Marine Biology (1998) 131: 347–360

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Water flow and prey capture by three scleractinian corals, *Madracis mirabilis*, *Montastrea cavernosa* and *Porites porites*, in a field enclosure

Received: 17 September 1996 / Accepted: 22 November 1997

Abstract Scleractinian corals experience a wide range of flow regimes which, coupled with colony morphology, can affect the ability of corals to capture zooplankton and other particulate materials. We used a field enclosure oriented parallel to prevailing oscillatory flow on the forereef at Discovery Bay, Jamaica, to investigate rates of zooplankton capture by corals of varying morphology and polyp size under realistic flow speeds. Experiments were carried out from 1989 to 1992. Particles (*Artemia salina* cysts) and naturally occurring zooplankton attracted into the enclosures were used as prey for the corals *Madracis mirabilis* (Duchassaing and Michelotti) (narrow branches, small polyps), *Montastrea cavernosa* (Linnaeus) (mounding, large polyps), and *Porites porites* (Pallas) (wide branches, small polyps). This design allowed corals to be used without removing them or their prey from the reef environment, and avoided contact of zooplankton with net surfaces. Flow speed had significant effects on capture rate for cysts (*M. mirabilis*), total zooplankton (*M. mirabilis*, *M. cavernosa*), and non-copepod zooplankton (*M. mirabilis*). Zooplankton prey capture increased with prey concentration for *M. mirabilis* and *M. cavernosa*, over a broad range of concentrations, indicating that saturation of the feeding response had not occurred until prey density was over 10^4 items m^{-3}, a concentration at least an order of magnitude greater than the normal range of reef zooplankton concentrations. Location of cyst capture on coral surfaces was not uniform; for *M. cavernosa*, sides and tops of mounds captured most particles, and for *P. porites*, capture was greatest near branch tops, but was close to uniform for *M. mirabilis* branches in all flow conditions. The present study confirms laboratory flume results, and field results for other species, suggesting that many coral species experience particle flux and encounter rate limitations at low flow speeds, decreasing potential zooplankton capture rates.

Introduction

A number of studies have shown that zooplankton are important dietary components of corals and related anthozoans (*Montastrea cavernosa*, Porter 1974; *Meandrina meandrites*, Johnson and Sebens 1993; *Montastrea cavernosa* and *Madracis mirabilis*, Sebens et al. 1996; various species, Sorokin 1991; octocorals *Alcyonium siderium*, Sebens and Koehl 1984). Replenishment of nitrogen, phosphorus, and other nutrients that cannot be supplied from symbiotic algae (zooxanthellae) must come from zooplankton capture, ingestion of particulates, or uptake of dissolved compounds (reviewed by Muscatine and Porter 1977; Sebens 1987). Phytoplankton, however, have rarely been observed in coelenteron contents of anthozoans and have been found to be an important dietary item only for certain alcyonacean corals to date (Fabricius et al. 1995).

Porter (1976) proposed a model in which corals with small polyps and large colony surface:volume ratios rely chiefly on zooxanthellar photosynthesis for most of their energy, and corals with large polyps and relatively low surface:volume ratios rely heavily on zooplankton capture. He noted that corals with large polyps and high

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Communicated by J.P. Grassle, New Brunswick

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surface:volume ratios are almost non-existent. The model assumed that vertical migration of zooplankton was the main mechanism leading to encounters between zooplankters and coral tentacles. In a general model of colony organization, Sebens (1979) examined the trade-off between polyp size, surface area, and the size of available prey; this model illustrated the great advantage of increased feeding surface area (per unit biomass) of small polyps for zooplankton capture. If water movement is the primary mechanism bringing zooplankton into contact with coral tentacles, rather than the vertical migration of the zooplankters themselves, then branched colonies, upright plates, or other complex forms might have enhanced particle capture as a consequence of the interaction between flow and colony morphology (Sebens and Johnson 1991; Helmuth and Sebens 1993).

In a previous study (Sebens et al. 1996) we used a field enclosure to examine prey capture for two coral species with contrasting morphologies: *Madracis mirabilis* has small polyps and a high surface:volume ratio as a consequence of its branching morphology, while *Montastrea cavernosa* has large polyps and a low surface:volume ratio as a consequence of its mounding form. We found that *M. mirabilis* captured far more prey per unit coral biomass than did *M. cavernosa*. We hypothesized that the high capture rate for the former species was primarily a consequence of the interaction between its branching morphology, high surface:biomass ratio, and flow conditions. When we examined the feeding selectivity and capture rates for different zooplankton taxa, and for organisms of a range of sizes, we found that both species captured primarily the less common, large prey items, and captured relatively few of the small copepods which dominated the zooplankton community. We attributed this apparent selectivity not to the corals themselves, but to escape behavior on the part of certain prey organisms and their interaction with the flow and capture surfaces (Heidelberg et al. 1997).

In the present study, we reexamined the data from the previous field experiments, which had used enhanced concentrations of natural zooplankton assemblages, and carried out additional experiments using brine shrimp (*Artemia salina*) cysts as tracer particles, to determine the combined effects of flow speed and prey concentrations on particle capture by corals with different morphologies. In addition to the two previous species, *Madracis mirabilis* (narrow branches, small polyps) and *Montastrea cavernosa* (mounding, large polyps), we also examined cyst capture by *Porites porites* (wide branches, small polyps). In all three species we also examined the locations of cyst capture on the surfaces of the coral colonies, to understand the interaction between flow speed and directionality and the probability of encounters between particles and colony surfaces. Our expectation was that capture success would increase with flow speed up to a maximum, and then decline at the higher flows experienced (model in Sebens 1984).

Methods

Experimental enclosures

Madracis mirabilis (Duchassaing and Michelotti) grows as an aggregation of narrow branches with small polyps (3 to 4 mm tentacle crown diameter); *Montastrea cavernosa* (Linnaeus) is a large mound-forming species with larger polyps (11 to 14 mm tentacle crown diameter), and *Porites porites* (Pallas) forms colonies of few wide branches with small polyps (3 to 4 mm tentacle crown diameter). All three species are common on the forereef at Discovery Bay (Andres and Witman 1995), and were much more abundant there before 1980 (Liddell and Ohlhorst 1987) when Hurricane Allen severely decreased the live coral cover (Woodley et al. 1981). Corals were collected on the forereef at Discovery Bay, Jamaica (November 1989 to January 1992 at depths of 12 to 18 m) and moved adjacent to experimental enclosures. Individual branches of *M. mirabilis* were positioned upright on four plastic tubing holders (15 × 10 × 10 mm) glued to Plexiglas plates, placing branches at least 5 cm apart laterally. Colonies (8 to 12 cm diameter) of *M. cavernosa* and branches of *P. porites* were attached to 15 × 30 cm Plexiglas plates (using Pettits underwater epoxy), being careful not to let the epoxy touch the living coral tissue. Corals on their mounting plates were placed in depressions on the reef for 1 d or more, then moved into an "isolator" at least 6 h (usually 24 h) before they were used in experiments. The isolator was a large Plexiglas enclosure 50 × 50 × 30 cm, with two ends covered by 40 μm Nitex mesh (cleaned daily). The isolator prevented corals from being exposed to ambient plankton until the experiment began, although a few zooplankton could move in and out of the isolator when the lid was open. Corals expanded completely in the isolator, as on the reef, then expanded again rapidly and were ready to feed within minutes when transferred to the enclosure, as long as their live tissue surfaces were not touched during the transfer.

The two enclosures used each consisted of a large, two-piece, Plexiglas channel (150 × 40 × 25 cm) painted black on all sides. Each end was covered by 180 μm Nitex mesh, which slowed flow by approximately 50%. For a diagram and details of enclosure construction refer to Sebens et al. (1996). Flow at this site (10 m depth) was generally oscillatory, with a slightly greater flux toward shore than away from shore (examples in Helmuth and Sebens 1993). Flow was measured 1.5 m away from the chamber (InterOcean S4 current meter, 0.5 m off the substratum) during each run, then was measured just above each coral specimen at the end of each run from video recordings of particle (hydrated *Artemia salina* cysts) tracks.

Zooplankton were attracted into the enclosure at the beginning of each experiment using one or more dive lights placed inside one end, facing through the enclosure such that plankton had to swim in through the opposite end or through the lid on top. Other potential methods of providing plankton to the corals would have involved collecting them with nets, which could damage them or potentially change their behavior. Attraction to light thus meant the plankton composition would not be identical to that on the reef at the same time, but the plankters would not be damaged. The possibility for plankters to be "blinded" by this technique was considered, although we noted that plankton in the chamber continued to show attraction to light and avoided obstacles, even after being exposed. Their normal swimming behavior also allowed them to avoid extreme exposure to the light (as for sunlight). The mesh (Nitex) end pieces were placed on the enclosure after the concentration of plankton in the flume had reached the desired density, and the light was removed; all dive lights were kept off within 5 m of the enclosure or isolator. The enclosure was painted black to prevent plankton from collecting on the upper surface on nights with strong moonlight.

After zooplankton were well distributed throughout the enclosure, corals were removed from the isolators, carried by the plastic holders, and placed into the enclosure. Live coral surfaces were never touched; most corals thus expanded and began feeding within a minute or two after being placed in the enclosure, and any corals that did not expand rapidly were omitted from the experiment. Zooplankton samples were taken by pumping plankton through three intake heads (see below) positioned 2 to 4 cm above coral surfaces, during the last 3 min of each run, so as not to deplete plankton in the enclosure before the corals had a chance to feed. Corals fed for approximately 20 ± 5 min and then all were tapped by hand repeatedly to cause polyp contraction. Video recordings (8 mm Sony V9 camcorder) were made of *Artemia salina* cysts added to the enclosure, using a 5 mm slit of light (Subatec video light on top of the enclosure, with a moveable set of black plastic parallel plates on a track under the flume lid) for less than 1 min per coral, with appropriate scale. After photography, corals were designated with pencil marks on their lower upstream side, and were removed and taken to the surface and preserved (10% formalin in seawater) within a few minutes. This insured that digestion of prey would be minimal before preservation. Experiments with *Artemia salina* cysts were conducted according to the same protocol, except that cysts were added (at 1 to 3 cysts ml^{-1} final concentration) and dispersed throughout the enclosure, instead of attracting zooplankton. Two 60-ml syringe samples were taken for cyst concentration three times during each run (beginning, middle, end) and averaged.

Zooplankton abundance and coelenteron contents

Plankton samplers incorporated a bilge pump (Rule 2500 gph) which pulled water through a 15 cm diameter PVC pipe; a 40 μm mesh (Nitex) plankton net was inserted upstream of the pump so plankton did not travel through the impeller (Sebens and Johnson 1991; Sebens and Maney 1992; Sebens et al. 1996). The flow speed was 7 cm s^{-1} or greater in the center of the net, and was >30 cm s^{-1} at each intake head. Intake heads were designed with two flat plates above and below the opening to orient intake such that water entered the head irrespective of ambient flow direction. Flow into heads was thus omnidirectional, lateral, and was faster than swimming speeds of most zooplankters; intakes could be positioned a few centimeters above the coral surface without the intake flow significantly affecting ambient flow near the coral. Pumps collected >200 recognizable zooplankters (usually 500 to 1000) per sample, and either entire samples or subsamples were quantified (in Sebens et al. 1996) depending on zooplankton abundance. Five field tests of pump samples, compared to complete collections of plankton in enclosures without corals, showed only minor differences in types and relative amounts of plankton captured (Sebens et al. 1996).

Zooplankton per 100 liters seawater moved through the pump (C) was calculated from the number of plankters in a subsample (P_s), the subsample volume (V_s, ml), the entire sample volume (V_t, ml), and the water volume moved through the plankton pump (V_p, liters) using the equation:

$$C = 100(P_\mathrm{s}V_\mathrm{t})/(V_\mathrm{s}V_\mathrm{p}) \ .$$

When the sampling pump removes water from the enclosure, new water (without zooplankton >180 μm) moves into the enclosure through the Nitex mesh, diluting the zooplankton concentration within. Oscillatory flow during the experiment moves equal volumes of water, without such zooplankton, in and out. If V_e is the total enclosure volume (120 liters), S is the volume pumped per second (1.0 liters), and n is the time the pump was used (180 s), then $V(n)$, the volume (liters) of the original enclosure contents (and plankters) that has been removed at time n, can be calculated as:

$$V(n) = \sum_{i=1}^{n}(S/V_\mathrm{e})[V_\mathrm{e} - V(n-1)] \ .$$

Zooplankton concentration also decreased during the 3 min of pumping at each run's end, during which 78% of the original enclosure volume (and plankton) was removed. Prey concentration is assumed to remain at the original concentration for 15 min, then to decrease from 100 to 30% of that value over the last 3 min; mean concentration (for 18 min) is thus 94% of the original concentration before pumping. The value C (above) must thus be multiplied by 0.94 $[S(n)/V(n)]$, which equals 1.8 [when $S = 1.0$ liter, $n = 180$ s, $V(n) = 93$ liters], to convert zooplankton concentration in the pumped sample to overall mean concentration in the enclosure during the run. Zooplankton captured by corals were also added to the original concentrations, since they were initially present during the run; this was especially important for rare categories. We also observed zooplankton concentrations to decrease during some runs, for zooplankton visible without magnification. This could be due to dispersal throughout the chamber, some escape, or settling onto surfaces. If the latter two processes are important, true mean concentrations during the run could be underestimated somewhat by sampling only at the end. Typical excursion distances of particles in the enclosure were around 3 to 30 cm in each direction. Since the enclosure was 150 cm long, most particles near the corals moved back and forth without coming near the ends. Zooplankton approaching the mesh on each end may have avoided contact by swimming, and a buildup of zooplankton at one end was not usually observed. Any plankton trapped at one end for most of the run were not available to the corals and would probably not have been sampled by the pump.

To examine coelenteron contents, corals were placed in 10% buffered formalin in seawater at the end of each experiment, and were kept in that solution until the polyp coelenterons could be examined. Polyps were searched (method in Sebens et al. 1996) and the identity and length of each prey item were recorded for each polyp, as were the location of each polyp on the coral head, and the number of polyps without prey.

Flow quantification

InterOcean S4 recording current meters were used to characterize near mainstream flow 0.5 m off the bottom, 1.5 m from the enclosure. Meters were bolted to rigid PVC pipe sunk into 4 × 4 × 10 cm concrete bases. The vertical position of the S4 meter was chosen to bring the unit as close as possible to the substratum, and to adjacent corals, without interfering with flow near those surfaces. Dye tests in the field showed that flow below the meter, above the base, was unobstructed and was approximately the same as that just above the meter. There was a narrow zone (approximately 5 to 10 cm) above the concrete base where flow was turbulent and clearly affected by the presence of the base. We placed the base in a shallow reef depression to minimize this effect. S4 current meters were programmed to sample flow continuously, recording flow speed, direction, and pressure (depth) each 0.5 s. Meters were used during the experimental runs (Fig. 1) and were also deployed for longer time periods to gather general information on the flow regime at 8 to 30 m on the forereef at Discovery Bay. Portions of these data were used by Helmuth and Sebens (1993) to describe flow as a function of depth under different surface wave conditions.

Flow above corals in the enclosures was visualized and quantified using particle tracks (hydrated cysts) from macro-video images with concurrent time recording and subsequent frame-by-frame analysis of tracks and captures. A 5 mm wide light "slit" produced by mounting parallel 6 × 6 cm plates of black plastic over an underwater video light, was used to illuminate the top polyps of coral colonies, for brief (<1 min) periods of filming. The light beam was oriented parallel to the main axis of flow, perpendicular to the coral surface (x, z plane). Video images (7 × 10 cm field of view) allowed us to quantify particle movement (technique similar to that described by Leonard et al. 1988 for crinoid particle capture). Each videotape segment of a single coral was examined for period of oscillation (complete oscillations per minute) and flow was quantified at 1 (± 0.5) cm above each coral. Each particle track consisted of 3 to 5 frames in which particle position was drawn on an acetate sheet taped to a flat screen video monitor; the outline of the coral and the scale were also drawn on the acetate. This was repeated for 20 particles over all peaks of flow speed during oscillations. Mean flow speed for the run (y) was calculated from the mean speed at peak flows (x) as $y = 0.65x - 0.16$ ($R = 0.999$)

based on a regression of mean flow to maximum (mean of all peak flows) for eleven 2-min records (S4 meter, 0.5 s, instantaneous) from this site and depth.

Data analysis

Capture rates were defined as the number of prey captured per number available per unit time, per polyp (or per 100 polyps) for each coral species. When comparing capture among coral species, 100 polyps represent very different amounts of coral biomass. Polyps of *Madracis mirabilis* contain only 0.011 the biomass of *Montastrea cavernosa* polyps (CHN analysis, Sebens 1997 and unpublished data) and thus the capture rate of 100 *M. cavernosa* polyps must be compared to that of 9000 *M. mirabilis* polyps if equal predator biomass is to be compared. Similarly, 4800 polyps of *Porites porites* represent equal biomass to 100 *M. cavernosa* and 9000 *M. mirabilis* polyps. Capture rates in Figs. 2 to 6 should thus be compared with this difference in mind.

Flux of zooplankton past coral tentacles was calculated as the number of zooplankters passing through a projected tentacle crown surface area (lateral view), which is 0.07 cm^2 for *Madracis mirabilis*, 0.40 cm^2 for *Montastrea cavernosa* (Sebens et al. 1996) and 0.03 cm^2 for *Porites porites*. This assumes cysts or plankters are being transported as passive particles at the mean flow speed for that run, and thus does not consider the effect of swimming speed or escape behavior of prey, which will affect actual encounter rates. It also assumes tentacle crowns are not collapsed by the higher flows, reducing surface area for capture. In *M. mirabilis*, collapse of upstream polyps occurs above 10 to 15 cm s^{-1}, for example (laboratory flume, Sebens et al. 1997).

Results

Particle capture versus flow speed

Flow speeds measured within enclosures during these experiments (Fig. 1) ranged from <2 to 16 cm s^{-1} at the peak of wave-induced oscillations; mean speeds were more than half those maxima. Flow speeds on the reef near the enclosure were approximately twice as high as inside the enclosure, with individual flow maxima even higher (to >40 cm s^{-1}). Surface waves that produced these flows were <0.5 to ≈ 2 m significant wave height (observations from boat) during the experiments. The flow speeds within the enclosure thus represent the lower half of the normal (non-storm) range experienced by these coral species at 10 m depth. The results of the experiments thus relate to this range of flow speeds and not to higher flows, which could have either positive or negative results on zooplankton capture.

The capture rate of *Artemia salina* cysts by *Madracis mirabilis* increased significantly with higher ambient flow speeds in the experimental enclosure (Fig. 2; Table 1), with branches capturing about twice as many cysts at 10 cm s^{-1} as those at 5 cm s^{-1}. This is as expected if delivery rate is the limiting factor, and if efficiency of capture is similar across this range of flow speeds. For *Montastrea cavernosa*, there was also a significant relationship between flow speed and cyst capture. *Porites porites* showed no significant change in capture with flow speed; there were many branches with low capture rates at all flow speeds, but the highest captures occurred at 9 to 11 cm s^{-1} (three coral branches), at the high end of the ambient flow range in the enclosure. Gravitational deposition of cysts (fall velocities 0 to 0.2 cm s^{-1}) during the runs could enhance capture by mounding or plating colonies in this experimental design, as in laboratory flumes (Johnson and Sebens 1993). This may explain why some of the *M. cavernosa* colonies had relatively high capture rates even at low flow speeds. This mechanism is less important for upright branches (*M. mirabilis*, *P. porites*) which have little surface area perpendicular to the direction of gravitational acceleration. Note that *M. mirabilis* had capture rates per polyp similar to those of *M. cavernosa* even though polyp biomass is only 0.011 that of *M. cavernosa*.

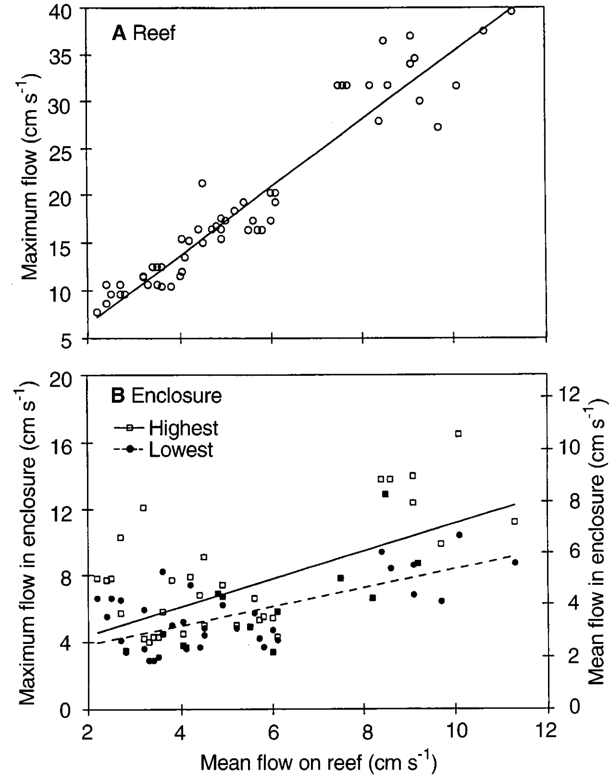


Fig. 1 **A** Maximum (single peak) flow speeds recorded by InterOcean S4 electromagnetic current meters 0.5 m off substratum at 9 to 10 m depth, near experimental enclosures, compared to mean flow speeds for same periods as experiments ($y = 3.6x - 0.75$, $R = 0.95$). **B** Flow speeds measured above each coral in enclosure (highest and lowest of all coral positions in each experiment) compared to mean flow (at S4) outside enclosure (High: $y = 1.36 + 0.42x$, $R = 0.60$; Low: $y = 1.36 + 0.28x$, $R = 0.61$). Flow within enclosure is expressed as maximum (mean of all peaks of oscillatory flow) and as mean flow (see "Methods" for calculation). Note that enclosure mesh slowed flow by approximately half. Periods of oscillation measured from video recordings were 4 to 9 s ($N = 61$)

The same data were examined to determine capture efficiency (capture rate per arriving cyst), by adjusting for the increasing flux of cysts with greater flow speed (Fig. 2). This analysis determined whether or not capture efficiency declined with increasing flow, which would be expected if nematocysts, spirocysts, or mucus were less effective at holding cysts as flow speed increased. There was no decline in capture efficiency for

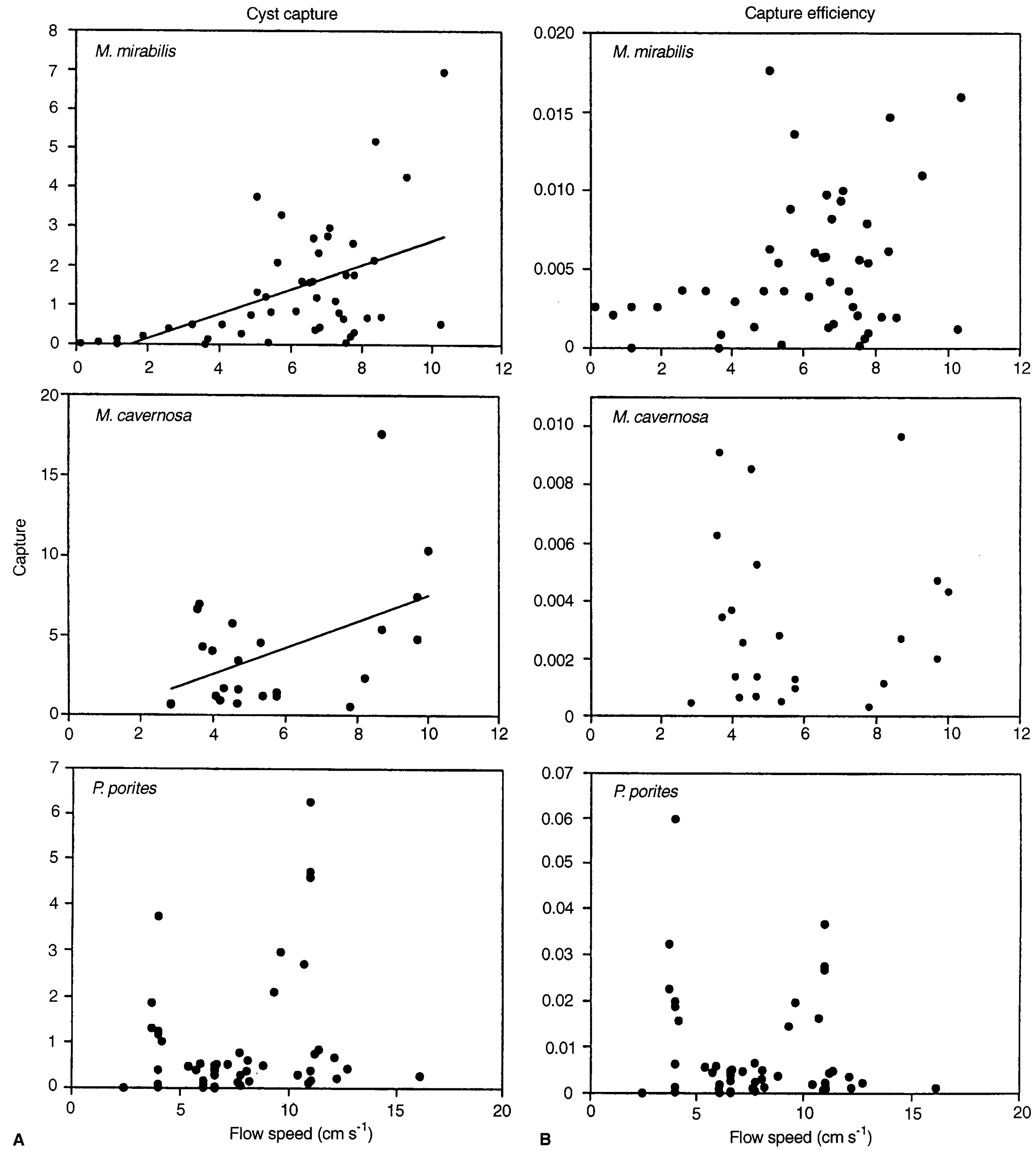


Fig. 2 *Madracis mirabilis*, *Montastrea cavernosa*, *Porites porites*. **A** Capture rates for hydrated brine shrimp cysts expressed as number of cysts captured per polyp per 20 min of experiment, per available cyst (standardized to 1 cyst ml^{-1}). Branch and mound tops, those regions nearest where flow was measured, were used for this comparison. **B** Capture efficiency (flux adjusted capture rate) for cysts expressed as number of cysts captured per polyp per number available cysts arriving at coral polyp (flux) during experiment. Flow speeds (cm s^{-1}, measured 1 ± 0.5 cm above coral tops 20 times during peaks of oscillatory flow)

Madracis mirabilis with increasing flow speed (Table 1). *Montastrea cavernosa* showed no significant relationship between flow and capture efficiency. *Porites porites* showed the highest efficiencies at the lowest speeds, but the relationship was not significant. Cysts have a hard proteinaceous coat that is not easily penetrated by most nematocysts, although surface agglutinant cnidae (spirocysts and some nematocysts) are probably more effective at retaining such impenetrable items.

Table 1 *Madracis mirabilis*, *Montastrea cavernosa*, *Porites porites*. Results of statistical tests (regression) on relationships between particle or plankton capture and flow speed for three coral species. Prey are denoted as brine shrimp (*Artemia salina*) cysts, total combined zooplankton, or subsets of zooplankton prey. The significance level (p) of the test is given, with the F-value and degrees of freedom. Flux is delivery rate of particles (see "Methods") (* significant at $p \leq 0.05$ level; *** $p \leq 0.001$)

Coral	Prey	*df*	*F*	*p*
M. mirabilis	Cysts	1,44	15.5	0.0003***
	Cysts (flux)	1,44	0.50	0.48
	Plankton	1,50	12.4	0.0009***
	Plankton (flux)	1,50	0.41	0.52
	Oithona sp.	1,50	0.90	0.35
	Oithona sp. (flux)	1,50	0.002	0.97
	Calanopia sp.	1,49	0.20	0.66
	Calanopia sp. (flux)	1,49	0.63	0.43
	Non-copepods	1,50	5.5	0.02*
	Non-copepod (flux)	1,50	0.41	0.53
M. cavernosa	Cysts	1,22	6.8	0.02*
	Cysts (flux)	1,22	0.17	0.69
	Plankton	1,24	6.8	0.02*
	Plankton (flux)	1,24	1.9	0.18
	Oithona sp.	1,24	1.4	0.25
	Oithona sp. (flux)	1,24	0.96	0.34
	Calanopia sp.	1,27	2.9	0.10
	Calanopia sp. (flux)	1,27	1.4	0.25
	Non-copepod	1,23	2.9	0.10
	Non-copepod (flux)	1,23	1.1	0.31
P. porites	Cysts	1,46	1.7	0.20
	Cysts (flux)	1,46	2.1	0.15

Location of capture on colonies

For each species used in the experiments, capture rates were determined for defined regions of each branch or mound. The data were divided at the median flow speed into high and low flow groups for comparison. Capture rates in each region were calculated as the percent of total capture for each branch or mound individually. For *Madracis mirabilis*, there were no significant differences among regions of the branch in high (ANOVA on arcsine transformed data, $p < 0.06$) or low ($p < 0.12$) flow groups although tops of branches had somewhat higher capture rates in both cases (Fig. 3).

Montastrea cavernosa showed a significant difference among colony regions in both low ($p < 0.008$) and high ($p < 0.008$) speed groups (Student–Newman–Keuls multiple comparison test, $p \leq 0.05$; Fig. 3). Sides of the corals captured significantly more cysts than did tops, fronts, or rear surfaces in both flows. As flow reverses, either the front or rear may develop a turbulent but lower flow (wake) region, whereas the top and sides always experience the higher flow, which is speeded up as water is diverted around the colony. If gravitational deposition were very important for this species, we would expect the flat top surface to receive more cysts than any other, but this was not the case even in the low speed group. The reason for the difference between tops and sides is thus not apparent.

Porites porites showed nearly equal capture rates on all surfaces at low flow speeds, with tops capturing somewhat more cysts ($p < 0.16$). At high flow speeds, differences were significant ($p < 0.0001$); the top (seaward) front sections were different from all other surfaces and top rear surfaces were different from top front and bottom rear surfaces (Student–Newman–Keuls multiple comparison test, $p \leq 0.05$). This indicates that the difference between top and bottom of these larger branches became more important with increasing flow speed, possibly because the branches (8 to 10 cm tall) spanned a greater part of the velocity gradient near the substratum, even though a stable boundary layer was not present.

Zooplankton capture versus flow speed

We examined capture rates for total combined zooplankton and for several categories of zooplankton versus flow speed in the experiments. *Madracis mirabilis* showed a significant positive relationship between capture rate and flow speed (Fig. 4) when all zooplankton were combined ($p < 0.009$; Table 1), and when all non-copepod prey were analyzed ($p < 0.02$). There was no significant relationship between flow and capture rate for the two most common copepods, the cyclopoid *Oithona* sp. and the calanoid *Calanopia* sp. *Oithona* sp. was often the most abundant copepod in plankton samples, but was rarely captured by either coral species. *Calanopia* sp. had higher capture rates throughout the range of flow speeds. *Montastrea cavernosa* (Fig. 4) capture rates were also significantly affected by flow speed for combined zooplankton prey ($p < 0.02$; Table 1). There was not a significant relationship for non-copepod prey, or for the copepods *Oithona* sp. and *Calanopia* sp. In all three cases, however, the highest capture rates occurred near the upper end of the range of flow speeds (5 to 6 colonies).

There was no significant relationship between capture efficiency (capture adjusted for flux of zooplankton) and flow speed for *Madracis mirabilis* (Fig. 4). There was also no significant relationship between capture efficiency and flow speed for *Montastrea cavernosa*, either

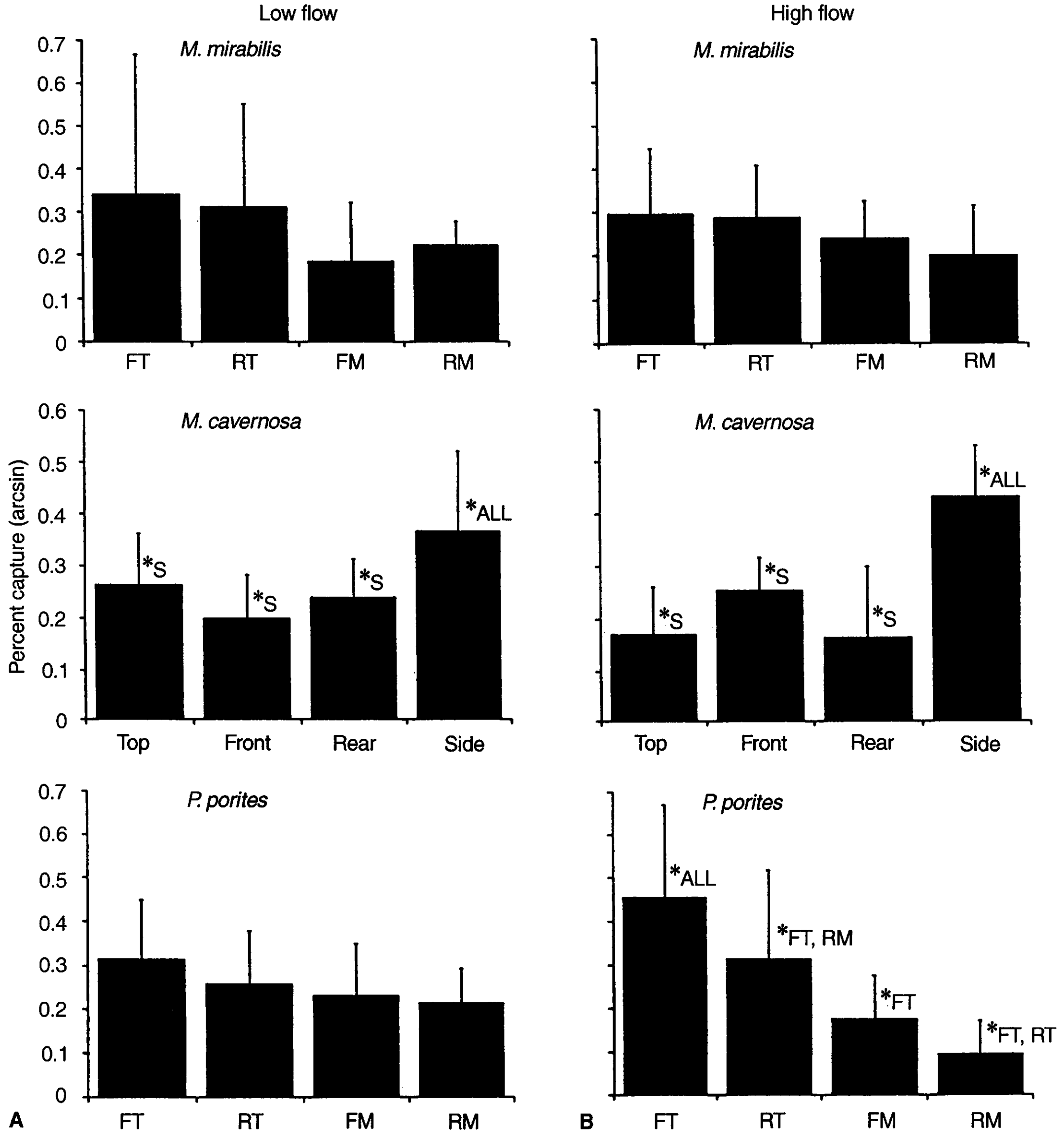


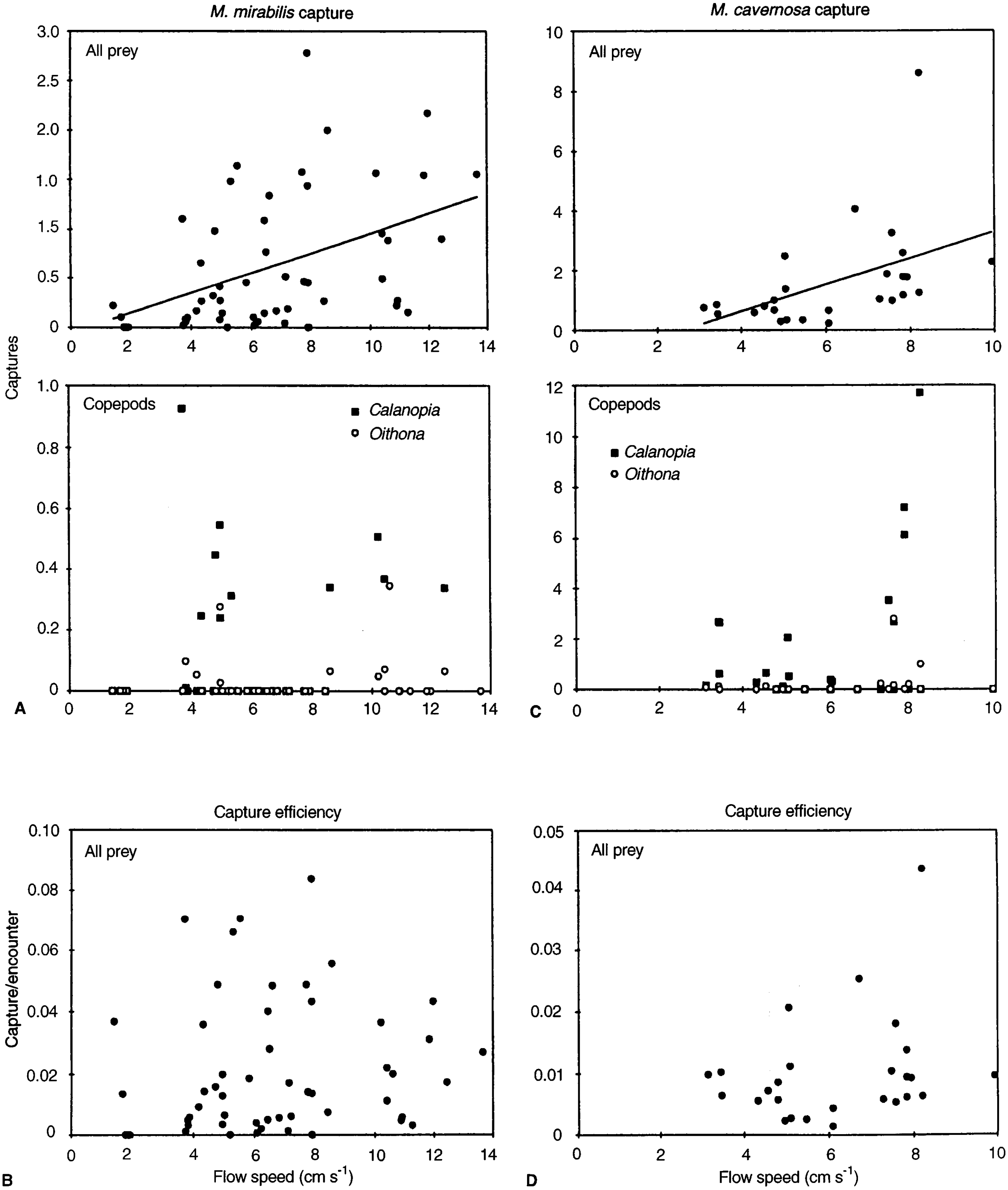
Fig. 3 *Madracis mirabilis*, *Montastrea cavernosa*, *Porites porites*. Capture rates for cysts in each colony region expressed as number of cysts captured per 20 min of experiment, as percent of total cysts captured by all polyps. Flow speeds were divided into **A** "low" and **B** "high" groups at the median flow speed (see Fig. 1) (* significant differences at $p \leq 0.05$; abbreviations above bars denote which groups are significantly different; *F* front, seaward side of colony; *R* rear; *FT* front top; *RT* rear top; *FM* front middle; *RM* rear middle)

for all prey combined or for any prey category (Fig. 4). In this case, the highest efficiencies occurred near the upper end of the flow speed range in all categories, but these comprised only two to four colonies. In general, it appears that some prey are captured more efficiently at low flow speeds and some at higher speeds but, overall, these effects may cancel out when all prey types are considered. The flow speeds used in the experiments do not include the higher flows experienced by these corals, and it is possible that efficiency could be affected, either positively or negatively, at higher speeds.

Capture rates differed based on region of the corallum at higher but not at lower flows (Fig. 5). The tops of *Madracis mirabilis* branches captured the most zooplankton per polyp. Front (seaward) and rear (landward) sides of branches captured equal numbers of zooplankton at low flows and both tops and fronts captured significantly more at higher flows (ANOVA, Student–Newman–Keuls multiple comparisons test, $p \leq 0.05$). Captures by *Montastrea cavernosa* were approximately equal at all locations in low flow, whereas tops and sides captured somewhat more prey at high flows (not significant).

Zooplankton capture versus concentration

The concentration of zooplankton in the enclosures varied greatly, over more than two orders of magnitude. For calculations of capture versus flow speed, only those experiments in the middle range were used (1000 to 30 000 ind m^{-3}), thus omitting variance due to



"swamping" of corals and possible saturation of the feeding response at the high end, and error because of extremely low numbers of prey captured per colony at the low end. Published studies of zooplankton concentration on reefs (night) using pumps or nets (not emergence traps) report concentrations in the range of 240 to 16 000 ind m^{-3} for individual samples (site means 1900 to 2300 ind m^{-3}) (203 μm mesh net, Herman and Beers 1969), 635 ± 551 SD ind m^{-3} (234 μm mesh net, Alldredge and King 1977), 508 to 2098 ind m^{-3} (250 μm mesh net, Ferraris 1982) and 70 to 1133 ind m^{-3} (pump with 150 μm net, Jakubczak 1989). Our experimental

Fig. 4 *Madracis mirabilis*, (**A**, **B**) *Montastrea cavernosa* (**C**, **D**). **A** Rates of zooplankton capture, expressed as number of plankters captured per 100 polyps per 20 min of the experiment, per available plankter (standardized to 1 plankter of that type per liter). **B** Capture efficiency (flux adjusted capture rate) for zooplankton captured by the corals expressed as number of plankters captured per available plankter arriving at the coral polyp (as in A, adjusted for flow speed). **C** Rates of zooplankton capture, expressed as number of plankters captured per 100 polyps per 20 min of the experiment, per available plankter (as in A). **D** Capture efficiency (flux adjusted capture rate) for zooplankton captured by the corals expressed as number of plankters captured per available plankter arriving (flux) at the coral polyp (as in A, adjusted for flow speed). Flow speeds determined as in Fig. 2

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concentrations were thus about 1 to 15 times these values (using a 40 μm mesh plankton net; most items in the plankton samples were well above 200 μm length, Sebens et al. 1996). Corals in our experiments were allowed to feed for approximately 20 ± 5 min, which is only 1/30 of the night/crepuscular feeding time available to corals, and most polyps still did not capture prey. Thus we expect most prey densities were well under saturation values, where feeding receptivity (and capture rate) could be lowered (e.g. Lasker et al. 1982; Patterson 1991).

Madracis mirabilis prey capture rates increased relatively linearly with concentration up to 10 000 ind m^{-3} (copepods) and 3000 ind m^{-3} (other zooplankton) (Fig. 6). When data were separated into high and low flow groups, it was evident that capture rates were higher in the high flow groups for the same numbers of zooplankton available (Table 2). The presence of numerous *Oithona* sp. and *Calanopia* sp. in plankton samples can bias this relationship severely because they affect total zooplankton concentration strongly, but are often not captured by the corals or are captured at very low rates (Sebens et al. 1996). Omitting these copepods from the calculations, it was clear that capture still increased with availability, and that higher flow resulted in more captures than occurred under low flow conditions (Table 2). For *Montastrea cavernosa*, the pattern was the same. Considering all prey, *M. cavernosa* captured more prey under higher flow conditions, and prey capture continued to increase up to > 40 000 ind m^{-3}. The relationship was most clear for non-copepod prey, where there was increased capture over a range of concentrations, to > 4000 ind m^{-3}. Analysis of covariance (Table 2) demonstrated significant relationships between capture and abundance for *M. mirabilis* (non-copepod prey) and for *M. cavernosa* (all prey, copepod prey), and significant differences between high and low flow groups for *M. mirabilis* (non-copepod prey) and *M. cavernosa* (non-copepod prey).

Discussion

Water flow and particle capture by passive suspension feeders

Water flow is a primary factor affecting feeding success of passive suspension feeders. The relative importance of each physical mechanism causing prey to contact feeding structures can be estimated from flow speed, particle size, density, and size and spacing of filter elements (Rubenstein and Koehl 1977; LaBarbera 1984; reviewed by Shimeta and Jumars 1991). At most flow velocities relevant to anthozoans, and for most sizes of zooplankton, direct interception (including sieving) is the

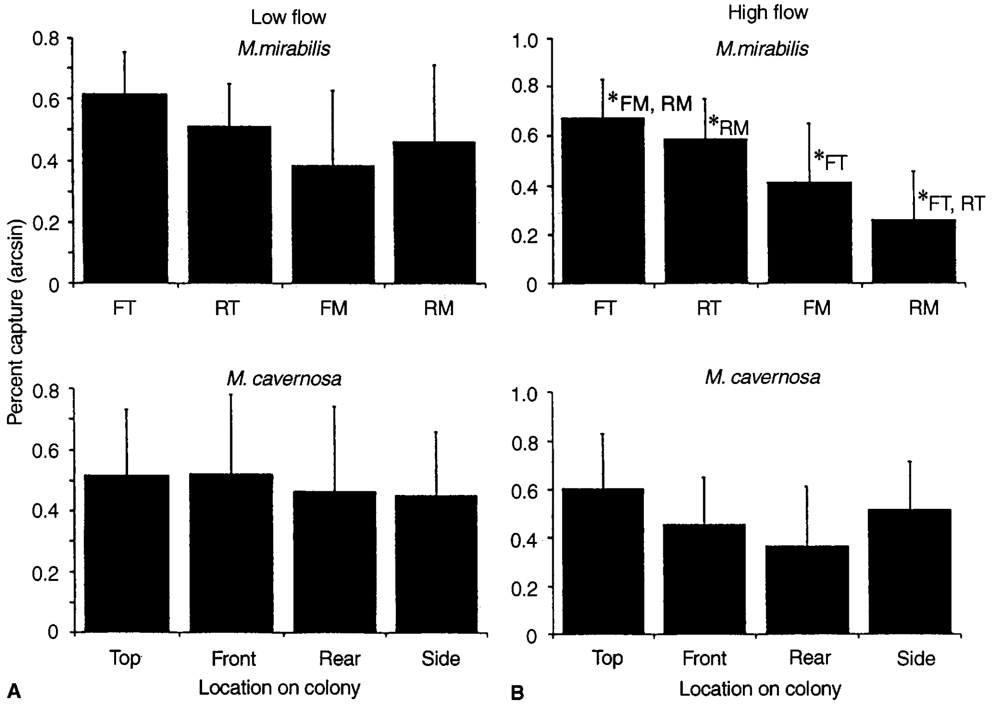

Fig. 5 *Madracis mirabilis*, *Montastrea cavernosa*. Capture rates for zooplankton in each colony region expressed as number of plankters captured per 20 min of the experiment, as percent of total plankters captured by polyps in all regions. Flow speeds were divided into **A** "low" and **B** "high" groups at the median flow speed (see Fig. 1). Abbreviations as in Fig. 3

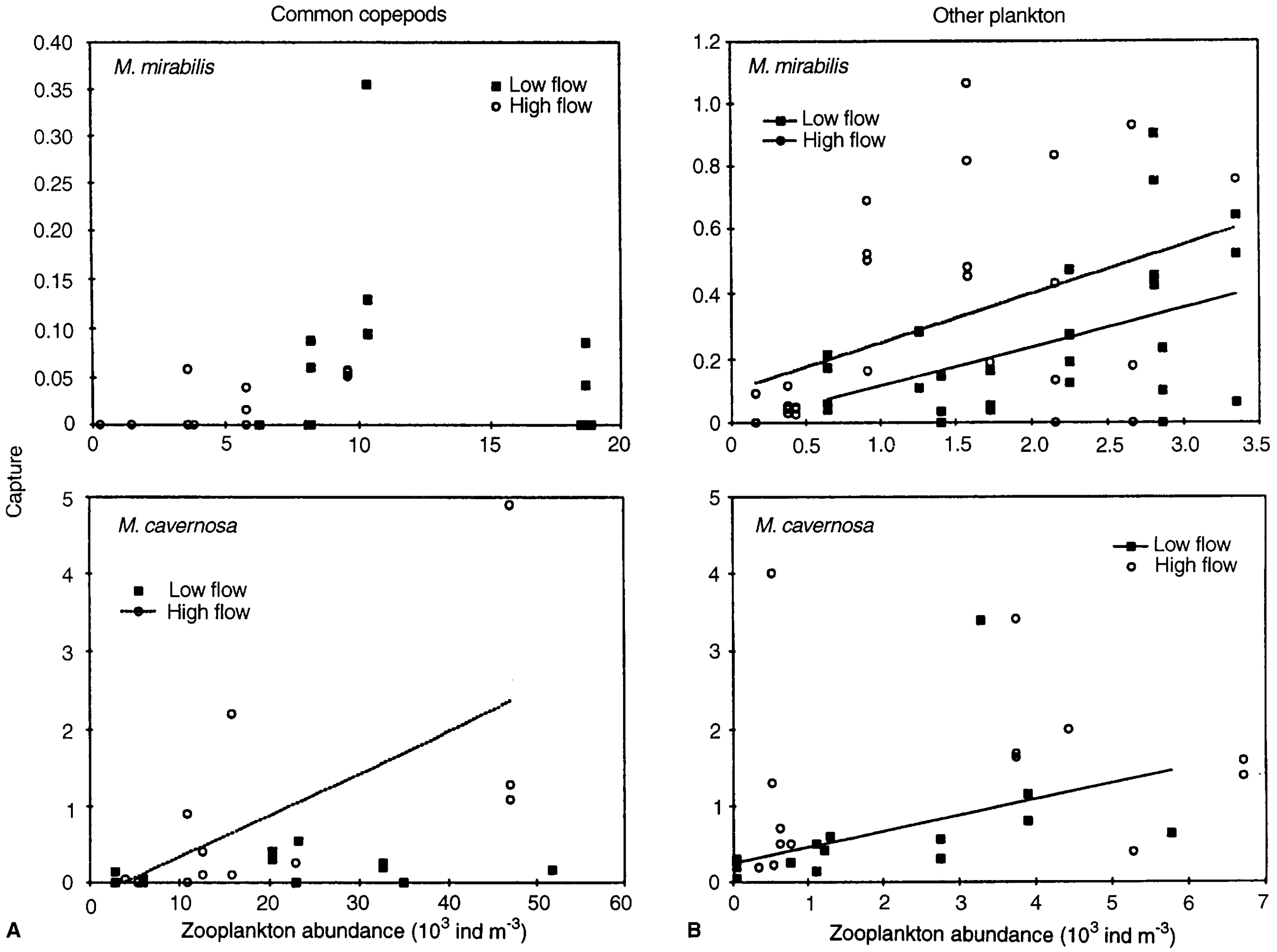

Fig. 6 *Madracis mirabilis*, *Montastrea cavernosa*. Capture rates for zooplankton ingested by corals expressed as number of plankters captured per 100 polyps min^{-1} during the experiment, versus total concentration of available zooplankton (10^3 ind m^{-3}) **A** for the numerically dominant copepods (*Oithona* sp., *Calanopia* sp.) and **B** for all other prey. Flow speed groups were determined by dividing the data set at the median value for flow speed (see Fig. 1)

primary mode of capture. Particles carried by the ambient flow contact tentacles directly as streamlines are diverted around them. Inertial impaction occurs when the momentum of dense particles causes them to deviate from streamlines and to contact a suspension-feeder's tentacle; this could be important for large (and dense) prey at velocities approaching 0.5 m s^{-1} (Sebens and Koehl 1984). Gravitational deposition can be important for capture of particles denser than water at low flow speeds, as in lagoonal and deep reef habitats (e.g. zoanthids, Koehl 1977; corals, Sebens and Johnson 1991; model in Abelson et al. 1993). Particles captured by the octocoral *Alcyonium siderium*, for example, were mostly larger than the spacing of pinnules (branches) on tentacles and could have been caught by sieving, whereas anemones and scleractinian corals captured zooplankton that were mostly smaller than the tentacle spacing (Sebens and Koehl 1984; Sebens et al. 1996). Especially at low to moderate speeds, flow has a positive effect on particle capture because it increases the flux of particles into the vicinity of filter elements.

Table 2 *Madracis mirabilis*, *Montastrea cavernosa*. Results of analysis of covariance with capture as dependent variable and prey availability as independent variable, with two flow speed groupings (high and low, see "Results"). The *F*-value for the interaction of flow and availability ($F_{f \cdot a}$) is equal to the *F*-value for heterogeneity of slopes. "Other" includes all zooplankton except the very abundant copepods *Oithona* sp. and *Calanopia* sp. Significant *F*-values are in *bold type* (* significant at $p \le 0.05$ level; ** $p \le 0.01$)

Species	Prey	F_{flow}	$F_{\mathrm{avail.}}$	$F_{\mathrm{f \cdot a}}$	$F_{\mathrm{elev.}}$
M. mirabilis	All	**8.28****	1.52	**15.32****	–
	Copepod	3.13	0.001	1.70	1.45
	Other	0.45	**11.92****	0.15	4.20
M. cavernosa	All	0.08	**10.43****	**4.41***	–
	Copepod	0.35	**8.23****	**6.45***	–
	Other	**5.27***	1.74	1.69	**3.60***

Zooplankton, however, are not passive particles. The swimming behavior of zooplankton causes them to contact tentacles, even at low flow speeds (as in diffusional deposition, Rubenstein and Koehl 1977), but rapid bursts of swimming also allow zooplankton to escape. The effects of prey behavior have been considered for pelagic tentaculate predators; Greene et al. (1986) calculated a vulnerability index for capture, by the ctenophore *Pleurobrachia bachei*, of the copepods *Calanus pacificus* and *Acartia clausi* relative to *Pseudocalanus* sp., although escape responses of prey were not examined. Purcell et al. (1987) quantified the frequency of escape by herring larvae, from tentacles of the hydromedusan *Aequorea victoria*. Trager et al. (1994) also noted successful evasive behavior by copepods encountering feeding barnacles, but not by *Artemia salina* nauplii, which were readily captured. Sebens and Koehl (1984) calculated electivity indices for *Metridium senile* (anemone) and *Alcyonium siderium* (octocoral) and found that strongly swimming prey were underrepresented in the diets, especially of the latter species, whose diet included primarily meroplankton. The corals used in the present study also showed very low capture rates for certain zooplankton categories, such as the abundant copepods *Oithona* sp. and *Calanopia* sp. (Sebens et al. 1996). These copepods, especially *Oithona* sp., exhibited strong escape responses to coral (*Meandrina meandrites*) tentacles in laboratory experiments (Heidelberg et al. 1997).

As for many active predators, success or failure in prey capture by passive feeders depends on the escape ability of the prey as well as on the detection and capture ability of the predator. Prey selection indices (e.g. Vanderploeg and Scavia 1979) for passive suspension feeders measure prey avoidance ability as well as, or instead of, any predator "preference" (Sebens and Koehl 1984; Sebens et al. 1996). The ability of corals to capture a particular type of zooplankter is also likely to depend on the behavior of those zooplankton in flow. It is entirely possible that the swimming behavior of some types of zooplankton would bring them into contact with tentacles at low flow, whereas they would have lower contact rates if they moved less. On the other hand, potential prey that are strong swimmers may be able to avoid tentacles at low to moderate flow speeds, but not at high and turbulent flows where increased direct interception or inertial impaction come into play (present study). Avoidance by these zooplankton may depend on mechanoreception, detecting a change in flow as the plankter approaches a surface, and such detection may be difficult in very turbulent flow. Conversely, it may be difficult for a zooplankter to detect a tentacle if flow is very slow, and there is no clear gradient or pattern of flow separation upstream (Heidelberg et al. 1997). The results of the present study suggest that, at the lower flow speeds, capture rate is directly proportional to prey flux. When there were differences in locations of cyst or zooplankton capture on colonies, capture rates were greatest in regions expected to experience higher mean flow (branch tops, mound tops and sides). For *Madracis mirabilis*, cyst capture was not statistically different among regions. This differs from laboratory flume results where there was a significant effect of position on the branch in unidirectional flow (Sebens et al. 1997), but is consistent with known differences between unidirectional and oscillatory flow. In the latter case, there is no stable boundary layer, and flow speeds near the substratum (e.g. 2 to 3 cm above) are expected to be similar to those a few centimeters higher, although there can still be a gradient of mean speed near the substratum (Denny 1988; Helmuth and Sebens 1993). Differences between front (seaward) and rear sides of branches are also not important when flow is reversing every 2 to 4 s, and is almost equal in magnitude, as was commonly the case at this location.

Particle capture by reef corals involves items other than zooplankton (e.g. particulate organic matter, POM), supplied to the corals by moving water. Corals have been shown to use mechanisms of capture (such as muco-ciliary feeding) suitable for POM intake (Lewis and Price 1975), and such particles thus have the potential to fulfill a portion of the coral's nutritional requirements. POM uptake has been documented for cerianthids (Tiffon 1976) and for anemones (Van Präet 1980). Recent studies showed substantial phytoplankton capture by certain octocorals (e.g. *Dendronepthya hemprichi*), and demonstrated the importance of water flow affecting delivery of this resource (Fabricius et al. 1995). The importance of such sources of nutrition for scleractinian corals, and effects of flow on their delivery, are at present unknown. Water movement undoubtedly affects the composition of the near-substratum plankton as well as its delivery. On days with low flow, a layer of increased zooplankton abundance can develop near the substratum whereas on days with strong currents or heavy wave action, locally released larvae (e.g. Graham and Sebens 1996) and any crustaceans that venture off the substratum will be rapidly mixed into the surrounding water via eddy diffusivity (reviewed by Denny 1988), and more detritus and fragments of benthic organisms will be scoured off the substratum (resuspended) than during calm water periods. Two common temperate zone anthozoans examined in a previous study (*Metridium senile* and *Alcyonium siderium*, Sebens and Koehl 1984) relied heavily on such substratum-associated prey (both meroplankton and demersal plankton).

Water flow near reef surfaces: effects on coral feeding and energetics

Coral reefs are complex physical structures and thus display a variety of flow regimes (Hamner and Wolanski 1988; Andrews and Pickard 1990; Sebens and Done 1992; Shashar et al. 1996) and flow microhabitats, from protected spaces among coral heads to exposed surfaces of spurs and buttresses. The surf zone, reef crest, and adjacent reef flat habitats experience strong wave-induced flow (bidirectional), which can pump water over the reef crest and into backreef or lagoonal areas creating a varying unidirectional flow (Kjerfve 1982; Roberts and Suhayda 1983; Pickard 1986; Sebens and Done 1992). On forereef slopes, flow regimes are usually wave-dominated to at least 15 to 20 m depth, especially on reefs without strong currents (e.g. Sebens and Johnson

1991; Helmuth and Sebens 1993). Where currents are strong (Roberts et al. 1975; Wolanski and Pickard 1983), they provide the primary source of water movement past corals at all depths below the reef crest. Corals in deep reef habitats typically experience slow unidirectional flows at sites where currents are minimal (Helmuth and Sebens 1993). In unidirectional flow, speeds within the benthic boundary layer (i.e. near corals) are generally lower than those measured at mid-depth (Shashar et al. 1996). In most studies of flow in reef habitats, vector-averaged flows have been recorded (5- to 10-min records), removing the high-frequency wave effects (but see Frith 1983; Andrews et al. 1984; Sebens and Johnson 1991; Sebens and Done 1992; Helmuth and Sebens 1993; present study). Vector-averaged data are not appropriate to describe the flow experienced by individual coral colonies, which may benefit substantially from high-frequency oscillations. Considering particle flux to corals, flows in opposite directions do not cancel each other out.

Examples of typical flow speeds on reefs (0.5 m above unobstructed surfaces, 0.5 s readings) are: maximal non-storm flows of almost 1.0 m s^{-1} during oscillations on a reef crest (means 7 to 34 cm s^{-1}), lagoonal (1 m depth) unidirectional mean flows of 1 to 16 cm s^{-1}, shallow (7 m) forereef oscillatory flows of 9 to 16 cm s^{-1} (see also Fig. 1, 10 m depth), and deeper forereef flows (18 m) with means of 5 to 7 cm s^{-1} (GBR, Australia, Sebens and Done 1992). These values are almost identical to those recorded in St. Croix (Sebens and Johnson 1991), and in Jamaica (Helmuth and Sebens 1993), except that flows in deep habitats were even lower at the latter sites (<5 cm s^{-1}). Such flow speeds are often well below the optimum speeds for particle capture by corals (Johnson and Sebens 1993; Helmuth and Sebens 1993; present study), and are in the range where increased flow can provide greater particle flux, higher encounter rates with prey, and thus enhanced prey capture (as in present study). The type of flow regime also matters; wave induced oscillatory flow, and the consequent lack of a steady-state boundary layer (Grant and Madsen 1979), can provide definite benefits to passive suspension feeders. Such animals rely on particles and dissolved substances moving from mainstream flow to their surfaces via simple advection and "eddy diffusivity" resulting from turbulent shear above the rock and organism surfaces (Denny 1988). Up to some optimum flow speed, more flow results in higher particle encounter rates (including zooplankton), and is thus energetically advantageous (Sebens 1984; McFadden 1986). Flow speed thus has the potential to be a limiting factor for particle capture (zooplankton and non-motile particles), and for energy intake by many species of reef corals; flow regimes may therefore limit coral growth rates and thus determine the types of reef habitats in which a particular coral species can succeed.

At low flow speeds, development of a thick momentum and/or diffusive boundary layer over organism surfaces inhibits particle movement and diffusion of dissolved substances (Atkinson and Bilger 1992; Helmuth et al. 1996; Shashar et al. 1996) and absolute horizontal flux is decreased. Reduction of gas exchange resulting from diffusive boundary layer limitations at low flow speeds results in decreased rates of coral respiration and photosynthesis by symbiotic algae (Patterson and Sebens 1989; Shick 1990; Patterson et al. 1991), reduced energy available for growth, and reduced calcification rates (Jokiel 1978; Dennison and Barnes 1988). Recent evidence of steep gradients of oxygen concentration within the diffusional boundary layer at low flow speeds supports the concept of diffusional metabolic limitation (Shashar et al. 1993; Kühl et al. 1995). Strong near-substratum flow can also have negative effects on corals and can increase the probability of organism dislodgment. Accelerational forces dominate during wave surge; these are the major forces tending to remove sessile organisms from the substratum (Denny et al. 1985). The "optimal" flow environment for any particular species of coral thus depends on an array of species-specific positive and negative effects of the local flow regime.

Rates of zooplankton capture, as functions of abundance and of flow speed, are important components of ecosystem models developed for coral reefs (e.g. Johnson et al. 1995). The present study demonstrates that an increase in zooplankton concentration, especially at the low concentrations usually found on reefs, is likely to result in a proportional increase in flux of food items to corals, and ingestion by them. Similarly, adjacent microhabitats that differ in mean flow speed should also experience a proportional difference in prey flux, capture rate, and ingestion. The species composition of the zooplankton assemblage is also critical, given that the most common copepods (e.g. *Oithona* sp.) are captured at very low rates. The species of coral used in ecosystem-scale models is extremely important, especially since capture rates per unit coral biomass can vary by more than an order of magnitude among species (Sebens et al. 1996).

This study demonstrates that water flow determines particle flux and thus capture rates of non-motile particles and of live zooplankton by two of these species under realistic field conditions. Flow in the enclosures was oscillatory (bidirectional, wave-generated) and varied from <2 to >16 cm s^{-1} during oscillations. This represents a good portion of the normal range of flows corals experience at 8 to 30 m on this reef, under non-storm conditions (i.e. ≤ 2 m significant wave height, Helmuth and Sebens 1993). Based on these results, it is clear that increased flow, in this range of speeds, enhanced particle and zooplankton capture, and thus energy and nutrient intake for these coral species. The distribution of flow speeds at 10 m depth, outside the enclosure, indicates that flow is often well below the optimum for zooplankton capture, and that periods of high waves or strong current may be beneficial to coral energetics and growth. Similarly, corals living in exposed microhabitats may also benefit from increased flow, compared to those in protected microhabitats on the same reef.

Acknowledgements This study was supported by NSF Grants OCE 8911421 and 9302066 and a NOAA/NURC award (to K. Sebens). The Discovery Bay Marine Laboratory (University of the West Indies), the Marine Science Center (Northeastern University, Nahant, Massachusetts), the Department of Zoology (University of Maryland at College Park) and the Horn Point Laboratory (University of Maryland System, Center for Environmental Studies, Cambridge, Maryland), all provided laboratory space and equipment, for which we are grateful. We thank the following individuals for valuable field and laboratory assistance: L. Savina, K. Graham, K. Vandersall, E. Thomsen Porter, S. Zamojski. We also thank A. Gauzens for help with copepod identification, and K. Heidelberg and M. A. Chen for providing helpful comments on the manuscript. This is Contribution No. 593 of Discovery Bay Marine Laboratory and No. 228 of Northeastern University's Marine Science Center.

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