

FLEXIBILITY: A MECHANISM FOR CONTROL OF LOCAL VELOCITIES IN HYDROID COLONIES

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ABSTRACT

A design conflict exists in passive suspension feeding colonies between maximizing surface area for feeding and minimizing drag-related forces on the colony. The importance of colony flexibility as a homeostatic mechanism was demonstrated experimentally on the scale of both the entire colony and the polyp. On the colony scale, flexibility reduces the relationship between drag and water velocity from a square to a first power dependence. This finding is consistent with the discovery that flexion in trees also reduces drag to a linear function of velocity. On the polyp scale, colony flexibility strongly damps flow velocity changes at the polyp over at least an order of magnitude change in ambient velocity. This previously unappreciated consequence of flexibility may be an important selective force affecting the evolution of colony form. The separate consequences of flexion at the polyp and whole colony level are considered in a simple conceptual model incorporating polyp feeding success and colony detachment probability over a range of flow velocities. Inspection of the model reveals that the lower velocity limit at which a colony can survive is likely to be constrained by polyp feeding success, while the upper velocity limit may be constrained by either polyp feeding success or the probability of colony detachment.

INTRODUCTION

Suspension feeding is a common trophic mode among colonial marine invertebrates. For a broad range of invertebrate taxa in the Cnidaria (Gorgonacea; Hydrozoa: Plumulariidae, Sertulariidae) (Warner, 1977) and Bryozoa (Cheilostomata; Cyclostomata), colonies that live in habitats with uni- or bi-directional currents maximize their feeding area with a planar morphology perpendicularly oriented to the prevailing current direction. However, a design constraint arises from the conflicting demands to increase surface area to maximize food intake and to decrease surface area to minimize drag forces. Most of these colonies appear to solve the design dilemma of increased drag by being flexible, thus bending rather than breaking as current-induced drag forces increase (Murdoch, 1976; Wainwright and Koehl, 1976; Patterson, 1983).

Although drag on a rigid object is proportional to the square of ambient velocity, flexibility can reduce the exponent relating velocity to drag. For example, Fraser (1963) reported that drag on trees is directly proportional to velocity rather than to velocity squared; this drag reduction is attributable to a bending of the branches and consequent streamlining of the tree, yielding changes in both the cross sectional area exposed to the flow and the drag coefficient. Koehl (1977) and Vogel (1984) have also demonstrated that drag is reduced in sea anemones and trees respectively, by such profile changes.

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An analysis of the effects of current-induced drag is complicated in colonial forms because hydrodynamic forces act on two spatial and functional scales: on the architecture and stature of the entire colony, and on the stature and behavior of individual polyps. Drag forces can dislodge colonies (Birkeland, 1974; Patterson, 1983) and disrupt the success in particle capture of polyps (Leversee, 1976; Okamura, in press). It is useful to discriminate between these scales because the consequences of increasing colony size and high drag forces differ at the two levels. For example, drag-induced dislodgement becomes an increasing source of mortality in larger colonies (Birkeland, 1974), while the drag forces on individual polyps are more disruptive to the feeding of small colonies (Okamura, in press). Although drag reduction on the whole colony is a frequently cited consequence of flexibility, an important and seldom discussed consequence of colony flexion is the resulting change in flow regime around the feeding units. As a colony flexes and streamlines, ambient flow will increasingly tend to pass around a colony rather than through it. We postulate that colony flexion is an important homeostatic mechanism operating to buffer changes in the hydrodynamic forces both for the individual polyp and the entire colony.

To test our hypotheses about colony design and hydrodynamics, we investigated the behavior of colonies of the hydroid *Abietenaria rigida* to variable currents in a flow tank. *Abietenaria rigida* is a planar branched hydroid whose colonies consist of one or more erect stipes bearing alternating, symmetrical side branches (Fig. 1). This morphology is a common architectural arrangement in hydroids from high current habitats. *A. rigida* is locally abundant in Puget Sound at 15–30 m depth in high current areas; at the locale where our colonies were collected, maximum average current speeds measured at 0.10 m above the substrate range from 0.2 to 0.4 m/s (Schopf *et al.*, 1980). At these sites colonies are oriented perpendicular to the predominant current direction in a stable, but maximum, drag configuration (Wainwright and Dillon, 1969). To interpret the consequences of flexion for *A. rigida*, we experimentally altered the stiffness of colonies and measured (1) how drag on stiff or flexible colonies varied with velocity and (2) how flow velocity at the polyp location varied with mainstream velocity for stiff or flexible colonies.

MATERIALS AND METHODS

For rigid objects at high flow velocities (high Reynolds number) drag is given by:

$$D = \frac{1}{2} C_d \rho S U^2$$

Over a limited range of Reynolds number the coefficient of drag (C_d) can be considered a constant; drag is thus proportional to the surface area (S) perpendicular to the flow and the flow velocity (U) squared (see Vogel, 1981). The density of water (ρ) is assumed constant.

Drag on the colonies was measured in a 15 by 15 cm square cross section flow tank (Vogel and LaBarbera, 1978). A foil strain gage bonded to a 0.130-cm thick aluminum beam was attached to the colony by a lever arm. The signal from the strain gage was amplified through an Intersil ICL7605 integrated circuit using the manufacturer's recommended circuit and recorded on a Brush 2200 chart recorder. The gage was calibrated by hanging known masses off the lever arm. Net sensitivity was approximately 10^{-4} N. Water velocities were calculated from the measured drag on a 3.7 cm diameter disc attached to a second strain gage beam. This provided an accurate measure of velocity at high speeds because the force measured (drag) is

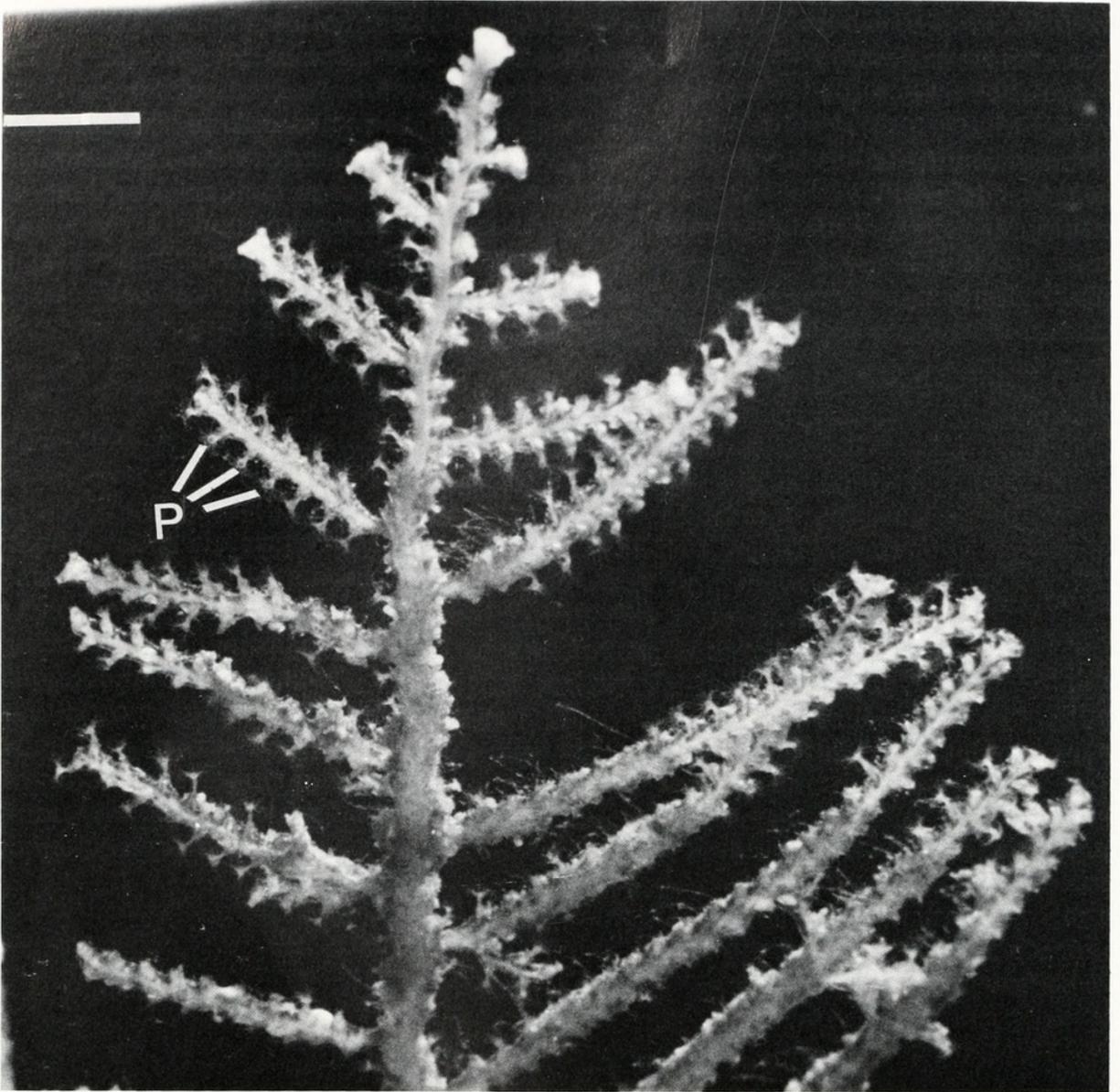


FIGURE 1. Colony architecture and polyp placement on *Abietenaria rigida*. P, polyp; scale, 1 cm.

proportional to velocity squared and the coefficient of drag for a disc is constant over a broad range of Reynolds numbers (Vogel, 1981). At low velocities, water velocity was measured by timing the passage of a dye cloud over a known distance.

Stiffened colonies were prepared by soaking selected fresh colonies in distilled water for two hours and drying them overnight at 60°C. A steel wire (0.030 cm diameter) was carefully threaded up the central axis of the colony, the colony was impregnated with cyanoacrylate cement, and then sprayed with five coats of an aerosol acrylic plastic. To quantify the difference between natural and stiffened colonies, the flexural stiffness EI (see Wainwright *et al.*, 1976) was determined by measuring the force necessary to deflect the specimens through known distances and applying the standard formula for deflection of a cantilever beam. The mean value of EI for fresh *A. rigida* colonies was $6.84 \times 10^{-6} \text{ Nm}^2$; the mean EI for stiffened colonies was $1.02 \times 10^{-4} \text{ Nm}^2$.

Detachment strength, the force required to detach a colony from the substrate, was measured on 21 colonies ranging from 2.8–7.0 cm high. Force was applied

parallel to the colony axis with a Schaevitz model FTD-G-1K force transducer. The signal was recorded on a Brush 2200 chart recorder; accuracy was ± 0.05 N.

Local current speeds around colonies were measured with a thermistor flowmeter modified after the design of LaBarbera and Vogel (1976). Spatial resolution was 0.5 mm; precision and accuracy were $\pm 5\%$. Measurements at the polyp locations were made by positioning the probe 1 mm above branches where the polyps are normally positioned. The probe was positioned about 1/2 way down the stipe, and at the midpoint of a side branch.

RESULTS

The drag on flexible *A. rigida* colonies is directly proportional to mainstream current velocities (Fig. 2), but the drag on artificially stiffened colonies is proportional to the square of mainstream velocity. The decreased drag on naturally flexible colonies relative to artificially stiffened colonies is a function of colony profile changes due to flexion; as a colony flexes, more water can move around or over the colony rather than through it and a reduced surface area is presented to the current. At velocities of 20–30 cm/s, flexible colonies experience an order of magnitude lower drag forces than artificially stiffened colonies of similar size.

Detachment strength, the force required to dislodge an *A. rigida* colony from the substrate, ranged from 1.4–6.0 N and was independent of colony size. In 95% of the colonies tested, failure occurred at the interface between the holdfast and the substrate, not within the colony itself. A linear regression of detachment force measured in newtons versus colony height measured in centimeters yielded the equation: detachment force = 0.222 (height) + 1.95 (n = 21; r = 0.284). This poor fit to a linear model suggests that there is little correspondence between colony size measured as height and detachment force. Extrapolating the data in Figure 2, a

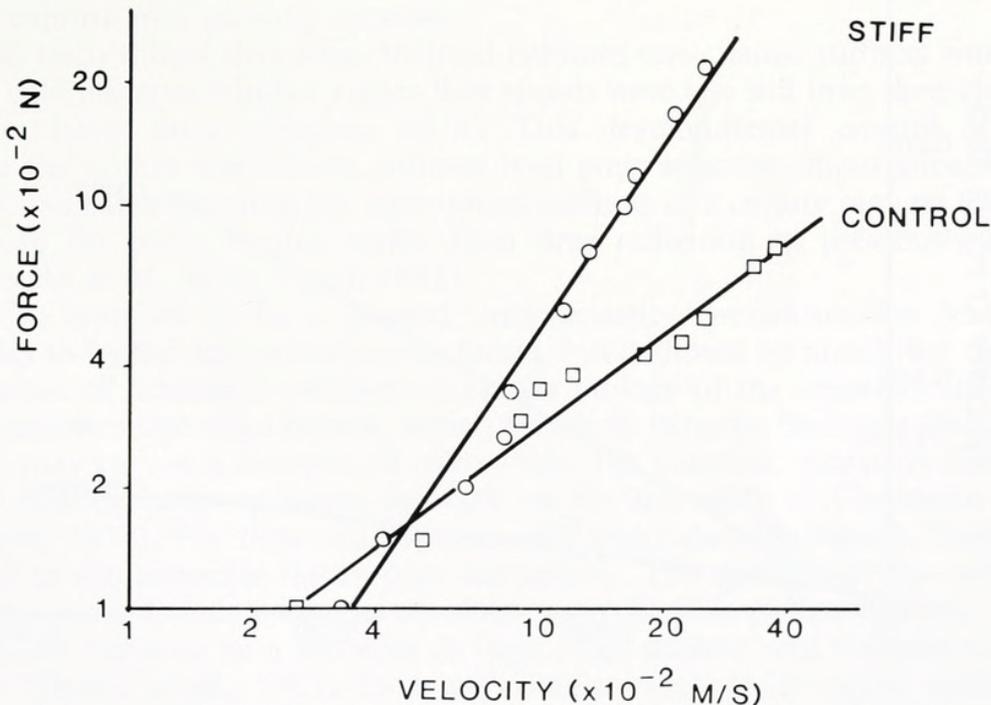


FIGURE 2. Drag force as a function of flow velocity for experimentally stiffened (O) and normal, flexible colonies (\square). The least squares linear regressions fit to these log plot data are: log force (N) = 1.91 U (m/s) - 0.46 (stiffened) and log force (N) = 0.94 (m/s) - 1.65 (controls).

stiffened colony would be dislodged by drag at a mainstream velocity of about 5×10^2 cm/s; a flexible colony would only be dislodged by currents in excess of 1.5×10^4 cm/s. These values far exceed the velocities that would ever be experienced by subtidal populations. Thus colonies are far more flexible than they need to be to avoid dislodgement. From this, we conclude that reduction of whole colony drag forces is not the primary selective force favoring colony flexion.

The local flow velocity around different portions of *A. rigida* colonies varies considerably, from values nearly equivalent to mainstream velocities to essentially still water. The high degree of spatial variation in flow speeds provides an opportunity for polyps to behaviorally mediate their flow environment. At low velocities, polyp tentacles are rigid and outstretched, creating a complete mesh between the branches through which water flows. As mainstream velocity increases and the colony flexes, the polyps themselves bend and the tentacles move behind the branch to areas of lower velocity, perhaps capturing food particles in eddy currents (Leversee, 1976; Patterson, 1983). The local flow velocity in regions where the polyps normally are located remains approximately constant (2–3 cm/s) over a 17 cm/s range of mainstream velocities (Fig. 3). For artificially stiffened colonies, the variation in velocity at the polyp locations with increases in mainstream velocity is much greater. In addition, although velocity at the polyp on both stiffened and flexible colonies increases in almost direct proportion to increases in mainstream flow, the slope of the increase in flexible colonies is considerably less than that for stiffened colonies (Fig. 3). Thus, polyps on normal, flexible colonies experience a damped flow environment with reduced variability in flow speeds relative to stiffened colonies.

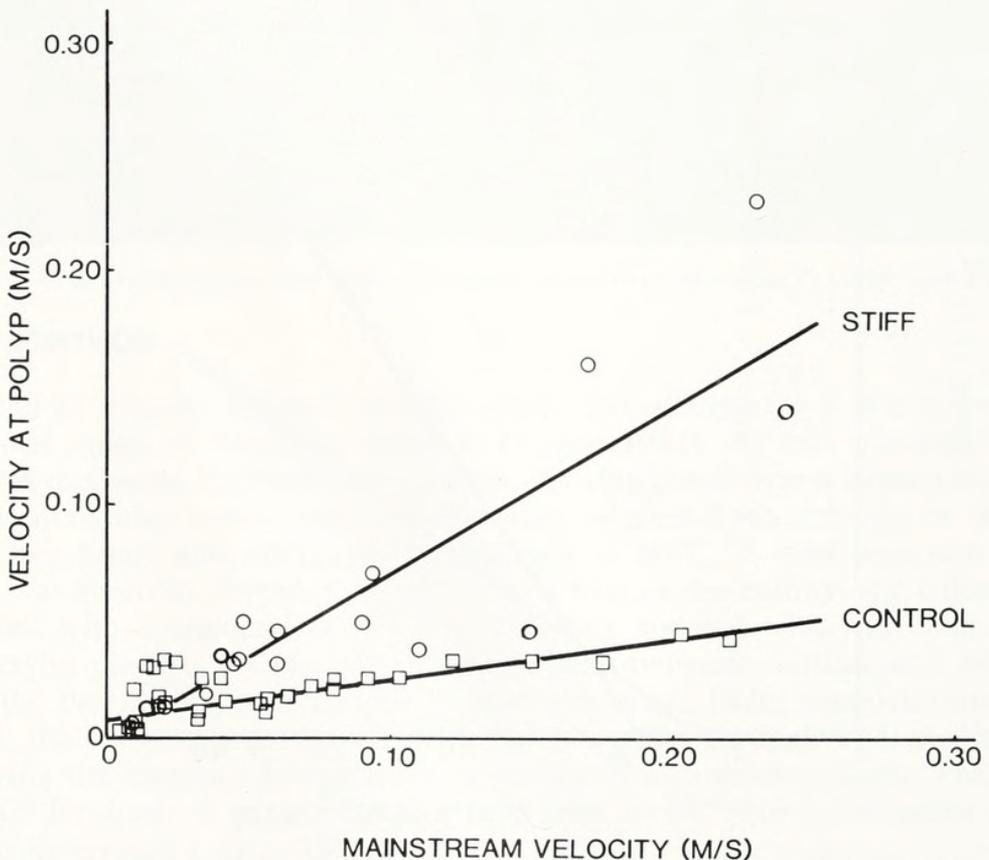


FIGURE 3. Velocity at the polyp as a function of mainstream velocity for experimentally stiffened (○) and normal, flexible control colonies (□).

DISCUSSION

The design of passive suspension feeding colonies appears to be constrained by the conflicting requirements of minimizing total drag and maximizing the flux of capturable particles through the feeding structures. Colony flexion resolves this conflict and allows simultaneous maximization of colony surface area and minimization of flow variability at the feeding units. The striking constancy of flow velocity at the polyp over a wide range of mainstream flow speeds is a previously unappreciated consequence of flexibility.

LaBarbera (1984) has argued that the hydrodynamics of small particles near surfaces implies that suspension feeders may capture particles with maximal efficiency only over a narrow range of flow velocities. Okamura (in press) reports reduced feeding of zooids from small, upright bryozoan colonies at faster velocities. Larger colonies are less sensitive to increases in flow velocity. We predict that several mechanisms exist to minimize flow variability at the polyp in variable mainstream flows, ranging from colony flexion and reorientation to polyp behavioral changes. Passive suspension feeders can be categorized on the basis of the mechanism of particle capture (LaBarbera, 1984). *A. rigida* appears to use a combination of aerosol particle capture mechanisms, depending upon the mainstream water velocity and the density of particle. The benefits of decreased flow variability may be greater with some feeding mechanisms than others. For example direct interception, which is likely to be the predominant particle capture mechanism in *A. rigida*, may be strongly dependent upon polyp posture and local flow velocities. For all mechanisms, success in feeding is highly dependent upon surface area exposed to flow, which is in turn affected by flow speed. As flow speed changes, colony and polyp postures change, and at the highest flow speeds, hydroid polyps retract and thus do not feed at all. A simple mechanism to circumvent (or at least reduce) the requirement for frequent changes in polyp posture is colony flexion. The cost of changing postures is probably a decreased gross efficiency in particle capture, although the rate of particle capture may actually increase.

It has been shown that some hydroid colonies can change stiffness with current regime; colonies grown under higher flow speeds were less stiff than their clonemates grown in lower flows (Hughes, 1978). This developmental control of stiffness supports the notion that colony stiffness is of great selective importance. However, the major variable dictating the appropriate stiffness of a colony may be the optimal flow range for polyp feeding rather than drag reduction as previously suggested (Wainwright *et al.*, 1976; Vogel, 1981).

Flexion appears to be a general, interphyletic mechanism for dealing with variability in hydro- and aerodynamic forces, but it should be noted that the specific implications of flexibility will depend on the biology of the organism involved. In marine passive suspension feeders, design trade-offs between feeding units and whole colonies may vary as a function of colony size. For example, mortality due to drag-induced dislodgement accounts for 80% of the mortality of Caribbean sea fans (Birkeland, 1974). For these sea fans, as with hydroids in this study, failure often occurred in the substrate rather than the colony. The strength of the substrate or colony-substrate interface sets an absolute upper limit to colony stiffness and size, and is more likely to be a problem in large, high surface area colonies than small colonies (Denny *et al.*, 1985). In small colonies, such as *A. rigida*, dislodgement due to drag forces does not appear to be a large source of mortality. We have shown that the force required to dislodge a colony is far in excess of the drag normally encountered. In general, we postulate that the evolutionary effects of drag on colony

design will be dependent on colony size: selection will act on large colonies to minimize drag, while for small colonies, constancy of flow at the polyp may be of greater selective importance.

A simple conceptual model of the relative constraints imposed by the sometimes conflicting requirements of drag minimization *versus* particle capture maximization is presented in Figure 4. A successful colony is likely to maximize the combined probabilities of surviving dislodgement and particle capture over some range of flow velocities. Viewing the probabilities of these events separately and then in combination allows us to determine which level constrains performance at any given velocity. The probability of surviving dislodgement over a range of flow velocities is plotted in Figure 4a as one minus the probability of dislodgement. This probability is one at low velocities and declines as some function, here shown as a sigmoid, of increasing flow. At some extreme high velocity, the colony will eventually detach, either due to substrate or colony failure; at this point the probability of survival is zero. Similar functions and the rationale for a sigmoid curve are presented in Denny *et al.* (1985). Because there is no single good measure of the feeding success of a colony and because the true shape of the curve is not known, we will plot some function of the probability of polyp capture success over a range of flow velocities in Figure 4b. We can assume the curve is peaked with low probabilities at extreme low and high velocities. Viewing the combined probability of surviving dislodgement and polyp capture success (Fig. 4c) allows us to determine which level is constraining

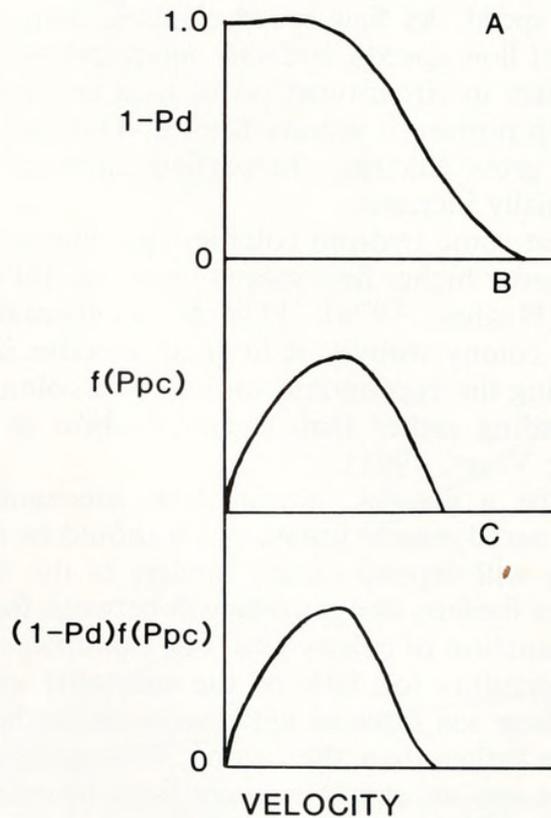


FIGURE 4. Model incorporating the probability of surviving colony detachment and polyp particle capture success as a function of velocity. A. The probability of surviving detachment. B. A function of the probability of polyp capture success. C. The combined probability of surviving detachment and polyp particle capture success. Pd—Probability of detachment. Ppc—Probability of polyp particle capture.

performance. In the example shown, the probability of particle capture (Fig. 4b) drops to zero at a lower velocity than the probability of surviving dislodgement (Fig. 4a). This is analagous to the situation measured for *A. rigida* and represents a situation where the requirements of particle capture set the upper velocity at which a colony can succeed. In the model, the zero probability of polyp capture success forces the resultant probability depicted in Figure 4c to be zero at the same velocity. The upper velocity at which a colony survives can be determined by either low polyp feeding success or a low probability of surviving dislodgement. From the model, the lower velocity limit is set by polyp capture success since the probability of surviving detachment is always one at low velocities. The measurements made on *A. rigida* provide an example of a colony where the upper velocity limit is set by particle capture success. An example where the upper limit may be set by dislodgement is that already discussed for tropical gorgonians. In general, we expect that the maximum velocities tolerated by large colonies are more likely to be limited by whole-colony drag or the risk of dislodgement than by polyp capture success.

For *A. rigida*, an abundant hydroid frequenting high flow environments, flexion acts to reduce drag and minimize variability in local flow velocities. Mechanisms promoting constancy in local flow may prove to be important adaptations possessed by many colonies living in high flow environments.

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