The influence of colony morphology and orientation to flow on particle capture by the scleractinian coral *Agaricia agaricites* (Linnaeus)

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(Received 14 January 1992; revision received 29 July 1992; accepted 28 August 1992)

**Abstract:** The scleractinian coral *Agaricia agaricites* (Linnaeus) is a common component of reef systems throughout the Caribbean. The morphology of *A. agaricites* is extremely variable, including flat unifacial plates, upright bifacial plates, and encrusting forms. Transects conducted on the fore reef of Discovery Bay, Jamaica, indicated that the morphology of colonies growing on horizontal substrata was strongly related to depth. Colonies in shallower water (7–12 m) tended to encrust or form unifacial plates, while deeper colonies (20 m) were primarily upright and bifacial. Furthermore, 90% of all bifacial colonies were oriented directly perpendicular to (feeding surface facing) the dominant direction of flow. Bifacial colonies also tended to have larger corallites, and possessed ridges which angled upward away from the substratum.

Measurements of flow conducted at this site indicated that ambient flow speeds generally decrease with increasing depth. A series of feeding trials was conducted in a laboratory flume over a range of flow speeds characteristic of those found on the reef (3–50 cm·s⁻¹) to address the hypothesis that variations in colony morphology and orientation to flow represent mechanisms for maximizing particle capture. Upright bifacial colonies oriented perpendicular to flow fed at significantly higher rates than bifacial colonies oriented parallel to flow. Bifacial colonies were never, however, able to capture more particles per unit surface area than were unifacial plates, at any flow speed. In all colony morphologies tested, capture shifted from upstream to downstream areas with increasing flow speed, suggesting that feeding did not involve the inertial impaction of particles. Particle capture was highest at intermediate flow speeds, although horizontal-plating colonies were able to feed well over the entire range of flow speeds tested. Behavioral observations suggest that particle capture was aided by currents originating within the polyps, and apparently did not involve mucus entrapment, as previously suggested.

Measurements of flow at points near the surface of colonies in the field indicated that flow conditions at 20 m roughly match flow conditions in the experimental flume, suggesting that the results of the feeding trials may be extrapolated to feeding in situ. The results thus suggest that colony morphology does not represent a mechanism for maximizing particle capture per unit tissue, but instead may have evolved as the result of other selective pressures such as spatial competition or gas exchange. Thus, by growing away from the substratum, colonies could potentially increase particle capture, and colony biomass, per unit of available substrate. The orientation of colonies into flow, however, does increase food capture, and may have arisen secondarily as a compromise between selective pressures.

**Key words:** *Agaricia agaricites*; Colony morphology; Scleractinian coral; Suspension-feeding
INTRODUCTION

Sessile passive suspension-feeders depend on moving water for the delivery of food, nutrients and gases, the removal of waste and sediments, and the transport of larvae and gametes (Koehl, 1977; Sebens, 1984; Denny, 1988; Patterson, 1988; Yoshioka & Yoshioka, 1989; Hill, 1991; Patterson et al., 1992; Atkinson & Bilger, 1992; Bilger & Atkinson, 1992). Concurrently, these organisms must contend with limits imposed by ambient flow, including the risk of being broken or dislodged (Koehl, 1984; Denny et al., 1985) and the mechanical deformation of feeding structures (Leversee, 1976; Lasker, 1981; Patterson, 1984; McFadden, 1986; Johnson, 1988). As a result, sessile organisms which frequently experience high flow tend to exhibit morphologies which minimize drag, while organisms for in slower-moving water display features which increase the amount of surface area exposed to flow, potentially increasing the exchange of materials with the water column (Chamberlain & Graus, 1975; Wainwright & Koehl, 1976; Koel, 1977).

Operating within the constraints imposed by flow, however, are a number of additional selective pressures which may also strongly influence colony morphology, such as light capture by symbionts (Barnes, 1973; Porter, 1976) and spatial competitive pressures (Jackson, 1979). These often conflicting selective pressures have resulted in an enormous diversity of morphologies and life-history traits which are often, to some extent, a function of the ambient flow regime (e.g., Foster, 1979; Sebens, 1984; McFadden, 1986; Sebens & Johnson, 1991).

In recent years a number of studies have examined the effects of colony size, morphology and ambient flow on the feeding capabilities of colonial sessile suspension feeders (e.g., bryozoans: Okamura, 1984, 1985, 1988, 1990; corals: Sebens & Johnson, 1991; deep-sea epifauna: Mullineaux, 1989; hydroids: Harvell & LaBarbera, 1989; Hunter, 1989; octocorals: Lasker, 1981; Lasker et al., 1983; Patterson, 1984, 1991a; Sebens, 1984; McFadden, 1986; zoanthids: Koehl, 1977), and a few studies have established correlations between feeding success and distributional patterns observed in the field (Mullineaux, 1989; Sebens & Johnson, 1991). Recent work by Sebens and Johnson (1991) has suggested that the morphology of the scleractinian coral *Madracis decactis* may be significantly influenced by the ability to feed. Hermatypic reef-building scleractinian corals capture zooplankton and other particulates from the water column on a regular basis, and several studies have described the various mechanisms by which corals feed (Yonge, 1930; Muscantine, 1973; Porter, 1974, 1976; Lewis & Price, 1976; Lewis, 1976, 1977; Sebens, 1987). To date, however, the work of Sebens and Johnson (1991) represents the only published investigation of the interaction of color morphology and flow on the feeding success of scleractinian corals, despite their obvious importance to reef ecosystems. The purpose of the present study, therefore, was to quantify the effects of ambient flow speed and intraspecific variability in color morphology on particle capture by the scleractinian coral *Agaricia agaricites* (Linnaeus,
and to attempt to relate feeding ability to the observed distribution of the various morphologies in the field.

*A. agaricites* is a ubiquitous member of most reef systems throughout the Caribbean and is found over a wide depth distribution (e.g., Jamaica: 3–75 m; Goreau & Wells, 1967). As a result, it must contend with the wide range of flow conditions encountered in a reef ecosystem (Done, 1982; Graus & Macintyre, 1989; McGuiness, 1990). *A. agaricites* possesses relatively shallow calices and has very short tentacles, and displays a variety of growth forms including flat unifacial plates, upright bifacial plates and irregular encrusting colonies (Fig. 1). In some cases, morphologies are sufficiently distinct to warrant splitting *A. agaricites* into several species or subspecies (Wells, 1973), although intermediate forms are often encountered. Preliminary transects on the fore reef at Discovery Bay, Jamaica, suggested that colony morphology may be correlated with depth, with upright bifacial forms oriented into flow becoming dominant in deeper water (20 m). Often, these colonies form aggregations in which one colony is oriented directly behind another. This trend in colony morphology is in marked contrast with many other corals (e.g., *Montastrea annularis*), which become more flat and plate-like with depth, probably as a means of increasing light capture (Barnes, 1973). The contrasting trend exhibited by *A. agaricites*, coupled with the apparently consistent orientation to flow therefore suggested that colony morphology probably does not represent a morphology designed to maximize light capture, but instead may be some form of adaptive response to the ambient flow regime at different depths.

The goals of this study thus were the following:

1. To discern whether colony morphology and orientation significantly vary as a function of depth, and hence as a function of ambient flow.

2. To determine if the magnitude and location (sensu Patterson, 1984; McFadden, 1986) of particle capture by *A. agaricites* varies as a function of ambient flow speed.

3. To quantify the effects of colony morphology and orientation to flow on particle capture under differing flow conditions.

![Flow](image)

**Fig. 1.** Categories of morphologies displayed by *A. agaricites* colonies. Unifacial plating colonies are found on both horizontal or vertical substrata. Bifacial colonies typically are oriented with their feeding surfaces facing directly into flow. Colonies may also be amorphous and encrusting (not shown).
Specifically, by comparing particle capture under controlled conditions to patterns observed in the field, this study addresses the hypothesis that intraspecific variation in colony morphology and orientation under differing flow conditions in the field represents a mechanism for maximizing the rate of particle capture. All experiments were conducted at the University of the West Indies' Discovery Bay Marine Laboratory (DBML), in Discovery Bay, Jamaica, between October 1989 and June 1991.

**Materials and Methods**

**Transects**

To determine the distribution of each morphology over a depth gradient, a series of transects was conducted on the west fore reef (LTS mooring) of Discovery Bay at 7, 12, and 20 m between February and June 1991. Transect lines were placed haphazardly at several locations at each depth, and all colonies within 1 m of either side of the transect line were included. Colony size (diameter), morphology (amorphous/encrusting, horizontal-plating, vertical-plating or bifacial), and orientation to flow (determined with sodium fluorescein dye) were recorded for a total of 264 colonies growing on horizontal substrata (sea floor and tops of coral heads) and 271 colonies growing on vertical substrata (sides of coral heads). Contingency table analysis was used to determine any differences in the frequency of each morphology over the depth gradient. A $\chi^2$ analysis of morphology was completed for each depth, using an equal frequency of each morphotype as the expected result. For these tests, horizontal and vertical substrata were considered separately.

**Feeding in Flow**

A series of feeding trials was conducted to assess the interaction of colony morphology and ambient flow on particle capture. Small (6–8 cm diameter) colonies of *A. agaricites* free of any obvious damage or bleaching were collected from 12–20 m depth on the fore reef at DBML. Animals were then transported to the laboratory, where they were maintained in seawater tables. All feeding experiments were completed within 3 days of collection.

Feeding trials were conducted in a recirculating Plexiglas flume [design of Vogel & LaBarbera, 1978; working section: 15 cm (depth) × 15 cm (width) × 93 cm (length); constructed by M. LaBarbera]. Flow speeds were controlled by means of a Minarik solid state speed controller coupled with a Bodine series-400, 1/15-hp motor. Flow speeds were measured by tracking particles (brine shrimp cysts) at points near the feeding surface of each colony using a video camera (Sony V9 8-mm camcorder) and slit illumination parallel to the direction of flow (Johnson & Sebens, MS). Particle positions in successive video frames (1/30 s apart) were traced onto acetate (method
of Leonard et al., 1988), and distances measured with an image analysis system [Apple Macintosh II with RGB camera, ColorImage 1.29 software (J. Ayers, Northeastern University)]. Only particles which could be traced for a minimum of four successive frames were utilized, to reduce error due to the movement of particles oblique to the plane of the illuminated slit (Johnson & Sebens, MS). Feeding trials were completed in flow speeds of 3, 6, 18, 30, and 50 cm·s⁻¹, for each of the following morphologies: perpendicular bifacial (facing flow), vertical unifacial (parallel to flow), and horizontal unifacial (n = 4–7 per speed, per morphology). All colonies were tested in the orientation in which they were found in the field. These flow speeds corresponded roughly to Reynolds numbers (Re) ranging from 1700 to 28700 for colonies oriented parallel to flow and from 600 to 9600 for bifacial colonies facing into flow (l = length of colony oriented parallel to flow). Because the maximum projected surface area of each coral was small relative to the cross-sectional area of the flume (normally ≤10–15%) wall effects were considered to be negligible (Nowell & Jumars, 1987; Denny, 1988). Furthermore, as cyst speeds were recorded at points directly adjacent to the colony surface rather than using an average for the entire flume, any potential influence of a boundary layer formed by the walls would have been reflected in the flow speed recorded and would therefore have been incorporated into the analysis.

At the beginning of each run, a colony was transferred from the seawater table without exposing it to air, and was placed in the center of the flow tank on the upstream edge of a small (1.5 cm tall) platform. Normally, colonies needed no support, but occasionally, and particularly in high flow, it became necessary to brace the downstream side of colonies with a small lead weight wrapped in paraflim or, alternatively, to embed the base of the colony in modeling clay. This support was placed such that local flow was not affected prior to contact with the colony.

Feeding by \( A. \textit{agaricites} \) is believed to occur primarily through the entrapment of small nonmotile particulates (Lewis & Price, 1975). Neutrally buoyant \( \textit{Artemia} \) cysts (diameter ≥ 200 μm), which are proteinaceous and are readily ingested by colonies, were therefore used as experimental particles. Prior to each run, cysts were hydrated and all approximately neutrally buoyant particles were removed for use by siphoning. Because a previous study suggested that \( A. \textit{agaricites} \) feeds most actively at night (Lewis & Price, 1975), the flow tank was maintained in darkness throughout the run by covering it with black plastic.

Each colony was allowed to acclimate in flow until the tentacles were visible. Following acclimation, a small amount of cysts was released downstream from the colony, to yield an approximate concentration of 1 cyst·ml⁻¹. Cyst concentrations were quantified by removing 20-ml samples from a point downstream and level with the height of the colony every 3 min with a 50-ml syringe. These values were then averaged to obtain the mean number of available cysts throughout the run. All runs in which significant gravitational deposition was observed (linear regression of cyst concentration vs. time) were eliminated from the analysis, to reduce any potential influence of particle capture by this mechanism, which may be highly variable depending upon the
relative density of the particle being captured (Rubenstein & Koehl, 1977; LaBarbera, 1984; Shimeta & Jumars, 1991). The volume of the tank was sufficiently high that the feeding of the specimen could not result in any detectable differences in cyst concentrations throughout the run. Each colony was permitted to feed for exactly 15 min; after which time it was removed and gently rinsed in cyst-free water to remove any uncap-tured cysts which may have adhered to the surface of the coral without being ingested. Cysts were then removed from the flow tank with a 180-μm Nitex mesh screen, and the next colony allowed to acclimate.

Following each run, the colony was dried in air for a minimum of 3 h, and normally overnight. As each colony dried, the corallites expelled all cysts contained in the co-elenteron. This was verified by dissection. Due to the thick outer covering of the cysts, digestion of the particles was not observed during the drying period, so that particle capture could be quantified by counting the number of cysts in each corallite. Each unifacial colony was divided into upstream and downstream sections to determine particle capture by different regions of the colony (Patterson, 1984). Bifacial colonies were similarly divided into upper and lower portions for both the upstream and downstream faces of the colony. Particle capture over each 15-min feeding period was standardized for each region and for the entire colony as:

\[
\frac{\text{number of cysts captured}}{\text{(number of polyps) (available cysts} \cdot \text{ml}^{-1})}
\]

Data were square-root transformed, and the effects of flow speed and colony morphology on particle capture were compared using a two-way ANOVA with multiple comparisons, and Fisher's protected LSD test for posthoc analysis (SuperANOVA). Because each morphology was found to have a significantly different number of calices per unit area (bifacial = 8.1 ± 2.0; horizontal = 12.0 ± 3.3; vertical = 13.7 ± 3.2 calices·cm⁻¹; ANOVA, \(F = 26.3, \text{df} = 2, p \leq 0.0001\)) analysis was conducted on both a per polyp and per unit surface area basis (Fisher's PLSD posthoc analysis of calices per unit area: bifacial vs. horizontal: \(p \leq 0.0001\), bifacial vs. vertical: \(p \leq 0.0001\), horizontal vs. vertical: \(p \leq 0.05\)). Colony surface area was calculated by covering the surface of the colony with aluminum foil, which was then weighed and compared to a regression of foil weight vs. surface area (\(y = 233.4x - 0.6, r^2 = 1.0\)). Localized capture by the regions of each colony at each flow speed were compared using a series of goodness-of-fit tests (χ²) against a model of expected capture values based on the percentage of total polyps represented by each region (a modification of the methods of Young & Cameron, 1989).

A set of feeding trials was also conducted to determine the effect of colony orientation on particle capture by bifacial colonies at two flow speeds (3 and 6 cm·s⁻¹; Re≈600–1200 for bifacial colonies facing flow, and 1700–3400 for colonies oriented parallel to flow). Bifacial colonies were oriented parallel to flow, and were otherwise treated as above. Particle capture by these parallel colonies was then compared to
FEEDING AND CORAL-COLONY MORPHOLOGY

capture by previously run bifacial colonies oriented perpendicular to (facing) flow. Results were analysed on a per-polyp basis using an ANOVA with square-root transformation.

FLOW ON THE REEF

Although flow conditions on the reef may vary significantly on both spatial and temporal scales, a relative comparison of ambient flow characteristics at different locations may nonetheless be described. An extensive catalogue of flow conditions on different parts of the reef at Discovery Bay has been compiled using paired electromagnetic current meters (InterOcean Model S4; K. Sebens, unpubl. data) and has demonstrated a fairly consistent, negative relationship between flow speed and depth on the forereef, as well as generally lower flows in more protected portions of the backreef environment (Fig. 2). The use of current meters for measuring flow on the reef is advantageous in that it accurately and quickly measures fluctuations in water motion each 0.5 s over long periods of time, and is fully automated. However, due to the size of the meter, flow data may only be collected at points ∼0.5 m off the bottom, and are integrated over a rather large sensing volume (1 m³).

In benthic boundary layers (Denny, 1988), organisms living close to the substratum do not necessarily experience flow of the same magnitude as points higher above the bottom. In an attempt to relate flow data collected by a current meter (S4) and the actual flow speeds experienced by the corals, a series of paired runs using an S4 meter and a video camera with synchronized internal clocks was completed in June 1991 at the LTS mooring at 20 m.

Just prior to dusk, an S4 meter was deployed, and was programmed to measure flow speed and direction at a sampling rate of 2 Hz (120 data points·min⁻¹). Flow adjacent to unobstructed A. agaricites colonies near the meter (within 3–4 m) was then recorded by video taping hydrated Artemia cysts with slit illumination parallel to the main axis of flow. Slit illumination was accomplished by connecting a Plexiglas cone over an underwater video light, which was held ∼10 cm above the area being recorded. By conducting these runs at dusk, particles were more readily distinguishable than during the day, while interference by zooplankton was less than that encountered during full darkness. A total of five runs were completed. Flow was recorded at points 10–15 cm above the bottom, level with the tops of colonies.

To compare flows near the bottom to flow recorded by the current meter at 0.5 m, one 10-s "snapshot" of flow was analysed for each replicate by calculating the flow speeds in 10 consecutive 1-s intervals. Cyst speeds were computed for the first half of each 1-s interval using methods similar to those previously described, with the substitution of a Sharp JX100 scanner for an RGB camera for the analysis of acetate tracings. Flow measurements made by each device could then be compared almost simultaneously (within 0.5 s).

Measurements of flow above colonies in the field were also used for a rough com-
Fig. 2. Flow transects on the forereef and at a protected backreef site, Columbus Park, within Discovery Bay (1989). Each point represents mean flow (from square-root transformed continuous data, recorded each 0.5 s) for a 4–8-min InterOcean S4 current meter deployment at a given depth, 0.5 m off substratum in areas of unobstructed flow. Error bars represent mean plus and minus one standard deviation, back-transformed Lines connect data points collected within 1 h of each other on a given date. Columbus Park transects were completed within 1 h before or after those on forereef. Note that flow at 6–8 m depth is more than twice as high on forereef as at protected site on same day (depth axis has been expanded for lower graph). A, 24 February with 2 m (maximum third) waves on forereef; B, 27 February; C, 10 March; D, 11 March; B–E with 0.8–1 m waves on forereef.
parison to conditions in the experimental flume. Because turbulence is measured as the variance in flow speeds at any given point turbulence intensity (TI) was calculated as the $\text{sd} \cdot \bar{X}^{-1}$ for each 0.5-s interval (Denny, 1988), and compared to particles moving at the same speed in the flume.

RESULTS

FIELD DISTRIBUTION OF MORPHOLOGIES

The distribution of each morphotype (unifacial and plating, upright and bifacial, and encrusting) on horizontal substrata was strongly related to depth at the LTS site on the west fore reef ($G = 25.19$, df = 3, $p \leq 0.0001$; Fig. 3a). Most colonies inhabiting shallower water were plating and encrusting, although bifacial morphs were also en-

Fig. 3. (a) Distribution of each morphotype on horizontal substrata. Distribution of each morphotype at LTS mooring was found to vary significantly along a depth gradient, with bifacial colonies becoming dominant in deeper water. 90% of these colonies were oriented perpendicular to normal direction of ambient flow. (b) Frequency distribution of each morphotype on vertical substrata. Although bifacial colonies were found growing on vertical substrata, their frequency of occurrence was never high, and did not change significantly with depth.
countered. With increasing depth, bifacial colonies became more prevalent, and were the dominant morphotype at 20 m ($\chi^2 = 21.3$, df = 2, $p \leq 0.0001$). 90% of the bifacial colonies growing on horizontal substrata were oriented perpendicular to (long axis of the colony-facing) flow. Orientation to light (compass direction) indicated that colonies were oriented into the predominant direction of flow (north-north-east) rather than into the east-west direction of sunlight (depth range 7–20 m; $n = 43$; N/S = 15, NE/SW = 17, E/W = 9, NW/SE = 2; $\chi^2 = 12.45$, df = 3, $p \leq 0.01$).

In contrast to colonies growing on horizontal surfaces, *A. agaricites* on vertical substrata did not vary significantly in their morphology over the depth gradient (Fig. 3b). Bifacial colonies did occur at a low frequency at each depth, but plating forms were by far the most common morphotype. The bifacial morphology therefore appeared to be a growth form limited to colonies growing on horizontal surfaces.

**FEEDING AND COLONY MORPHOLOGY**

Particle capture rates were extremely variable for all three morphologies tested, and particularly at higher flow speeds. Colonies feeding in slightly higher concentrations of cysts captured proportionately more particles, indicating that saturation of the polyps did not occur (Lasker et al., 1982). An ANOVA indicated a significant effect of both morphology ($F = 5.72$, df = 2, $p \leq 0.005$) and flow speed ($F = 3.66$, df = 4, $p \leq 0.01$) on particle capture, when compared on a per-polyp basis (Fig. 5). The interaction of these two parameters was not significant. Posthoc analysis by Fisher’s protected LSD test indicated that bifacial colonies captured significantly fewer particles per polyp than either horizontal ($p \leq 0.01$) or vertical colonies ($p \leq 0.005$). Colonies tended to capture the most particles at intermediate flow speeds (18–30 cm·s$^{-1}$), although bifacial colonies achieved a maximum rate at a flow speed lower than those of either vertical or horizontal unifacial colonies (Fig. 4). Posthoc analysis indicated that particle capture at a flow speed of 30 cm·s$^{-1}$ was significantly higher than that at either 3, 6, or 50 cm·s$^{-1}$ (morphologies grouped, all $p \leq 0.05$).

Horizontal-plating colonies were able to feed successfully over a surprisingly wide range of flow speeds, and a separate ANOVA considering this morphology alone indicated no significant effect of flow speed on particle capture rate (Fig. 4). A second ANOVA also indicated no significant effect of flow speed on particle capture by bifacial colonies. Vertical colonies, in contrast, captured a significantly larger number of particles at intermediate flow speeds, at least partially explaining the results of the above posthoc analysis (ANOVA; $F = 7.37$, df = 4, $p \leq 0.001$). It should be noted, however, that particle capture rate is not equivalent to capture efficiency, due to an increasing encounter rate at higher flow speeds (Shimeta & Jumars, 1991). When capture was adjusted for encounter rate, particle capture efficiency was found to decrease with increasing flow speeds for all morphologies tested (ANOVA; horizontal: $F = 6.33$, df = 4, $p \leq 0.005$; bifacial: $F = 5.95$, df = 4, $p \leq 0.005$; vertical: $F = 5.15$, df = 4, $p \leq 0.01$).
Fig. 4. (a) Feeding by each morphotype on a per-polyp basis over 15-min periods. Feeding by all three morphologies was highest at intermediate flow speeds, although bifacial colonies achieved a maximum rate at a flow speed lower than that of either horizontal or vertical plating colonies. A two-way ANOVA indicated a significant effect of both flow speed and colony morphology on particle capture (see text). Plating colonies were always at least as efficient as bifacial colonies, and were able to feed well over a large range of flow speeds (bars indicate standard deviation; \( n = 4–7 \) per morphology, per flow speed). For typical-sized colonies, these flow speeds roughly corresponded to \( Re \) ranging from 1720 to 28,650 for colonies oriented parallel to flow and from 573 to 9550 for bifacial colonies facing into flow. (b) Feeding by each morphotype on a per-unit surface area basis. Because bifacial colonies were found to possess fewer coralites per unit area than either plating morphology, particle capture was also compared on a per-unit surface area basis. Results were very similar to those found by analysis on a per-polyp basis (bars indicate standard deviation; \( n = 3–7 \) per morphology, per flow speed).
Results of $\chi^2$ analysis of location of particle capture by horizontal plating colonies. Particle capture was compared to a model of symmetrical capture, and is reported as a percentage of expected capture (U, upstream; D, downstream).

<table>
<thead>
<tr>
<th>Flow speed (cm·s$^{-1}$)</th>
<th>Position</th>
<th>Capture (% of expected)</th>
<th>$\chi^2$</th>
<th>df</th>
<th>p value</th>
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<tbody>
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<td>114</td>
<td>6.0</td>
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<td>NS</td>
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<tr>
<td></td>
<td>D</td>
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<td>8.8</td>
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<tr>
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Analysis on a per-unit surface area basis also indicated a significant effect of both morphology ($F = 10.87, \text{df} = 2, \ p \leq 0.0001$) and flow speed ($F = 4.56, \text{df} = 4, \ p \leq 0.005$; Fig. 4) on particle capture. The interaction of morphology and flow speed was also significant ($F = 2.81, \text{df} = 8, \ p \leq 0.01$). Again, bifacial colonies captured fewer particles than either horizontal ($p \leq 0.0005$) or vertical colonies ($p \leq 0.0001$), and particle capture was highest at flow speeds of 18 and 30 cm·s$^{-1}$ ($p \leq 0.05$).

LOCATION OF CAPTURE ON COLONY

The location of particle capture on the surface of colonies of all three morphologies shifted dramatically from upstream to downstream regions with increasing flow speed ($\chi^2$; Tables I–III; Fig. 5). While the change from upstream to downstream capture by horizontal plating colonies occurred at flow speeds of 6–18 cm·s$^{-1}$ ($Re \approx 3500–10300$;...

Results of $\chi^2$ analysis of location of particle capture by vertical colonies (U, upstream; D, downstream).

<table>
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<th>Capture (% of expected)</th>
<th>$\chi^2$</th>
<th>df</th>
<th>p value</th>
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</table>
Table III
Results of $\chi^2$ analysis of location of particle capture by bifacial colonies (UT, upstream (front) Top; UB, upstream bottom; DT, downstream (rear) Top; DB, downstream bottom).

<table>
<thead>
<tr>
<th>Flow speed (cm·s$^{-1}$)</th>
<th>Position</th>
<th>Capture (% of expected)</th>
<th>$\chi^2$</th>
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Fig. 5a), the shift in capture by vertical plating colonies did not occur until a much higher flow speed of $\approx 30\, \text{cm} \cdot \text{s}^{-1}$ (Re $\approx 17\,200$; Fig. 5b).

Bifacial colonies also displayed a marked shift from the upstream to the downstream face of the colony at a flow speed of $18–30\, \text{cm} \cdot \text{s}^{-1}$ (Re $\approx 3400–5700$; Fig. 5c). Changes in the efficiency of capture by upper and lower portions of each face were also evident, and particle capture tended to be restricted to the upper portions of the colony. Particle capture by the upper half of the upstream face was highest at the lowest flow speeds, and capture by the upper half of the downstream face was highest at the fastest flow speeds (Fig. 5c). The bottom portions of both faces generally captured fewer particles than the upper portions. Capture by the upstream bottom region was highest at a flow speed of $6\, \text{cm} \cdot \text{s}^{-1}$ (Re $\approx 1100$). At all other flow speeds tested, capture by this region was significantly lower than that predicted by a model of symmetrical capture (Fig. 5c). Similarly, the bottom, downstream region was highest at a flow speed of $30\, \text{cm} \cdot \text{s}^{-1}$ (Re $\approx 5700$), but was lower than predicted by the model for all other flow speeds.

FEEDING AND COLONY ORIENTATION

Colony orientation was found to affect particle capture by bifacial colonies. Capture by colonies facing into flow was higher than by colonies oriented parallel to flow for
Fig. 5. (a) Location of particle capture by horizontal plating colonies. Capture shifted dramatically from upstream half to downstream half of colony at a flow speed of 6–18 cm·s⁻¹ (Re≈3500–10300). Capture was compared against a model of symmetrical capture with a χ² (see text). A value of 100% indicates completely symmetrical capture, in which upstream and downstream portions of colony captured an equal number of cysts polyp⁻¹. (b) Location of capture by vertical plating colonies. Capture by unifacial colonies oriented parallel to flow also shifted to downstream polyps, but this shift occurred at a much higher flow speed of ≈30 cm·s⁻¹ (Re≈17200). (c) Location of particle capture by bifacial colonies. Bifacial colonies feeding in low flow speeds (3–18 cm·s⁻¹, Re≈600–1700) caught particles on upstream side of colony; capture shifted to downstream face in higher flow speeds. Capture tended to be concentrated in upper half of colony at most flow speeds tested.
both flow speeds tested, although a significant difference ($p \leq 0.05$) was found only at the lowest flow speed (Fig. 6).

**BEHAVIORAL OBSERVATIONS**

Both particle ingestion and sediment clearing involved active water movement originating from within the polyps. In still water, *Ariemia* cysts were frequently observed to be transported by weak currents to points directly above the center of a coralite. Judging from the movement of detritus on the surface of the colony, these currents appeared to be initiated after the addition of cysts or other food particles, but prior to any physical contact, suggesting chemosensory activity (Lewis & Price, 1975). After spinning for several seconds, the cyst was normally drawn downward into contact with the surface of the oral disk. At this point, the entire polyp quickly initiated a slight "jerk", in which the stomodeum was briefly retracted inward. The cyst was then drawn into the mouth and ingested. Although conclusive evidence is lacking, particle capture may involve the reversal of cilia, which normally pump water outwards as a cleansing mechanism (Lewis & Price, 1976). Mucus did not appear to be used in the entrapment of these relatively large ($\approx 200 \mu m$) particles.

Sediment rejection involved a similar process, and was usually initiated within 1 min. Upon contact with large pieces of debris, polyps generally pumped water outwards, forcing even large particles out of the coralite. The process was repeated by adjacent polyps until the particle was transported to the edge of the colony. Occasionally, sand
particles were ingested in the manner described above for cysts, perhaps due to the presence of food particles on their surface.

Lewis & Price (1975) indicated that *A. agaricites* is primarily a mucus feeder, and captures particles from the water column with mucus nets and strands, which are subsequently drawn into the mouth. Such strands were only occasionally observed during runs in the flow tank, and were rarely observed during numerous dives on the reef, both during the day and night. These observations did not utilize dye to stain for mucus. However, mucus production was very commonly observed without the use of dye in the laboratory during stressful events, such as elevated water temperature or excessive handling.

**MORPHOLOGICAL OBSERVATIONS**

*A. agaricites* is extremely variable in both overall colony morphology and individual corallite structure. Wells (1973) describes six species of *Agaricia* in Jamaica, although up to 21 names have been used to describe members of this genus in the West Indies. The specimens used in this study were considered to represent different morphologies of *A. agaricites*, rather than distinct species, as intermediate forms (plates with small bifacial regions) are readily encountered on the reef. This classification remains to be verified by genetic analysis.

As mentioned above, one consistent difference between bifacial and unifacial platting colonies is the number of corallites per unit area. In addition to possessing larger corallites, bifacial colonies also tended to display corallites in which the ridges were angled upward, so that the polyps faced away from the substratum, rather than at right angles to the surface of the colony (Fig. 7).

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**Fig. 7.** (Left) Corallite structure of a typical bifacial colony. Bifacial colonies tended to possess ridges that were oriented upwards, away from substratum, rather than facing directly into flow (≈ 10 x). This position may increase particle capture by gravitational deposition, as well as assist in ingestion of particles traveling over colony's surface. (Right) Corallite structure of a horizontal, platting colony. In contrast to bifacial colonies, horizontal colonies typically possessed calices in which intervening ridges were directed normal to surface of colony (≈ 12 x).
NATURAL FLOW CONDITIONS ON THE REEF

The interaction of depth, geomorphology, and sea state can cause significant variation in the characteristics of flow encountered on various portions of the reef. The effect of surface swell, however, is most pronounced in shallower water, and flow velocities at 20 m probably exceed 10 cm·s⁻¹ only during days with high surface waves (Fig. 2). When conditions on the surface are calm, flow speeds at 20 m would be expected to decrease to values of <4–5 cm·s⁻¹. The mean flow speed recorded by the current meter during this experiment was 5 cm·s⁻¹ (Fig. 8a), and was recorded on a day with moderate surface swell. This value is well within the normal range of flow speeds recorded at this site, and probably represents approximately average flow conditions (K. Sebens, unpubl. data).

Flow was found to be oscillatory, although complete reversals were often preceded by fairly long intervals of unidirectional flow (Fig. 8b). Flow near the bottom was found to be strongly related to fluctuations in the direction of current, and on a short time scale, showed no linear relationship with flows recorded by the current meter. For example, in unidirectional flow, flow speed near the bottom (15 cm) was lower than that.

Fig. 8. 5-min “snapshot” of flow at LTS mooring (20 m), showing (a) flow speed (b) direction. Mean flow speed on this day was 5 cm·s⁻¹, a typical value for this site. Flow was fairly unidirectional, with occasional changes of 180°.
recorded by the current meter (e.g., \(2.8 \pm 1.3\) vs. \(6.0 \pm 3.4\) cm·s\(^{-1}\); Fig. 9), potentially due to the formation of a boundary layer. In oscillatory flow, in contrast, flow was slightly higher closer to the bottom (e.g., \(5.6 \pm 2.7\) vs. \(4.1 \pm 3.2\) cm·s\(^{-1}\); Fig. 10), probably reflecting local increases in flow velocity resulting from the flattening of wave orbitals near the bottom.

![Graphs showing flow speed, direction, and turbulence intensity over time.](image)

Fig. 9. Unidirectional flow at LTS mooring (20 m). An electromagnetic current meter was used to measure current speed (a) and direction (b) in a field originating at a point 0.5 m above substratum. This was then compared to current speed (a) and turbulence intensity (c) measured by video taping cysts at a point level with surface of a colony near bottom. During unidirectional flow, flow speeds recorded at points close to the bottom were much lower than values recorded by current meter.
TI values (Figs. 9c, 10c) were found to be similar to those recorded in the laboratory flume (mean field $\text{TI} = 0.19$, mean flume $\text{TI} = 0.15$), although values recorded in the field were slightly higher in unidirectional ($\bar{x} = 0.22$) than in oscillatory flow ($\bar{x} = 0.15$).

Fig. 10. Bidirectional flow at LTS mooring (20 m), showing (a) current speed, (b) direction, and (c) turbulence intensity recorded by a current meter and a video camera. In contrast to unidirectional flow, oscillatory flow resulted in higher current speeds at points closer to substratum. Thus, although current meter is a useful tool for relative comparisons, it does not reflect flow characteristics experienced by organisms near the substratum.
FLOW AND FEEDING IN NATURE

The advantage of conducting feeding studies in a laboratory flume rather than in the field lies in the ability to precisely control and quantify the flow conditions experienced by the feeding animals. However, flow on a coral reef is often turbulent and oscillatory, particularly in shallow water. This necessarily limits the validity of extrapolation from laboratory studies to field situations. For example, Hunter (1989) found large differences in the feeding abilities of the hydroid Obelia in oscillatory vs. unidirectional flow, due to bending of the stalk. Harvell & LaBarbera (1985) similarly found the flexibility in hydroids may represent a means of increasing particle capture in high flows. Flexibility is not an uncommon occurrence in nature, and is probably utilized by a number of organisms to withstand moving wind and water (Vogel, 1981). One advantage to studying inflexible organisms such as corals, however, is that there is no a prior reason to expect the relative feeding abilities of different morphologies to vary between oscillatory and unidirectional flow, particularly when the feeding structures are relatively short, as in A. agaricites.

Although highly variable, the measurements of flow conducted in the field suggest that the flow characteristics experienced by corals feeding in the laboratory flume may represent a fair representation of conditions at moderate to deeper parts of the reef. The results of this experiment also indicate, however, that although large instrument such as current meters may provide useful information about near-mainstream or bull flow in different habitats, measurements must be conducted on the scale of the organism before any true predictive power can be attained.

Despite the fact that the theory of boundary layer formation has been in existence for a long time, relatively few measurements of shear stress or boundary layer thickness have been made in field situations (Denny, 1988; but see Caldwell & Chris, 1979; Frechet et al., 1989). Although boundary layer thickness may not be accurately calculated from flow velocities measured at only two points in nonequilibrium flow (Nowell & Jumars, 1984), flow measurements conducted in this experiment at least suggest an effect of the bottom even as high as 10–15 cm in unidirectional flow. This result may to a large extent, reflect the influence of roughness elements on the bottom, in particular the carpet of algae which has overgrown the reef as a result of hurricane damage and a decrease in urchin grazing, as well as the corals themselves. Periodic reversal in flow, however, disrupt this boundary layer, potentially increasing the vertical flux of materials to and away from the bottom. These periodic disruptions may be particularly important to sessile suspension-feeders growing in low-flow environments, which have been shown to deplete food concentrations in steady-state boundary layers (e.g., Wildish & Kristmanson, 1984; Frechet et al., 1989).
PARTICLE CAPTURE MECHANISMS

Observations of feeding by A. agaricites suggest that feeding is accomplished by the ingestion of particles from the boundary layer formed over the surface of the colony through the use of ciliary currents, and may involve the formation of small-scale eddies in the wake of the ridges on the surface of the colony. This qualitative observation is supported by the location of capture by unifacial plating colonies, as particle capture was found to increase in the downstream direction in higher flows, while upstream regions were comparatively more successful in lower flows, potentially due to the depletion of particles in the boundary layer. Similar results have been obtained for octocorals with more flexible polyps (Patterson, 1984; McFadden, 1986), but this is the first clear evidence of a shift in particle capture by an inflexible suspension-feeder, and is the first time this effect has been reported for a scleractinian coral.

Unlike some other corals (e.g., Meandrina meandrites; Johnson & Sebens, MS), A. agaricites possess extremely short tentacles, which are unlikely to be affected significantly by deformation. Instead, the limit to capture rate may be the speed at which particles are transported past the polyp, and the degree to which they are slowed by the viscous boundary layer overlying the colony’s surface. Differences in particle capture by the upstream and downstream portions of unifacial colonies may be further augmented by the asymmetrical distribution of particles which occurs in boundary layers formed in slow laminar flow (Einav & Lee, 1973; Patterson, 1984).

Bifacial colonies appear to feed by a mechanism similar to that of unifacial forms. Because the ridges of the calices are angled upward, rather than directly into flow (Fig. 7), feeding by polyps on the upstream face of the colony probably occurs via a mechanism similar to plating unifacial colonies. Furthermore, this angled structure might also be expected to increase particle capture by gravitational deposition in very low flows. Particle capture apparently is affected by the structure of the calices, rather than just by the orientation of the colony, as vertical plating colonies were always at least as successful as bifacial colonies (Fig. 4). The absence of capture by the upstream face in high flow strongly suggests that inertial impaction is not involved. Capture by the downstream face may involve the formation of larger-scale eddies, as feeding by this side occurs only in higher flows (Patterson, 1984; Fig. 11). Thus, the shift from the upper portion to the lower portion of the downstream face may reflect differences in the size of the eddies formed in higher flow.

ADAPTIVE SIGNIFICANCE OF UNIFACIAL PLATING MORPHOLOGY

Perhaps the most striking result of the feeding experiments is the ability of plating, unifacial colonies to feed well under an extremely broad range of flow conditions. Although flow conditions vary significantly with depth and with the geomorphology of the reef, ambient flow velocities may also be quite variable within a habitat, and on relatively short time scales. This heterogeneity is particularly apparent on reefs such
as those on the north coast of Jamaica, which display a highly variable topography (Liddell & Ohlhorst, 1981). The ability to feed under this wide range of flow conditions may provide a marked advantage to horizontal plating *A. agaricites*.

**ADAPTIVE SIGNIFICANCE OF BIFACIAL MORPHOLOGY?**

**Feeding**

Because unifacial plates appear to always capture at least as many particles as bifacial colonies feeding in the same ambient flow speed, the question naturally arises as to why the bifacial morphology exists at all. Bifacial colonies might be expected to experience slightly higher ambient flow velocities than unifacial morphologies, particularly in the presence of a thick boundary layer. However, when feeding rates of bifacial colonies are compared to unifacial colonies feeding in flows as much as 15 cm·s⁻¹ lower (e.g., 18 vs. 3 cm·s⁻¹; Fig. 4), no increases in particle capture are found to occur.

To understand the significance of any reputed adaptation requires knowledge of the resources and processes which limit the survival and reproduction of the colony. Barnes (1973) and others have suggested that the deposition of skeletal material may limit the
growth of scleractinian corals at depth. As such, *A. agaricites* might grow in a bifacial morphology in deeper water as a means of maximizing particle capture per amount of structural material. To examine this hypothesis, experimental coral skeletons were weighed and particle capture compared on a per unit calcium carbonate basis. Results again indicated that unifacial, plating corals were more efficient at capturing particles than were bifacial forms (ANOVA: $F = 4.02$, df = 2, $p \leq 0.05$; Fisher’s protected LSD posthoc analysis: horizontal > bifacial, $p \leq 0.05$).

Quite clearly, the results of this study indicate that the bifacial morphology does not represent a mechanism for increasing particle capture per unit of structural material. The orientation of bifacial colonies does, however, increase particle capture significantly, and may have arisen secondarily as a mechanism for maximizing particle capture within the constraints set by the bifacial morphology. It is interesting to note that other reef organisms may utilize a similar growth strategy. For example, observations of the hydrocoral *Millepora* spp. suggest that bifacial fans of this species also orient directly into flow (Denny, 1988). Flattened lobes of *Montastrea annularis* have also been observed to face directly into flow (B. Heimth, pers. obs.).

Although the precise role of heterotrophy in coral energetics remains unclear (reviewed in Sebens, 1987), mechanistic studies of coral feeding may become increasingly crucial in the near future given the recent widespread bleaching events experienced in tropical regions throughout the world (Brown & Suharsono, 1990; Jokiel & Coles, 1990; Williams & Bankley-Williams, 1990; Glynn, 1991). Following the expulsion of zooxanthellae, scleractinian corals would be expected to be much more dependent on particle and prey capture for nutrition until symbiont populations can recover. As such, studies of prey capture may provide powerful predictors of the recovery of corals from bleaching and anthropogenic alterations of reefs.

*Other selective pressures on colony form*

Like other scleractinian corals, the morphology of *A. agaricites* may be influenced by many selective pressures, including particle capture, light capture, sediment removal, gas and nutrient exchange, and spatial competition. The results of this study indicate that the upright morphology probably arose as a result of selective pressures other than feeding. These pressures may be (or have been) more prevalent at depth, or, conversely, the upright morphology may not be able to withstand drag forces encountered in shallower water, particularly during storm or hurricane conditions.

Discovery Bay has experienced two major hurricanes within the last decade. The interpretation of patterns observed on the present reef system may, therefore, be confounded by the historical effects of these storms, which radically altered the structure of the reef. For example, most branching corals were destroyed by the impact of Hurricane Allen, while larger, more massive corals survived (Woodley et al., 1981). The observed distribution of *A. agaricites* could thus be interpreted as the result of the selective removal of the bifacial morphology in higher-current areas.
Fortunately, *A. agaricites* is a rapidly growing coral, and has recruited fairly quickly after the most recent hurricane. To assess the effect of Hurricanes Allen (1980) and Gilbert (1988) on the observed distribution of *A. agaricites*, a separate analysis was conducted on small (≤8 cm diameter) colonies only, which are probably <3 yr old and thus recruited after Hurricane Gilbert and certainly after Hurricane Allen (J. D. Woodley, DBML, pers. comm.). The results of this analysis were identical to those obtained from the entire data set (contingency table analysis, $G = 15.14$, df = 3, $p \leq 0.01$), suggesting that the observed distribution of the bifacial morphology is not due to the effects of the hurricanes, but instead arose in response to other selective pressures.

Previous studies have shown that one of the most limiting resources to sessile benthic invertebrates such as corals is space (e.g., Connell, 1961; Chadwick, 1991). In a prehurricane study, Lang (1973) reported that overgrowth interactions by and against *A. agaricites* were extremely common on the forereef of Discovery Bay. A fairly weak aggressor, such as *A. agaricites*, may thus be very susceptible to overgrowth by competitors (Lang, 1973; but see Chornesky, 1989), particularly during the conditions of high coral cover existing prior to the effects of the two hurricanes (Woodley et al., 1981).

Previous work (Sebens, 1982) has suggested that temperate zone soft corals may adopt an upright morphology as a means of escaping spatial competition with other species such as ascidians, which are able to overgrow smaller colonies. Similar trends have been found among both extant and fossil bryozoan species (Jackson, 1979; Cheetham, 1986; McKinney & Jackson, 1988). By conforming to an upright morphology, *A. agaricites* could potentially increase the rate of particle capture per unit of available substratum, thus achieving more biomass and higher growth and reproductive rates in habitats where neighboring organisms prevent or slow lateral growth.

One further advantage to adopting an upright morphology may lie in the formation of turbulence in the low-velocity flows often encountered at depth. Jokiel (1978) first demonstrated that increased water movement alone may increase the growth, survival, and fecundity of scleractinian corals. Patterson & Sebens (1989) were further able to show that, in very low flows, the diffusion of gases into and out of the tissue of cnidarians may be limited by the formation of a boundary layer overlying the surface of the colony. Increased water movement during the daytime has the effect of increasing the removal of O$_2$ across the coral's tissue, as well as increasing CO$_2$ flux into the coral. For hermatypic corals, such as *A. agaricites*, this leads to higher rates of photosynthesis by the endosymbiotic zooxanthellae (Patterson et al., 1991; Patterson, 1992). Concurrently, however, the respiration rate of the coral tissue in the dark also increases in higher flows because O$_2$ delivery to tissues is enhanced (Sebens, 1987; Patterson & Sebens, 1989; Patterson et al., 1991). Similarly, recent studies have indicated that the rate of phosphate uptake by corals increases with increasing water flow, again suggesting an advantage to corals exposed to higher flows (Atkinson & Bilger, 1992; Bilger & Atkinson, 1992).

Sebens (1984) previously demonstrated that *Alcyonium siderium* colonies on vertical rock walls increase in mean size and growth rate as a function of higher ambient flow.
This suggests a significant effect of ambient flow on colony energetics, potentially due to the trade-offs between increased respiration rate and particle capture (Sebens & Johnson, 1991). Similar compromises between photosynthesis, respiration, nutrient exchange, and particle capture might also be expected to affect the morphology of *A. agaricites* colonies growing under different conditions of flow and light on the reef.

Bak (1976) previously showed that *A. agaricites* colonies in water as deep as 13 m may be exposed to light levels that are sufficiently high to limit colony growth. Thus, although some self-shading probably occurs in bifacial morphologies, this may effectively optimize the interception of light under some high-light conditions. By increasing water movement over the surface of the colony, bifacial morphologies could potentially increase the photosynthetic and nutrient uptake rates of the endosymbionts during periods of low flow, at little or no expense to particle capture. Colonies in shallower water, however, may be limited in their morphology by drag forces.

Although the results of this study do not elucidate all selective pressures controlling the morphology of *A. agaricites*, they do suggest that feeding ability may not be as strong a selective pressure in deeper waters as are other processes such as spatial competition or gas exchange. The orientation of bifacial colonies into flow in these environments may therefore represent a compromise between these selective pressures and capturing food.

**ACKNOWLEDGEMENTS**

This project has benefitted greatly from the advice and support of M. R. Patterson and J. Witman. E. A. LaPointe provided invaluable assistance with the collection and analysis of data. The authors wish to thank J. D. Woodley and the Staff of the Discovery Bay Marine Laboratory for the use of the facilities. Critical reviews of the manuscript were provided by D. Cheney, T. L. Daniel, A. Kohn, R. T. Paine, M. R. Patterson, C. Pfister, N. Sholtz, J. Witman, and two anonymous reviewers. This research was submitted in partial fulfillment of the requirements for the M.Sc. degree in the Department of Biology of Northeastern University by B. Helmuth. Funding was provided by NSF Grant OCE-891421 to K. Sebens and a grant from the Lerner-Gray Fund for Marine Research to B. Helmuth.

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