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Zooplankton capture by two scleractinian corals, *Madracis mirabilis* and *Montastrea cavernosa*, in a field enclosure

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Abstract Capture of zooplankton by scleractinian corals has been noted for several species, yet quantitative information on rates of capture and differential capture by prey taxon has been lacking. We used field enclosures to examine prey capture for two coral species, *Madracis mirabilis* (Duchassaing and Michelotti) and *Montastrea cavernosa* (Linnaeus), on the north coast of Jamaica (Discovery Bay) in November 1989, February and March 1990, and January 1992. *M. mirabilis* has small polyps and a branching colony morphology (high surface/volume ratio), whereas *M. cavernosa* has large polyps and mounding colonies (low surface/volume ratio). Corals were isolated from potential prey, then were introduced into enclosures with enhanced zooplankton concentrations for 15- to 20-min feeding periods. Corals were fixed immediately after the experiment to prevent digestion, and coelenteron contents were examined for captured zooplankton. Plankton pumps were used to sample ambient zooplankton in the enclosures near the end of each run. Selectivity and capture rates were calculated for each prey taxon in each experiment; both indices were high for relatively uncommon large prey, and low for copepods, which were often the most common items in the plankton. Sizes of zooplankton captured by both species were generally larger than those available considering all prey taxa combined, but were almost the same for both coral species, even though the corals' polyp sizes are very different. This occurred primarily because small copepods, with low capture rates, dominated most plankton samples. For specific prey species, or group of species, there were few significant differences in size between the prey available and the prey captured. *M. mirabilis*, with small polyps, also captured far more prey per unit coral biomass than did *M. cavernosa*, with much larger polyps. We hypothesize that the large differences in capture rate of prey taxa are related to escape or avoidance behavior by those potential prey, and to the mechanics of capture, rather than to any selectivity by the corals.

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Introduction

Although corals are known to feed on zooplankton and other particulate material, quantitative data on natural prey are available for only two species of scleractinian corals (*Montastrea cavernosa*, Porter 1974, and *Meandrina meandrites*, Johnson and Sebens 1993). Zooplankton feeding is likely to be important to most scleractinian corals, since replenishment of nitrogen, phosphorus, and other nutrients that cannot be supplied from photosynthesis by the coral's symbiotic algae must come from zooplankton capture, from particulate matter, or from dissolved compounds (Muscatine and Porter 1977, review; Sebens 1987). Corals and other anthozoans use both nematocyst adhesion (Muscatine 1973), and cilia with mucus entrapment (Yonge 1968; Goreau et al. 1971; Lewis and Price 1975) to capture prey, although the latter mechanism is probably most often used to capture small nonmotile particles. For a variety of anthozoans, polyp size appears to be positively correlated with prey size captured (Sebens 1987, review), although the generality of this pattern is untested for corals.

Zooplankton are crucial to the nutrition of certain anthozoans; Edmonson (1928) fed zooplankton to corals kept in darkness; large-polyp corals lived >45 d, small-polyp corals <18 d. Yonge and Nicholls (1931) fed five coral species zooplankton in light and dark laboratory experiments (228 d); starved colonies lost tissue but fed colonies did not. Wellington (1982) used field enclosures with plankton netting around corals to exclude zooplankton. His experiments showed that both small and large polyp corals relied on zooplankton for a significant fraction of their growth. Lewis (1992) also found high rates of zooplankton capture for the hydrocoral *Millepora alcicornis*, with very small polyps. Sebens (1977) demonstrated that three zoanthid species captured small zooplankton and that light alone, with filtered seawater, was insufficient for colony mass increase. Sorokin (1991) found high rates of heterotrophy for a wide range of coral reef Cnidaria. Thus, even for shallow-water anthozoan species with abundant zooxanthellae, prey capture may be critical. Porter (1976) proposed a model in which corals with small polyps and large colony surface/volume ratios (S/V) are expected to rely on photosynthesis for most of their energy, whereas those with large polyps and lower S/V ratios are predicted to be zooplankton capture specialists. Data collected during this study can be used to provide a partial test of this hypothesis.

Near-substratum zooplankton on coral reefs are partially demersal (originating on the substratum) with a strong diel pattern of upward migration at dusk and downward migration at dawn (Emery 1968; Glynn 1973; Alldredge and King 1977, 1980; Porter and Porter 1977; Porter et al. 1977, 1978; Hobson and Chess 1979; Rützler et al. 1980; Robichaux et al. 1981; Ohlhorst 1982). Coral reef zooplanktivores capture much of their prey during these two periods of migration, as well as through the night (corals, Porter 1974; zoanthids, Sebens 1977; fish, Hobson and Chess 1979; Jakubczak 1989). Benthic zooplanktivores thus have two potential prey resources: (1) zooplankton originating from the open-water plankton community, and (2) substratum-related prey, including the larvae of benthic invertebrates, adult benthic crustaceans that spend some time swimming, and epibenthic organisms resuspended off the bottom by water flow. Corals use mechanisms of capture (such as muco-ciliary feeding) suitable for intake of protozoa, small microzooplankton, and other very small particles (Lewis and Price 1975), and thus particulate organic material (POM) has the potential to fulfill some portion of their nutritional requirements. Uptake of POM has been documented for cerianthids (Tiffon 1976) and for a sea anemone (Van Präet 1980). Phytoplankton were rarely observed in coelenteron contents in the present study, although the methods used were not designed to quantify such small particles. In general, cnidarians are not known to consume phytoplankton, although recent studies on alcyonaceans (Fabricius et al. 1995) indicate that the octocoral, *Dendronephthya hemprichi*, can ingest and digest significant amounts of phytoplankton. Detrital material also provides substratum for growth of bacteria, which are known to be a potential food source for corals (DiSalvo 1971; Sorokin 1973).

This study examined the zooplankton prey captured by two scleractinian corals, *Madracis mirabilis* and *Montastrea cavernosa*, on the fore-reef at Discovery Bay Jamaica. The former is a mounding species with polyps >10 mm diameter (tentacle crown), whereas the latter forms narrow branches with small polyps <5 mm crown diameter. Both species are common on the fore-reef, and were much more common there before 1980 (Liddell and Ohlhorst 1987) when Hurricane Allen cleared much of the live coral off the shallow reef zones. Experiments were conducted in large field enclosures which allowed natural bidirectional water movement and enhanced plankton concentrations. Corals were never removed from the water before the experiment, and plankton were attracted into the flume, such that both predator and prey were likely to behave normally. Corals were preserved in situ at the end of each 15- to 20-min experiment to prevent digestion of prey, and concurrent plankton samples were taken in the chamber using an omnidirectional plankton pump (Sebens and Johnson 1991; Sebens and Maney 1992). These methods allowed us to compare prey capture to prey availability and to calculate selectivity indices for each experiment.

Materials and methods

Experimental procedures

Corals were collected on the fore-reef at Discovery Bay, Jamaica (depths 8 to 15 m) for experiments conducted in November 1989, February/March 1990 and January 1992. Branches of *Madracis mirabilis* (Duchassaing and Michelotti) (Fig. 1A) were positioned upright in four plastic tubing holders (15 × 10 × 10 mm) glued to Plexiglas plates, such that branches were at least 5 cm apart laterally. Small heads (8 to 15 cm diameter) of *Montastrea cavernosa* (Linnaeus) (Fig. 1B) were glued to 15 × 30 cm Plexiglas plates using dabs of Pettits underwater epoxy, being careful not to let the epoxy touch the coral tissue. Corals on plates were placed in depressions on the reef for one or more days, then transferred to an "isolator" at least 6 h before being used in experiments (usually 24 h). The isolator consisted of a large Plexiglas enclosure 50 × 50 × 30 cm, with two ends covered by 40 μm Nitex, cleaned daily. This prevented corals from being exposed to plankton until the time of the run, although a few zooplankton could move in and out of the isolator whenever the lid was opened. The isolator prevented corals from being contacted by demersal migrating plankton during the early evening hours before the experiment. Corals expanded fully in the isolator, comparable to those on the reef, and were thus ready to feed when transferred to the field enclosure.

The experimental feeding enclosure (Fig. 1C) consisted of a two-piece Plexiglas channel (150 × 40 × 25 cm), painted black on all surfaces. Each end was covered by 180 μm Nitex mesh which slowed flow through the channel (< 50%). Flow straighteners inside each end consisted of racks of white plastic gird with 1 cm square openings, stacked 10 cm deep. Two adjustable vanes on each end of the enclosure allowed flow to be slowed below ambient, retaining the same period of oscillatory flow. The center of the enclosure had a removable lid that allowed corals on their plastic holders to be placed into the enclosure and held down with Velcro tabs. Flow at this site was oscillatory, with a slightly greater mass transport toward than away from shore (examples in Helmuth and Sebens

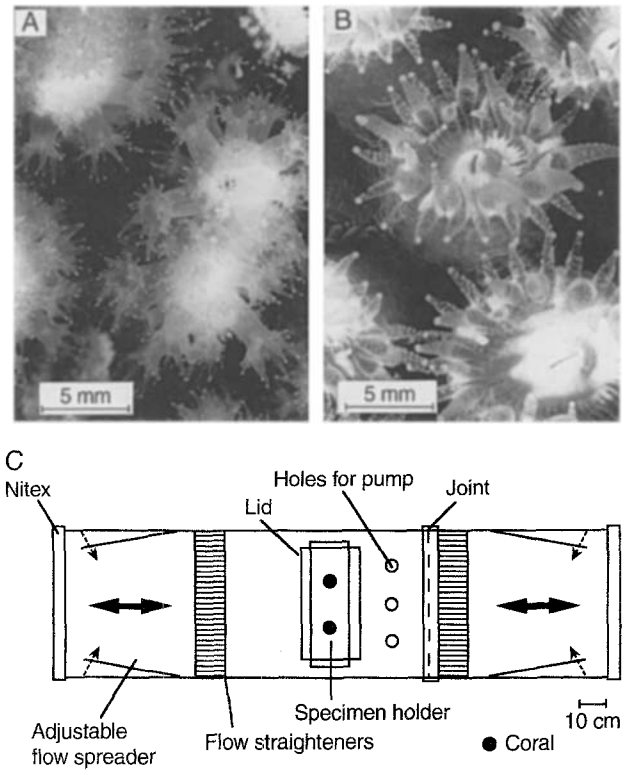

Fig. 1 **A** *Madracis mirabilis*, **B** *Montastrea cavernosa*. Polyps fully expanded at night (scale: 5 mm). Note prominent acrospheres on tentacle tips of both species. **C** Diagram of enclosure used for field experiments (scale: 10 cm)

1993). The same oscillations, at a lesser magnitude, were produced inside the chamber. Flow was measured outside the chamber (Interocean S4 current meter, 0.5 m off bottom) during each run and was also measured 1 to 2 cm above each coral specimen at the end of each run with video recordings of particle (*Artemia salina* cyst) tracks (method of Sebens and Johnson 1991). Flow was not necessarily equal across the width of the enclosure, so flow was measured over the center of each coral.

Low concentrations of prey, and consequent low numbers captured (e.g. <1 per 100 polyps, Porter 1974), made it necessary to use higher concentrations for feeding experiments. To initiate an experiment, zooplankton were attracted using a wide-beam light placed inside one end of the enclosure, facing through the enclosure so that plankton had to swim into the enclosure through the opposite end or through the lid. Any other method of providing zooplankton would have involved collecting them with nets which could damage them or change their behavior. Attraction to a light meant that the composition of the plankton might be different from that on the reef at the same time, but the plankters would not be physically damaged. The possibility that plankters are "blinded" by this technique is a real one, although we noted that plankton in the chamber continued to show attraction to light, and avoided obstacles, after being exposed to the initial attractor. Their swimming behavior also allowed them to avoid direct contact with the light (as they would do for sunlight). The Nitex end pieces were placed on the enclosure after the concentration of plankton in the flume had reached the desired point, and the light was removed, after which all dive lights were kept off within 5 m of the enclosure or isolator. Preliminary trials demonstrated that the enclosure had to be covered with black plastic or be painted black to prevent plankton from congregating on the upper surface as they moved toward surface light; this was noticeable on nights with strong moonlight. Even with full darkness, it was evident that the concentration of plankton dropped during the 15- to 20-min run, and it is probable that some plankton escaped and/or settled onto surfaces. All experiments were conducted 1 to 4 h after sunset.

Once plankton were distributed throughout the enclosure, corals were added by removing them from isolators, carrying them by the plastic holders, placing them in the enclosure, then quickly closing the lid. Living coral surfaces were never touched by hand, and corals usually expanded and began feeding within a minute or two after being placed in the enclosure. Corals that did not expand within the first few minutes were omitted from the experiment. Zooplankton samples were taken during the last 3 min of each run by pumping plankton through three intake heads positioned 5 cm above coral surfaces. Corals were allowed to feed for 15 to 20 min, then were tapped to cause polyp contraction. Videos (8 mm Sony V9 camcorder) were taken of *Artemia salina* cysts injected into the enclosure, using a 5-mm slit of light provided by a Subatec video light positioned on top of the enclosure, with a moveable set of black plastic parallel plates on a track under the flume lid (0.5 to 1 min per coral). Scale was provided by the plastic holders of *Madracis mirabilis* branches, and by a ruler glued to the light slit above each coral. Photographs of each coral were also taken after collection, with scale, such that measurements of particle movement (for flow speed calculation, Sebens and Johnson 1991) could be calibrated to coral size as well. After video photography, corals were marked with pencil on their lower upstream (seaward) side, then were removed and taken directly to the boat; corals and zooplankton samples were preserved within minutes of the end of the experiment such that minimal digestion occurred before preservation.

Zooplankton quantification

The plankton pumps used were similar to the HOPLASA system developed by Rützler et al. (1980) in that water is forced through a small plankton net held inside a rigid tube. In our design (Sebens and Johnson 1991; Sebens and Maney 1992), a bilge pump (Rule 2500 gph) pulls water through a 15 cm diameter PVC pipe with a 40 μm mesh Nitex plankton net upstream of the pump, so plankton does not travel through the impeller. This produces a speed of 12 cm s^{-1} or greater in the center of the net, or >36 cm s^{-1} at each of the three intake heads. Flat plates above and below the openings orient intake such that water moves in horizontally from around the intake head, irrespective of ambient flow direction; organisms are not sucked off the substratum below the heads. This design offers several advantages: (1) flow into the intake heads is omnidirectional and lateral; (2) flow at the intake is more rapid than swimming speeds of most zooplankters; and (3) intake heads can be positioned within a few centimeters of a coral surface without impacting the coral or the flow around it. Sampling times were sufficient to collect >200 recognizable zooplankters, usually 500 to 1000, per sample. Samples were preserved in 5% buffered formalin in seawater.

The total volume of each plankton sample was determined by weight. Random subsamples were then taken to determine the abundance and sizes of plankters in the sample. The sample was mixed by vigorously shaking (not swirling) the Whirl-pak bag. A dipper (1 × 2 cm cylinder with one end closed, glued to a plastic rod) of 6 ml volume was inserted before shaking, and was used to draw a subsample which was poured into a gridded petri dish. All zooplankters in subsamples were counted and measured until at least 200 identifiable zooplankton had been counted. The number of dishes (and squares of partial dishes) searched was recorded. Due to the loss of the preserved coelenteron samples for 1989, no sizes were recorded for that year. The 1989 and 1990 zooplankton samples were reanalyzed subsequently for copepod identifications. A random subsample was drawn from each sample, and the first 50 copepods were identified to genus and measured. The percentages from this copepod analysis were then applied to the previously calculated total copepods to determine the total numbers of copepods in each genus.

Both the time and the number of turns of the plankton pump flowmeter were recorded for each run. For 1989 and 1990 a pump

calibration of 0.35 liter per turn of the pump flowmeter was used to determine the volume sampled. In some cases the flowmeter was not operating, and the volume was calculated using the time calibration of 57.7 liter min^{-1}. For the 1992 samples a time calibration of 60 liter min^{-1} was used to calculate the volume sampled. The number of zooplankters per 100 liter of seawater moved through the pump (C) was calculated using the number of zooplankters in the subsample (P_s), the volume of the subsamples (V_s, ml), the total volume of the sample (V_t, ml), and the volume of water pumped through the plankton pump (V_p, liter) in the following equation:

$$C = 100(P_s V_t)/(V_s V_p) \ .$$

The mean concentration of zooplankton (each category) during the entire experiment was determined by summing the numbers removed by the pump, the calculated numbers remaining in the enclosure, and the numbers captured by the coral. Zooplankton concentrations decreased during each run, due to escape from the chamber, capture, and setting of plankton onto chamber walls. Runs in which pumped samples were taken at the beginning and end of the run showed that the mean concentration in the enclosure during the run was 1.8 times the final concentration in pumped samples. This factor was used to adjust final pumped sample concentrations to calculate availability during the run, for capture rate determinations. Concentrations of the most common zooplankton were usually <30 000 individuals per 1000 liter (= 1 m^3). These values are, on average, 10 to 30 times the published values for concentrations of reef zooplankton (≤1100 m^{-3}: Alldredge and King 1977; Hobson and Chess 1979; Jakubczak 1989 and 508 to 2098 m^{-3}: Ferraris 1982). Corals in experiments fed for about 1/40 the normal feeding period for one night, and thus their total exposure to prey was not greatly elevated, if at all. Most polyps on each colony were still without prey, and thus corals were not likely to be prey saturated.

Pump selectivity

Plankton pumps, as well as plankton nets, are known to be selective (in Sebens and Maney 1992); large zooplankton with strong swimming capabilities can detect the flow field around pump intakes and potentially avoid capture. Pumps must therefore be compared to some other method of plankton sampling to determine if they are providing an accurate estimation of available plankton, yet most other methods are also potentially selective. To provide an unbiased sample of zooplankton, we used the 1.0 m long rectangular section of the feeding enclosure with all internal structures removed and with a large 40 μm mesh Nitex bag fitted tightly over one end. A plunger was constructed with 40 μm Nitex mesh over a rectangle of plastic grid that fit snugly into the enclosure, with a 1.5 m wooden handle attached to its center. This plunger was left in one end of the enclosure after zooplankton had been attracted into the enclosure as in experiments. The plankton pump intake heads had already been mounted in the enclosure as in the experiments; the pump was turned on for 2 min, then removed. The plunger was then pushed through the enclosure into the mesh bag at the other end, then removed, and the bag was tied off. All zooplankton in the enclosure were thus captured in either the plankton pump bag or in the large mesh bag; the two samples combined represented the initial concentration of all zooplankton in the enclosure (≥ 40 μm). These samples were analyzed as for all other zooplankton samples (see "Zooplankton quantification"). The initial concentration and distribution across taxa was then compared to what the pump actually captured and what remained, providing an accurate description of any selectivity (contingency table method, Pearre 1982). This experiment was repeated five times over two nights to get different relative abundances of zooplankton in the enclosure.

Coelenteron contents

After each run, corals were placed in 10% formalin in seawater until the polyp coelenterons could be examined. In the laboratory, each coral head or branch was rinsed with (40 μm) filtered seawater to remove any plankton that may have been on the coral but not in the polyps. The coral was then immersed in filtered seawater. Each polyp was probed with a dissecting needle and fine forceps under a dissecting microscope (20 to 200×), removing all obvious prey items, then scraping the coelenteron to expose any remaining prey for removal. Any items that were not a part of the coral polyp were identified, counted, removed, and preserved in 70% ethanol. The number, type, and length of each prey item were recorded for each polyp, as was the general location of the polyp on the coral head. The total number of polyps without prey was also recorded.

Data analysis

Prey capture rates are defined here as the number of prey captured per number potentially encountered during each experiment. We considered the number of prey available to be the mean number per 100 liter in the enclosure during the 20-min run. Prey availability was modified by flow speed, which varied from around 2 to 9 cm s^{-1} (mean values) on different nights; flow changes the potential encounter rate of prey with coral tentacles as well as the lateral surface area of the tentacle crown. Zooplankton flux was calculated as the number of zooplankters passing through the projected (lateral) surface area of the tentacle crowns (0.07 cm^2 per polyp for *Madracis mirabilis*, 0.4 cm^2 for *Montastrea cavernosa*) during the experiments (for N polyps), assuming prey (prey × 100 l^{-1}) were transported as passive particles at the mean flow speed for 20 min. This calculation omits differential swimming speeds of the zooplankters, which can further affect encounter rates. The relationship of capture to flow will be the subject of a separate paper.

Capture rates for each experiment were quantified for 78 to 369 polyps of *Madracis mirabilis*, representing three or four branches, and 49 to 415 polyps of *Montastrea cavernosa*, representing one or two colonies. Captures were standardized as captures per 100 or 9000 polyps of *M. mirabilis*, or as captures per 100 polyps of *M. cavernosa* per 20-min experiment. Based on nitrogen per polyp, (CHN analysis, corrected for skeletal nitrogen), *M. cavernosa* polyps are approximately 90 times the biomass of *M. mirabilis* polyps (Sebens unpublished data). Capture rate, incorporating zooplankton availability and flow speed, was calculated by dividing captures by zooplankton flux (see above) for each experiment (20 min) that had enough prey of a given type. Capture rates defined in this way are independent of the presence and abundance of other potential prey, which influence prey-selection indices.

Vanderploeg and Scavia's (1979) index E was used to compare prey-selection for all prey taxa found in coelenteron contents and in plankton samples for both species of corals, omitting only species or groups that were rare in plankton samples and in coelenteron contents. This index ranges from +1 to −1 with 0 representing "no selection". Any species or group that made up either 5% or more of the plankton, or was represented by two or more prey in the coelenterons, was included. Those prey that were represented by only one individual captured were included for the calculation of E for other groups, but were not included in subsequent analyses. Prey items abundant in coelenterons but rare in the plankton were thus included, as were those common in the plankton but rare or absent in coelenterons. Statistical tests of significance were applied to all selectivity measures using the contingency table method of Pearre (1982).

Results

Pump selectivity

The results of five experiments indicate that plankton pumps generally captured all available prey in direct proportion to their relative abundance in the chambers (Fig. 2). There were no significant differences between

pump and remaining zooplankton distributions (contingency table, G-test, $p > 0.05$) in any of the experiments except in the second run on 8 November 1989 (contingency table, G-test, copepods $p < 0.005$, other zooplankton $p < 0.05$). This method overestimates selectivity; comparing pumped plankton to initial plankton would be preferable, but would necessitate combining parts of pumped and remaining plankton subsamples. Because copepods dominated the samples, we first tested all copepods against all other prey, then tested all other prey independently. Observations and video photography of the pump intakes indicate that some zooplankton reacted to the flow field. Chaetognaths, in particular, were observed to reverse direction and to make rapid "jumping" movements after entering the flow field; this did not, however, result in undersampling of chaetognaths by the pump.

Zooplankton captured: prey taxa

Madracis mirabilis and *Montastrea cavernosa* captured numerous zooplankton during most experiments. Examples of capture and prey availability are given in Fig. 3 for four of the experiments with the largest number of prey captured by the corals. Histograms representing prey capture are not very similar to those for available plankton, indicating there was selection by the coral, or avoidance by prey. In most experiments, the abundant copepods, such as the cyclopoid *Oithona* sp. and the larger calanoid *Calanopia* sp., were rarely captured by either species. For *M. mirabilis*, the other zooplankton groups having low capture rates include copepod nauplii, isopods, and cumaceans; high rates were noted for the large copepod *Monstrilla* sp., polychaetes, crab zoea, and decapod shrimp. *M. cavernosa* showed high capture rates for decapod shrimp, isopods, cumaceans, chaetognaths, polychaetes, and gammarid amphipods and low rates for zoea, mysids and copepod nauplii.

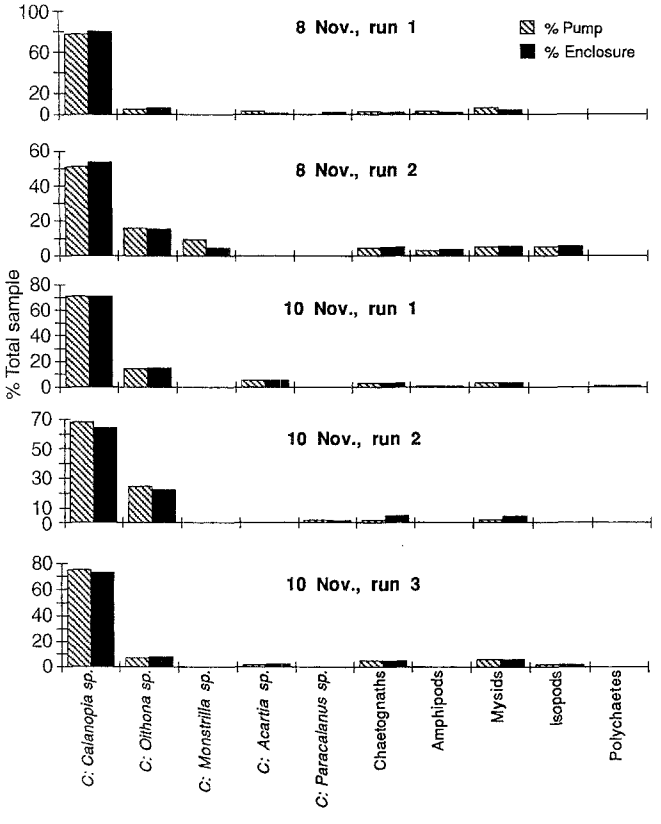

Fig. 2 Five tests of plankton pump selectivity in the field enclosure using plankton attracted into the enclosure, without corals present. Histograms compare numbers of individuals in each category of zooplankton for pumped samples (*crosshatched bars*) to numbers in total sample within the enclosure when the experiment began (*filled bars*); both are represented as percent of sample. There were no significant differences between pumped and total samples, except for Run 2 on 8 November (*C:* indicates copepod genus or group)

Under the same conditions, in this set of field experiments, *Madracis mirabilis* captured over 36 times as many prey in most categories (Fig. 4). The mean capture for all zooplankton combined was 994 ± 792 SD for *M. mirabilis* ($N = 26$) and 27.4 ± 21.9 SD for *Montastrea cavernosa* ($N = 19$), over all experiments, based on equal predator biomass (9000 polyps *M. mirabilis*, 100 polyps *M. cavernosa*, 20-min period). Spearman rank correlations of captures to prey abundance (Fig. 4) were significantly negative for both coral species ($p \leq 0.008$ *M. mirabilis*, $p \leq 0.003$ *M. cavernosa*) for all experiments combined. Considering only those experiments with $\leq 10\,000$ prey m^{-3}, most comparable to natural reef plankton concentrations, this relationship was even more significant ($p \leq 0.006$ *M. mirabilis*, $p \leq 0.002$ *M. cavernosa*).

The mean capture rate, or probability of capturing a plankter as it passes through the tentacle crown, was higher for *Madracis mirabilis* than for *Montastrea cavernosa*. Considering all zooplankton combined, this probability was 0.023 ± 0.021 SD for *M. mirabilis* and 0.012 ± 0.009 SD for *M. cavernosa*. This analysis (Fig. 5) also shows that, for both corals, large and relatively rare prey types were captured more readily than were the abundant copepods *Calanopia* sp. and *Oithona* sp., which made up most of the zooplankton in nearly every sample (Fig. 4). Capture rates for only these two copepod genera were 0.004 ± 0.009 for *M. mirabilis* and 0.003 ± 0.004 for *M. cavernosa*. For all prey other than these two copepod genera, capture rates were much higher; 0.113 ± 0.086 for *M. mirabilis* and 0.078 ± 0.103 for *M. cavernosa*. Several zooplankton groups had capture rates >1.0, indicating that more of that prey type were captured than were encountered, where encounter rate was calculated for flow transporting prey as passive particles. Prey swimming, for example, would cause additional encounters. These high values could also result from underestimation of prey abundance in pump samples, especially for rare prey.

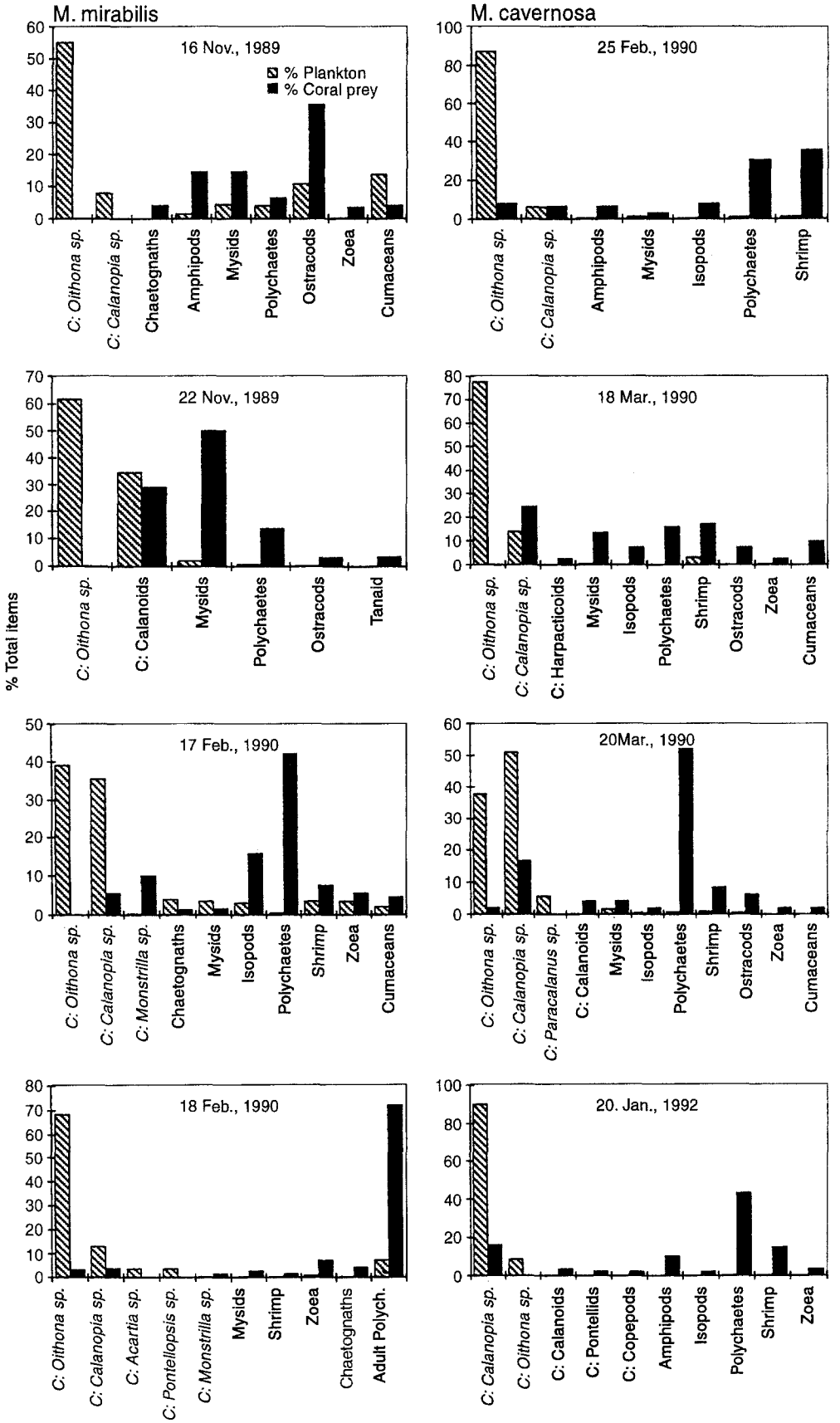

Fig. 3 *Madracis mirabilis*, *Montastrea cavernosa*. Coral coelenteron contents and prey availability (by taxon) for 4 of 17 experiments, as percent of total sample. Note major differences between amount of prey in the enclosure and in the coelenteron contents for most categories (*C:* indicates copepod genus or group)

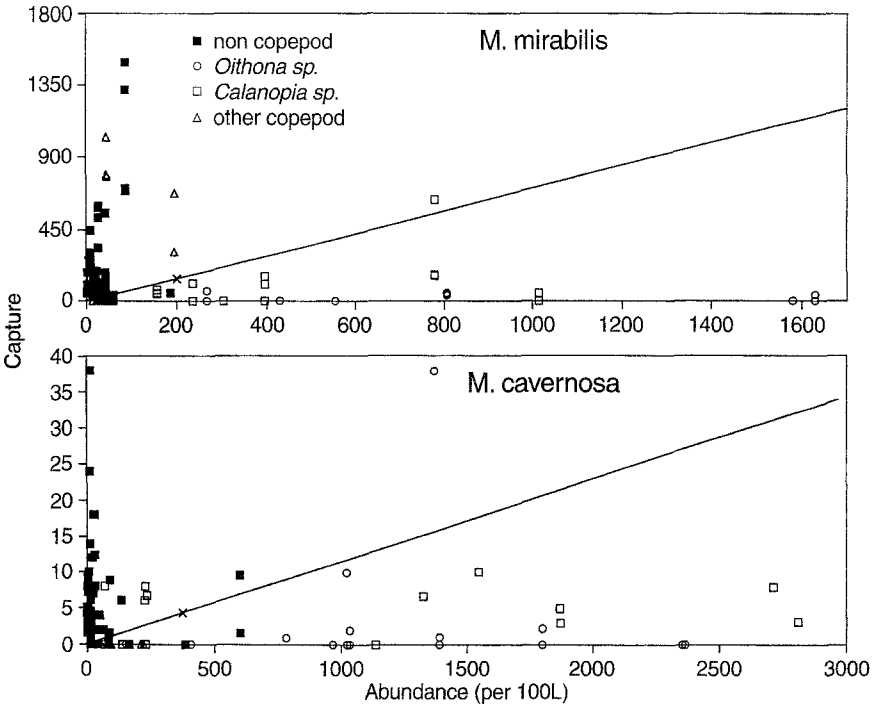

Fig. 4 *Madracis mirabilis*, *Montastrea cavernosa*. Number of prey captures for all zooplankton taxa in all experiments, as a function of prey abundance (N per 100 liter) irrespective of flow speed. Captures were calculated as prey per equal coral biomass (9000 polyps *M. mirabilis*, 100 polyps *M. cavernosa*) per 20 min. $N = 127$ for *M. mirabilis*, $N = 113$ for *M. cavernosa*. Straight lines pass through mean x, y-values ("x" on graph) and represent the expected capture rate based on abundance alone. Points above lines are capture rates higher than predicted; points below lines are lower than predicted. Note that the most abundant prey were copepods, most of which were captured at very low rates compared to other taxa. See "Results – Zooplankton capture" for statistical tests

Prey selection

Both corals showed high values of selectivity (E) and capture rate (C) for decapod shrimp, polychaetes, chaetognaths, isopods, and crab zoea (Fig. 5). Copepods were generally at the bottom of the prey-selection hierarchy, even though they were often the most abundant zooplankton. *Oithona* sp. had the lowest selection index; *Oithona colcarva* was identified as the most abundant member of the plankton captured in emergence traps in previous studies at this site (Ohlhorst 1985). Exceptions include the large copepod *Monstrilla* sp., which was captured regularly by *Madracis mirabilis*, but not by *Montastrea cavernosa*, and the category of "other calanoids" which had moderately low prey-selection values for both coral species.

Prey-selection indices were calculated a second time, considering only copepod prey (Fig. 6). This analysis showed that the large and relatively rare species had high prey-selection values whereas *Oithona* sp. had low values in all but one experiment. *Calanopia* sp. prey-selection values were split into two groups, one representing experiments in which *Oithona* sp. was abun-

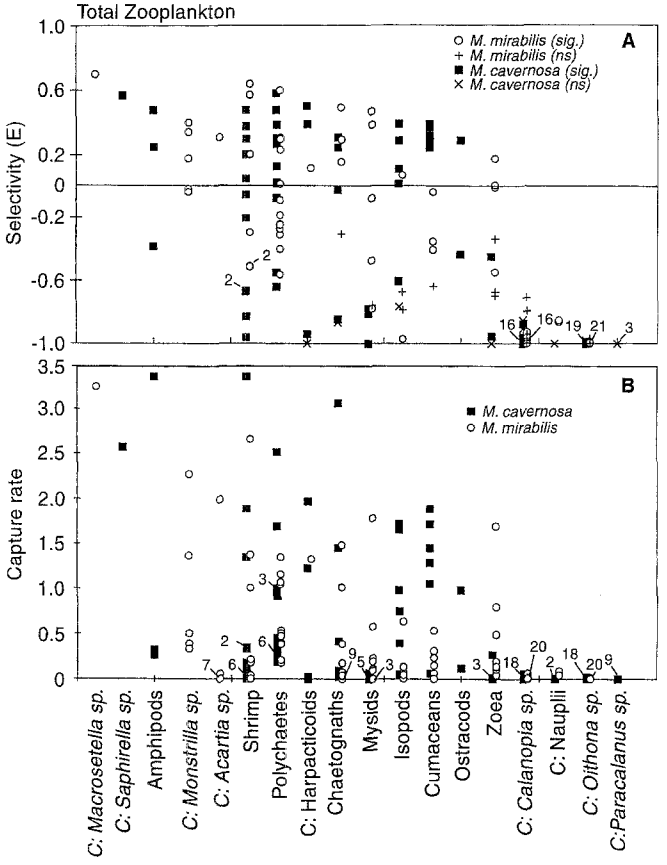

Fig. 5 *Madracis mirabilis*, *Montastrea cavernosa*. **A** Prey selection (E) for all prey taxa, graphed from highest to lowest. **B** Capture rates per zooplankter (probability of capture) passing through the tentacle crown where $C = P/B$; C is the capture rate, P is the number of prey of that category caught and B is the number of prey potentially encountered (zooplankton flux, see "Results – Zooplankton capture") for that category. Capture rates were calculated for each individual coral in which two or more items of that category were caught by the coral, and/or that group was ≥ 5% of all zooplankton. Capture rates >1.0 indicate more prey captured than passed through the tentacles as passive particles. This could result from prey swimming, for example, which would increase encounter frequency, but is not accounted for here. Numbers next to points on the graph indicate number of overlapping data points (*C:* on y-axis indicates copepod genus or group). See "Results – Prey selection" for statistical tests

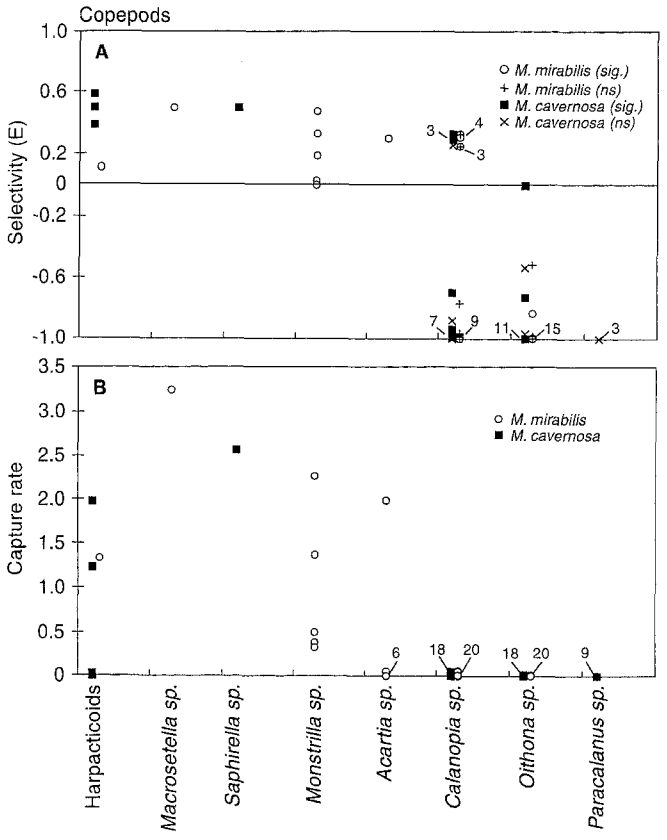

Fig. 6 *Madracis mirabilis*, *Montastrea cavernosa*. **A** Prey selection (E) for copepods by genus, graphed from highest to lowest. Note there are two groups of values for *Calanopia* sp. representing experiments in which *Oithona* sp. was abundant (*upper group*) and rare (*lower group*). **B** Captures rates per zooplankter passing through the tentacle crown. Calculations as in Fig. 5. Numbers next to points on the graph indicate number of overlapping data points

dant, which produced a high prey-selection value for *Calanopia* sp., and those where other copepods were common and *Oithona* sp. was not, producing the low prey-selection values for *Calanopia* sp. Note that capture rates do not show this split pattern, since they are not affected by the presence of other species.

Zooplankton captured: prey sizes

The sizes of zooplankton captured by both coral species were larger than those available in most experiments (Table 1), primarily because small copepods, with low capture rates, dominated most plankton samples. Examples of prey and plankton size–frequency histograms are given in Fig. 7. On one night, for each coral species, small copepods were captured in relatively large numbers. These nights (14 and 18 February 1990) had higher flow speeds, which may have contributed to the greater capture rates for copepods, if the copepods were unable to avoid coral tentacles under conditions of high (and/or turbulent) flow. The sizes of all prey captured were compared to the sizes of the same species or groups in plankton samples for each experiment and for all experiments combined (Fig. 8). Experiments which had sufficient numbers of prey and plankton of a given type are listed in Table 1, with the results of analysis of variance. There were significant differences in sizes of available prey and prey captured for relatively few prey types. In most cases, the sizes of prey and zooplankton of that type were approximately equal for both coral predators. For *Madracis mirabilis*, the *Calanopia* sp. captured were significantly larger than those available in all experiments, and the *Oithona* sp. were significantly larger in one experiment. Isopods and cumaceans were significantly larger in coelenteron contents than in the plankton, whereas decapod shrimp were smaller. For *Montastrea cavernosa*, the *Calanopia* sp. were larger in coelenteron samples, although the *Oithona* sp. were not. Harpacticoid copepods were not significantly larger as prey than in the plankton for both species of coral.

That both coral species captured prey of approximately the same size distribution (Fig. 9) is surprising given the large difference in size between the polyps of *Madracis mirabilis* and *Montastrea cavernosa* (Fig. 1). A Kolmogorov–Smirnov test (Sokal and Rohlf 1981) showed a significant difference (p <0.005) between the size distributions of prey for both coral species. This result was based on the largest absolute difference between the distributions, which occurred in the second to smallest size category; *M. mirabilis* captured more of the two smallest size categories compared to *M. cavernosa*. Considering only prey above the two smallest categories (>1 mm), there were no significant differences between the distributions.

Differences in plankton and prey sizes could be an artifact if zooplankton recovered from coelenterons were biased to large sizes because of digestion or poor recognition of small items. However, experimental techniques stopped digestion no more than 10 min after the experiment (35 min since first possible capture). Digestion of zooplankton takes at least 4 h for similar corals, with a few prey remaining in coelenterons for up to 12 h (Purcell unpublished data). It is therefore unlikely that substantial digestion occurred in this study. Most of the small copepods were at least 500 μm in length; these are very easy to see under 40× magnification and would be hard to miss in the polyps. We are confident that prey items 200 μm in length were being recognized consistently, and many smaller items were also found. The mesh used in plankton sample bags was 40 μm, and that on each end of the enclosure was 180 μm. Prey 200 μm in width (about 600 μm long) would thus be retained in the enclosure, whereas smaller items were free to move in and out. The latter were also available to the corals and were sampled adequately by the plankton pump (40 μm mesh).

Table 1 *Madracis mirabilis, Montastrea cavernosa*. Size differences between plankton categories in the coelenterons and in the available plankton for the six experimental runs with the greatest number captured and for all dates combined. For each date, any category with three or more individuals in both captured prey and plankton, and the combined categories, were tested by analysis of variance. Categories with insufficient data to test were left blank. The first number in each entry is the number of the plankter type in the captured prey, the second is the number measured from the plankton subsample, and the final is the *p*-value. Significant results are in *bold type*. *P* indicates plankton items are significantly larger than those in the coelenteron, *C*, indicates the reverse

	M. mirabilis						
	14 Feb 1990	15 Feb 1990	17 Feb 1990	17 Feb 1990	18 Feb 1990	24 Feb 1990	Combined dates
Oithona sp.	(35, 35, 0.84)				**C(5, 147, 0.007)**	(3, 42, 0.85)	**C(135, 1145, 0.0001)**
Calanopia sp.		**C(3, 8, 0.02)**	**C(7, 23, 0.009)**	(14, 37, 0.91)	**C(6, 28, 0.03)**	**C(3, 6, 0.005)**	**C(47, 322, 0.0001)**
Harpacticoids							(5, 7, 0.66)
Chaetognaths				(3.6, 0.65)			(15, 23, 0.38)
Amphipods							(3, 7, 0.28)
Mysids						(3, 3, 0.10)	(16, 19, 0.43)
Isopods			**C(6, 18, 0.03)**				**C(28, 20, 0.0006)**
Polychaetes					(7, 107, 0.10)		(182, 14, 0.14)
Shrimp			**P(5, 7, 0.04)**				**P(33, 11, 0.0001)**
Zoea			(7, 8, 0.18)				(27, 9, 0.17)
Cumaceans			**C(4, 6, 0.02)**	(7, 3, 0.17)			**C(11, 15, 0.042)**
Combined zooplankton	(157, 203, 0.06)	**C(90, 218, 0.0001)**	**C(112, 202, 0.0001)**	**C(53, 213, 0.0001)**	**C(145, 204, 0.0001)**	**C(52, 213, 0.0001)**	
	M. cavernosa						
	18 Feb 1990	25 Feb 1990	18 Mar 1990	20 Mar 1990	19 Jan 1992	20 Jan 1992	Combined dates
Oithona sp.	(9, 42, 0.34)						**C(24, 2628, 0.0006)**
Calanopia sp.			**C(7, 7, 0.004)**	**C(6, 27, 0.30)**	**P(189, 18, 0.0001)**	**C(14, 341, 0.0001)**	**C(252, 1357, 0.0001)**
Pontellopaia sp.							(7, 12, 0.18)
Harpacticoids					**C(11, 8, 0.0002)**		(23, 41, 0.41)
Nauplii					(5, 5, 0.97)		(5, 51, 0.22)
Chaetognaths							(13, 41, 0.61)
Amphipods							(17, 23, 0.22)
Mysids							**C(18, 57, 0.05)**
Isopods							**C(34, 20, 0.0001)**
Polycheates							**C(120, 26, 0.004)**
Shrimp			(12, 7, 0.26)				**P(78, 26, 0.0001)**
Ostracods							**C(15, 19, 0.002)**
Zoea							**C(35, 42, 0.02)**
Cumaceans							**C(34, 24, 0.03)**
Cyprids							**C(4, 9, 0.01)**
Combined zooplankton	**C(30, 213, 0.0001)**	**C(56, 252, 0.0001)**	**C(68, 232, 0.0001)**	**C(45, 244, 0.0001)**	**C(317, 258, 0.0001)**	**C(78, 379, 0.0001)**	

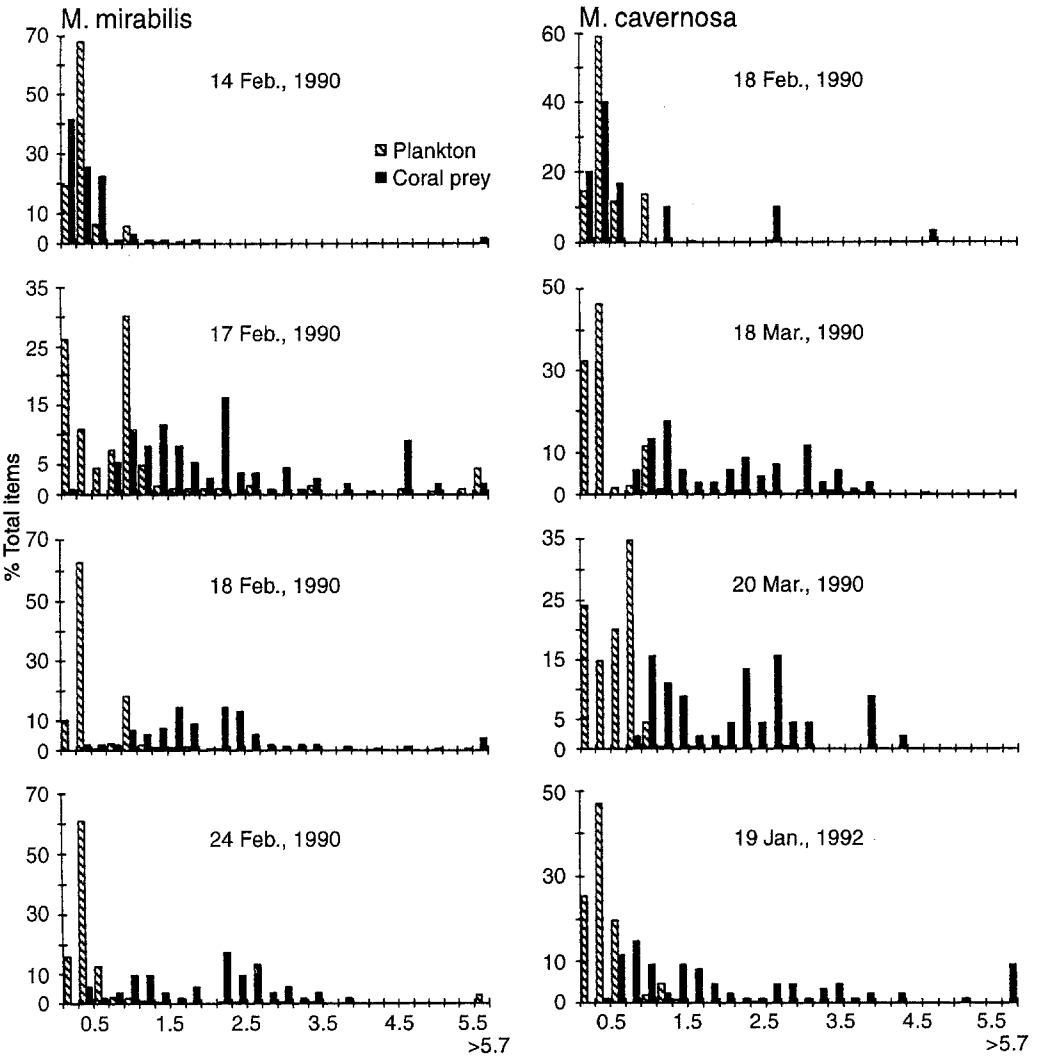

Fig. 7 *Madracis mirabilis*, *Montastrea cavernosa*. Coral coelenteron contents and prey availability (by size) for 4 of the 17 experiments, as percent of total sample. Note major differences between sizes of prey in the enclosure and in the coelenteron contents for most dates, for both coral species. Statistical comparisons given in Table 1

Discussion

Mechanisms of capture, selectivity and prey behavior

Zooplankton capture by corals is influenced by the mechanics of particle interception, adhesion, and motility as well as by any potential predator selectivity for particular types of prey. Mechanisms of particle contact and capture by suspension feeders were described by Rubenstein and Koehl (1977) who introduced "aerosol filtration theory", a concept developed by engineers, as a way of examining biological particle capture. Shimeta and Jumars (1991) have provided a recent review of this topic, and a critical analysis of mechanisms identified to date. The relative importance of various physical mechanisms causing prey to contact a suspension-feeder's tentacles can be estimated from knowledge of flow speeds, particle sizes and densities, and size and spacing of capture structures (Rubenstein and Koehl 1977). One important mechanism by which passive suspension feeders capture prey is by sieving; all items larger than the space between two adjacent food-catching structures (e.g. tentacles) are retained as the water flows between the structures. In the present study, most prey of *Madracis mirabilis* were larger than the tentacle spacing (600 μm) and about half of the prey items for *Montastrea cavernosa* were larger than the space between tentacle tips (1700 μm), and could have been captured by sieving (as in octocorals, Sebens and Koehl 1984).

For most types of particles, and at most flow velocities that anthozoans encounter, direct interception is likely to be the primary mode of particle capture (i.e. particles in streamlines close enough to tentacles will contact them). However, inertial impaction (i.e. the momentum of dense particles causes them to deviate from the streamlines of ambient flow and to contact a suspension-feeder's tentacle as the water is deflected

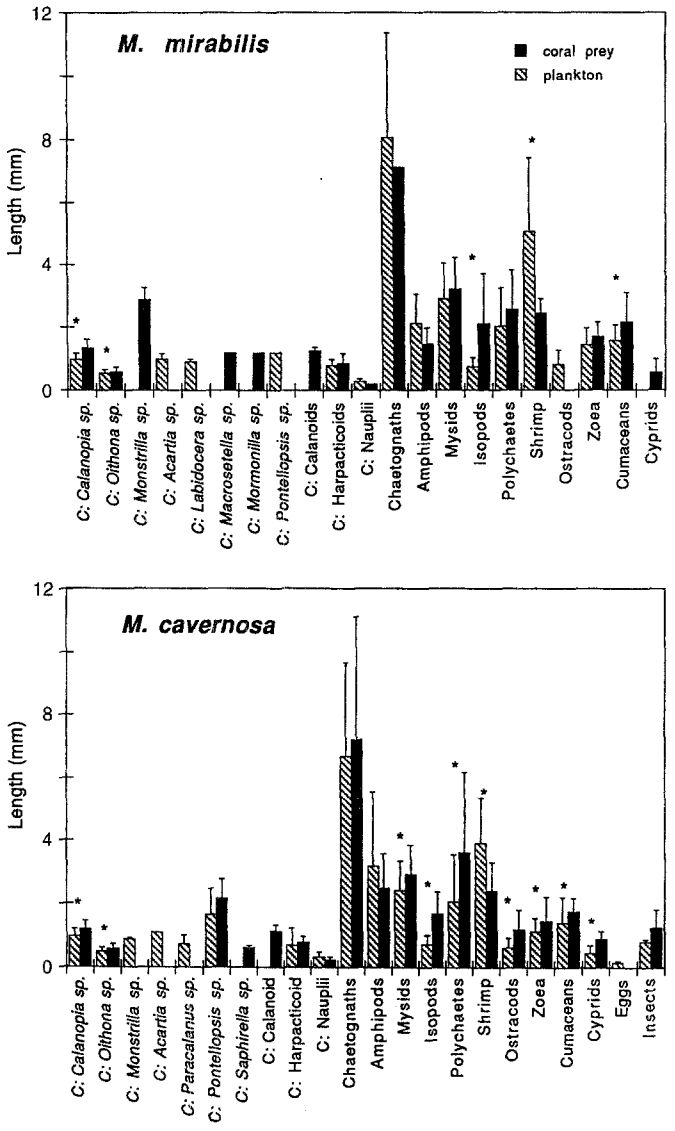

Fig. 8 *Madracis mirabilis*, *Montastrea cavernosa*. Sizes of all prey captured by the two species compared to sizes measured from plankton samples. In most cases, there were no significant differences in mean sizes. Those that were significantly different are noted with (*) and are listed in Table 1 (*C:* indicates copepod genus or group)

around it) appears to be involved in the capture of particles at the large end of the spectrum of prey at peak velocities approaching 0.5 m s^{-1}. Diffusive deposition (Rubenstein and Koehl 1977) occurs when movement of particles (Brownian motion, swimming) affects contact with a filter element. Gravitational deposition may also be important for capture of particles denser than water at low flow speeds, such as those that occur in lagoonal and deep reef habitats (e.g., zoanthids, Koehl 1977; corals, Sebens and Johnson 1991; Johnson and Sebens 1993; Abelson et al. 1993). Such mechanical aspects of particle capture will directly affect both capture rates and indices of prey selection, as used in this study, because each may interact with prey behavior to determine the observed differences in capture success.

Although aerosol filtration theory considers the effects of general particle motility on capture success by filter elements, behavior of prey can be complicated and directed. First, the swimming behavior, directionality, and rate of directional change all affect the probability of encounter between predators (stationary or moving) and prey (Gerritsen 1984). Pastorok (1981) defined a vulnerability function which depends on prey size and developmental stage, showing that apparent prey-size selection by the freshwater predator *Chaoborus* sp. could be explained by prey vulnerability rather than by predator behavior or choice (see also Drenner and McComas 1980; Greene et al. 1986; Purcell et al. 1987). Escape behavior affects vulnerability of prey, and can be very specific to external stimuli (Ohman 1988, review). Capture of copepods by the predatory copepod *Euchaeta elongata* was highest for intermediate size classes because small ones were not detected efficiently and large ones had very effective escape behaviors (Yen 1985). Escape behavior of copepod prey can be elicited by the flow field of a predatory species (Yen and Fields 1992). This result may also explain the situation for some copepods encountering coral polyps very accurately as well, based on our preliminary data and observations.

The same behaviors that allow zooplankton to escape from planktonic predators may or may not be effective against benthic suspension feeders such as corals. For example, a common avoidance mechanism of certain zooplankton is akinesis (cessation of movement, slow sinking) (Ohman 1988, review). This behavior may hide prey from pelagic predators, but is likely to drop them directly into fields of coral tentacles (Johnson and Sebens 1993). In general, swimming by prey that do not have good avoidance behavior could increase their encounters with tentacles above that produced by flow alone (Figs. 5, 6). Finally, prey that cannot escape successfully before ingestion may do so afterward; bivalve veliger larvae survived ingestion and egestion by scyphozoan (*Chrysaora quinquecirrha*) medusae and ephyrae, although benthic scyphistomae of *C. quinquecirrha* and pelagic ctenophores (*Mnemiopsis leidyi*) digested a large percentage of the veligers (Purcell et al. 1991). Differential digestion of the prey types captured by the corals in this study is currently being examined.

Prey-selection indices (e.g. electivity) compare how likely certain prey types are to be captured when in the presence of other potential prey. They were originally formulated to investigate preference by predators, such as fish, for different prey types that varied in their abundance and availability (Ivlev 1961). Prey-selection indices have been used for other anthozoans; Sebens and Koehl (1984) sampled coelenterons and available prey, and calculated prey-selection indices, for *Metridium senile* (anemone) and *Alcyonium siderium* (octocoral). *M. senile*, with relatively large tentacles, captured most types of plankton at sizes similar to those available, whereas *A. siderium*, with small pinnate tentacles, consumed only small prey (e.g. ascidian larvae). For passive suspension feeders such as these, and the corals in the

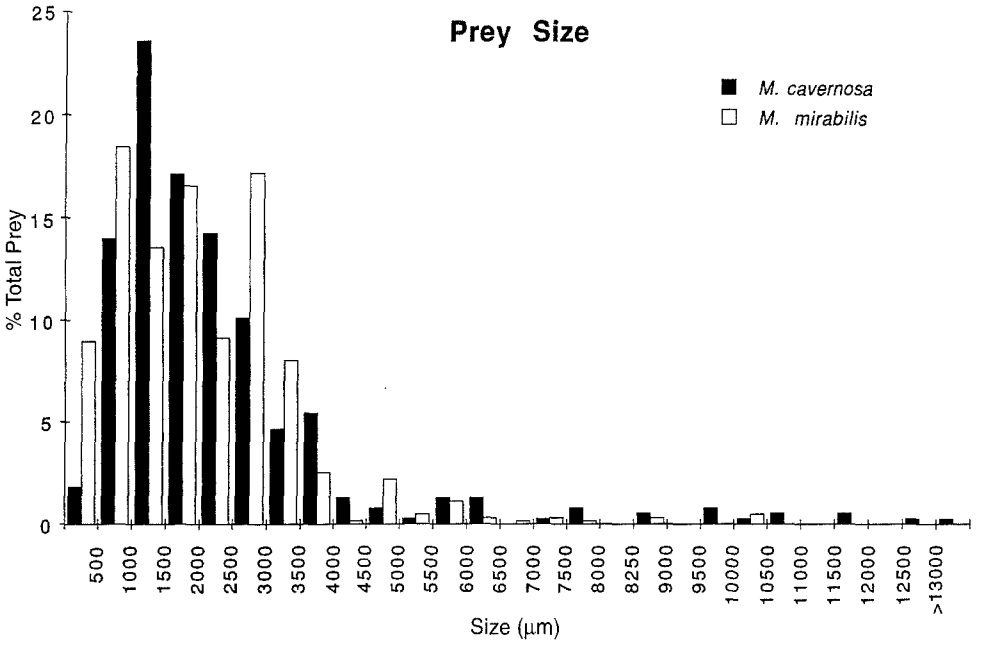

Fig. 9 *Madracis mirabilis*, *Montastrea cavernosa*. Sizes of all prey from coelenteron contents, combining data from all experiments (N = 635, N = 386, respectively). Note the almost identical distribution of prey sizes. See "Results – Zooplankton captured" for statistical comparisons

present study, success or failure in prey capture probably depends more on the escape ability of the prey than on any preference by the predator. Therefore, prey-selection indices (e.g. Vanderploeg and Scavia 1979), when used for passive suspension feeders, measure prey avoidance ability and mechanical aspects of capture as well as (or instead of) any predator preference (Sebens and Koehl 1984).

The ability of corals to capture a particular zooplankton category may well depend on the behavior of those zooplankton, which can also be modified by water movement. For example, zooplankton that are normally able to avoid tentacles may not be able to do so under conditions of strong or turbulent flow. This study illustrates another problem with the use of prey-selection indices, the potentially confounding effect of alternate prey which are sometimes absent but are frequently captured when present (e.g. *Monstrilla* sp., Fig. 5) and those which are very abundant but are infrequently captured (e.g. *Oithona* sp., *Calanopia* sp., Fig. 5). If the predator is completely nonselective and all factors affecting capture success relate to the behavior of the prey and the mechanisms of capture, then capture rate alone (number captured per number encountered) provides the most useful information on the ability of the predator to capture a particular type of prey. Prey-selection indices may lead to erroneous conclusions because of their reliance on relative abundances of multiple categories of prey.

In the present study, the zooplankton captured most readily were relatively large individuals, some with strong directional swimming abilities (shrimp, mysids) and others with less-directed motion (polychaetes). Small zooplankton that are strong swimmers (copepods, especially *Oithona* sp.) were captured much less readily, even when extremely abundant. Decapod shrimp larvae, zoea, and polychaetes were also abundant as prey. Some copepods, such as harpacticoids, are dominant members of the migrating demersal plankton. Porter (1974) found a large percentage of copepods (unidentified) in coelenteron contents of *Montastrea cavernosa* as did Johnson and Sebens (1993) for *Meandrina meandrites,* which also captured *Calanopia* sp. more readily than *Oithona* sp. Demersal plankters must swim past coral tentacles as they leave the bottom after dusk, and as they return again at dawn. Although they migrate to the surface, many are still swimming near the bottom for at least 4 h after dusk, which was when our experiments were carried out. These zooplankters are carried horizontally by water movement, either currents or wave-induced flow.

Other types of zooplankton, such as *Oithona* spp., are local reef holoplankton (Robichaux et al. 1981) which swarm during the day and disperse at night; these also pass by coral tentacles on a regular basis. *Oithona* spp. are known to avoid predation by certain fish (Paffenhöfer 1991); they may also be able to avoid tentaculate predators effectively. Alternatively, the swimming behavior of some prey may keep them away from any substratum and thus from benthic suspension feeders. In our apparatus, zooplankton were collected a few centimeters above each coral. It is unlikely zooplankton which were abundant in that location were not coming within range of the tentacles. At present, we hypothesize that certain copepods have avoidance or escape behaviors that make them unlikely to be captured by corals. Either they sense the coral (structure) hydrodynamically and avoid contact entirely, or they have rapid escape movements that take them away from the corals once they contact, or come close to, the tentacles. Such escape behaviors were observed for predation on zooplankton by barnacles (Trager et al. 1994). Copepods that live on

or near the substratum and migrate daily into the water column and back constantly run the gauntlet of tentaculate predators, fish, and other types of zooplanktivores. Given this strong and continuous selection pressure, it comes as no surprise to find they have evolved mechanisms to avoid capture.

Polyp size, colony morphology and zooplankton capture

Zooplankton capture is an important source of energy and limiting nutrients for corals (Sebens 1987, review), yet it is clear that not all corals have the morphology necessary for zooplankton capture and retention (Muscatine 1973). Porter (1976) proposed a model to explain the wide variation in polyp sizes and colony forms among scleractinian corals. In that formulation, corals with high S/V ratios (branching, plating) and small polyps were considered light-capture specialists. Corals with low S/V ratios (mounding, solitary, clusters) and large polyps were considered zooplankton-capture specialists. By far the majority of corals were arrayed close to the axes of a graph of S/V to polyp size; corals with large polyps and a high S/V ratio are very rare. Porter explained the high S/V ratio as an adaptation for light capture, especially in shallow water where high-energy light quanta come from all sides. Having small polyps also provides a mechanism for increasing light-capture surface by spreading out tissue biomass over the larger skeletal area. Large polyp size, however, was proposed as necessary to capture the full range of zooplankton sizes.

Porter (1976) considered the corals with high S/V morphologies less appropriate for zooplankton capture because he assumed vertical migration of zooplankton to be the main mechanism leading to encounter with coral tentacles. Adding more surface area per square meter of substratum would not increase the maximum number of plankton encountered and captured according to his model; a single sheet of polyps could thus capture all plankters swimming down and encountering a given area of substratum. Sebens (1979) proposed a general model for clonal and colonial organisms which emphasized the trade-off between polyp size, surface area, and the size of prey available. Having smaller polyps per unit biomass of coral does indeed increase surface area, for feeding or light capture, but it potentially restricts the size of zooplankton that can be handled. For a given size spectrum of zooplankton, there is a minimum polyp size below which energy intake decreases substantially. Sebens' (1979) model examined the trade-off between gain due to greater feeding surface area and cost due to lost prey capture opportunity as polyp size decreases. If water movement (currents, wave-induced motion), rather than vertical migration, is the primary mechanism bringing zooplankton into contact with coral tentacles, then branched colonies, upright plates, or other complex forms can enhance particle capture by providing greater contact area and by creating turbulent eddies behind plates and branches where capture can occur even at high flow speeds (Sebens and Johnson 1991; Helmuth and Sebens 1993). The same argument applies if zooplankton swim laterally or randomly. High colony surface area, or S/V ratio, thus has the potential to increase zooplankton capture as well as light interception.

The results of the present study provide a partial test of these theories. First, the coral with the smaller polyps and high S/V ratio in this study, *Madracis mirabilis*, captured far more plankton (over 36 times) than did the low S/V ratio coral *Montastrea cavernosa* with much larger polyps, when compared for equal biomass of each coral. Both corals have well-developed tentacles with prominent acrospheres (nematocyst batteries) on their tips. However, it is still surprising that the sizes of zooplankton captured by *M. mirabilis* were very similar to those captured by *M. cavernosa* under identical field conditions, and only differed for a few zooplankton taxa. For the most part, both corals captured zooplankton of almost the full size range available. It should be noted that most zooplankton were below 1 mm in length, and very few were above the 3.2- to 4.0-mm span of *M. mirabilis* tentacles; even prey larger than this tentacle crown diameter, such as chaetognaths, were captured and folded to fit into a polyp. *M. cavernosa* has somewhat larger and potentially stronger tentacles (1.3 to 2.0 mm length for *M. mirabilis*, 2.5 to 4.4 mm for *M. cavernosa*), with larger contact area per tentacle and thus greater nematocyst adhesion capabilities and a wider tentacle crown diameter (8 to 13 mm). Certainly, this could be important for the retention of some of the larger and stronger swimmers among the zooplankton. When compared by biomass of prey captured, these larger zooplankton could make up a significant amount of the total capture for *M. cavernosa*. The increased S/V ratio of *M. mirabilis* is, however, likely to be the factor allowing the high capture rates per unit coral biomass (as in Sebens' 1979 model). Prey were frequently captured on all surfaces of the coral, especially on downstream sides of branches in high flow conditions (laboratory flume, Sebens et al. 1996). Although the smaller polyp size of *M. mirabilis* may lose them a few large zooplankton, the increased feeding surface area (more tentacles, acrospheres, nematocysts) per unit coral biomass, and the slightly higher capture rate for zooplankton < 1 mm in length, seem to more than compensate. Small polyp size, and high S/V ratios, therefore do not correlate with low feeding rates on zooplankton.

The advantage in feeding surface area for *Madracis mirabilis* is substantial. The total (tentacle crown, oral view) feeding surface of *M. mirabilis* polyps is approximately 0.10 cm^2, while that of *Montastrea cavernosa* is 0.78 cm^2. For equal coral biomass (90 polyps *M. mirabilis*), the feeding surface of *M. mirabilis* is 9.0 cm^2, 12 times that of a *M. cavernosa* polyp. Using projected (lateral) surface of the tentacle crown, which is the surface through which water flows, *M. mirabilis* has 0.07 to 0.40 cm^2 area for *M. cavernosa*. For equal coral biomass, this gives 6.3 cm^2 for 90 polyps of *M. mirabilis*, which is

16 times the area of a *M. cavernosa* polyp. Feeding surface, therefore, cannot explain the high capture rates of *M. mirabilis*, which were more than twice as high as expected by surface area relationships alone. Polyp number may also affect capture rates; if capture rates are constrained by handling time, polyp number (more mouths) could also be a major determinant of feeding rates, along with the increased area for encounter.

Why are corals grouped into those with relatively small polyps and high S/V ratios; and those with larger polyps and low S/V ratios? Corals with large polyps and high S/V ratios are almost nonexistent, as noted by Porter (1976). Small polyp size alone does not appear to limit zooplankton feeding, although it may limit the upper sizes captured for some kinds of prey. The type of tentacles and nematocysts present are likely to be more important for prey capture than is polyp size alone. Similarly, high S/V ratios appear to be important for particle capture as well as for light capture, especially in shallow water where flow speeds can be very rapid. Corals with small polyps and high S/V ratios may be light-capture specialists (sensu Porter 1976) if tentacles are reduced in size or in nematocyst content, or if the tentacles function primarily as photosynthetic organs (dense zooxanthellae, expanded all day). However, corals with small polyps and fully functional feeding tentacles, and with high S/V ratios, cannot be considered light-capture specialists, but may instead represent an adaptation for feeding under conditions of high flow. They may also be favored when the primary prey resource is small zooplankton. Corals with large polyps may be good zooplankton feeders, and can probably capture some larger prey, but incur a large cost in lost feeding surface area. The combination of large polyps and low S/V ratio, however, may have more to do with competition for space than with feeding adaptations. Large polyps have large coelenteron volumes, long mesenteric filaments, and large or long sweeper tentacles used in agonistic encounters (Lang and Chornesky 1988, review). Mounding corals (low S/V) have relatively low skeletal growth rates, but are very persistent in the face of physical disturbance (e.g. hurricanes).

Following these arguments, it is possible that the large-polyp corals with mounding, solitary, or clustered morphologies (low S/V) represent the competitively dominant species in moderate to deep zones of coral reefs. They have the ability to defend themselves from overgrowth, due to large polyp size, and to survive catastrophic events. High S/V corals generally have high growth rates, whether they depend primarily on zooplankton or on light for energy and nutrient intake, but are very susceptible to storm damage. Their small polyp size gives them a high feeding surface to respiring biomass ratio (Sebens 1979), which can maximize energy gain. Their small polyp size, however, also makes them poor competitors by means of mesenteric filaments and sweeper tentacles although, with rapid growth, they can frequently overtop, shade, and/or smother competitors. It may be this separation along the lines of competitive ability and persistence, rather than nutritional mode, that maintains the observed dichotomy in polyp size and colony morphology.

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References

Abelson A, Miloh T, Loya Y (1993) Flow patterns induced by substrata and body morphologies of benthic organisms, and their roles in determining availability of food particles. Limnol Oceanogr 38: 1116–1124

Alldredge AL, King JM (1977) Distribution, abundance and substrate preferences of demersal reef zooplankton at Lizard Island Lagoon, Great Barrier Reef. Mar Biol 41: 317–333

Alldredge AL, King JM (1980) Effects of moonlight on the vertical migration patterns of demersal zooplankton. J exp mar Biol Ecol 44: 133–156

DiSalvo LH (1971) Ingestion and assimilation of bacteria by two scleractinian coral species. In: Muscatine L, Davis LV (eds) Experimental coelenterate biology. University of Hawaii Press, Honolulu, pp 129–136

Drenner RW, McComas SR (1980) The roles of zooplankter escape ability and fish size selectivity in the selective feeding and impact of planktivorous fish. Am Soc Limnol Oceanogr Spec Symp 3: 587–593

Edmondson CH (1928) The ecology of an Hawaiian coral reef. Bull Bernice P. Bishop Mus 45: 1–64

Emery AR (1968) Preliminary observations on coral reef zooplankton. Limnol Oceanogr 13: 293–303

Fabricius KE, Genin A, Benayahu Y (1995) Flow-dependent herbivory and growth in zooxanthellae-free soft corals. Limnol Oceanogr 40: 1290–1301

Ferraris JD (1982) Surface zooplankton at Carrie Bow Cay, Belize. In: Rützler K, Macintyre IG (eds) The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize. I. Smithsonian Institution Press, Washington, DC, pp 143–151

Gerritsen J (1984) Size efficiency reconsidered: a general foraging model for free-swimming aquatic animals. Am Nat 123: 450–467

Glynn P (1973) Ecology of a Caribbean coral reef. The *Porites* reef-flat biotope. Part II. Plankton community with evidence for depletion. Mar Biol 22: 1–21

Goreau TF, Goreau NI, Yonge CM (1971) Reef corals: autotrophs or heterotrophs? Biol Bull mar biol Lab, Woods Hole 247–260

Greene CH, Landry MR, Monger DC (1986) Foraging behavior and prey selection by the ambush entangling predator, *Pleurobrachia bachei*. Ecology 67: 1493–1501

Helmuth B, Sebens KP (1993) The influence of colony morphology and orientation to flow on particle capture by the coral *Agaricia agaricites* (Linnaeus). J exp mar Biol Ecol 1889: 1–28

Hobson ES, Chess JR (1979) Zooplankters that emerge from the lagoon floor at night at Kune and Midway Atolls, Hawaii. Fish Bull US 77: 275–280

Ivlev VS (1961) Experimental ecology of the feeding of fishes. Yale University Press, New Haven
Jakubczak RS (1989) The nutrition and neurophysiology of reef corals. PhD dissertation, Department of Biology, University of Georgia, Athens, Ga
Johnson AS, Sebens KP (1993) Consequences of a flattened morphology: effects of flow on feeding rates of the scleractinian coral *Meandrina meandrites*. Mar Ecol Prog Ser 99: 99–114
Koehl MAR (1977) Water flow and the morphology of zoanthid colonies. In: Taylor DL (ed) 3rd int coral Reef Symp. University of Miami, Miami, Fla., pp 437–444
Lang JC, Chornesky EA (1988) Competition between scleractinian reef corals: a review of mechanisms and effects. In: Dubinsky Z (ed) Ecosystems of the world: coral reefs. Elsevier Press, Amsterdam, pp 209–252
Lewis JB (1992) Heterotrophy in corals: zooplankton predation by the hydrocoral *Millepora complanata*. Mar Ecol Prog Ser 90: 251–256
Lewis JB, Price WS (1975) Feeding mechanisms and feeding strategies of Atlantic reef corals. J Zool Lond 176: 527–544
Liddell WD, Ohlhorst S (1987) Patterns of reef community structure, North Jamaica. Bull mar Sci 40: 311–329
Muscatine L (1973) Nutrition of corals. In: Jones OA, Endean R (eds) Biology and geology of coral reefs, 2nd edn. Academic Press, New York, pp 79–115
Muscatine L, Porter JW (1977) Reef corals: mutualistic symbiosis adapted to nutrient-poor environments. BioSci 27: 454–459
Ohlhorst SL (1982) Diel migration patterns of demersal reef zooplankton. J exp mar Biol Ecol 60: 1–15
Ohlhorst SL (1985) Reef zooplankton collected along a depth gradient at Discovery Bay, Jamaica. In: Reaka M (ed) The ecology of coral reefs. NOAA Symp Ser Undersea Res 3: 101–116
Ohman MD (1988) Behavioral responses of zooplankton to predation. Bull mar Sci 43: 530–550
Paffenhöfer G (1991) Some characteristics of abundant subtropical copepods in estuarine, shelf and oceanic waters. Proc 4th int Conf on Copepoda. Bull Plankton Soc Japan 1991: 201–206
Pastorok RA (1981) Prey vulnerability and size selection by *Chaoborus* larvae. Ecology 62: 1311–1324
Pearre SP (1982) Estimating prey preference by predators: uses of various indices and a proposal of another based on χ^2. Can J Fish aquat Sciences 39: 914–923
Porter JW (1974) Zooplankton feeding by the Caribbean reef-building coral *Montastrea cavernosa*. In: Cameron et al. (eds) Proc 2nd int coral Reef Symp. Great Barrier Reef Committee, Brisbane, pp 111–125
Porter JW (1976) Autotrophy, heterotrophy and resource partitioning in Carribbean reef building corals. Am Nat 110: 731–742
Porter JW, Porter KG (1977) Quantitative sampling of demersal plankton migrating from different coral reef substrates. Limnol Oceanogr 22: 553–556
Porter JW, Porter KG, Batac-Catalan Z (1977) Quantitative sampling of Indo-Pacific demersal reef plankton. In: Taylor DL (ed) Proc. 3rd int. Coral Reef Symp. University of Miami, Miami, Fla., pp 105–112
Porter KG, Porter JW, Ohlhorst SL (1978) Analysis of resident reef zooplankton composition and habits. In: Stoddart DR, Johannes RE (eds) Coral reefs: research methods. Monogr oceanogr Methodol (UNESCO) 5: 499–514
Purcell JE, Creswell FP, Cargo DG, Kennedy VS (1991) Differential ingestion of bivalve larvae by the scyphozoan *Chrysaora quinquecirrha* and the ctenophore *Mnemiopsis leidyi*. Biol Bull mar biol Lab, Woods Hole 180: 103–111
Purcell JE, Siferd TD, Marliave JB (1987) Vulnerability of larval herring (*Clupea harengus*) to capture by the jellyfish *Aequorea victoria*. Mar Biol 94: 157–162
Robichaux DM, Cohen AC, Reaka ML, Allen D (1981) Experiments with zooplankton on coral reefs, or will the real demersal plankton please come up? Mar Ecol Prog Ser 2: 77–94
Rubenstein DJ, Koehl MAR (1977) The mechanism of filter feeding: some theoretical considerations. Am Nat 111: 981–994
Rützler K, Ferraris JD, Larson RJ (1980) A new plankton sampler for coral reefs. Pubbl Staz Zool Napoli (I. Mar Ecol) 1: 65–71
Sebens KP (1977) Autotrophic and heterotrophic nutrition of coral reef zoanthids. In: Taylor DL (ed) Proc 3rd int coral Reef Symp. University of Miami, Miami, Fla., pp 397–406
Sebens KP (1979) The energetics of asexual reproduction and colony formation in benthic marine invertebrates. Am Zool 19: 683–697
Sebens KP (1987) Coelenterata. In: Vernberg FJ, Pandian TJ (eds) Animal energetics, 1st edn. Academic Press, New York, pp 55–120
Sebens KP, Johnson AS (1991) The effects of water movement on prey capture and distribution of reef corals. Hydrobiologia 226: 91–101
Sebens KP, Koehl MAR (1984) Predation on zooplankton by the benthic anthozoans *Alcyonium siderium* (Alcyonacea) and *Metridium senile* (Actiniaria) in the New England subtidal. Mar Biol 81: 225–271
Sebens KP, Maney EJ Jr (1992) A portable diver-operated plankton sampler for near-substratum use. In: Cahoon LB (ed) Proceedings of the American Academy of Underwater Sciences, 12th Annual Symposium. A.A.U.S., Wilmington, NC
Sebens KP, Witting J, Helmuth B (1996) Effects of branch spacing and water flow on particle capture by the reef coral *Madracis mirabilis*. J exp mar Biol Ecol (in press)
Shimeta J, Jumars Pa (1991) Physical mechanisms and rates of particle capture by suspension feeders. Oceangr mar Biol A Rev 29: 191–257
Sokal RR, Rohlf FJ (1981) Biometry, 2nd edn. W.H. Freeman and Company, San Francisco
Sorokin YI (1973) On the feeding of some scleractinian corals with bacteria and dissolved organic matter. Limnol Oceanogr 18: 380–385
Sorokin YI (1991) Biomass, metabolic rates and feeding of some common reef zoantharians and octocorals. Aust J mar freshwat Res 42: 729–741
Tiffon Y (1976) Nutrition experimentale chez les cerianthaires. In: Mackie GO (ed) Coelenterate ecology and behavior. Plenum, New York, pp 147–154
Trager G, Achituv Y, Genin A (1994) Effects of prey escape ability, flow speed, and predator feeding mode on zooplankton capture by barnacles. Mar Biol 120: 251–259
Van Präet M (1980) Absorption des substances dissoutes dans le milieu, des particules et des produits de la digestion extracellulaire chez *Actinia equina* L. Reprod Nutr Dev (Paris) 20: 1391–1399
Vanderploeg HA, Scavia D (1979) Two electivity indices for feeding with special reference to zooplankton grazing. J Fish Res Bd Can 36: 362–365
Wellington GM (1982) An experimental analysis of the effects of light and zooplankton on coral zonation. Oceologia 52: 311–320
Yen J (1985) Selective predation by the carnivorous marine copepod *Euchaeta elongata*: laboratory measurements of predation rates verified by field observations of temporal/spatial feeding patterns. Limnol Oceanogr 30: 577–597
Yen J, Fields D (1992) Escape responses of *Acartia hudsonica* (Copepoda) nauplii from the flow field of *Temora longicornis* (Copepoda). In: Sprules GO, Schulze PC, Williamson CE (eds) Advanced techniques for in situ studies of zooplankton abundance. Plenum, Stuttgart, pp 123–134
Yonge CM (1968) Living corals. Proc R Soc (Ser B) 169: 329–344
Yonge CM, Nicholls AG (1931) Studies on the physiology of corals. V. The effect of starvation in light and in darkness on the relationship between corals and zooxanthellae. Scient Rep Gt Barrier Reef Exped 1: 177–211