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Effects of water flow and branch spacing on particle capture by the reef coral *Madracis mirabilis* (Duchassaing and Michelotti)

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Abstract

The scleractinian coral *Madracis mirabilis* forms colonies composed of many narrow branches whose spacing varies across habitats; this is especially evident along a depth gradient. Environmental factors such as irradiance and water movement co-vary along this gradient and both factors could have effects on branch spacing. We examined the effects of water flow on particle capture by *Madracis mirabilis* in a laboratory flume at Discovery Bay, Jamaica, using hydrated *Artemia* cysts as experimental particles. Isolated branches of *Madracis* showed highest particle capture rates in the 10–15 cm s^{-1} range of flow speeds, although capture was still occurring at about one fourth the maximum rate even at 40–50 cm s^{-1}. The ability to capture particles at these higher flow speeds results from polyps on downstream sides of branches capturing particles from turbulent eddies in the wake of the branch. At high flows, these polyps are not deformed (flattened) as are the upstream polyps. Two aggregation densities were tested at three flow speeds and both flow and particle capture were measured at each branch. Low density aggregations, comparable to those in low flow and deep reef habitats, captured particles best at the lowest flow speeds tested and capture was relatively uniform through the aggregation. High density aggregations captured particles best at high flow speeds, especially near the downstream end of the aggregation. At low flow speeds, the highest capture rates occurred at the upstream end of the aggregation. Flow speed decreased downstream within aggregations at both low and high densities, especially at higher flow speeds. Turbulence intensity also changed within aggregations, increasing behind the first row of branches at all flow speeds and in both aggregation densities. Total capture rate per polyp was highest at intermediate flow speeds (10–15 cm s^{-1}) for single branches and for aggregations due to high encounter rates, while capture efficiency (flux adjusted capture rate) was greatest at low flow speeds. Patterns of flow and particle capture within aggregations suggest that high density aggregations function better in high flow environments. Low density aggregations were able to capture only one fourth as many particles as high density

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aggregations at the higher speeds used in these experiments. Conversely, high density aggregations captured only about half as many particles at the low flow speed, compared to low density aggregations. Factors other than flow, especially light interception, are likely to affect branch spacing as well. Shallow reef habitats, with high irradiance and high flow conditions, may thus favor tight branch spacing as a response to both environmental variables. © 1996 Elsevier Science B.V.

Keywords: Madracis mirabilis; Colony morphology; Scleractinian coral; Suspension feeding

1. Introduction.

Corals and related anthozoans capture zooplankton and other particulate matter from the water column using both nematocyst adhesion (Muscatine, 1973) and cilia with mucus entrapment (Yonge, 1968; Goreau et al., 1971; Lewis and Price, 1975; Lewis, 1976; Helmuth and Sebens, 1993). Data on natural prey are available for only three species however (*Montastrea cavernosa*, Porter, 1974; *Meandrina meandrites*, Johnson and Sebens, 1993; *M. cavernosa* and *Madracis mirabilis*, Sebens et al., 1996). Zooplankton appear crucial to the nutrition of at least some corals. Edmondston (1928) and Yonge and Nicholls (1931) fed zooplankton to several coral species in laboratory experiments and found prolonged survival in the dark. Wellington (1982) used field enclosures to exclude zooplankton; growth rates of both small and large polyp corals were negatively affected by this treatment.

Particulate feeding is likely to be very important to most corals for several reasons. Even in shallow water, replenishment of nitrogen, phosphorus, and other nutrients which cannot be supplied by the coral's symbiotic algae must come from particle capture, or from uptake of dissolved compounds (reviewed by Muscatine, 1973; Muscatine and Porter, 1977; Sebens, 1987). In deep reef habitats, where zooxanthellae cannot meet all of the coral's energy needs, particulate feeding may be necessary to provide energy for maintenance and growth as well as potentially limiting nutrients (Stambler and Dubinsky, 1992). Water flow determines the delivery rate of particles to suspension feeders, including corals (Sebens, 1984; Sebens and Johnson, 1991), and affects the ability of such species to capture particles (Shimeta and Jumars, 1991 review). Flow also affects gas exchange (Patterson et al., 1991), nutrient uptake (Atkinson and Bilger, 1992) and breakage and dislodgement (Denny et al., 1985). Given the strong observed flow gradients, and the multiple effects of flow, several authors have hypothesized flow-related patterns of coral distribution across and among reefs (Done, 1982; Graus and MacIntyre, 1989; Sebens and Done, 1992).

The effects of flow on suspension feeders of all taxa have been reviewed extensively by Shimeta and Jumars (1991). Leversee (1976), Lasker (1981) studied whole colony feeding in gorgonians, demonstrating the asymmetric nature of food capture (downstream side of colony). Porter (1974), Patterson (1984) and Helmuth and Sebens (1993) noted similar patterns for a soft coral and for two scleractinian corals, respectively. Patterson (1984) found greater prey capture on the upstream side of octocoral colonies

in slow flow and on the downstream side in more rapid flow, indicating that particle capture from downstream eddies was important; increased turbulence, however, removed this pattern. A prediction of particle capture models is that feeding success should increase as flow speed increases but at a rate less than directly proportional to flow speed, then should decrease with faster flow as particles fail to adhere. McFadden (1986) demonstrated this response for a temperate zone octocoral (see also Best, 1988 for sea pens).

Particle capture in aggregations is less well understood. However, McFadden (1986) showed that aggregations of *Alcyonium* captured particles better than did solitary colonies at high speeds, but that the reverse was true at low speed, indicating that spacing within aggregations was critical for particle capture. Buss (1981) showed decreased particle capture when erect bryozoans were crowded. Okamura (1984), (1985), (1992) demonstrated that bryozoan colony morphology interacts with flow environment to affect particle capture success. Erect bryozoans within aggregations exhibit decreased particle capture at low to moderate flows whereas encrusting bryozoans, especially at high flows, capture particles better when neighbors are present. Anthony (1997) also showed decreased prey capture within aggregations of sea anemones in a laboratory flume. Some of the negative effects of being within an aggregation are due to flow reduction, and thus decreased encounter rates with particles. However, aggregations of benthic suspension feeders also have the potential to deplete particles locally (Frechette et al., 1989), with consequences for morphology, growth and competitive interactions.

The purpose of the present study was to examine the relationship between water flow, branch spacing and particle capture for *Madracis mirabilis*, a common branching reef coral at Discovery Bay, Jamaica (Wells, 1973; Liddel and Ohlhorst, 1981). In Jamaica, as well as in Barbados (Lewis and Snelgrove, 1990) and other Caribbean reefs, this species grows as large densely packed aggregations up to several meters across, and as small isolated hemispherical colonies. It covers a broad depth range from a few meters in backreef locations to at least 24 m on the forereef and varies markedly in branch spacing (Fig. 1). Branch spacing is expected to determine the pattern, speed and turbulence of water flow through a colony and thus will affect particle delivery and capture rates. In this study, we examine particle capture by single branches of *M. mirabilis* in a laboratory flume over a broad range of flow speeds, and compare this to particle capture by aggregations of *M. mirabilis* in the flume for a range of branch spacings and flow speeds. We test the hypothesis that plasticity in branch spacing within aggregations affects particle capture under particular ambient flow conditions such that colonies can optimize particle capture in a given habitat and flow regime.

2. Methods

2.1. Field collection and measurements

Colonies of *Madracis mirabilis* were collected from the forereef at Discovery Bay, Jamaica, from depths of 10–15 m and were maintained in running seawater aquaria

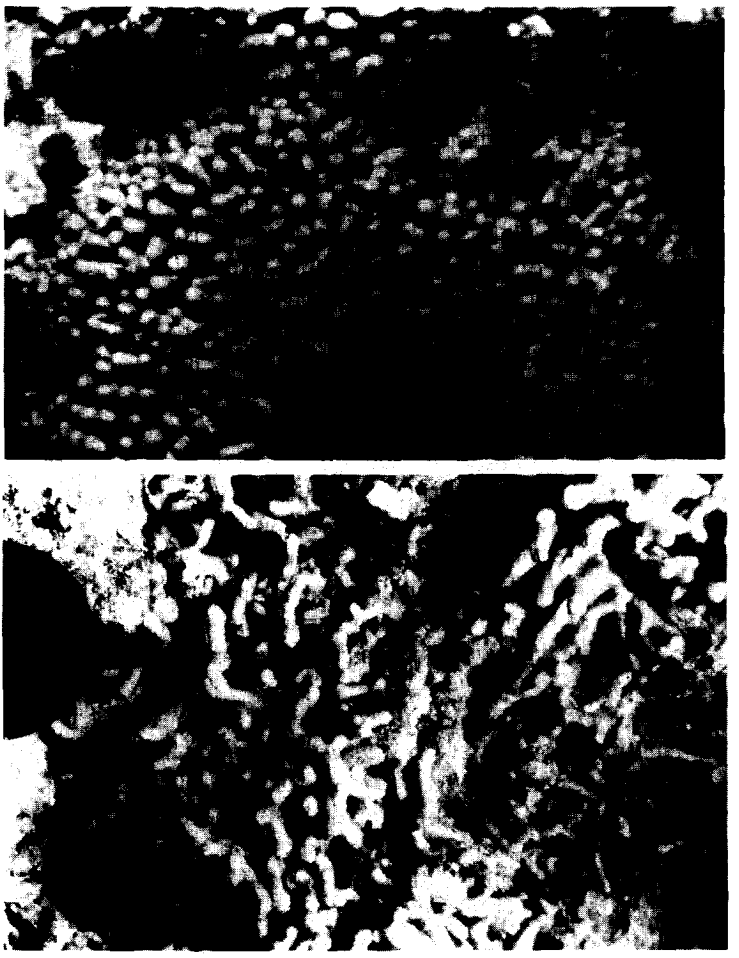

Fig. 1. *Madracis mirabilis* aggregations at 10 m (top) and 20 m (bottom) depths on the forereef at Discovery Bay, Jamaica. Note tighter branch spacing in the shallower habitat. Scale (black circle) is 8 cm across.

under low light conditions at the Discovery Bay Marine Laboratory (D.B.M.L.), University of the West Indies. After collection, colonies were divided into individual branches and were clipped with pliers to produce small (4–6 cm tall) branch fragments. These fragments were generally Y-shaped, sometimes with a third small branch. The bottom centimeter or two of each fragment often lacked living tissue. This species expands polyps completely almost immediately after breakage, but if kept in aquaria for more than about four days, polyps elongate to an extent rarely observed in the field. Their behavior aquaria is likely to be affected in other ways as well; branches were therefore used within four days of collection.

To determine branch tip spacing in the field, we photographed aggregations (haphazard selection) at depths of 8 to 22 m, from directly above with a scale in the

photograph. Branches in the center of each aggregation were chosen and all distances ($N = 30$) to direct neighbors (5–6) were measured using an image analysis system (Sony PHV-A7 slide scanner, Apple MacIntosh Quadra 900, NuVista video board, 'Image' Program (NIH)).

2.2. Particle capture by single branches

Individual branches were placed in the flume in groups of two or three, with enough lateral separation between branches such that no branch was in the wake of another, as determined by dye tests and observations of suspended cysts. When three branches were used, one was 6 cm upstream of the other two, centered, and the two downstream were 8 cm apart laterally. Branch centers were thus 3.5 cm from flume walls, and tips were at least 2 cm from walls. Since flow was measured directly at the corals, wall effects, manifested as reduced local ambient flow speed, were avoided and/or taken into account. Branches were mounted in 8 mm tall plastic tubing holders glued to a glass plate that fit the bottom of the flume. Once corals were placed in the flume, they were allowed to expand fully before the experiment was started. A small amount (< 0.5 ml) of macerated gastropod body fluid was added to the flume (downstream of the corals) to promote polyp expansion. When tests were attempted without this step, corals frequently delayed 30 min before expanding, whereas expansion occurred within 5 to 10 min with the fluid added.

The laboratory flume used was based on the design of Vogel and LaBarbara (1978) (constructed for use at D.B.M.L. by M. LaBarbera). This flume had a 1-m trough with a working section 0.4 m long and 15 by 15 cm in cross section, with a water depth of 15–20 cm. Recirculating flow was produced by a Bodine (TM) Series 400 1/15HP DC motor with Minarik (TM) variable speed controller with the propeller mounted in the vertical PVC pipe downstream of the working section. Upstream of the working section were two flow straighteners, each 6 cm deep, filling the flume width. Hexagonal channels in the flow straighteners were 4 mm diameter. Flow in the flume center was variable from under 2 to over 40 cm s^{-1} as determined by fluorescein dye release in the center of the flume's working area. Details of the construction and near-bottom boundary layer for this type of flume are given by Vogel and LaBarbara (1978) and Patterson (1985). Any flume can have substantial wall effects, where flow is decreased. Therefore, for this study, flow was measured in front of each branch tip, just above the tip, and in front of the midsection of the branch by video tracking of suspended hydrated brine shrimp (*Artemia salina*) cysts (Sebens and Johnson, 1991). Capture measurements were not made within 2 cm of the flume bottom or sides. Corals obstructed less than 5% of the cross sectional surface area of the flume, and flow speeds calculated from particle tracks (at sites of capture) were used rather than relying on mean flow in the flume. These precautions obviate the negative effects of most flume artifacts that can occur in flumes of small dimension used for suspension feeding studies (Nowell and Jumars, 1984).

Hydrated brine shrimp cysts were used as experimental prey in this study because they are readily ingested by coral polyps, are close to neutrally buoyancy, and (at > 200 diameter) are well within the size distribution of prey captured by corals in the field

(Johnson and Sebens, 1993; Sebens et al., 1996). The cysts are not digested by coral polyps and are egested after approximately 30–60 min when corals are kept out of water. It was possible to examine several hundred polyps per branch to determine rates of capture by region (top 1.5–2 cm, middle 1.5–2 cm, bottom 1.5–2 cm), using a dissecting microscope. Most egested cysts appeared in the open mouth area of each polyp; very few remained in the coelenteron and these were found rapidly by probing with a fine needle. The rate of capture was quantified for a range of cyst concentrations and times (Fig. 2) to determine if saturation and reduction of feeding rate had occurred. Cyst concentrations and duration of feeding bouts were selected such that most polyps had one or no cysts captured (at 1–2 cysts per ml).

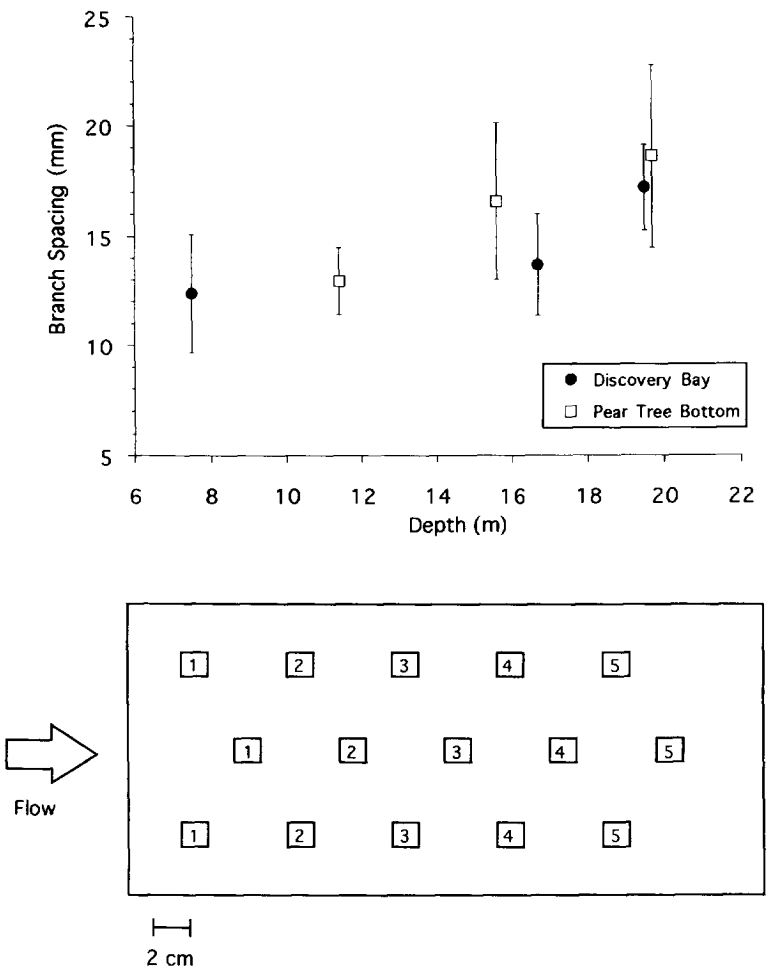

Fig. 2. (A) Branch spacing of *Madracis mirabilis* on the forereef at Discovery Bay (Mooring 1 site) and Pear Tree Bottom, Jamaica, 7–20 m depth. $N = 32$ colonies (30 measurements per colony), error bars are ± 1 SD (B) Artificial aggregations for feeding trials were constructed with high and low densities to mimic approximate densities found shallow and deep on the reef. Numbers refer to positions (rows) in aggregation (1 is upstream).

Colonies were allowed to acclimate to the flow for 15–30 min, then were fed during a 20 min period in flows ranging from 5–45 cm s^{-1}. Cysts were hydrated an hour or more before each run and floating cysts were then poured off. The volume of dry cysts was chosen such that final cyst concentrations were 1–2 cysts per ml in the flume. Cyst concentrations were determined during each run after 1, 7, and 13 min by taking water samples with a 25-ml syringe at the height of the coral tips. Contents of syringes were passed through a 180 μm mesh Nitex square which was then examined under a dissecting microscope. Cyst concentrations from the three time intervals were then averaged for each run. There were only small differences among counts at speeds over 10 cm s^{-1}, but at speeds below 10 cm s^{-1} there were substantial changes in cyst counts during the runs, due to gradual settling of cysts. Because we were working with upright branching corals, horizontal surface area subject to gravitational deposition was minimal; we, therefore, did not remove hydrated cysts that were negatively buoyant (see Helmuth and Sebens, 1993). Capture rates were standardized to 20-min run duration and to a 1 cyst per ml concentration by calculating cysts captured per N polyps per unit time, per cyst available.

During the last minute of each run, a macro video recording (Sony V9 8 mm camcorder with No. 2, 3 diopter lenses) was made of each coral's upper half, (with 5-mm slit lighting from above, holding the the slit parallel to flow, as in Sebens and Johnson (1991)). A small ruler was held 1 cm above the coral tip for scale, and tracks of illuminated cysts were measured by stop-frame analysis. When the tapes were played back, illuminated cysts just upstream of the coral tip were chosen if they remained in the slit of light for at least five consecutive frames, and 20 cysts were chosen haphazardly from the entire record. This technique provides flow speed in the x, z plane, but omits the component of flow in the y plane (across the flume). The flow components along the y and z axes were much smaller than along the x axis, and we were comparing capture rates at different heights (z) along the coral branch. Each cyst position was traced on acetate taped to a video monitor screen, with the coral and scale traced as well. In flows under 30 cm s^{-1}, successive positions of a cyst were drawn for five frames each 1/30 of a second apart. For higher speeds, the length of a particle track in one frame was traced and measured; this is the distance the particle travelled in 1/60 of a second. The mean of these 20 measurements was used to determine flow speed for that coral, quantifying differences in mean local flow speed due to the position of corals in the flume, and thus correcting for any potential wall or position effects.

Note that two flow speeds will be referred to in this study. The first is local unobstructed flow which is the flow directly upstream of the first central coral branch tip. It will be similar, but not identical, to the 'mainstream' flow in the center of the flume. Unless indicated differently, all flow speeds referred to will be local unobstructed flow. The second flow speed used is local incident flow, which is the flow speed measured directly in front of the coral branch region of interest. This flow can be influenced by upstream branches and by distance from the bottom or sides of the flume.

2.3. Particle capture in aggregations of branches.

In a second set of experiments, we used aggregations of 15 branches in a rectangular array (Fig. 3) with spacing of 3.0 + 1.4 cm between branch tips (low density) and

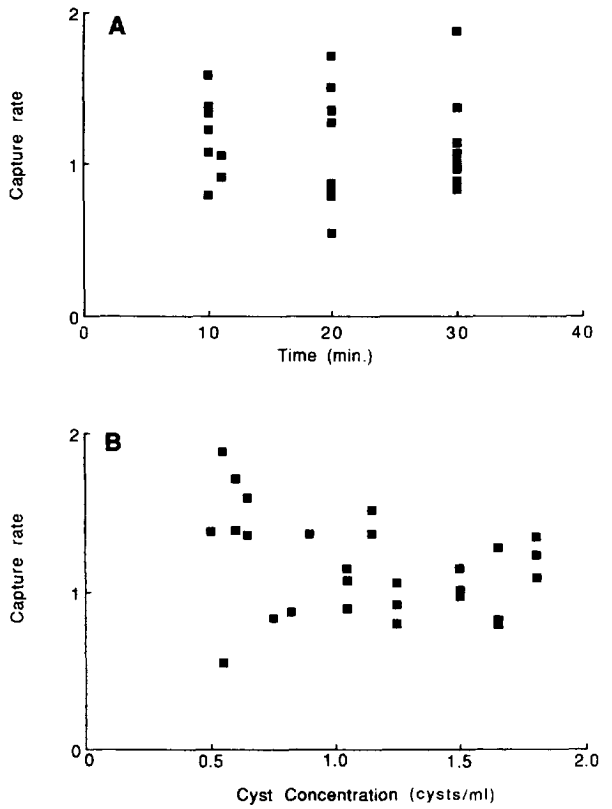

Fig. 3. Capture rates (cysts per polyp) per 10 min for corals exposed to (A) cysts for varying lengths of time (10–30 min) at one cyst concentration (2 cysts per ml) and to varying cyst concentrations (1–3 cysts per ml) for 10 min at 10 cm s^{-1} local unobstructed flow speed. Regression analysis showed no significant change in capture rate in either experiment, indicating corals were not nearing prey saturation under the conditions used in subsequent experiments.

2.1 + 0.7 cm between branch tips (high density). The latter configuration is close to the spacing observed in the field (Fig. 2), for colonies found in areas of moderate to low flow, especially below 20 m depth on the forereef. The rectangular array was formed by gluing 15 slices of square plastic cuvettes to a sheet of glass (each holder 8 mm wide, 8 mm tall) and placing coral bases in each holder. These were arranged in three rows, staggered so the middle row began slightly behind the outer two (Fig. 3). Coral branches were generally Y-shaped with the two top branches oriented across the flume (Y facing into flow, as in the field). If not enough Y-shaped pieces were available, branches with one major and one minor upper branch were used. A third partial branch was sometimes present as well.

In our experiments, the two densities were subjected to three flow speeds each (February 1990), determined a priori to be approximately 5, 10 and 25 cm s^{-1} by dye movement. These aggregations occupied much less than 10% of the flume's cross sectional area in any one cross section and side branches were positioned such that tips of each branch were more than 2 cm away from side walls to reduce potential wall effects (Nowell and Jumars, 1987). Flow speeds were measured before the first branches (local unobstructed flow), and at two levels for each visible branch in the array (local incident flow), by moving the video camera and slit light illumination sequentially to each branch for 10–20 s each. Therefore, no matter how the array and its position within the flume affected flow, flow speeds were known at each position in the array. Capture rates and flow speeds were calculated for all three corals in each of the five positions from upstream to downstream (Fig. 3).

3. Results

3.1. Particle capture by single branches

The highest capture rates by single branches occurred at flow speeds of 10–15 cm s^{-1} (unobstructed local flow, upstream of branch tip), with tops of branches capturing over 50% more cysts than middle sections, on a per polyp basis (Fig. 4 A,B). Lower capture rates were observed at flow speeds of 4–8 cm s^{-1}, indicating capture limitation due to decreased cyst delivery rate. At flow speeds above 20 cm s^{-1}, tops of branches still captured high numbers of cysts compared to lower branch segments, and overall capture was similar to the rates at 4–8 cm s^{-1}. Above 25 cm s^{-1}, to almost 50 cm s^{-1}, capture at the tops and middles of branches remained relatively high. Analysis of Variance showed significant differences between capture rates at six flow speed ranges; capture rates at 10–15 cm s^{-1} were significantly higher than those at other speeds (Table 1).

Observations indicate upstream polyps were flattened against the corallum at flow speeds above 20 cm s^{-1}, and that successful cyst captures were concentrated on the rear sides of branches at and above that speed (Fig. 4C, Table 2). Front polyps captured very few cysts at any speed above 20 cm s^{-1}. From these data, it is clear that relatively high cyst capture rates are possible over a wide range of flow speeds, and that capture from downstream eddies allows feeding at speeds that totally flattened upstream polyps. Although there was a peak capture rate just over 10 cm s^{-1}, the decrease of whole colony capture from 20 to 45 cm s^{-1} was relatively small.

Tests of capture rate as a function of run length (10–30 min) and cyst concentration (1–3 cysts per ml), showed no change in capture rate as either time or cyst concentration increased (Fig. 2). This result indicates that corals in these experiments were not reaching a saturation point, where feeding rate decreased because a large number of polyps already contained cysts. The highest numbers of cysts found in any polyps were in the range of 15–20 cysts, although most polyps in these experiments captured one or zero cysts in all runs.

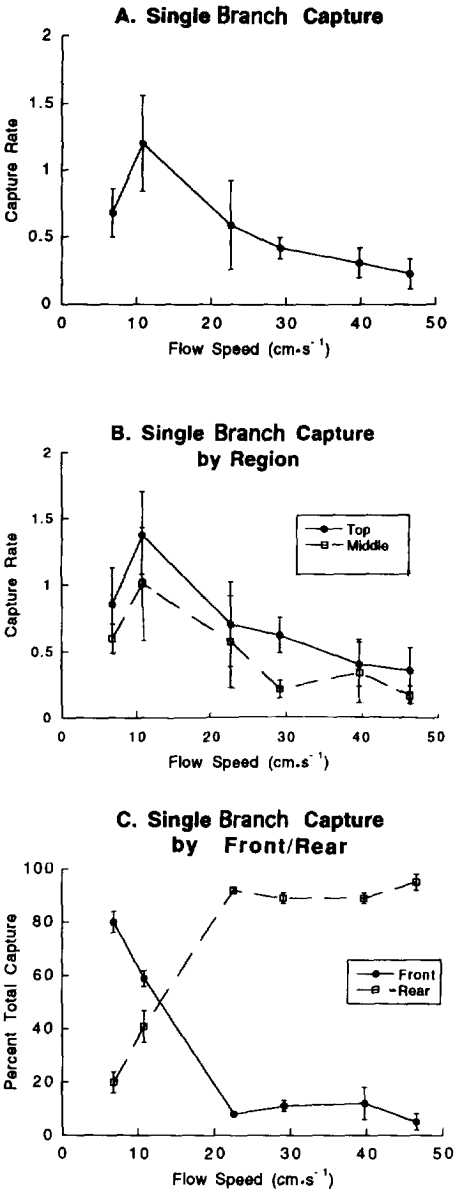

Fig. 4. (A) Single branch capture (normalized as (cyst per polyp) at 1 cyst per ml per 20 min period) by single branches feeding in unidirectional flow in a laboratory flume. Flow speeds are local unobstructed flow, upstream of branch tips. Capture was significantly higher at moderate than at low speeds then decreased again at high flow speed (see Table 1 for results of statistical analyses). (B) Particle capture by upper and middle regions of single branches. Capture rates were consistently higher in upper than in middle regions of branches. All regions exhibited a similar response to increasing flow speed. Fig. 8 shows flow speeds of middle regions of branches without upstream neighbors were about 2/3 the flow at branch tops. (C) Capture by front (upstream) and rear sides of single branches. Capture shifted significantly from front to rear sides of the branches with increasing flow speed. Error bars are ±1 SD, $N = 6$ branches per flow speed group.

Table 1
Analysis of variance for whole branch capture rates. See Figure 4 for graph comparing capture rates at all flow speeds. Group 1 is the lowest flow speed, group 6 is the highest. Capture rates differed significantly among flow speed groups, with group 2 (10–15 $cm \cdot s^{-1}$) having the highest capture rates

Source	DF	Sum of squares	Mean square	F	P ≤
Flow speed	5	1.90	0.38	3.16	0.02
Residual	35	4.20	0.12		

Multiple comparisons test: Fisher's protected LSD for whole branch capture rates

Flow speed groups compared	Difference	Critical difference	P ≤
1 vs 6	0.42	0.38	00.3
2 vs 4	0.37	0.33	0.03
2 vs 5	0.53	0.37	0.006
2 vs 6	0.63	0.37	0.001

All other groups not significant at the .05 level

3.2. Particle capture in aggregations of branches

Aggregations in the field had a spacing as low as 12.4 mm (+ 2.8 SD) in shallow habitats (7–11 m) and as high as 18.8 mm (+ 3.9 SD) in deep habitats (19–21 m). When spacing data were compared between shallow, deep and moderate (15–17 m) depths by Analysis of Variance (Fig. 3), there was a significant difference among groups ($F_{2,29} = 6.73$, $p < 0.004$); the shallow group was significantly different from the deep group ($p < 0.05$) and the moderate depth group was significantly different from the deep

Table 2
Two factor analysis of variance. Capture by front and rear sides of branches. Data presented in Fig. 4. Front and rear polyp location, and flow speed groups, are the two factors and capture rate is the dependent variable. Effects of flow speed and polyp location on capture rate are significant. Flow speed also has a highly significant effect on capture rate for both front and rear locations individually.

Source	DF	Sum of squares	Mean square	F	P ≤
Flow speed	5	4.02	0.80	5.23	0.0004
Front/rear	1	0.93	0.93	6.08	0.02
Flow speed front/rear	5	4.63	0.93	6.03	0.0001
Residual	70	10.77	0.15		
% Rear capture, flow speed	5	8.21	1.64	33.31	0.0001
Residual	34	1.68	0.05		
% Front capture, flow speed	5	5.20	1.04	44.41	0.0001
Residual	34	0.80	0.02		

Multiple comparisons tests: Numbers in parenthesis are (group A, group B, P value). Group 1 is lowest flow speed, group 6 is the highest (see Fig. 4). Rear: (1,2, .04), (1,3, .0001), (1,4, .0001), (1,5, .0001), (1,6, .0001), (2,3, .0001), (2,4, .0001), (2,5, .0001), (2,6, .0001) All others non-significant at the .05 level. Front: (1,2, .0002), (1,3, .0001), (1,4, .0001), (1,5, .0001), (1,6, .0001), (2,3, .0001), (2,4, .0001), (2,5, .0001), (2,6, .0001) All others non-significant at the .05 level

group ($p < 0.05$). Spacing therefore increased with depth at these sites, tripling between the most (26.0 mm) and least (8.0 mm) spaced colonies in the sample.

The three speed settings of the flume motor controller chosen produced a range of flow speeds, depending on the site of measurement within the aggregation. These ranges were measured as 3–5 cm s^{-1} for the slowest setting (local unobstructed flow), 5–10 cm s^{-1} for the medium, or moderate, setting and 12–24 cm s^{-1} for the high setting. For the purposes of subsequent discussion, these flow speed ranges will be referred to as 'low, 'moderate' and 'high'. The range of flow speeds resulted in different capture rates in all but two runs: High density low flow and high flow capture rates were not significantly different from one another (see Table 3 for results and analysis), although capture rate at the medium flow speed was significantly lower than the other two. In the low density aggregations, low flow speed runs clearly had the highest capture success, with high flow speed producing the lowest captures. Capture success was also analyzed for the position of each individual branch in the aggregation (Fig. 5). In the high density aggregations, the medium flow run exhibited a statistically significant trend of reduced capture toward the rear of the aggregation (regression analysis of capture vs. position of branch, $DF = 1$, $F = 7.93$, $p < 0.05$, $y = 0.97 - 0.10 \cdot X$, $R^2 = 0.38$). Other comparisons of capture rate to position within the aggregation were not statistically significant.

In these experiments, low density aggregations captured nearly twice as many cysts as high density aggregations at low flow speeds. In the high density aggregations, there was a clear reduction in capture rate from the front (upstream) to the rear of the aggregation at low and moderate flow speeds (Fig. 6), indicating either cyst depletion or slowing of flow speed such that encounter rates decreased. At higher flow speeds, high density aggregations captured 4–8 times as many cysts as did low density aggregations. There was a slight increase in capture rate with distance downstream for the high density aggregation. In low density aggregations, most captures were on branch fronts at low flow speeds and on rear sides at higher flow speeds, although the branches farthest downstream in the aggregation at both speeds had approximately equal capture on the front and rear sides. In high density aggregations (Fig. 6), there was a general decrease in captures on branch fronts at low speed, and front captures were higher than rear captures throughout. At higher speeds, rear captures were higher in the front of the aggregation, and front and rear captures were similar for the center to rear of the aggregation, with front captures slightly higher.

Table 3
Two factor analysis of variance. Capture rate within aggregations of branches (high and low flow speeds, high and low density aggregations). Data presented in Figure 5. Flow speed had a significant effect on capture rate in both high and low density aggregations. Row position did not have a significant effect.

Source	DF	Sum of squares	Mean square	F	P ≤
High density: flow speeds	1	4.49	4.49	29.66	0.0001
High density: rows	4	0.32	0.08	0.53	0.72
High density: residual	24	3.63	0.15		
Low density: flow speeds	1	3.92	3.92	22.03	0.0001
Low density: rows	4	0.14	0.03	0.19	0.94
Low density: residual	24	4.27	0.18		

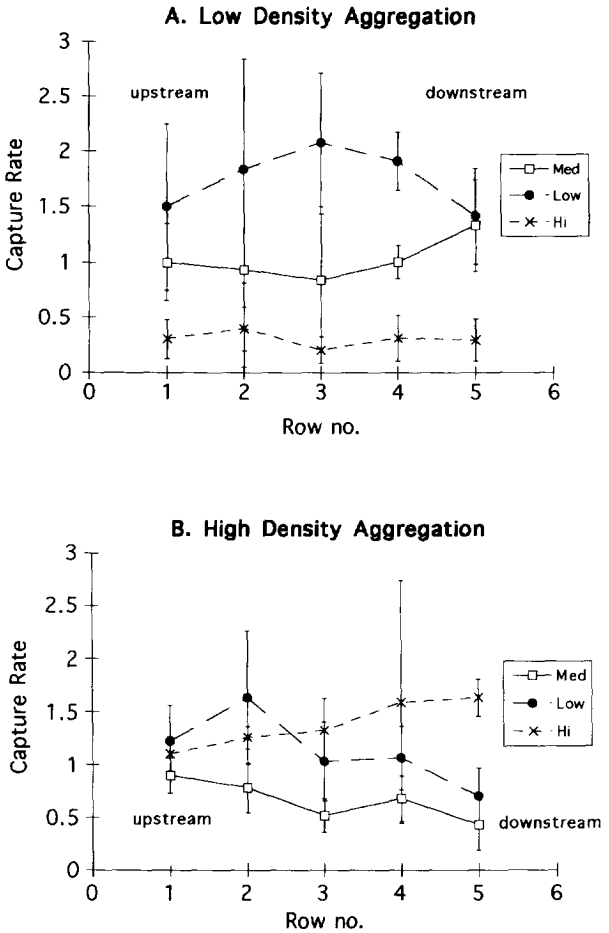

Fig. 5. Average capture rate (normalized as (cyst per polyp) at 1 cyst per ml per 20 min period) for polyps within rows (row 1 closest to the leading edge of the aggregation, as in Fig. 2). Comparison of capture by (A) low density and (B) high density aggregations at low (3–6 cm $^{-1}$), moderate (7–10 cm s^{-1}) and high (12–24 cm s^{-1}) flow speeds. Low density colonies, normally found on deeper parts of the reef, which experience slower flows, were twice as successful as high density aggregations at the lowest flow speeds, while high density aggregations caught four to eight times as many particles at the highest flow speed. Flow speeds are local unobstructed flow, upstream of the first branch tips. Error bars are ± 1 SD, $N = 3$ branches per row in each experiment.

3.3. Flow within aggregations

The position of a branch within an aggregation had a much lower impact on the local incident flow that any given polyp experienced than did the polyp's location on the branch. Fig. 7 shows a significant reduction in flow speed (local incident flow) towards the rear of the high density aggregations at high flow speed. Fig. 8 shows flow rates significantly reduced towards the mid-height position on the branches (statistics, Tables

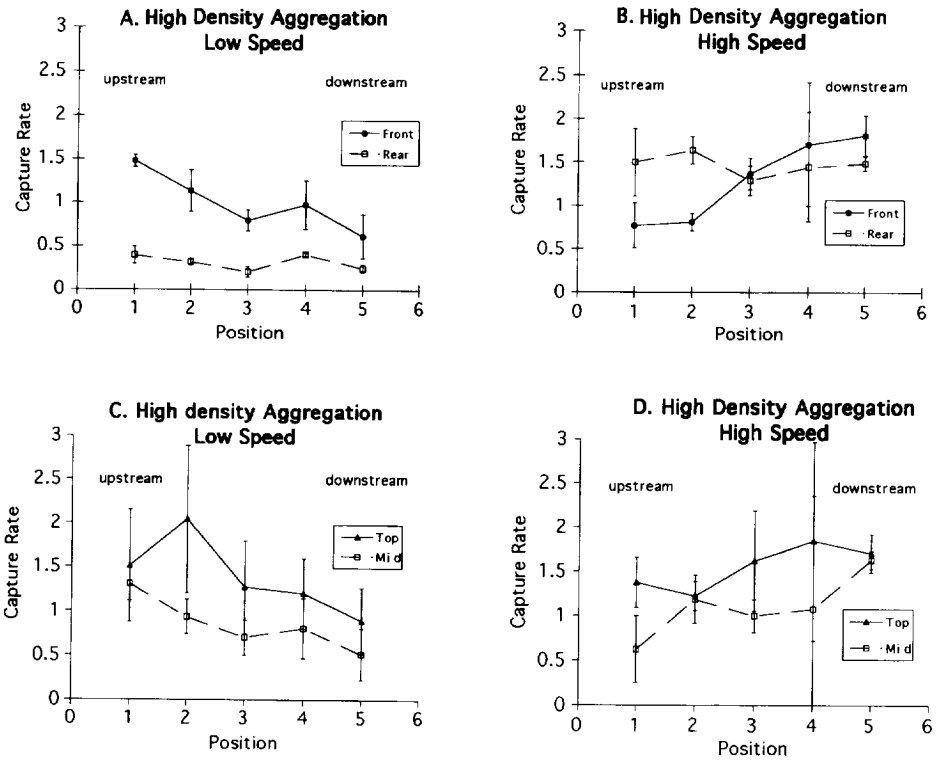

Fig. 6. Comparison of average capture rates (normalized as (cyst per polyp) at 1 cyst per ml per 20 min period) of polyps in high density aggregations. Capture by front and rear sides of branches in high density (A,B) and by top and middle sections of branches in high density (C,D) aggregations at mainstream flow speeds of (A,C) 7–10 cm s^{-1} and (B) 12–24 cm s^{-1}. Capture rates were consistently higher on the front sides of colonies at low speeds, but shifted to a more even distribution on branches feeding in the downstream regions of the aggregation in higher flows. Captures were always higher near branch tips than lower down. Flow speeds are local unobstructed flow, upstream of the branch tips. Error bars are ±1 SD, $N = 3$ branches per row in each experiment.

3 and 4). The effect of the aggregation on flow speed was examined in more detail by looking at how different positions within an aggregation (above, top and middle of branches) fared as the location of a branch moved downstream in the aggregation. A significant reduction in flow speed at the three branch height locations (above, top, middle) towards the downstream edge of the aggregation was evident for the high flow speed runs. Local incident flow at mid-level branch locations was approximately 30 to 50% lower than at branch tips for corals in the first (upstream) row. This is almost exactly the magnitude of the difference in capture rates between top and middle locations for single branches. This flow difference, and the resulting difference in particle delivery rate, can thus explain the pattern observed for single branches as well.

Besides reducing local incident flow speed, the aggregation might also increase the turbulent character of flow polyps experience, conceivably influencing capture ef-

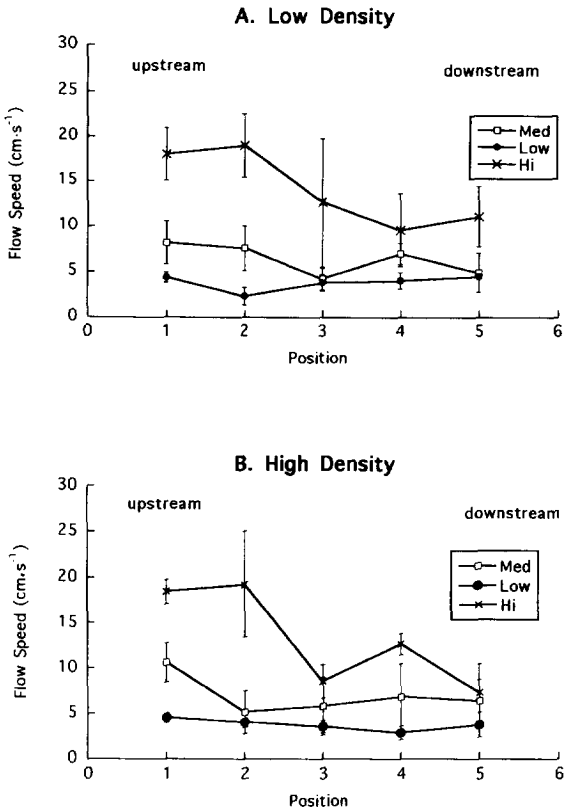

Fig. 7. Comparison of measured flow speeds (local incident flow), at tops of branches, between low (A) and high (B) density aggregations. $N = 30$ particle tracks measured for each point. Labels Low, Med, and Hi refer to the three flow speeds (Low 3–6 cm s^{-1}, Med 7–10 cm s^{-1}, Hi 12–20 cm s^{-1}). Error bars are ±1 SD.

ficiency. The turbulent character of flow can be expressed as turbulence intensity (TI), defined as the standard deviation of flow speed measurements in the XZ plane (Denny, 1988). In this study, turbulence intensity indices were divided by the average flow speed at each location, yielding a relative index of the turbulent character of the flow. This analysis showed a general trend of elevated TI in the aggregation compared to the leading edge for most runs. However, no significant relationship between turbulence intensity and capture rate could be determined statistically.

Capture efficiency (capture rate adjusted for particle flux) was calculated by dividing the (time- and particle-concentration) adjusted capture rates by local incident flow speed. In each graph of capture efficiency against corresponding flow speeds (Fig. 9 A,B), the data points were divided into two equal groups with median flow as the cut-off point; the resulting groups were then compared by ANOVA. In both high and low density aggregations, the high flow speed group had a significantly smaller (low density $p < 0.0001$, Scheffe $F = 22.52$, $DF = 1$, high density $p < 0.0001$, Scheffe $F = 22.89$, $DF = 1$) average capture efficiency (0.14 vs. 0.48 at low density and 0.15 vs. 0.35 at

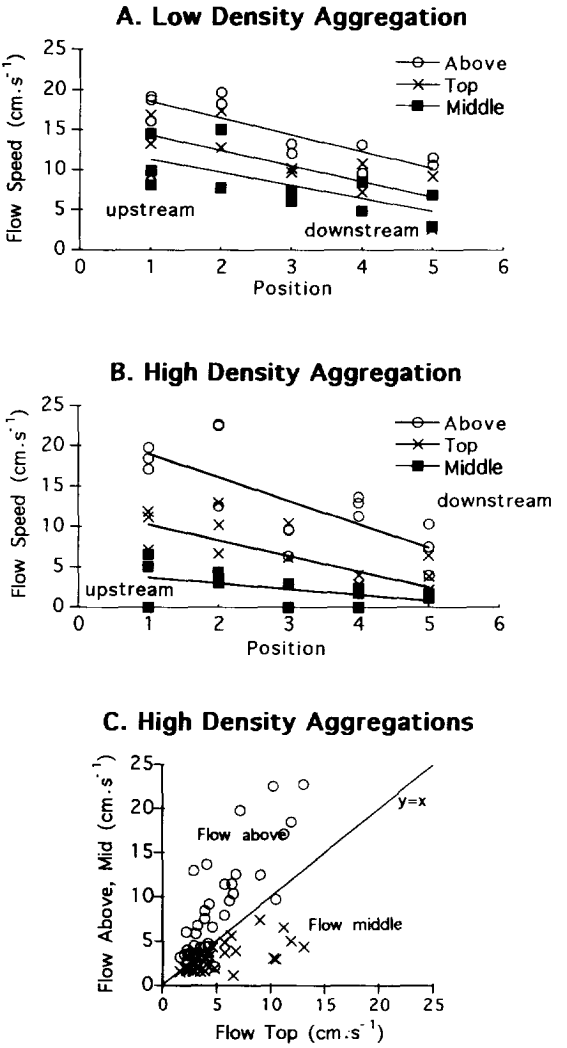

Fig. 8. Flow speeds (cm s^{-1}, local incident flow) at two heights on the colony (top, middle) and immediately above the branches. Figures A, B show the reduction in flow speed down the branches as well as downstream in the aggregation. All regression lines are significant (Table 4). (C) Flow speed measured at the middle and above locations plotted against flow at branch tips (Table 4). Both locations within the aggregation show reduced flow speeds, with the middle location exhibiting the greatest reduction in speed.

high density aggregations). Capture rates (Fig. 9 C, D) decreased with flow speed within the low density aggregations, but had no significant relationship to density in the high density aggregations. Clearly, while the efficiency of capture dropped above 5 cm s^{-1}, increased delivery rates compensated to enable high capture rates at flow speeds over 10 cm s^{-1} in the high density aggregation.

Table 4
A,B) Regression statistics of flow speeds within low and high density aggregations at the highest flow speeds used (app. 20 $cm \cdot s^{-1}$ upstream of aggregations. Decreases in flow speed are significant for all locations, in both aggregations. Changes in flow speed for medium and low flow speeds are mostly not significant within the aggregations. C) ANOVA for flow speeds compared among locations on branches. Flows are significantly different among all three regions.

A. Regression: Low density aggregation, high flow speed

	N	R^2	F	P ≤
Above	11	0.74	25.25	0.0007
Top	11	0.51	9.20	0.0001
Middle	11	0.46	7.52	0.0001

B. Regression: High density aggregations, high flow speed

	N	R^2	F	P ≤
Above	15	0.54	15.26	0.0002
Top	11	0.57	14.55	0.003
Middle	9	0.86	55.23	0.0001

C. ANOVA table

	N	Source	DF	F	P ≤
Above	41	Above vs. middle	1	33.38	0.0001
Top	39	Above vs. top	1	12.17	0.0008
Middle	37	Middle vs. top	1	12.23	0.0008

The possibility of particle depletion influencing capture by downstream branches in aggregations was investigated by calculating the percent of cysts moving through a typical aggregation that were actually captured by the polyps. In all runs, the captures stayed below 4% of the available flux (Table 5), suggesting that particle depletion was not the primary mechanism reducing capture by downstream branches in high density aggregations at medium to low flow speeds (Fig. 5B).

4. Discussion

Passive suspension feeders rely on water flow to carry prey and food particles to their surfaces. Those surfaces can be elaborated in a number of ways that might influence the probability of capturing particles. The types of structures needed to capture large swimming zooplankton, and those best for the capture of smaller particles, are likely to be very different. Sebens and Koehl (1984) compared the tentacles of the anemone *Metridium senile* and the octocoral *Alcyonium siderium*, and quantified coelenteron contents of both species by field sampling. The anemone captured most sizes of zooplankton available, using large simple tentacles, whereas the octocoral captured only smaller zooplankton, primarily larvae, and detrital particles using small thin tentacles with side branches (pinnules). Both species are common in the same wave-swept rocky shore habitats, and both manage to feed in rapid flow. Other passive suspension feeders

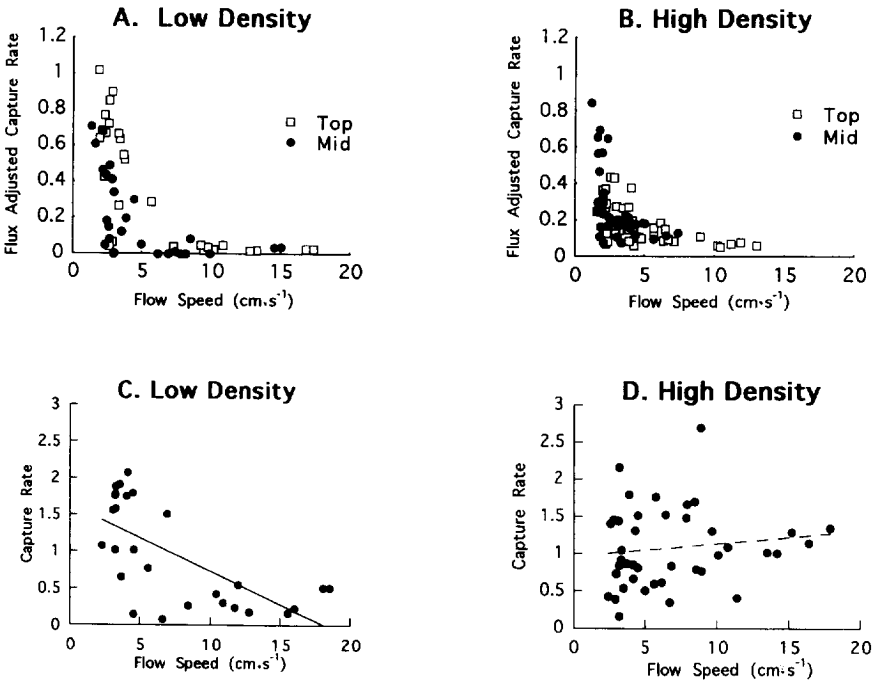

Fig. 9. Comparison of capture efficiencies (capture rate adjusted for the rate of particle delivery (flux) across a flow speed (local incident flow) gradient at top and middle levels for all (A) low density and (B) high density aggregations. For the purposes of this analysis, the data were divided into two groups, with the median flow speed as a divider (3.3 cm s^{-1} and 3.8 cm s^{-1} for figures A and B, respectively). In both low and high density aggregations, the capture efficiency decreased at higher flow speeds (Anova, $DF = 47$, $F = 22.52$, $p < 0.0001$ for low density and $DF = 67$, $F = 22.89$, $p < 0.0001$ for high density aggregations). There were no significant differences between top and middle level capture efficiencies ($DF = 47$, $F = 2.03$, $p < 0.16$ for low density and $DF = 67$, $F = 1.89$, $p < 0.17$ for high density aggregations). Figures C,D: regressions of all calculated capture rates for low (C) and high (D) density aggregations with corresponding local incident flow speeds. The regression is significant for low density runs ($DF = 1$, $F = 20.374$, $p < 0.0001$), but not for high density runs ($DF = 1$, $F = 2.108$, $p < 1.555$). High local incident flow within high density aggregations was turbulent, probably resulting in greater capture rates at those flows.

(e.g. crinoids, Leonard et al., 1988) produce large delicate capture structures that function best at relatively low flow speeds. The type of feeding structure, and the filter elements of that structure, are probably influenced by the most common ambient flow speeds, the types and sizes of particles available, and morphological constraints based on the evolutionary history of any particular group of suspension feeders.

Mechanisms of particle capture, several mechanisms of capture by filter elements of passive suspension feeders determine how those elements function in different flow conditions (Rubenstein and Koehl, 1977). In sieving, items larger than the space between two adjacent filter elements (e.g. tentacles) are retained as water flows between the structures. Octocorals, with their feathery tentacles, have finer meshes for sieving food out of the water than do anthozoans with more widely-spaced simple tentacles.

Table 5
Depletion of cysts form the water column by coral polyps. Percent depletion is calculated as the ratio of cysts captured by the entire aggregation to the number of cysts passing through the cross-sectional area of the aggregation. In the highest depletion case, less than four percent of the cysts were removed from suspension. These percentages are an overestimation, since this depletion is reached only after all branches have had a chance at capture. In reality, the branches are in five rows, any given row only seeing the depletion effect from the preceding branches.

	Flow speed	Cyst conc. (cysts · ml^{-1})	Cyst flux (cysts · $cm^{-2} \cdot s^{-1}$)	No. captures (captures · s^{-1})	% of available cysts depleted
Low density aggregations	low	1.39	188	2.39	1.27
	mid	2.47	287	10.27	3.58
	high	1.8	349	2.10	0.06
High density aggregations	low	0.96	332	2.59	0.78
	mid	1.9	312	7.84	2.51
	high	2.38	314	7.58	2.41

More than half the zooplankton captured by *A. siderium*, for example, were larger than the inter-pinnule spacing and thus could have been captured by sieving (Sebens and Koehl, 1984), although phytoplankton captured by the tropical octocoral *Dendronephthya hemprichi* (Fabricius et al., 1995) are much smaller than this spacing. Most prey of the anemone *M. senile* on the other hand, and the coral *Montastrea cavernosa* (Sebens et al., 1996), were smaller than the intertentacular gaps and were probably captured by direct interception.

The relative importance of various physical mechanisms causing prey to contact a suspension-feeder's tentacles can be determined from data on flow speeds, particle sizes and densities, and size and spacing of filter elements (Rubenstein and Koehl, 1977; LaBarbera, 1978, 1984; Okamura, 1990). For most types of particles, at the typical flow velocities that anthozoans encounter, direct interception is the most likely mode of particle capture. Particles carried by ambient flow contact tentacle surfaces because the particle diameter spans the distance from streamline to the tentacle surface. Inertial impaction occurs when 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 around it; this appears to be involved in the capture of heavy particles at the large end of the spectrum of prey for both octocorals and anemones at peak velocities approaching 50 cm s^{-1} (Sebens and Koehl, 1984). Okamura (1984), (1985), (1988) described similar patterns and mechanisms of particle capture for bryozoans. Gravitational deposition may also be important for capture of particles denser than water (some detritus) at low flow speeds, such as in lagoonal and deep reef habitats (e.g., zoanthids, Koehl, 1977; corals, Sebens and Johnson, 1991; reviewed in Shimeta and Jumars, 1991; Abelson et al., 1993).

Coelenteron sampling of more than sixty *Madracis mirabilis* branches, with several hundred polyps per branch, demonstrated that this species commonly captures zooplankton of a wide size range (<200 to >3000 μm, Sebens et al., 1996). Of the zooplankton captured, the most abundant copepods (*Oithona* sp., *Calanopia* sp.) were captured rarely whereas larvae, polychaetes, chaetognaths and other crustaceans were highly selected. Near-substratum zooplankton on coral reefs are in part demersal

(originating on or remaining near the substratum) swimming upward at dusk followed by downward migration at dawn (Emery, 1968; Glynn, 1973; Porter and Porter, 1977; Porter et al., 1977, 1978; Alldredge and King, 1977, 1980; Hobson and Chess, 1979; Rützler et al., 1980; Robichaux et al., 1981; Ohlhorst, 1982). Coral reef zooplankton feeders capture many of their prey during these two periods and at the night (corals, Porter, 1974; zoanthids, Sebens, 1977; fish, Hobson and Chess, 1979). Corals thus have two potential prey resources: zooplankton from the open-water planktonic community, and substratum-related prey. The latter group includes larvae of benthic invertebrates, adult benthic crustaceans that spend some time swimming, copepods that swarm near the bottom and benthic non-motile material resuspended off the bottom by flow. In addition to the particle capture mechanisms noted above, swimming behavior of zooplankton also increases their encounter rates with tentacles,(Sebens et al., 1996).

4.1. Flow speed and prey capture, and effects of aggregation.

Water flow clearly affected particle capture rates for *Madracis mirabilis*. At flow speeds less than 10 cm s^{-1}, capture rates by single branches were low and were probably limited by the encounter rates of particles with the corals' tentacles. Polyps on the fronts of branches captured many more particles than did those on rear surfaces at low flow speeds; this may have resulted in decreased availability of particles to the downstream sides of branches, further limiting capture rate. At intermediate flow speeds, more particles were encountered by polyps on both the front and rear surfaces of branches, such that capture rates on all surfaces were nearly equal. Downstream polyps received particles missed by polyps on upstream sides, and may also have captured particles advected into downstream eddies from the water bordering those eddies. At speeds of 20 cm s^{-1} and above, upstream polyps were clearly not capturing particles as efficiently as those on downstream surfaces. Observations indicate that upstream polyps were deformed (flattened) downstream whereas downstream polyps were fully expanded with tentacles extended (as in *Alcyonium siderium*, Patterson, 1984). At the highest speeds (over 40 cm s^{-1}), upstream polyps were fully flattened against the corallum surface yet downstream polyps still managed to remain extended and capture some particles, even while being agitated rapidly by eddy shedding. Efficiency of capture by whole branches, as opposed to capture rate, declined precipitously at speeds over 20 cm s^{-1}.

Flow can have important consequences for *Madracis mirabilis*. This coral lives in reef zones (10–15 m depth, forereef) that experience moderate oscillatory flow, as well as in deeper and shallower habitats with low unidirectional flow (>20 m forereef, some backreef habitats <5m). Flow measurements at Discovery Bay (Helmuth and Sebens, 1993) indicate that mean flows of 10–20 cm s^{-1} (0.5 m off the substratum) are common in the shallower part of this range, and that flows in deeper forereef zones, and in backreef habitats, are typically well below 10 cm s^{-1}, often below 5 cm s^{-1}. In oscillatory flow with mean speeds over 20 cm s^{-1}, maxima during oscillations can be more than twice that value. With high waves (1.5 to 2 m, Helmuth and Sebens, 1993) passing over the reef, corals commonly experience flows well above the optimum for particle capture by a single branch. However, within aggregations, flow is decreased and may be near the optimum even under high ambient flow conditions. In deeper reef

zones, aggregations have more space between branches, and most branches probably experience flows well below the optimum for particle capture, except during extreme surface conditions or periods when longshore currents are particularly strong. By modifying branching structures, spacing, and possibly polyp extension, this species can be an efficient passive suspension feeder over a wide range of ambient flow conditions. Given the flow regimes at Discovery Bay (Helmuth and Sebens, 1993), it seems likely that deep forereef habitats, and some backreef habitats, are frequently flow-limiting (as far as particle capture is concerned), whereas shallow forereef habitats are likely to be at or above the optimum (near 10 cm s^{-1}) much of the time.

Aggregation decreases particle capture for other suspension feeders, such as erect bryozoans (Buss, 1981; Okamura, 1984), although adjacent encrusting bryozoans can enhance capture by downstream neighbors in high flows by inducing local turbulence (Okamura, 1985). In conditions of low flow, aggregations in which branches or colonies further reduce the flow reaching the center of the aggregation may be disadvantageous. Slower flow in aggregations, with potential depletion of particles, results in fewer particle encounters by downstream branches or neighbors (e.g. mussel beds, Frechette et al., 1989; Okamura, 1986). This may be a problem for branches, or other units of the same genotype, where food competition is with 'self'. In a colony, there may be enough integration between the subunits such that this condition can be ameliorated by altered spacing. At high flow speeds, tight spacing can reduce flow speed and increase eddy diffusivity within an aggregation such that capture structures within an aggregation have as good or better chances to capture particles than those upstream (e.g. octocorals, McFadden, 1986). Branch spacing is variable in many corals (Lesser et al., 1994) and may be controlled by a specific chemical mediator (coral isomone, Rinkevich and Loya, 1985).

Whereas single branches have a distinct peak of capture (at flows near 10 cm s^{-1}), aggregations of branches can capture particles effectively over a broad range of flows by modifying their internal spacing. Aggregations of *Madracis mirabilis* branches (usually termed colonies, although potentially of mixed genotype), vary in branch height and branch spacing. In shallow forereef habitats in Jamaica, such colonies are typically less than a meter in diameter, and have branches up to 20 cm tall with spacing of one to two centimeters between branch tips. Extended polyps often fill the space between branches such that tentacle tips are almost touching. This densely-packed condition almost certainly slows flow reaching the center of an aggregation compared to flow experienced by edge branches. Because such flow is often oscillatory, two edges of the colony take turns being upstream or downstream, but the majority of branches in the center are always in the lee of neighboring branches. Such dense spacing is advantageous if flow is generally well above the optimum, because much of the colony experiences reduced flow near the optimum flow speed. However, during periods of calm surface conditions and lower flow speeds, dense packing of branches must limit particle capture by center individuals and may also pose problems for gas and nutrient exchange (Shick, 1990; Patterson et al., 1991; Lesser et al., 1994). Given the patterns observed, it appears that high flow is the common condition in forereef zones where *Madracis* exhibits a tight branching pattern, thus improving the capture success of center branches.

In deep forereef habitats, colonies are generally smaller, and branch tips are more

widely spaced (2 to 3 cm). Here, potential interference between branches presents a problem for particle capture, and additional spacing may help relieve that limitation. Slow unidirectional flow is the most common condition below 15 m (Helmuth and Sebens, 1993; Sebens, unpubl. data), and both photosynthetic capability and nutrient uptake could also be enhanced by wider spacing. Some of the largest colonies of *Madracis mirabilis* observed in Jamaica are in moderately deep backreef habitats within Discovery Bay (8–12 m depth). These aggregations can be several meters across and branch lengths may be over a meter at the center, although only the top 5 to 10 cm bear living tissue. Branch spacing here is similar to that in the deep forereef aggregations and ambient flow speeds are either low and unidirectional or low and oscillatory (Helmuth and Sebens, 1993). These appear to be very old aggregations that survived two major hurricanes (Woodley et al., 1981), and which surround freshwater seeps high in inorganic nutrients (D'Elia et al., 1981). Zooplankton and particulate capture here may be of lesser importance than on the forereef if this coral can take advantage of an alternative inorganic source of nitrogen and/or phosphorus (Cook et al., 1992). Alternatively, locally increased nutrients may result in high availability of plankton and particulates which then become available to corals growing in such habitats.

4.2. Flow on reefs and effects on coral biology.

The flow regime experienced by corals over a range of coral reef habitats is determined by several large and small-scale processes. The physical oceanography of coral reefs has been reviewed recently based on over 30 years of field studies (Hamner and Wolanski, 1988; Andrews and Pickard, 1990). Water flow over and along reefs can be broken down into components based on frequency (e.g., high frequency wave effects, intermediate frequency tidal effects, low frequency drift), and by the effects of reef topography. As a broad generality, reef crest and reef flat habitats experience strong wave-induced oscillatory flow (bidirectional), which can move water over the reef crest and into backreef or lagoonal areas (Kjerfve, 1986; Pickard, 1986; Roberts and Suhayda, 1983). When waves are minimal, reversing tidal flow often dominates these shallow habitats, but flow over the reef flat becomes unidirectional when strong wave overtopping occurs (Frith, 1983; Andrews et al., 1984). Lagoonal and backreef areas have modified and reduced wave effects (Rees, 1972; Roberts and Suhayda, 1983), and highly variable currents (both speed and direction) (e.g. Sebens and Done, 1992). Flows are further affected by tidal currents, low frequency drift through reef openings, and by the arrival of topographically-controlled eddies (Wolanski and King, 1990).

Recent studies have used electromagnetic current meters close to the substratum (0.5 m), with instantaneous (each 0.5 s) recording. These studies showed that, on the forereef slope, waves can dominate to at least 15 m depth, especially on reefs without strong tidal or prevailing currents (St. Croix, Sebens and Johnson, 1991; Australia, Sebens and Done, 1992; Jamaica, Helmuth and Sebens, 1993). Where currents are substantial (Cayman Islands, Roberts et al., 1975 Great Barrier Reef, Wolanski and Pickard, 1983; Sebens and Done, 1992), they can provide the major source of water movement (typically 10–30 cm s^{-1}) past corals at all depths at and below the reef crest. Corals living in deep (>20 m) reef slope habitats usually experience extremely slow

unidirectional flows (as in lagoonal habitats) where currents are minimal (≤ 5 cm s^{-1}), but can be impacted by very rapid unidirectional flow where prevailing currents are strong. In the Cayman Islands (Roberts et al., 1975), the strongest flows occurred shallow (wave-generated) and deep (prevailing current generated) with substantially lower flow at intermediate reef depths. The flow speeds used in our experiments thus span the usual range of (non-storm) flow on reefs.

Oscillatory flow induced by waves also prevents the buildup of a steady-state boundary layer (Grant and Madsen, 1979) as develops over smooth surfaces in unidirectional flow (reviewed by Denny, 1988). Turbulent mixing is important near organisms and between coral heads, and eddy shedding enhances turbulence in such regions. Dense, regular arrays of projections from the substratum (roughness elements) can increase boundary layer thickness and thus can slow flow between them, but when irregular, can have the opposite effect, increasing mean velocity and turbulence levels above and between them (Eckman et al., 1981; Eckman, 1983; Nowell and Jumars, 1984). An irregular substratum, for example, produces a sigmoidal velocity profile, rather than the log profile that forms above smooth surfaces (laminar flow), because eddies form at the edge of the overlying free shear (mainstream) flow and migrate down into the roughness element array (Denny, 1988). Coral reef surfaces are rough and irregular, and thus modify flow in a variety of ways providing a wide range of microhabitat flow regimes. Stable boundary layer theory has been used to model particle distributions over coral reefs (Abelson et al., 1993), but may not be representative of most reef conditions and habitats.

In habitats with strong wave-induced oscillatory flow, the lack of a steady-state boundary layer may be a benefit to passive suspension feeders. These organisms rely on particles moving from the water above down to their prey capture surfaces via 'eddy diffusivity', as a result of turbulent shear above the rock and organism surfaces (Denny, 1988). Development of a thick boundary layer (i.e. thick laminar or viscous sublayer) over organism surfaces inhibits particle or nutrient movement across that layer. Strong near-substratum flow, on the other hand, comes with an increased probability of organism dislodgment (Denny et al., 1985) as well as potentially increased prey encounter rates (Sebens, 1984; this study; McFadden, 1986). Accelerational forces dominate during a wave surge and these provide the largest force differential experienced by sessile organisms; this is the force that can remove them from the substratum (Denny et al., 1985). A coral that can alter its morphology, including branch spacing, can modify and potentially improve local flow patterns.

Water flow also has a direct effect on the physiology and energetics of corals and other anthozoans. Metabolic costs increase with water flow for two reasons. First, oxygen depletion occurs in the boundary layer over tissues at very low flows (Shashar et al., 1996). Respiration is generally passively related to ambient oxygen concentration (Sebens, 1987 review), therefore, the lowered oxygen concentration near the tissue surface (and in the coelenteron) can depress respiration. Second, there may be some cost associated with maintaining a given posture in moving water, for example, holding the tentacles erect by hydrostatic pressure. These potential effects were investigated for the reef coral *Montastrea annularis* (Patterson et al., 1991), and for the temperate zone anthozoans *Metridium senile* and *Alcyonium siderium* (Patterson and Sebens, 1989). All

species showed significant increases of respiration with flow. Productivity of *M. annularis*, however, increased with flow even more (Patterson et al., 1991) such that energy surplus was greater with higher flow. Dennison and Barnes (1988) and Shick (1990) also demonstrated positive flow effects on coral productivity, including calcification rates. The trade-off between positive flow effects on feeding and photosynthesis, versus additional metabolic costs, will determine the flow rates that optimize energy balance (intake minus cost, Sebens, 1982, 1984, 1987 review). Strong evidence of flow effects on nutrient (phosphate) uptake by corals has also been provided by field and laboratory studies (Atkinson and Bilger, 1992). The true 'optimal' flow environment for a particular coral thus depends on an array of positive and negative flow effects, and on the interaction between flow and variable colony morphology.

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