

At 12m, larger individuals re-emerged later, presumably because they are more conspicuous and therefore are at greater risk to predation. It has been reported that age is directly correlated to size (Hunte, 1990). Hence, it appears that older worms have either learned to be more cautious, or that individuals quick to re-emerge were differentially eliminated via predation.

Because a wide array of color patterns was observed across all depths, light alternation and its effect on color perception does not appear to be a force selecting color morphology. Predators may not be visually cued or individuals may benefit from variation in color and pattern by straying from a common visual search image. In this case, uniqueness would increase an individual's chance of survival. It appears that worms are palatable or else a convergence upon an aposomatic color pattern would have been observed (John J. Gilbert, pers. comm.). Crypticity may also play a role, although our methods were unable to provide evidence for this.

Worm location and orientation on coral heads change with depth presumably in response to currents. In shallow waters, the majority of *S. giganteus* seek refuge from waves and surge by positioning themselves on the sides of promontories. At depths greater than 6m, the filtering process may be limited by low ambient current. By locating themselves on top

of coral heads, current flow is maximized, filtering efficiency is enhanced, and the chance of refiltering is reduced.

Because this investigation shows that environmental factors and predation risk exert selective pressures on *S. giganteus*, further studies could possibly pinpoint the mechanisms behind these forces. Specific time trials between cryptic and non-cryptic individuals or comparative studies between sites with varying predation pressure would both delve deeper into the questions behind color patterns and overall morphology and behaviors of the worms.

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CAPTURE OF SMALL AND LARGE ZOOPLANKTON BY *MADRACIS MIRABILIS*

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ABSTRACT

Under laboratory conditions, this study examined the effect of prey size on polyp handling time, polyp investment per prey item, and capture rate by the coral *Madracis mirabilis*. Handling time was approximately 34 times greater with large prey (Mysids) than with small prey (*Artemia*). Polyp investment was higher, on average, with three polyps involved in subduing a mysid individual in contrast to the single polyp capture of *Artemia*. Also, capture rates of mysids were 50 times lower than those observed for *Artemia*. This suggests that it is potentially more costly to capture large prey than small prey if it results in a decrease in feeding efficiency by the coral polyp.

Key Words: *Madracis mirabilis*, coral polyp, tentacle capture, feeding strategy, nutrient acquisition.

INTRODUCTION

Research on coral feeding mechanisms has primarily focused on the role in symbiotic zooxanthellae providing photosynthate to the coral. However, corals use a variety of feeding strategies to exploit nutrients from dissolved organic and particulate matter, bacteria, and zooplankton found in the external environment (Clayton and Lasker, 1982). These strategies include prey capture by tentacles, entanglement by mucous nets, and feeding by ciliary currents (Lewis and Price, 1975). The relative importance of these feeding mechanisms for different coral species is not well understood.

In some Atlantic corals, prey capture by tentacles is the primary mode of acquiring nutrients from the external environment. Tentacles have been regarded by many researchers to be the most important organs involved in such nutrient uptake (Lewis and Price, 1975). Lewis and Price (1975) examined the feeding behavior of 35 coral species and found that the families Poritidae and Pocilloporidae incorpo-

rate external nutrients primarily by tentacle capture. Although only one feeding strategy is employed, the polyp tentacles are expanded both day and night thus allowing continuous prey capture.

The coral *Madracis mirabilis* (Pocilloporidae) uses this strategy for nutrient uptake. Polyp tentacles are particularly effective in the capture of zooplankton (Lewis, 1976). Gut content analysis of *M. mirabilis* show that small copepods are abundant in the coral diet while larger zooplankton species, i.e. mysids, have not been recovered (personal communication with Jan Witting). If the ability of the coral polyps to capture and digest these two different size classes of prey are the same, then one would expect to find the same ratio of small to large zooplankton in the coral diet as is found in the field. In Discovery Bay, Jamaica, small copepods are approximately 300 times more abundant than the larger zooplankton family Mysidae. Since mysids have not been to occur in the natural diet of *M. mirabilis*, it may be

that the coral is preferentially selecting the smaller prey items or, alternatively, the large prey may be more difficult to capture.

This study examines the feeding behavior of *M. mirabilis* focusing on the effect of prey size on polyp handling time, polyp investment per prey item, and capture rate. I predict that handling times and polyp investment will be greater with large prey items than with smaller ones and that capture rates will vary inversely with prey size.

METHODS

Madracis mirabilis colonies were collected on 1 and 3 March, 1994 from a reef located off of Columbus Park in Discovery Bay, Jamaica and transported to the Discovery Bay Marine Lab. Coral colonies were maintained in running, unfiltered sea water and all experiments were conducted within two days of *M. mirabilis* collection.

The capability of *M. mirabilis* to feed on small prey items (*Artemia salina*) and large prey items (mysids; Mysidae) was determined from laboratory observations. Once polyps attained feeding postures (horizontal and vertical positioning of the tentacles and elevation of the oral disk; Lewis and Price, 1975), a single prey item was injected into the vicinity of the coral polyps. Handling time of individual prey items was measured as the time from initial tentacle contact with the prey item to the resuming of polyp preparatory feeding postures. Observations were made on illuminated corals using a stereomicroscope. Polyp investment

was defined as the number of polyps involved in subduing and/or feeding on the prey item. For example, if multiple polyps are involved in subduing one prey item this would mean there was a high polyp investment.

M. mirabilis feeding rate was measured on four different colonies each broken into five smaller segments. Fragmentation of the colony did not produce any observable changes in coloration or polyp behavior. Each clonal segment was placed in 120ml seawater and its polyps allowed to expand. Fifty *Artemia* or fifteen mysids were then added and the segment allowed to feed, under dim light, for 30 minutes with small prey and 45 minutes with large prey. The clonal segments were then rinsed in seawater and the remaining prey items counted. The number of polyps on each clonal segment was counted to determine a capture rate defined as the number of prey captured per minute per polyp.

In an attempt to quantify the qualitative difference in small and large prey swimming behavior, a single prey item was placed in 20ml of seawater in a petri dish that was divided into 22 one centimeter squares. Observations were made using a stereomicroscope. The number of squares entered by an individual in one minute was noted. All data were analyzed using student t-tests.

RESULTS

There were no significant differences in prey handling time, polyp investment, or capture rates between day and night with either

Table 1: *M. mirabilis* handling times (seconds) of small and large prey items for day, night, and combined trials. Data are expressed as mean \pm SE.

	n	Handling Time(s)	Prey Type	p
Day	20	111.3 \pm 11.2	<i>Artemia</i>	0.39
Night	20	98.85 \pm 8.6	<i>Artemia</i>	
Day	8	2679.3 \pm 536.2	Mysid	0.10
Night	7	4461.4 \pm 837.0	Mysid	
Combined	40	105.1 \pm 7.0	<i>Artemia</i>	<<.001
Combined	15	3510.8 \pm 522.7	Mysid	

size class of prey (Tables 1 and 2). Therefore, in all subsequent analyses, day and night trials were combined.

The handling time of large prey was approximately 34 times greater than the handling time of small prey ($p < 0.001$; Table 1). In addition, the polyp investment increased with the larger prey items. Mysid capture always involved at least two polyps and, on average, three polyps to subdue the prey. In contrast, in each of 40 *Artemia* feeding trials one polyp was solely responsible for capturing the prey item.

Capture rates differed significantly for small and large prey. Approximately fifty times as many *Artemia* were caught per minute per polyp as mysids ($p < .001$; Table 2). Mysids were more active swimmers than

Artemia. They entered, on average, 44 squares in a minute in contrast to the 8 mean squares entered by the *Artemia*. Mysids were approximately five times the length of the *Artemia* (personal observation).

DISCUSSION

Madracis mirabilis captures prey primarily through the use of its tentacles. Therefore, the efficiency and rate at which the tentacles are able to capture prey has direct ramifications on the coral's net nutrient income. In these feeding experiments, *M. mirabilis* had shorter handling times, lower polyp investment, and higher capture rates with small prey items than with large prey items.

Table 2: Capture rate (number prey eaten/min \times (polyp $\times 10^3$)) at small and large prey items by *M. mirabilis* during day, night, and combined trials. Data are expressed as mean \pm SE.

	n	Capture Rate	Prey Type	p
Day	5	13.38 \pm 1.9	<i>Artemia</i>	>0.5
Night	5	12.35 \pm 1.2	<i>Artemia</i>	
Day	5	0.170 \pm .07	Mysid	>0.5
Night	5	0.335 \pm .11	Mysid	
Combined	10	12.80 \pm 1.07	<i>Artemia</i>	<<.001
Combined	10	0.2525 \pm .07	Mysid	

Polyp handling time was significantly lower with *Artemia* prey than with mysid prey. Presumably, this is due to the relative size differences between the two prey types. The *Artemia* were approximately one-fifth the size of the mysids and were therefore more readily processed by the polyp. This lower handling time, associated with smaller prey, incurs a greater ability to feed because the quicker the polyp can process prey, the sooner it will be able to resume a preparatory feeding posture.

A low polyp investment was characterized by a low number of polyps involved in subduing a single prey item. If several polyps are occupied with one prey item, as was the case with mysid individuals, there is a reduction in the number of foraging polyps available, at a given time, to capture other prey items. This could possibly result in a lower net nutrient income to the coral colony. In this study, *Artemia* were immediately captured upon first contact with a tentacle tip. Each tentacle then contracted around the prey and stuffed it into the polyp's mouth. In contrast, mysid capture involved at least two polyps. Multiple tentacles, from one or more polyps, would grasp the caudal end of the mysid while at least one other polyp wrapped its tentacles around the prey body. It was not clear if one polyp then ingested the whole prey item or if ingestion by multiple polyps was occurring. The polyps involved in subduing the mysid would remain contracted for up to three hours whereas the single polyp that captured an *Artemia* would be contracted for no more than three and a half minutes.

On several occasions, mysid individuals

were captured by one tentacle and then able to escape. In contrast, *Artemia* were never observed to escape once captured by tentacles. This difference in prey escape capacity is most likely a consequence on different prey size and different levels of swimming activity. Mysids are larger and more active swimmers than *Artemia*. Therefore, larger prey size seems to incur a greater polyp handling time while better swimming ability reduces polyp capture efficiency.

The size variation between *Artemia* and mysids is most likely correlated with different nutrient levels available in each prey item. If mysids confer a much higher nutrient return to the polyp than *Artemia*, this may offset the cost of high handling times and low capture efficiencies. However, if the net nutrient uptake to the coral colony is equal for these two prey types, it would be advantageous for the polyps to preferentially select the smaller prey that require less handling time and are easier to capture. The relative nutritional value of different prey types and the potential for polyp food selectivity need to be investigated.

This study has focused on one nutrient gathering mechanism employed by an Atlantic coral species. Previous discussions on coral nutrition have treated various feeding mechanisms as independent (Clayton and Lasker, 1982). However, this is probably not the case as some researchers suggest that zooplankton feeding is dependent on the energy derived from the coral's photosynthetic zooxanthellae. If the different feeding strategies function as inter related mechanisms, the efficiency of nutrient capture by one feeding mode (i.e. tentacle capture) may

have direct consequences on the overall feeding behavior on the coral colony. Therefore, the relative importance of different feeding modes and the efficiency with which each strategy is able to capture nutrients is vital for understanding resource partitioning and allocation within a coral species.

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