

EFFECTS OF PREY ESCAPE BEHAVIOR AND WATER FLOW ON PREY CAPTURE BY THE SCLERACTINIAN CORAL, *MEANDRINA MEANDRITES*K.B. Heidelberg¹, K. B. Sebens^{1,2}, and J.E. Purcell¹¹Horn Point Environmental Laboratories, Box 775, Cambridge, MD 21613, USA²Department of Zoology, University of Maryland, College Park, MD 20742, USA

ABSTRACT

Corals feed on zooplankton, mostly at night. Capture of zooplankton depends on delivery of prey to the tentacles and the ability of the corals to retain the prey, although mechanisms of prey capture are not well understood. We designed a recirculating laboratory flow tank that yielded oscillatory flow comparable to *in situ* reef conditions. This flow tank, in conjunction with high magnification video recordings with infrared illumination, allowed us to analyze small scale interactions using the coral *Meandrina meandrites* (Linnaeus) and zooplankton prey collected at a reef near Discovery Bay, Jamaica during 1994 and 1995. Prey behaviors (average swimming speed, avoidance and escape abilities) altered susceptibility to predation for five prey types (three copepod genera, copepod nauplii and chaetognaths). Flow conditions (still vs. oscillatory) and flow speed had significant effects on prey contact with the predator, with flow affecting both encounter and escape frequencies of the prey.

INTRODUCTION

Zooplankton provide much of the heterotrophic nutrition of corals and are crucial for replenishment of nitrogen, phosphorus, and other nutrients that cannot be supplied completely by the symbiotic zooxanthellae (reviewed by Muscatine and Porter 1977; Sebens 1987). The trophic position of scleractinian corals as predators on zooplankton is poorly understood, in part because research on their basic feeding biology is lacking. Strong patterns of selective feeding on zooplankton have been observed in corals (Johnson and Sebens 1993; Sebens et al. 1996a,b) and other anthozoans (e.g. Sebens and Koehl 1984). However, the factors that contribute to prey capture in these passive suspension feeders have not been studied. Aerosol filtration theory has been applied to suspension feeding (Rubenstein and Koehl 1977; Shimeta and Jumars 1991), but predator-prey interactions are much more complex. Properties of both predator (colony shape, polyp size, tentacle morphology, cnidae composition) and prey (size, shape, sensory capabilities, swimming speeds, avoidance/escape behaviors) influence the outcome of the interactions. Successful predation occurs only if the predator ingests its prey, so each step of the feeding process (encounter, contact, capture, and ingestion) can alter the probability of successful predation.

To date, specific studies on particle/zooplankton capture rates by corals and other benthic cnidarians in different flow regimes are limited to one species of hydroid, two octocorals, and four scleractinian corals (Hunter 1989; Patterson 1991; Lewis 1992; Helmuth and Sebens 1993; Johnson and Sebens 1993; Fabricius et al. 1995; Sebens et al. 1996b). These studies noted the importance of feeding structure morphology and flow for capture rates, but none examined the importance of prey escape behavior near the tentacles. Only the study by Trager et al. (1994) examined prey behavior and capture for a benthic suspension feeder, a barnacle, *Nobia grandis*.

Most zooplankton do not behave as passive particles. They have directed swimming and complex behavioral adaptations that increase their probability of survival (Ohman 1988). A few comprehensive studies have described escape behaviors among zooplankton species or from an artificially created flow field (Hauray et al. 1980; Yen 1985, 1988; Williamson 1987; Gilbert and Kirk 1988; Kirk and Gilbert 1988; Williamson and Vanderploeg 1988; Yen

and Fields 1992). In these studies, escape behaviors were elicited by a change in the hydrodynamics or by visual cues. Gilbert and Kirk (1988) suggested that some of these same responses may be elicited in the presence of a passive suspension feeder.

Copepods and other suspension feeding zooplankton form crucial links in the coral reef food web, so factors that affect coral feeding rates are important to quantify. Understanding prey behavior, associated with predator-prey interactions, is critical if we are to correctly assess the contribution of zooplankton to coral nutrition, energetics, and growth. The differences in zooplankton behaviors might help to explain both selective feeding by corals and zooplankton species composition within the reef. The objective of this study was to identify the effects of flow and prey behavior on zooplankton feeding by the scleractinian coral, *Meandrina meandrites*.

METHODS

Animal collection and maintenance

Small colonies (8-10 cm dia.) of *M. meandrites* were collected by SCUBA divers at 10-14 m depth from the forereef near Discovery Bay Marine Laboratory, Jamaica, West Indies. Corals were maintained in a laboratory flowing sea water table for 18-20 h under a normal day night light cycle. Colonies were transferred to isolation chambers made of 64 μ m Nitex netting 12 hours before an experiment, which prevented feeding on zooplankton but still allowed water exchange.

Zooplankton to be used as coral prey were collected on the forereef 1.5 h after sunset. A wide beam light was held inside a bucket for 5 to 10 min to attract and concentrate prey. The light was removed and the bucket was closed immediately. This method allowed collection of healthy copepods, mysids, chaetognaths, and other common reef zooplankton, whereas a pump or net often damaged zooplankton (Sebens et al. 1996b). In the lab, the bucket was kept in the dark and maintained at *in situ* temperature prior to experiments, which followed immediately.

Feeding Experiments

The Plexiglas recirculating flow tank (Fig. 1) used for feeding experiments was filled from the running seawater system. The flow tank could produce either unidirectional or oscillatory flow from 1-40 cm s^{-1} . Feeding experiments were conducted between 20:00-02:00, when corals would normally be feeding. The flow tank was covered by black plastic so that ambient light would not disturb feeding. Baseline swimming behaviors of prey were characterized in still water. Additionally, predator-prey interactions were analyzed in two oscillating flow speeds.

Flow speeds were measured by tracking clearly focused hydrated *Artemia* cysts (close to neutrally buoyant, ca. 230 μ m diam.) in the same region that zooplankton behaviors were observed. Cyst paths were tracked for 0.33 s along the top of the tentacle zone during three different phases of the oscillatory flow cycle (change in flow, accelerating/decelerating flow, and maximum flow). The oscillation period was 6 s for both flow treatments. The top of the tentacle zone was defined as the height above the coral where fully extended tentacle tips were located (ca. 8 mm above the coral polyps). This method provided an accurate way of determining flow

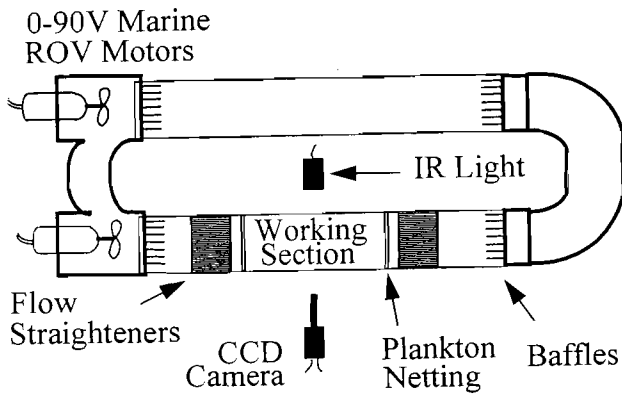


Fig. 1: The experimental flow tank consists of two channels (120 cm long and 14x14 cm in cross section) connected by PVC pipe (designed by K. Sebens and constructed at Horn Point Environmental Laboratory). The working section (30 cm long) is located in the middle of one channel. Alternating motors (ROV, 0-90v DC, J.W. Fisher, Mfg. Inc.) on a timer circuit yielded oscillating flow at specific flow patterns similar to in situ conditions. A baffle (3 cm wide) and flow straightener (10 cm wide tightly stacked drinking straws) were located at each end of the channel. Baffles were adjusted before use to correct for faster moving water along the outside edge of the flume, and the flow straighteners reduced the size of turbulent eddies. These produced a uniform horizontal and vertical flow field in the center of the working section of the channel. To prevent zooplankton from encountering propellers, 180 μ m Nitex screens were inserted on each end of the working section.

conditions at the most appropriate location relevant to predator-prey interactions (Sebens et al. 1996a, b).

Three coral colonies were used in each flow treatment. A single colony was placed at the center of the flume working area and allowed to fully extend feeding tentacles. Zooplankton were gently transferred in a beaker to the flume and allowed to disperse for 5 minutes. Predator-prey interactions were videotaped (CCD camera, Pulnix Model TM-9700) for 10 to 15 minutes. The camera has an adjustable shutter speed, high infrared sensitivity, and an adjustable field of view (0.5-1.0 cm). At magnification levels used in this study, the depth of field was less than 1 mm. Video footage was recorded using either a High 8 mm Video Camcorder (Sony, V99) or a High 8 mm VCR deck (Sony, EV-2000). An infrared light source (> 700 nm) was positioned 15 cm behind the working section of the flume to produce a backlit image of the feeding coral. Infrared light was used because it

has a higher wavelength than the typical spectral sensitivity range of crustacean zooplankton (Forward 1976), which are positively phototactic to visible light (Stearns and Forward 1984). A scale bar was videotaped at the completion of each run.

For accurate zooplankton identification in video images, a subsample of the available zooplankton was preserved each night in 5% formalin in seawater. A Folsom plankton splitter was used to obtain a random subsample of each sample. Zooplankters (≥ 200 individuals) were identified and measured to determine percent composition of the available prey. In addition, copepod cephalothorax, body, and antennae lengths were measured to further aid in videotape identifications.

Behavioral observations

During video analysis, all zooplankton that were in focus were categorized by type, and copepods were further identified to genus. After identification, each zooplankton-coral interaction event was characterized as one of the following: **No Reaction** - Zooplankter and tentacle were within 3 mm, but there was no change in swimming speed or angle; **Avoidance** - Zooplankter changed swimming speed and/or direction while approaching a tentacle (no contact); **Escape** - Zooplankter made contact with tentacle, but was not captured; **Capture** - Zooplankter made contact with tentacle and was captured. When a zooplankter remained in clear focus throughout the encounter, the swimming path was traced, frame-by-frame, from a high resolution 19" monitor (Panasonic, CT-2084VY). Two-dimensional swimming speeds and angles were calculated using a digitizer board (Jandel Scientific) and SigmaScan software (version 3.92) for interactions in still water. The small depth of field minimized error associated with three-dimensional swimming angles of the zooplankter.

RESULTS

Flow measurements

The two flow treatments had average speeds of 2.0 ± 1.4 SD (Slow Flow) and 4.9 ± 2.4 SD cm s^{-1} (Moderate Flow), measured along the top of the tentacle tips and averaged over the entire flow cycle. The oscillatory flow was further divided into three phases: 1. change in flow direction (characterized by low flow), 2. increasing or decreasing flow, and 3. maximum flow. Flow speeds were measured at the coral tentacle tips and within the tentacle zone for each phase of the flow cycle where zooplankton behaviors were observed (Fig. 2). During all phases, flow was significantly slower within the tentacle zone (ANOVA, LSD, all $p \leq 0.01$). Flow several centimeters above the coral would be much higher and comparable to in situ flow speeds above the tentacle tips (Johnson and Sebens 1993).

Table 1: Sizes and swimming speeds (Means ± 1 SD) of abundant prey types measured in still water. The numbers of measurements are in parentheses. Average swimming speeds represent swimming speeds prior to interactions with the coral. Different superscript letters indicate means which were significantly different with no significant difference between means indicated by the same letter (one way ANOVA at $p = 0.05$; LSD analysis). Means without letter designations were not compared in LSD analysis.

	Body length (mm)	Average Swimming Speed (cm/s)	Avoidance Speed (cm/s)	Escape Speed (cm/s)	Escape Speed (body lengths/s)	% Change in Speed (Escapes)
Copepods						
<i>Oithona</i> sp.	0.65 ± 0.15 (162)	0.76 ± 0.90^a (14)	3.06 ± 4.15 (5)	6.81 ± 2.56^a (6)	105	1598 ± 1460^a (6)
<i>Calanopia</i> sp.	1.29 ± 0.12 (162)	2.62 ± 1.08^b (34)	3.66 ± 2.35 (5)	8.32 ± 4.99^a (16)	65	185 ± 143^b (16)
<i>Temora</i> sp.	0.96 ± 0.07 (162)	0.83 ± 0.78^a (24)	3.24 ± 2.64 (7)	7.92 ± 4.06^a (13)	82	1859 ± 1775^a (13)
nauplii	0.21 ± 0.09 (41)	0.16 ± 0.23^c (5)	0.02 (1)	0.01 ± 0.0004^b (2)	< 1	23 ± 5.8 (2)
Chaetognaths	7.22 ± 2.21 (68)	0.48 ± 0.40^d (12)	4.10 ± 2.51 (7)	10.96 ± 1.42^c (4)	15	4388 ± 2254 (4)

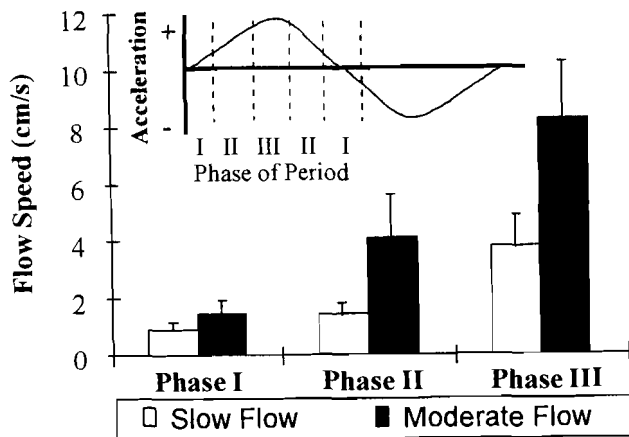


Fig. 2: Flow speed (Mean \pm 1 SD) as a function of phase of the oscillatory flow cycle. The flow cycle was divided into three phases: Phase I, change in flow; Phase II, accelerating or decelerating flow; Phase III, maximum flow. All measurements were taken along the top of the tentacle tips, approximately 8 mm above the coral colony.

Copepods

The cyclopoid, *Oithona* sp. and the calanoid, *Calanopia* sp., were the numerically dominant zooplankton throughout the study, but the calanoid, *Temora* sp. also was common in the still water feeding experiments. All had significantly different body lengths and body length to antennae ratios (one-way ANOVA, $p < 0.001$, $n=162$), which aided in video footage identification (Table 1).

Copepods that interacted with the predator had a relatively constant swimming speed and direction preceding an interaction. As a coral tentacle was approached, the copepod either performed an avoidance reaction or made contact, resulting in an escape response or a capture. Avoidance and escape responses were characterized by a distinct change in swimming speed and trajectory (Fig. 3). The percent occurrence of contacts was highest in still water as evidenced by the high proportions of escapes and captures and relatively low avoidance responses (Fig. 4). The addition of flow significantly decreased contacts with coral tentacles; 57% of copepods observed within 3 mm of a tentacle contacted the predator in still water treatments, while only 15% made contact in flow treatments.

Both *Oithona* sp. and *Temora* sp. had significantly slower average swimming speeds than *Calanopia* sp. (One-way ANOVA, $p < 0.001$) (Table 1). Slower swimming speeds corresponded to higher percent occurrence of avoidance behaviors for both *Oithona* and *Temora* (Fig. 4). Avoidance speeds of the three copepod genera were highly variable and not significantly different. Although escape speeds were not significantly different among genera, the percent change in swimming speed was significantly greater for both *Oithona* and *Temora* than for *Calanopia* (Table 1, ANOVA with arcsine transformation, $p \leq 0.003$).

Chaetognaths

In still water, chaetognaths had lower percent occurrences of contact than did the copepods and maintained controlled positions around the coral (Fig. 4). Chaetognaths frequently swam in a head-down or head-up hop and sink motion, with a slow average swimming speed of 0.48 ± 0.40 cm s^{-1} . Although chaetognaths have very good avoidance and escape responses, speeds could not be as accurately determined as for other zooplankton because the distances traveled took many off camera in one frame (avoidance and escape speeds reported in this study are probably underestimates of true means). Most (87%) of the contacts with the corals occurred along the

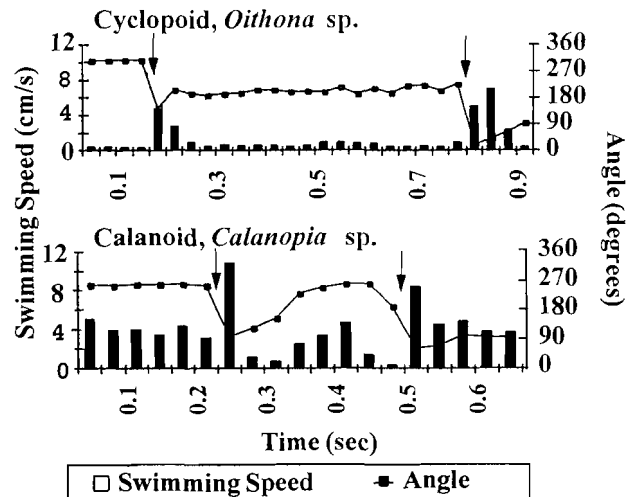


Fig. 3: Swimming speed (bars) and direction (line) exhibited by two typical copepods, the cyclopoid, *Oithona* sp. and the calanoid, *Calanopia* sp. Escape behaviors are characterized by both a change in swimming speed and trajectory (indicated by arrows). Plotting the direction of movement on a 360° scale relative to an x-axis parallel to flow = 0° to 180° and a y-axis = 90° to 270° determined the trajectory. The two copepods differed significantly in baseline cruising speed in still water (One-way ANOVA, $p < 0.001$) and percent change in swimming speed during an escape (ANOVA on arcsine transformed data, $p < 0.001$).

chaetognath mid-body or tail. Flow did not significantly affect contact rates or behavioral responses (Chi-square contingency table, $p > 0.05$).

Copepod nauplii

Nauplii were weak swimmers (average speed = 0.16 ± 0.23 cm s^{-1}). In still water, nauplii were slightly negatively buoyant when not swimming, and they sank into tentacles in 57% of the contacts (gravitational deposition). Once contact was made, 67% of the nauplii were able to escape (Fig. 4). Escape speeds were actually slower than the average cruising speed because of temporary retention by the predator. In both flow treatments, nauplii behaved like neutrally buoyant particles. The few contacts observed in the slow flow experiments did not elicit a strong tentacle response, and the nauplii were almost always dislodged, probably by hydrodynamic drag forces exceeding the holding strength of the mucus or cnidae attachment.

Oscillatory flow effects

Unlike copepod nauplii, both copepods and chaetognaths had distinct behavioral responses in flow treatments. We further analyzed these responses by grouping the copepods and chaetognaths. The oscillatory flow cycle was divided into three phases with different mean flow speeds (Fig 2). For copepods and chaetognaths, the phase in which the interaction occurred significantly altered the frequency of prey behavioral responses in the moderate flow treatments, but did not have an effect on the low flow experiments (Fig. 5). In low flow, there was no difference in the expected frequencies of avoidance reactions throughout the entire flow cycle (Phases I-III) (Chi-square $p > 0.05$). However in moderate flow, the copepod and chaetognath encounter rates were significantly lower than expected during Phase III (Chi-square, $p < 0.0001$) (Fig. 5). During Phase III tentacles were flattened against the coral and the water flow streams controlled the paths of the zooplankton. Almost all active interactions occurred during Phase I, which had the lowest flow speeds and fully extended tentacles.

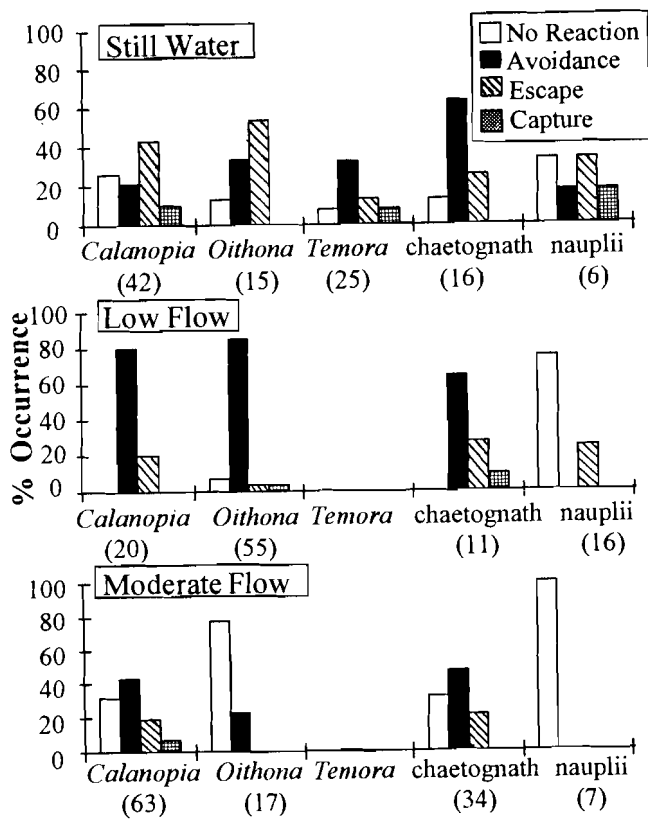


Fig. 4: Percent occurrences for each of the prey behavior categories in each flow treatment (still water, oscillatory Slow and Moderate). Chi-square contingency table analysis showed that *Calanopia* sp., *Oithona* sp., and nauplii all had significant differences in proportional behavioral responses with flow ($p \leq 0.001$), but there was no flow effect on chaetognaths ($p > 0.05$).

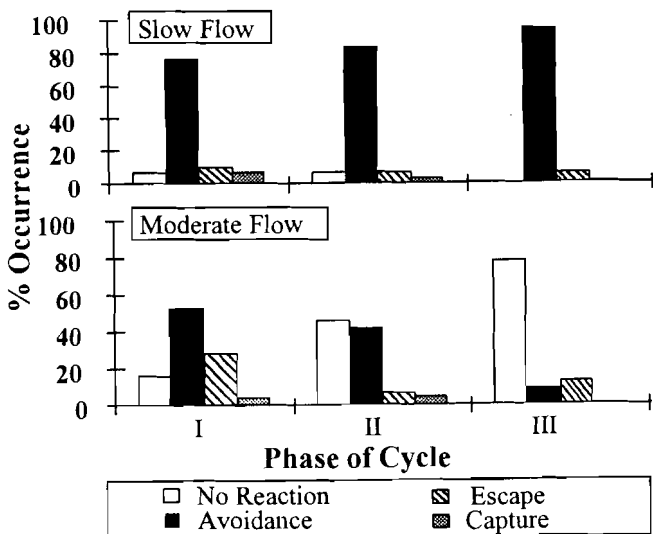


Fig. 5: Percent occurrences for each of the prey behavior categories as a function of the phase in the oscillatory flow cycle. Copepod and chaetognath data from Fig. 4. were summed and reanalyzed in a contingency table to determine response differences throughout the flow cycle. Low flow had no difference in the expected frequencies of behavioral responses during the flow cycle (Chi-square $p > 0.05$). Encounter rates were significantly lower than expected during Phase III (Chi-square, $p < 0.0001$).

DISCUSSION

We found that both prey behavior and water flow help explain selective feeding by the coral, *M. meandrites*. Zooplankton on coral reefs have complex behavioral adaptations that promote their survival within the reef ecosystem. Most studies that have quantified coelenteron contents from cnidarians show a strong negative selection for copepods (e.g. Fancett 1988; Johnson and Sebens 1993; Fabricius et al. 1995; Sebens et al. 1996a,b). Additionally, selection differences have been observed among copepod genera; *Calanopia* sp. was captured much more frequently than *Oithona* sp., even though the latter was more abundant in ambient water samples adjacent to three coral species (Johnson and Sebens 1993; Sebens et al. 1996a,b).

Zooplankton capture

For copepods, baseline swimming speed was important for both encounters and capture success. Both *Oithona* and *Temora* had lower swimming speeds than *Calanopia*. A slower approach meant a better opportunity to perform a successful avoidance behavior and a contact with less force than the faster moving, larger, *Calanopia*. Nematocyst discharge is affected both by prey mechanical and chemical cues (Thorington and Hessinger, 1988; Watson and Hessinger 1988). Prey items that contact feeding tentacles with greater force should be captured more readily; however, this has yet to be investigated. In both flow treatments, *Oithona* sp. had less contact with coral tentacles than *Calanopia* sp. These results help explain the higher selectivity for *Calanopia* sp. previous studies.

Cheetognath behavior was not affected by the flow speeds tested in this study. When swimming in a head-down position, they rarely made contact with tentacles. However, when swimming horizontally or in a head-up position, they often made contact both by floating down into tentacles and direct interception. Most contacts were along the mid-body or tail section, but they were rarely captured. Sebens et al. (1996b) found that chaetognaths were highly selected for in field feeding experiments. Potentially in higher flows, encounter rates would increase, and chaetognaths avoidance abilities might decrease.

Copepod nauplii are rarely captured by *M. meandrites*. However, the adhesion apparently was not sufficiently strong to transfer prey to the oral disks before swimming behavior (in still water) or accelerating or drag forces (in oscillatory flow) resulted in escape of the nauplius. *M. meandrites* uses mucus strands for feeding on particulate material (Lewis and Price 1975), but this does not appear to be an effective mechanism for zooplankton feeding. Unlike Green and Landry (1985), who found the calanoid *Euchaeta* naupliar stages more susceptible to predation by active suspension feeders, because of their slow swimming speeds, we found that the naupliar stages escaped predation by this coral possibly because their small size did not trigger significant nematocyst discharge.

Flow Effects

Corals are passive suspension feeders, relying on water flow patterns to bring potential prey items into proximity with feeding structures. Water flow has profound effects on benthic suspension feeders (reviewed by Shimeta and Jumars 1991). Differences in flow affect suspension feeding by altering plankton contact rates, behaviors, and feeding structure effectiveness (Sebens and Johnson 1991; Johnson and Sebens 1993; Helmuth and Sebens 1993). We found a highly significant effect of flow on zooplankton behavior. Our data suggest that not only is flow speed important for determining particle encounter rates, but that the phase of the oscillatory flow is also important for predation by corals. Hunter (1989) characterized scleractinian corals as rigid organisms regarding flow effects. However, for a coral with large polyps and long tentacles, such as *M.*

meandrites, this is not the best classification. Zoo-plankton-tentacle interactions occur on a scale smaller than the average height of the flexible tentacles of *M. meandrites*. Water flow can deform the long tentacles of this coral at flow speeds well below 10 cm s^{-1} (Sebens and Johnson 1991 and this study). During deformation, the tentacles collapse together, and water carrying prey items passes over the tentacles following streamlines. Mechanical deformation of the tentacles on top of the colony occurred during Phase III of the faster flow speed in this experiment. During this time, there is less surface area available for prey capture. However, tentacles become fully extended during Phase I. During this phase the zone below the tentacle tips has a lower flow than ambient, and prey are mixed or fall down into the zone below tips (Johnson and Sebens, 1993). Sebens and Johnson (1991) also found that particle capture rates of *M. meandrites* were higher at flow speeds below 5 cm s^{-1} . Phase I of the oscillatory flow cycle always had the highest amount of prey contact. Flow regimes that have shorter periods would have less time during which tentacle deformation occurs, and possibly greater turbulence, both of which could increase plankton contact rates.

As heterotrophs, an important aspect of the success of corals is their ability to retain and ingest prey items after contact with feeding structures. The design of this study was to quantify specific prey behaviors that enhanced or prevented capture by predators. Our results suggest that in low flow, differences in prey avoidance and escape abilities explain the selective feeding. Oscillatory flow always has a phase where flow speeds are low, and differences in avoidance and escape behaviors of zooplankton would be important. We found that copepods and chaetognaths had excellent behavioral adaptations that prevented capture by corals. During periods of higher flow, tentacle deformation and prey size are more important.

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