Flow patterns and velocities around a suspension-feeding gorgonian polyp: evidence from physical models

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Abstract: The influence of polyp posture on local velocity profiles around the suspension-feeding tentacles was determined using a scale model of a polyp of the tropical gorgonian *Pseudopterogorgia acerosa* (Pallas). Polyp flexion was found to be an important mechanism for maintaining reduced and less variable flow velocities at the level of the polyp: local velocities were reduced by 40% in mainstream velocities of \( \frac{5 \text{ cm}}{\text{s}} \), by 80% in mainstream velocities of \( \frac{10 \text{ cm}}{\text{s}} \), and by \( \frac{20 \text{ cm}}{\text{s}} \). Flow patterns indicated a recirculation of water behind the polyp at intermediate mainstream velocities that may further enhance particle capture. Polyp flexion may act in conjunction with colony flexibility to increase the range of current velocities over which suspension-feeding is successful.

Key words: Cnidarian; Flow pattern; Gorgonacean; Suspension-feeding

INTRODUCTION

Most suspension-feeders capture food particles from fluid media at low Reynolds numbers. In this realm, viscous forces dominate and flows are reversible, creating an environment where a limited number of particle capture mechanisms are feasible. LaBarbera (1984) characterized these mechanisms as: (a) scan and trap, (b) sieving, (c) direct interception, (d) inertial impaction, (e) gravitational deposition, and (f) diffusive deposition. Regardless of the specific capture mechanism involved, an important factor dictating particle capture success is the velocity of the flow encountered by the suspension feeding apparatus (Rubenstein & Koehl, 1977; LaBarbera, 1984); mainstream velocities affect both the flow pattern around elements in the suspension-feeding apparatus and the probability of particle loss after capture.

Gorgonians (Cnidaria: Gorgonacea) are an important component of tropical coral reefs. Research on cnidarian nutrition has demonstrated that many cnidarians obtain nutrients through a combination of three processes: incorporation of photosynthetic products of symbiotic zooxanthellae, active transport of dissolved nutrients across epidermal membranes, and suspension feeding (Muscatine, 1973; Johannes, 1974; Lewis & Price, 1975; Lewis, 1976; West et al., 1977). Because most of this work has been conducted with scleractinian corals, not all of these processes can be assumed to
function in gorgonians. Particle capture, however, has been documented for four species of gorgonians (Leversee, 1976; Lasker, 1981), an octocoral (Patterson, 1983), and juvenile *Pseudopterogorgia* spp. colonies (Sponaugle & LaBarbera, 1991).

As passive suspension-feeders, gorgonians are highly dependent on ambient currents to drive particle-laden fluids through the colony. Recent work evaluating the feeding success of *Pseudopterogorgia acerosa* (Pallas) colonies in various current velocities has suggested that colony-feeding rates are highest during moderate mainstream flow velocities (10–15 cm·s$^{-1}$), and reduced at low (0–5 cm·s$^{-1}$) and high (20–25 cm·s$^{-1}$) velocities (Sponaugle & LaBarbera, 1991). Several processes may contribute to this enhanced feeding. With increased flow velocities, more prey items are transported across the colony. However, at high speeds, mechanical deformation of polyps and increased difficulty in capturing or retaining particles may reduce feeding success. Flow velocities in the vicinity of the polyps can be kept relatively constant, however, through the reversible deformation of the colony (Sponaugle & LaBarbera, 1991). Similar results were reported by Harvell & LaBarbera (1985), who found that the maintenance of reduced and less variable velocities in a hydroid is an important consequence of flexibility. This buffering of local flow velocities may in part account for the relatively broad range of velocities over which successful particle capture occurs in *P. acerosa* (Sponaugle & LaBarbera, 1991).

Close examination of colony behavior reveals that in addition to colony flexion, individual polyps deform as higher flows are encountered. Increasing current flows produce distinct shifts in the polyp orientation as the polyp is deflected away from the oncoming flow. In experiments with live colonies, simultaneous flexion of both the entire colony and individual polyps prevents the isolation of the effects of each component. This study was designed to examine the local flow around a gorgonian polyp through the use of a scale (10×) model under conditions of dynamic similarity (identical Reynolds numbers; see Vogel, 1981). Flow patterns and local velocities were measured and mapped to clarify events occurring at the polyp level during particle capture. Comparisons were then made with direct measurements of local flow velocities in live colonies to trace the relative contributions of each level of flexibility.

**METHODS AND MATERIALS**

A model polyp was constructed 10 times life size based on close-up photographs of *P. acerosa* polyps (Fig. 1). Tentacles were modeled using catheter tubing of the appropriate diameter stiffened by the insertion of thin copper wire; the pinnules were modeled by small pieces of the wire inserted perpendicularly through the catheter tubing. The eight model tentacles were glued to a 4-mm high plastic cylinder, and the entire structure attached to a clay cylinder ("polyp stalk"). The stalk was then molded onto a steel cylinder ("branch") propped up on either end with clay support mounds. The clay stalk permitted adjustments in orientation, as did the wire-reinforced tentacles. The model
was placed in the center of a 15 × 15-cm cross-section, recirculating flow tank (Vogel & LaBarbera, 1978) and oriented horizontally and normal to the flow direction with the polyp stalk extending vertically from the top surface of the model branch.

Three orientations were used for the polyp: (1) vertical stalk with tentacles spread, corresponding to observed live polyp orientations in an ambient velocity of 5 cm · s⁻¹, (2) moderately bent (~45°) stalk with tentacles compressed slightly, corresponding to observed live polyp orientations in an ambient velocity of 10 cm · s⁻¹, and (3) bent (~90°) stalk with tentacles more compressed, corresponding to observed live polyp orientations in an ambient velocity of 20 cm · s⁻¹. Mainstream velocities were adjusted to maintain Reynolds numbers consistent with the in vivo situation (Table I).

Flow patterns were observed and mapped with use of fluorescein dye released continuously from catheter tubing positioned 5–10 cm upstream from the model. The level and position of the dye release was adjusted with a micromanipulator attached to the catheter device.

Local velocities were obtained from strobe-illuminated photographs (Vogel & Feder, 1966) of fluorescein-dyed Pharmacia Sephadex G-50 beads. Beads suspended in dilute dye were released from a syringe ~25 cm upstream of the polyp. The camera (35 mm with attached macroscopic lens) shutter was manually controlled and opened as the particles travelled around the model. An electronic stimulator driving the strobe trigger
TABLE I


<table>
<thead>
<tr>
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<th>Actual</th>
<th>Model</th>
</tr>
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<tbody>
<tr>
<td>Fluid density (10^3 kg·m⁻³)</td>
<td>1.02</td>
<td>1.00</td>
</tr>
<tr>
<td>Fluid dynamic viscosity (10⁻³ Pa·s⁻¹)</td>
<td>0.97</td>
<td>1.31</td>
</tr>
<tr>
<td>Characteristic length (polyp stalk diameter) (10⁻³ m)</td>
<td>0.55</td>
<td>5.50</td>
</tr>
<tr>
<td>Flow velocity (cm·s⁻¹) generating:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Re = 29</td>
<td>5.0</td>
<td>0.7</td>
</tr>
<tr>
<td>Re = 58</td>
<td>10.0</td>
<td>1.4</td>
</tr>
<tr>
<td>Re = 116</td>
<td>20.0</td>
<td>2.8</td>
</tr>
</tbody>
</table>

permitted adjustments to the frequency of stroboscope firing. Photographs produced multiple images of the particles on the film, tracing streamlines. Local flow velocities could be calculated from the multiple particle images and known strobe frequencies (strobe frequency divided by the number of particle images per cm). Real, or “actual” velocities could then be backcalculated from the measured velocities. These “actual” velocities were comparable to the in vivo local velocities measured with a thermistor flow probe on live colonies during whole colony and polyp flexion (Sponaugle & LaBarbera, 1991).

RESULTS

Flow patterns around the model gorgonian polyp varied with mainstream current velocity (Fig. 2). In the first orientation, which corresponded to polyps in a mainstream velocity of 5 cm·s⁻¹, flow was laminar around the polyp and rarely penetrated the tentacles. Some eddying of the water occurred several polyp diameters downstream and behind the model gorgonian branch. In the second orientation, which corresponded to polyps in a mainstream velocity of 10 cm·s⁻¹, downstream eddies were more developed, with flows travelling back upstream directly towards the polyp tentacular crown (Fig. 3A). Water flowing around the stalk eddied behind the stalk and also circled back up towards the tentacular crown (Fig. 3B). Flow tended to pass around the polyp rather than through the tentacles, although streams occasionally passed through the distal third of the space between the tentacles. Flow around the polyp in the third orientation, corresponding to a mainstream velocity of 20 cm·s⁻¹, remained laminar, and penetrated the tentacles more frequently than in the previous orientations and velocities. Recirculation occurred several polyp diameters downstream but rarely travelled far upstream. At this Reynolds number, small eddies also formed directly downstream of the model branch.

Strobe-illuminated photographs enabled the calculation of local flow velocities at
Fig. 2. Flow patterns around the model polyp in a mainstream velocity equivalent to in vivo velocities of (A) 5 cm·s⁻¹, (B) 10 cm·s⁻¹, and (C) 20 cm·s⁻¹. Flow streams were drawn by hand based on fluorescein dye patterns. Scale is in mm.
Fig. 3. Downstream circulation of fluorescein dye released from catheter tubing positioned upstream of the (A) modelled polyp and (B) modelled stalk. Polyp orientation corresponded to a mainstream velocity of 10 cm·s⁻¹. Scale is in mm.
Fig. 4. Flow velocities around the model polyp at speeds corresponding to in vivo mainstream velocities of (A) 5 cm·s⁻¹, (B) 10 cm·s⁻¹, and (C) 20 cm·s⁻¹. Velocities were calculated from multiple exposure strobe-illuminated photographs of fluorescein-dyed Sephadex beads moving around the model polyp. Scale is in mm.
Reduction of mainstream current velocities due to polyp flexion alone (model) or whole colony and polyp flexion (live colonies; data from Sponaugle & LaBarbera, 1991) for three mainstream velocity ranges, corresponding to three different polyp orientations.

<table>
<thead>
<tr>
<th>Mainstream velocity (cm·s⁻¹)</th>
<th>Local velocity and percent reduction due to Polyp flexion (cm·s⁻¹)</th>
<th>Whole colony and polyp flexion (cm·s⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>3</td>
<td>1.5</td>
</tr>
<tr>
<td></td>
<td>40%</td>
<td>70%</td>
</tr>
<tr>
<td>10</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>80%</td>
<td>80%</td>
</tr>
<tr>
<td>20</td>
<td>10</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>50%</td>
<td>75%</td>
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Average velocities at or just below the tentacle tips were substantially reduced relative to mainstream velocities (Table II). The effect of polyp flexion on local flow velocity was variable across the three mainstream velocities, with the greatest difference occurring in the intermediate velocity (second orientation). Calculations based on measurements of live colonies (i.e., polyp and whole colony flexion; Sponaugle & LaBarbera, 1991) demonstrated that during the lowest and highest flow velocities, local velocities were lower than in the modelled case, while in the intermediate mainstream velocities, local flow velocities in the two situations were approximately equivalent. In the live colonies, velocity reduction across all three mainstream velocities was less variable (70–80%) than for the model polyp.

**DISCUSSION**

Based on hydrodynamics, maximally efficient suspension-feeding should occur over a relatively narrow range of flow velocities (LaBarbera, 1984). Okamura (1984, 1985) observed that high ambient velocities reduced zoid feeding in small colonies of an arborescent bryozoan, and in large and small colonies of an encrusting species. In larger arborescent species, however, feeding remained relatively constant with increasing velocities, presumably due to flow deflection by more branches (Okamura, 1984). Although also dependent on a number of other parameters, the feeding activity of stalkless crinoids appears to be greatest at intermediate current flows (Leonard, 1989). Juvenile colonies of *P. acerosa* have recently been reported to feed most successfully in an intermediate range of current velocities (Sponaugle & LaBarbera, 1991). This intermediate feeding success may be a function of the increased transport of particles across the colony with increasing flow, coupled with increased difficulty in capturing prey. By minimizing the variability in local velocities at the polyp, flexibility may function in extending the range of velocities over which successful particle capture can occur.

Flexibility in these two gorgonians occurs at two levels: at the whole colony/branch and at individual polyps. Comparison of the local velocities in the vicinity of the polyp during polyp flexion (as modelled in this study) with measured local velocities at the
polyp during both whole colony and polyp flexion (Sponaugle & LaBarbera, 1991) demonstrates that both levels contribute to the maintenance of relatively less variable flow velocities at the polyp (Table II). While neither the colony nor the polyps flex much at the lowest velocity (5 cm·s⁻¹), polyp orientation alone can greatly reduce the mainstream flow velocity. This reduction is most likely due to flow deflection around the polyp and branch. Local velocities at the polyps within a colony appear to be further reduced as flow is deflected by neighboring polyps. By the second flow regime (mainstream velocity of 10 cm·s⁻¹), live colonies are deforming in the flow as well as the polyps. Because colony deformation could act to reduce the initial flow encountered by the polyps, it is difficult to determine the relative contributions of each level of flexibility. Polyps within a colony may be encountering relatively lower flows, so the flow reduction due to polyp flexion may not be as great as that predicted by the model. Where polyps encounter a 10 cm·s⁻¹ flow, however, polyp flexion alone can contribute substantially to the maintenance of reduced local velocities (Table II). In the third orientation corresponding to a high mainstream velocity (20 cm·s⁻¹) local velocities in the vicinity of the polyp were greater than those measured on the live colony, suggesting that while polyp flexion could reduce flow by as much as 50%, colony flexion is necessary for further flow reduction.

The velocity measurements and flow patterns around the model gorgonian polyp support the observation of enhanced feeding success at intermediate velocities. The greatest reduction in flow velocities at the level of the polyp occurred in the second orientation corresponding to intermediate mainstream velocities. This may reflect a situation where a relatively large number of particles can be carried to the colony while the velocity of the flow encountered at the polyp level is relatively low. Observed flow patterns also suggest that recirculation of water back to the polyp may contribute to enhanced feeding success at intermediate flow velocities. Only in intermediate mainstream velocities did eddies forming downstream of the polyp circle back directly into the tentacular crown. The recirculation of water downstream of the polyp may reintroduce prey items, providing additional opportunities for capture at low local velocities (Leversee, 1976). During in vivo experiments, Artemia nauplii were seen within these eddies behind P. acerosa polyps, and often remained there for several seconds before being either caught or carried downstream (Sponaugle, unpubl. data).

Flow patterns around the modelled polyp revealed that most of the water flows around the polyp rather than through the tentacles, suggesting that sieving of the flow through the pinnules may not be a primary feeding mechanism. Although the particle size most frequently caught in nature is unknown, during laboratory observations, live gorgonian colonies feeding on relatively large prey (Artemia nauplii ≈ 0.5 mm in length) appeared to use a combination of direct interception and diffusive deposition (see LaBarbera, 1984) to capture prey. As the prey travels near the polyp tentacles, either passively or by active swimming, it is captured by the tentacles and inserted into the polyp mouth. As prey is moved into the gut, tentacles re-expand to feed again.

Scale models can permit the delineation of processes occurring on live organisms. In
this study, modelling a gorgonian polyp enabled the separation of the effects of whole colony and polyp flexion on the flow encountered by a suspension-feeder. While polyp flexion can account for a substantial portion of the flow reduction at the polyps, whole colony flexion is also important for reducing velocity fluctuations, particularly during high mainstream velocities. Whole colony and polyp flexion interact to reduce the range of velocities encountered by the suspension-feeding polyps, thus extending the range of mainstream velocities over which suspension-feeding is successful.

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REFERENCES


