted of 3 zooplankton taxa: amphipods, isopods, and crab zoea. Each of these 3 taxa accounted for approximately 25% of the zooplankton captured by each coral species, while polychaetes and nematodes played minor and variable roles in the diet of all species (Fig. 4). This consistency in zooplankton taxa ingested is emphasized by the non-significant results of a Model III MANOVA (Table 2), wherein species, depth, and upwelling did not have statistically significant effects on the proportionate contribution of each zooplankton taxon to the assemblage of captured zooplankton.

Table 2. *Pocillopora damicornis*, *Pavona clavus* and *Pavona gigantea.* Captured zooplankton assemblage. Results of Pillai's trace statistic of fully factorial 3-way Model I MANOVA assessing proportionate contribution of zooplankton taxa to feeding rate of corals, with species, depth and upwelling as main effects. $p < 0.05$ indicates significant difference in captured zooplankton assemblage

Source	Value	Approx. *F*	df	p > *F*
Model	1.14	0.90	66	0.69
Species	0.15	0.53	12	0.89
Upwelling	0.24	1.53	6	0.20
Depth	0.18	1.10	6	0.38
Species × Upwelling	0.23	0.83	12	0.62
Species × Depth	0.21	0.74	12	0.70
Upwelling × Depth	0.09	0.55	6	0.77
Species × Upwelling × Depth	0.25	0.90	12	0.55

Relative abundances of captured zooplankton

A highly significant difference was found to exist between the zooplankton assemblage fed to the corals and the assemblage ingested by the corals ($T^2_{6,55}$

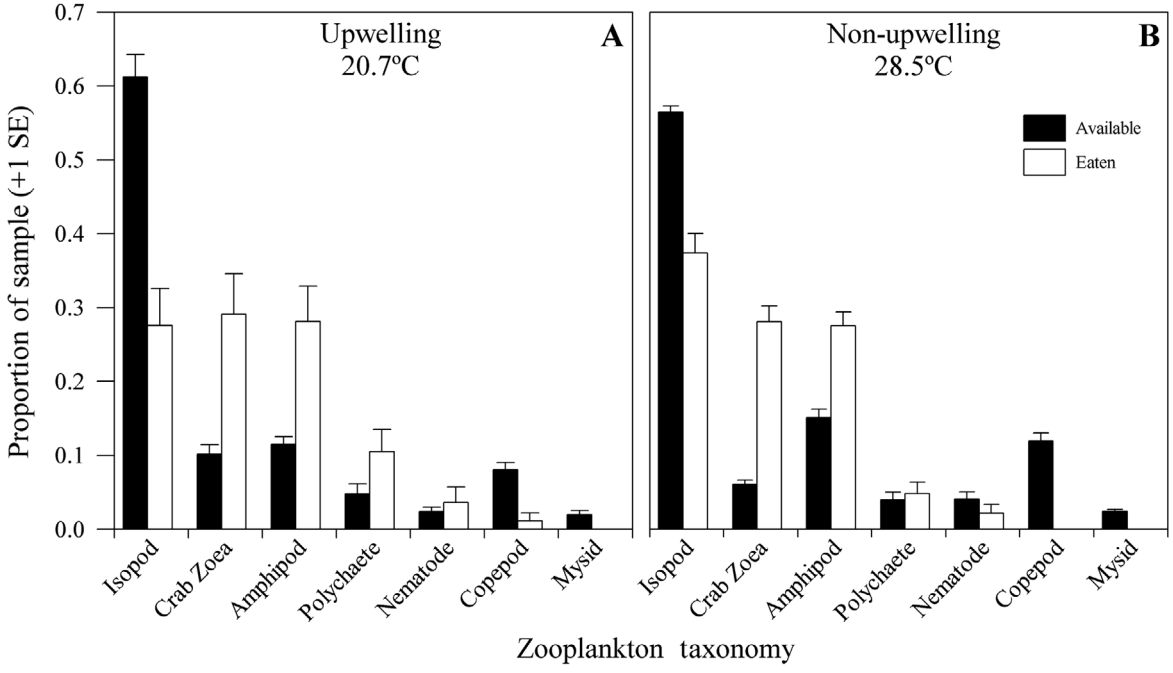

Fig. 5. *Pocillopora damicornis*, *Pavona clavus*, *Pavona gigantea* (combined data). Average zooplankton availability (n = 4) and zooplankton ingested by all corals (A: n = 30; B: n = 24) by taxon, as proportion of total sample during (A) upwelling and (B) non-upwelling conditions. Note major differences between proportion of zooplankton available and proportion captured by corals

$p < 0.0001$) (Fig. 5). Although accounting for an average of 61 ± 3.1% of available zooplankton, isopods represented only 28.7 ± 4.9% of zooplankton captured (Fig. 5). Other highly mobile taxa, copepods and mysids, were never observed in any coral gut. In comparison, crab zoea and amphipods accounted for 29.1 ± 5.5 and 28.1 ± 4.8% of captured zooplankton while representing only 10.2 ± 1.3 and 11.5 ± 1.0% of the total zooplankton available, respectively (Fig. 5).

DISCUSSION

Corals are active carnivores (Titlyanov et al. 2000, Grottoli 2002, Ferrier-Pagès et al. 2003) who are known to capture large quantities of natural zooplankton. Most studies that have investigated feeding rates of corals *in situ* on natural zooplankton (Porter 1974, Sebens et al. 1996, 1998) occurred using Caribbean species. To complement previous studies, we present a direct test of resource partitioning in morphologically different scleractinian corals in a new geographic location (eastern Pacific), as well as addressing the composition of captured zooplankton and the effects of upwelling and depth on coral feeding.

Feeding rates were standardized to zooplankton captures cm^{-2} of skeletal area h^{-1}. Although not ideal (Edmunds & Gates 2002), standardizing to skeletal surface area is consistent with many results in the published literature, and enables the comparison of the present results with those of many previous studies.

Water flow through the feeding chambers was observed to be between 5 and 10 cm s^{-1}. This is typical ambient flow velocity and should not have limited prey capture rates (Sebens et al. 1998). Additionally, relative capture rates observed between *Pocillopora damicornis* and *Pavona gigantea* were similar during exposure to ambient flow conditions at the same location (J. E. Palardy et al. unpubl. data), indicating that the feeding rate of each fragment was independent within the chamber.

Feeding rates during non-upwelling periods (average seawater temperature 28.5°C) were significantly greater, by an average of 35.6%, than during upwelling (average seawater temperature 20.7°C) (Table 1, Fig. 3), when ambient zooplankton concentrations were 3.2 times higher (J. E. Palardy unpubl. data). As such, the data support the hypothesis that feeding rates are lower during periods of upwelling. As the assemblage of zooplankton captured did not differ significantly between upwelling and non-upwelling conditions, one possible mechanism for the marked decrease in feeding rates during periods of low temperature is a slowing of polyp contraction (Johannes & Tepley 1974) or a loss of nematocyst function that may allow certain organisms to escape prior to ingestion,

rather than changes in ambient zooplankton composition. A decrease in heterotrophic ability may be one factor leading to mortality in symbiotic corals exposed to water temperatures below normal. As cooler water temperatures have been observed to decrease photosynthetic efficiency (Saxby et al. 2003), corals may not be able to increase heterotrophic intake sufficiently to compensate for this decrease in fixed carbon. Alternatively, increased nutrient concentration (Ferrier-Pagès et al. 2000) and reduced heterotrophic intake (Wellington 1982, Ferrier-Pagès et al. 2003, Holbrèque et al. 2003) during upwelling may reduce skeletal extension to such an extent that corals cease to be effective competitors. Another possible reason for the reduction in feeding during upwelling is seasonal variability in nutrient supply. If zooplankton capture is necessary to supply nitrogen, phosphorus and other nutrients, corals may need to capture fewer prey items to become nutrient-replete during upwelling, when concentrations of these nutrients in the water column are higher (D'Croz & Robertson 1997). Alternatively, if zooplankton capture is a necessary source of fixed carbon to the coral, decreases in metabolic rate with decreasing temperature may reduce carbon needs to such an extent that photosynthesis may provide sufficient carbon for the coral's daily metabolic needs.

Decreases in feeding rates with upwelling were not consistent across either depth or species (Fig. 3). Changes in feeding rates with upwelling varied significantly between species, with *Pavona gigantea* < *Pavona clavus* < *Pocillopora damicornis* (Table 1). This seems to indicate that larger-polyped species are more affected by upwelling than small-polyped species.

All coral species captured more zooplankton at 6 m than at 1 m depth (Fig. 3, Table 1), supporting the hypothesis that feeding rate increases with increasing depth. Our observation is consistent with $\delta^{13}C$ evidence obtained from *Pavona clavus* and *P. gigantea* collected from the same site. Grottoli & Wellington (1999) showed zooplankton to be responsible for a greater proportion of fixed carbon in the skeletons of *P. clavus* and *P. gigantea* at 6 m than at 1 m. Decreases in skeletal $\delta^{13}C$ with increasing depth have also been observed in other coral genera at various sites (Muscatine et al. 1989, Ferrier-Pagès et al. 1998, Grottoli 1999).

As feeding rates increased with increasing depth for *Pocillopora damicornis*, *Pavona clavus* and *Pavona gigantea*, it is unlikely that any of these species feed maximally in shallow depths. As all 3 coral species increased feeding rates proportionately with increasing depth, the data display similar degrees of phenotypic plasticity between low S:V and high S:V corals as well as between corals with small and large polyps. Since all corals were collected at the same intermediate depth, selection for increased feeding with increased depth may be excluded from consideration. Instead, the data suggest that corals are able to increase heterotrophic intake with changes in environmental conditions in order to compensate for the decrease in fixed carbon translocated by zooxanthellae. Increased feeding rates are probably the result of physiological plasticity or behavioral adaptation of corals placed in environments with reduced light due to depth (this study), similar to the increase in capacity to use suspended sediment as a food source in high-turbidity environments (Anthony 2000, Anthony & Fabricius 2000).

Feeding rates per 100 polyps in *Pavona gigantea* (3.0 mm polyps) were 45% higher than in *P. clavus* (1.3 mm polyps), which is consistent with Porter's (1976) hypothesis. However, when feeding rates were normalized cm^{-2}, they did not differ (Fig. 3B, Table 1). These results indicate that surface area, not polyp size, is critical for zooplankton capture and that *P. gigantea* is not a more efficient feeder than *P. clavus.* It is known that heterotrophy alone is not responsible for a greater proportion of carbon incorporated into the skeleton of shallow *P. gigantea* than in the skeleton of shallow *P. clavus* (Grottoli & Wellington 1999), and that zooplankton limitation reduces the growth rates of *P. clavus* and *P. gigantea* to a similar extent (Wellington 1982). Thus, although the tentacles of *P. gigantea* remain extended throughout the day (a behavioral adaptation that may influence the quantity of prey captured in a single day), this species does not appear to be more reliant upon heterotrophy to fulfill its daily metabolic requirements than *P. clavus*.

Feeding rates were higher in the mounding coral *Pavona clavus* (low S:V ratio) than in the branching coral *Pocillopora damicornis* (high S:V ratio) with similar polyp sizes (Fig. 3, Table 1). These results support the hypothesis that feeding rates increase as the S:V ratio decreases. From low to high S:V ratios, feeding rates per 100 polyps increased by 95%, and feeding rates cm^{-2} increased by 46% (Fig. 3). This is consistent with previously published linear skeletal extension data for these species at Playa Cacique on Isla Contadora. Under reduced zooplankton conditions, linear skeletal extension rates of *P. clavus* decreased to a greater extent than did linear skeletal extension rates of *P. damicornis* (Wellington 1982). The results obtained in the Gulf of Panamá (Wellington 1982, this study) contradict the results obtained by direct observation by Sebens et al. (1996) in the Caribbean, where the high S:V coral *Madracis mirabilis* was found to feed to a greater extent than the low S:V coral *Montastrea cavernosa*. This discrepancy between geographical locations may be attributable to regional differences in plankton availability, species-specific feeding

abilities (Sebens et al. 1998), or morphological differences. Because of limited species availability in Panamá, polyp sizes ranged from only 1 to 3 mm, while the polyp sizes used by Sebens et al. (1996) varied from 3 to >10 mm. Although the species tested in this study do not display the full range of either colony morphology or polyp size that exist, this study expands the range of polyp sizes in which direct quantification of feeding has been observed.

Although polyp size was not observed to have a significant effect on feeding rates in this study, an effect may become pronounced as polyp diameter increases beyond the sizes present in the Gulf of Panamá. When combined with previously published results, the data may suggest a threshold polyp size above which a negative relationship exists between polyp size and normalized heterotrophic intake (Sebens et al. 1996) and below which a positive correlation exists between polyp size and heterotrophic intake (this paper). Further study is required to fully test this threshold hypothesis.

The assemblage of captured zooplankton did not differ among species, between depths, or between seasons (Table 2, Fig. 4). These results suggest that season, depth, colony morphology and polyp size do not affect the size or type of zooplankton a coral is able to capture, and are consistent with those of Sebens et al. (1996), who showed that the size and taxon of zooplankton captured by the Caribbean corals *Madracis mirabilis* and *Montastrea cavernosa* were not different. Thus, neither polyp size nor morphology limit heterotrophic intake in either Caribbean or Pacific corals, suggesting that zooplankton capture is limited by effective feeding surface area (Sebens et al. 1996, this study), the type of nematocysts and tentacles present (Sebens et al. 1996, 1998), or feeding effort (this study).

The 3 coral species differed in both ease of dissection and plankton identification. The small polyp size, light coloration, and short tentacles of *Pocillopora damicornis* allowed for quick identification of polyps that fed, and permitted easy zooplankton identification. For both *Pavona clavus* and *Pavona gigantea*, dark coloration made sighting and identifying captured zooplankton more difficult. Consequently, it is likely that the zooplankton captures reported here for these corals are conservative, and differences in feeding rates between low and high S:V corals may be even greater than reported here.

A highly significant difference between available zooplankton prey items and captured items was observed in this study (Fig. 5). The zooplankton taxa most commonly captured in relation to their abundance were observed to have poor swimming abilities and are between 200 and 500 µm (crab zoea, polychaetes, amphipods) (Fig. 5). Extremely large (mysids, >2000 µm) or small (copepods, <200 µm) prey items and faster-swimming taxa (isopods, 200 to 500 µm) were captured rarely in relation to their relative abundance (Fig. 5). These results are similar to those of Sebens et al. (1996), who hypothesized that variable predation-avoidance techniques accounted for the difference between prey availability and capture.

Compared to plankton samples collected in a bucket using a flashlight, plankton tows (J. E. Palardy unpubl. data) did not contain greater taxonomic diversity, but demonstrated that highly motile taxa were over-represented in the assemblage fed to the corals. As these highly motile taxa were exposed to shearing forces and abrasion during collection, it is possible that the zooplankton were injured, leading to a loss of escape behavior and therefore to capture rates higher than would be expected under ambient conditions. Since all fragments were exposed to zooplankton collected in the same manner, reduced zooplankton motility will not affect the relative capture rates among species, nor between seasons. Additionally, as there was no difference in captured zooplankton assemblage between coral species (Table 2, Fig. 4), relative feeding rates among coral species exposed to ambient zooplankton assemblages are unlikely to have differed.

This study provides a direct test of the effects of upwelling, depth and morphological traits on resource partitioning in eastern Pacific scleractinian corals *in situ* and presents direct evidence of increased coral feeding with increasing depth and with a decreasing S:V ratio, and decreased feeding in upwelling conditions. The data obtained corroborate previously published estimates of heterotrophic input via indirect linear skeletal extension and $\delta^{13}C$. As some of the data conflict with other direct observations of heterotrophic intake, significant regional or species-specific differences may exist.

The feeding rates of corals in this study were plastic, varying with changes in light intensity due to depth, and to environmental changes associated with upwelling. Such plasticity may allow for large shifts in energy input from heterotrophic means during stressful conditions. Coral species exhibiting plastic feeding rates may be able to offset reduced energy from photosynthesis during bleaching events and thereby experience lower mortality rates.

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