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With our compliments,
Larry Sanford

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A new explanation of particle capture in suspension-feeding bivalve molluscs

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Abstract

Using video endoscopy, we examined water flow through the infrabranchial cavity and observed particle capture by the ctenidia (gills) of several species of suspension-feeding bivalve molluscs. We found that previously published interpretations of the particle capture process did not adequately explain our in vivo observations. Instead, we propose that particle capture in bivalves can be explained in terms of hydrosol filtration theories that have been shown to apply to a wide diversity of aquatic suspension feeders. Particles are captured by direct interception with the ctenidial filament and then transported along the frontal surface of the filament by mucociliary processes. Two primary mechanisms aid in capture. First, the low angle at which particles approach the filaments increases the probability of encounter with frontal cilia. Second, vortical flow patterns set up by the beating of the laterofrontal cilia or cirri reduce or block flow through the interfilamentary spaces and redirect it toward the frontal surface of a filament. This flow pattern further increases encounter efficiency with the frontal cilia and promotes particle retention on the frontal surface. Our studies indicate that the suspension-feeding complex as a whole (incurrent siphon/margin, ctenidia, and mantle) functions in a highly integrated manner and is critical for particle capture. This observation calls into question previous explanations developed from examination of surgically altered bivalves.

Suspension feeding is one of the most common methods of food collection among aquatic invertebrates. During the last several decades, numerous workers have examined the physical and behavioral factors that mediate particle capture in various suspension-feeding invertebrate groups (*see* reviews by Rubenstein and Koehl 1977; LaBarbera 1984; Jørgensen 1989; Shimeta and Jumars 1991). While the anatomy and location of feeding structures vary considerably among taxa, the actual physical and hydrodynamic mechanisms involved in particle capture, at the scale of the capture structure, are often similar (Shimeta and Jumars 1991). Computer-aided video imaging techniques have enabled researchers to examine species with exposed feeding structures under nearly natural conditions; such species include adult cnidarians, annelids, and arthropods (Patterson 1984; Mayer 1994; Trager et al. 1994; Yen and Strickler 1996), as well as larval arthropods, molluscs, and echinoderms (Strathmann 1982; Gallager 1988; Hart 1991; Merritt et al. 1996). These studies have greatly increased understanding of suspension-feeding mechanisms, and they have allowed testing of theoretical models for particle capture and establishment of general rules for suspension-feeding processes (Koehl and Strickler 1981; LaBarbera 1984; Shimeta and Jumars 1991).

Concurrently, the development of video endoscopy has also allowed in vivo observations of organisms in which the feeding apparatus is concealed, such as adult bivalve molluscs (Ward et al. 1991). This research has led to a more accurate understanding of many suspension- and deposit-feeding processes in bivalves (Beninger et al. 1992; Ward et al. 1993, 1994; Levinton et al. 1996; Ward 1996). However, the mechanisms by which particles are captured by the cte-

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nidia (gills) of bivalve molluscs remain poorly defined, at least in part due to problems associated with studying small-scale processes in animals that are enclosed within opaque shells. In fact, current explanations of particle capture in bivalves have been largely based on surgically altered specimens or on isolated ctenidial filaments and their associated tracts of cilia. Extrapolation of in vitro results to explain in vivo mechanisms (e.g., Nielsen et al. 1993; Silverman et al. 1996*a,b*) implicitly assumes that the filaments and other feeding structures function realistically as discrete units in the absence of other constituent parts. While valid under certain circumstances, results obtained from dissected animals should be interpreted with caution because surgery can stimulate excess mucus production and cause feeding structures to function abnormally (Jørgensen 1976). Furthermore, isolation of pallial organs can alter the hydrodynamics of flow across these organs and destroy the subtle interactions between adjacent feeding structures (e.g., ctenidia and labial palps; Beninger et al. 1992; Ward et al. 1993). Therefore, mechanisms of bivalve feeding cannot be understood simply from studies on exposed ctenidia or ctenidial filaments (e.g., Jørgensen 1981, 1990).

Consequently, mechanisms underlying particle capture in suspension-feeding bivalves remain uncertain and controversial. Some workers maintain that particles are mechanically trapped by rows of laterofrontal cilia or cirri and are transferred onto frontal ciliary tracts of the ctenidial filaments (Tammes and Dral 1955; Dral 1967; Moore 1971; Silverman et al. 1996*b*). Others suggest that particles are retained by hydrodynamic forces, such as shear stresses, that might arise at the level of the interfilamentary spaces (i.e., spaces between adjacent filaments; Jørgensen 1981, 1990). Neither explanation, however, adequately explains our in vivo observations of the capture phenomenon, and aspects of both explanations violate some of the physical and biological constraints imposed by the intact feeding system, such as the constraint of low Reynolds number flow. In addition, current explanations of particle capture in bivalves largely ignore accepted principles of hydrosol filtration that have been successfully applied to the study of other suspension-feeding species, both pelagic and benthic (cf. Jørgensen 1990; Shimeta and Jumars 1991). Finally, no current explanation takes into account the different types of laterofrontal ciliary structures found on the ctenidial filaments of different bivalve species. Ignoring this morphological diversity implicitly assumes that it has little influence on particle capture.

Previous endoscopic studies have focused predominately on postcapture processes (e.g., Ward et al. 1993) or presented observations of particle capture in specific bivalve species with little explanation of the mechanisms involved (e.g., Beninger et al. 1992; Ward et al. 1994). In this study, we examined particle capture in living, intact bivalves by means of video endoscopy. Assays were conducted in vivo with dyes, different size particles, and neurotransmitters to address questions pertinent to the capture process. We then critically evaluated previously published reports on suspension feeding and developed a new model of particle capture in bivalves, one that can be explained in terms of accepted principles of hydrosol filtration.

Table 1. In vivo observations of particle capture were made on six species of bivalves with different ctenidial forms and different laterofrontal tracts on the ordinary filaments. Particle approach velocities were measured at 12 to 15°C for all species except for those of *A. zebra* and *C. virginica* which were measured at 24°C. *n* = number of measurements made for each mean value; error estimates are standard deviations (SD).

Species	Laterofrontal tracts	Particle approach velocity (10^3 μm s^{-1}) ($\pm$SD)	*n*
Filibranchiate*			
Arca zebra	simple cilia†	1.66±0.63	15
Geukensia demissa	large cirri‡	NA§	—
Modiolus modiolus	large cirri	0.56±0.06	6
Mytilus edulis	large cirri	1.96±0.83	22
Pseudolamellibranchiate‖			
Crassostrea virginica	small cirri¶	1.77±0.32	10
Ostrea edulis	small cirri	0.89±0.21	9

* Flat, homorhabdic ctenidia.
† Length, 10–17 μm.
‡ Each had 22–26 pairs of cilia 20–30 μm in length.
§ Qualitative data only.
‖ Plicate, heterorhabdic ctenidia.
¶ Each had 6–11 pairs of cilia 14–25 μm in length.

Materials and methods

Video endoscopy was performed according to methods described in detail by Ward et al. (1991), Beninger et al. (1992), and Ward et al. (1993, 1994). The endoscope, equipped with either straight or side-viewing (90° angle) optical insertion tubes (OIT) measuring 1.7 mm in diameter, was attached to a video camera and mounted on a micromanipulator. The resolution of the video endoscope was about 3 μm at a maximum magnification of about 150×. Video signals were recorded (Sony, Hi8), digitized (RasterOps), and contrast enhanced (Jandel Scientific; Adobe Systems) prior to analysis (Ward et al. 1991).

Six bivalve species were studied, each possessing one of three types of laterofrontal ciliary tracts on the filaments of the ctenidia (Table 1). During endoscopy, bivalves were held in aerated seawater, either static or flowing at salinities similar to those of their natural environments. Specimens were allowed to feed freely on natural seston supplemented with cultured microalgae (*Thalassiosira* sp., *Tetraselmis* sp., and *Dunaliella* sp.) and various synthetic particles (polystyrene, alumina, and silica) ranging in diameter from 4 to 95 μm. To increase particle concentrations above background levels, particles were added to the seawater with a peristaltic pump just before entering the holding chamber (flowing system) or delivered to the inhalant margin of bivalves using a peristaltic pump or Pasteur pipette (static system). The OIT of the endoscope was introduced into the pallial cavity of a bivalve, and recordings were made after the animal had acclimatized to experimental conditions and exhibited normal feeding behavior. Bivalves that had extended mantle edges and that were drawing particles into the pallial cavity were considered to be feeding normally.

In vivo dye studies were conducted using a solution of either Evans Blue dye (Sigma Chemical; Gilmour 1986) or, when studying *Crassostrea virginica,* soluble pen ink (permanent blue; Parker). These dyes did not disturb feeding behavior of the bivalves when introduced into the pallial cavity. Dye was prepared with water isotonic with that of the holding chamber and adjusted with small amounts of higher or lower salinity seawater to obtain near neutral density. Dye was delivered to the bivalves using a low-flow peristaltic pump connected to fine-bore surgical tubing and a drawn glass micropipette mounted on a micromanipulator. Dye was slowly released close to the inhalant margin or within the infrabranchial chamber of the pallial cavity at the level of the ctenidial filaments.

To determine the role of the laterofrontal cirri in particle capture, we exposed *Mytilus edulis* to serotonin (5-hydroxytryptamine; Sigma Chemical). Serotonin affects the activity of laterofrontal cirri by reducing the angle of beat, and at concentrations of 10^{-5} to 10^{-4} M, the cirri remain immobile at the end of their effective stroke (Jørgensen 1976, 1990). Mussels were placed in separate 1-liter containers filled with seawater (20°C) supplemented with 10–20 μm polystyrene microspheres. Particle capture by the ctenidia was observed for a 10–15-min control period. Each mussel was then exposed to 10^{-4} M serotonin. After 15–30 min of exposure, the ctenidia were again observed for 10–15 min. The effect of immobilizing the laterofrontal cirri on particle capture was quantified by examining sections of the ctenidia (14–17 filaments wide), selecting 25 particles that encountered the section, and scoring whether they were retained or lost by the ctenidium. Particles were scored only when the mussel was actively pumping (flow speeds over the ctenidium $>1.6 \times 10^3$ μm s^{-1}). We also qualitatively examined the way in which particles were handled by the ctenidium before and after exposure to serotonin.

Morphometric analyses of digitized images were calibrated by isolating the ctenidia of several specimens of each bivalve species and measuring the width of filaments or plicae with a calibrated ocular micrometer under a compound microscope. Particle velocities were determined by counting the number of frames required for a particle to traverse a known distance just above or along a given structure; recording speed was 30 frames s^{-1} (NTSC format). Approach velocity could be estimated in animals with flat, nonplicate ctenidia (e.g., mussels, ark clams) because the approach vectors were largely in two dimensions (anteriorly and laterally). Filament width at point of particle contact was used as a scale to determine distance travelled above the ctenidia. Although there was some error associated with particles "wandering" in the third dimension, this movement was small compared to the other two approach vectors, especially at a location midway between the dorsal and ventral margins of a lamella. It was also possible to estimate the approach velocity of particles in bivalves with plicate ctenidia when particles were clearly moving only anteriorly and laterally. Particle approach velocities were calculated primarily from measurements with polystyrene microspheres. Because of their small diameter (10–20 μm) and low relative density (s.g. = 1.05), measured particle velocities were essentially equivalent to flow speeds through the infrabranchial chamber.

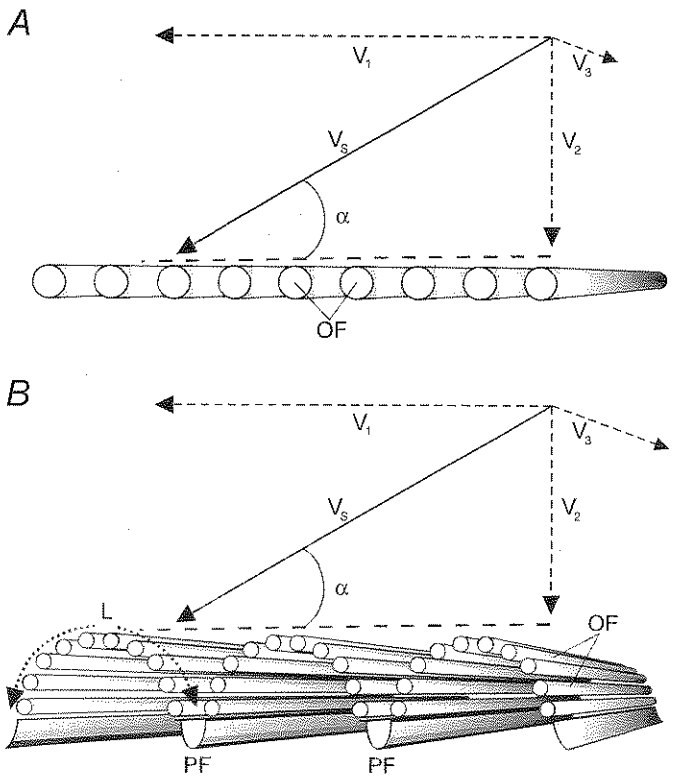

Fig. 1. Cross-sectional diagrams of ctenidial filaments, as viewed looking dorsally, showing components of flow within the infrabranchial chamber of bivalves. Component V_1 is directed anteriorly and parallel to frontal surfaces, component V_2 is directed laterally and perpendicular to frontal surfaces, and component V_3 is directed dorsally and parallel to frontal surfaces. The vector sum of flows (V_s) is the measured particle approach velocity with associated angle α. (A) Flat ctenidium in which α is measured with respect to the frontal surface of ordinary filaments (OF). (B) Plicate (heterorhabdic) ctenidium in which α is measured with respect to the frontal surface of the plical crests. Dotted arrows indicate localized flow (L) around plical crests and into the principal filaments (PF).

Results

Particle capture was examined in six different species of bivalves (Table 1). These species possess feeding structures that represent the major types of lamellibranch ctenidia, including the filibranchiate and pseudolamellibranchiate conditions. They also possess laterofrontal cilia of three different types (Table 1), including "large" laterofrontal cirri composed of 22–26 pairs of cilia each (20–30 μm in length), "small" laterofrontal cirri composed of 6–11 pairs of cilia each (14–25 μm in length), and "simple" cilia (10–17 μm in length) (Atkins 1938; Owen and McCrae 1976; Ribelin and Collier 1977; Owen 1978).

Analysis of flow—Analysis of the movement of particles and dye streams within the infrabranchial chamber of intact

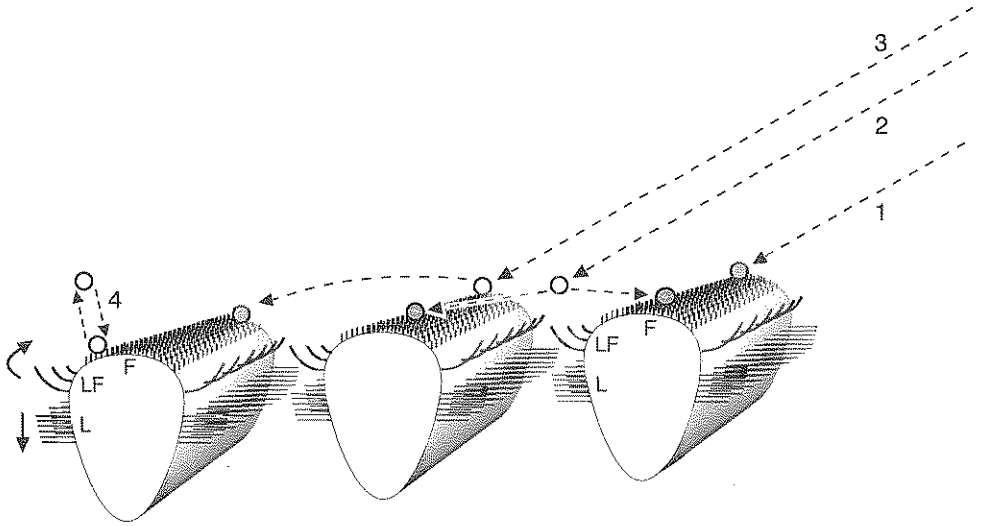

Fig. 2. Cross-sectional diagram of three ordinary filaments on a typical bivalve ctenidium showing particle capture kinematics. Dashed arrows show particle paths during capture: 1 = direct interception, 2 = trap and flip, 3 = skip, 4 = bounce (*see* text for details). Open and closed circles indicate preretention and postretention particles, respectively. Relative positions of frontal (F), laterofrontal (LF), and lateral (L) ciliary tracts are indicated. Small, solid arrows indicate effective stroke of laterofrontal and lateral cilia.

bivalves indicated that flow through this chamber can be decomposed into three vector components. One vector was directed parallel to the frontal surfaces of the ctenidium and another was directed perpendicular to the surfaces of the ctenidium (Fig. 1, components V_1 and V_2, respectively). Even within 10–20 μm of the filaments, there was a component of flow parallel to the ctenidial surface (V_1). A third component of flow was directed dorsally (Fig. 1, component V_3) and was stronger in bivalve species with plicate, heterorhabdic ctenidia (i.e., ctenidia composed of more than one type of filament; *Ostrea edulis, Crassostrea virginica*; Fig. 1B) than in species with homorhabdic ctenidia (i.e., ctenidia composed of only ordinary filaments; *Arca zebra, Geukensia demissa, Modiolus modiolus, Mytilus edulis*; Fig. 1A). In addition, in species with heterorhabdic ctenidia, there were components of flow directed around each plical crest and into the plical troughs (Fig. 1B, component L). In all species, flow appeared to be laminar across the ctenidial lamella.

The resultant vector sum of flows described above (V_s) causes particles to approach ctenidial filaments at a low angle with respect to the frontal surface plane ($\alpha \approx 30°$; Figs. 1, 2). In bivalves with plicate ctenidia, the angle of approach is low with respect to the frontal surface of the plica, or entire ctenidial plane, but it might be steeper with respect to ordinary filaments on the sides of the plical ridge (Fig. 1B). Pumping activity, as estimated by particle approach velocity and extension of the inhalant mantle margin, affected the angle of approach. When a given specimen was actively pumping, the approach angle was low ($\alpha < 30°$); when pumping activity decreased, as measured by a decreased approach velocity, the angle of approach became steeper ($\alpha > 30°$).

Particles approached the ctenidia of bivalves at velocities that differed with species and pumping activity (Table 1). Velocity measurements represent data from actively feeding animals (gaping individuals with extended mantle edges); velocities in nonfeeding animals approached zero.

Particle capture—The process of particle capture by ctenidia was similar among species and occurred on the ordinary filaments and, if present, principal filaments. We consider particle capture a sequence of three interrelated processes: encounter, retention, and transport. The exact movement of particles just prior to encounter was exemplified by several different patterns and was dependent on the morphology of the ctenidium.

Direct interception occurred on the ordinary filaments of the ctenidia when a particle encountered the centerline of a filament, was retained, and immediately transported along the frontal surface (Figs. 2, 3A,C; path 1). A modification of direct interception occurred in a frequently observed pattern we term "trap and flip." As the particle approached the lateral edge of an ordinary filament, or sometimes the interfilamentary space, all forward movement would abruptly stop. After 0.03–0.23 s, the particle was deflected laterally and encountered the filament; thereupon, it was retained and transported on the frontal surface in the same manner as particles captured by direct interception (Figs. 2, 3B; path 2). Particle capture by the ordinary filaments of the ctenidia was not always instantaneous. Often, particles encountering the centerline of one filament would "skip" across several adjacent filaments before being retained by a filament downstream (Figs. 2, 3D; path 3). This observation is striking, because such particles traversed several interfilamentary spaces without passing through and without being lost by the ctenidia. Some particles were also deflected away from

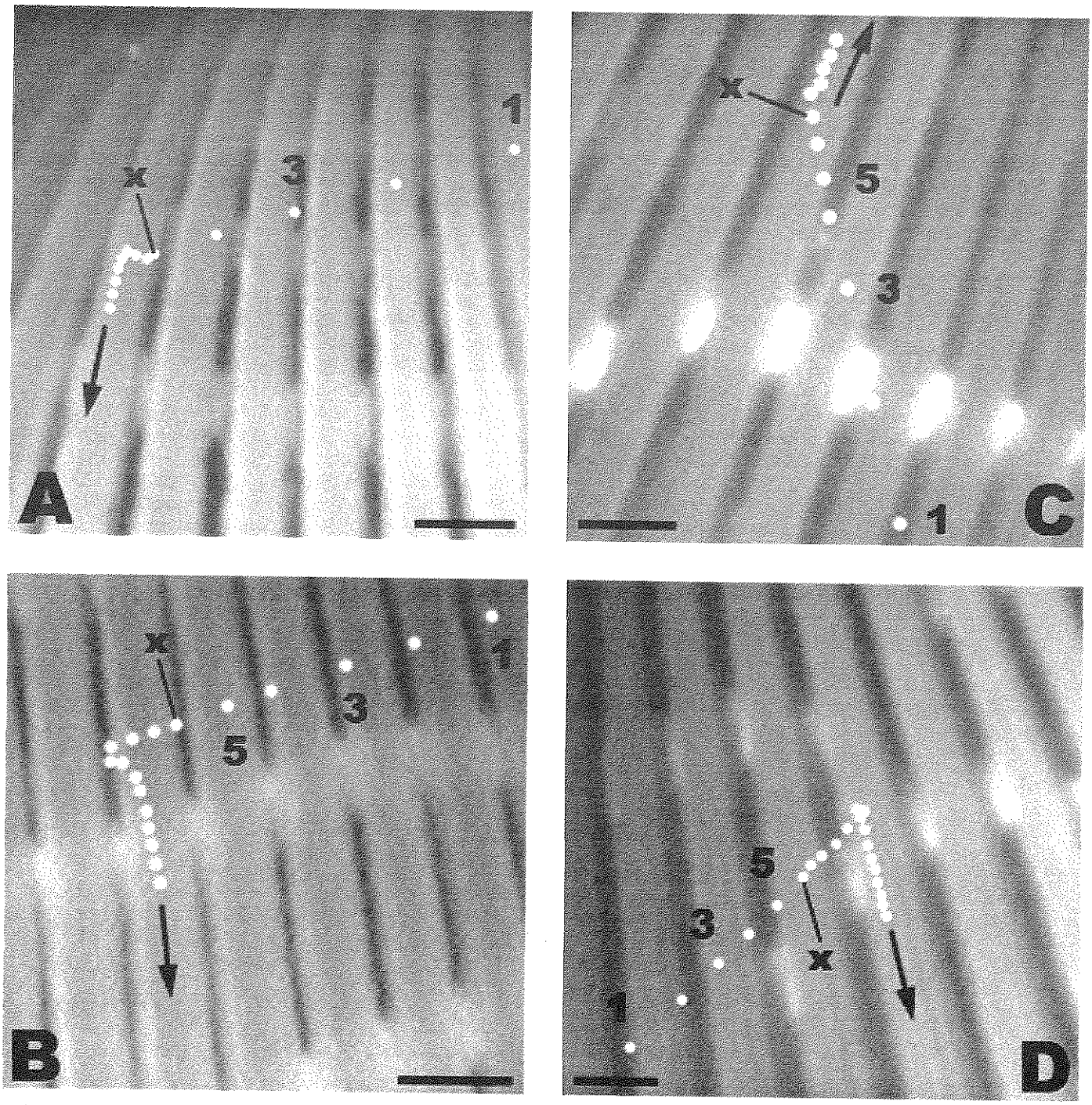

Fig. 3. Digitized, video micrographs of particle kinematics above and along the frontal surface of the ctenidia of two filibranchiate bivalves. Particles (white dots) were positioned on micrographs to illustrate specific paths obtained by motion analysis. Numbers indicate cumulative frame advances for a given position of the particle (0.033-s time steps, NTSC). The *x* indicates position of particle when it first contacted a given ctenidial filament. Scale bars are about 100 μm. (A) *Mytilus edulis* ctenidium showing direct interception of particle (path 1 in Fig. 2). (B) *M. edulis* ctenidium showing trap-and-flip capture of particle (path 2 in Fig. 2). (C) *Arca zebra* ctenidium showing direct interception of particle (path 1 in Fig. 2). (D) *A. zebra* ctenidium showing particle traversing an interfilamentary space at the level of the frontal surface (skip, path 3 in Fig. 2).

the frontal surface of a filament, only to accelerate toward the frontal surface of the same or an adjacent filament (Fig. 2; path 4). These particles appeared to be "bouncing" from one filament to another and moved perpendicularly to the long axis of ctenidial filaments. In bivalves with heterorhabdic ctenidia, these particles often moved into the plical troughs, where they were captured by the principal filaments *(see below)*.

In bivalves with plicate, heterorhabdic ctenidia, particles were also drawn directly into the troughs between adjacent plicae. Particles were entrained in the components of flow that were directed around each plical crest and into the plical troughs (Fig. 1B; component L). At the base of each plical trough is a principal filament. The actual mechanism of capture on the principal filaments could not be determined because the surrounding plical crests occluded the view. However, particles retained in the plical troughs were carried dorsally in a flow presumably induced by the frontal cilia of the principal and adjacent, transitional filaments (Ward et al. 1993, 1994).

Infrequently, some particles were lost by the ctenidia. These lost particles exhibited rapid, lateral oscillations as they passed through the spaces between adjacent ordinary filaments. In addition, on the ctenidia of *A. zebra*, particles were retained on the lateral edges of filaments where the laterofrontal ciliary tract is located. These entrained particles moved rapidly in a circle and appeared to be trapped in a vortex. They were eventually directed onto the frontal surface of the filament.

Effects of serotonin—During the control period, mussels were observed to capture particles (10–20 μm) with 100% efficiency. In contrast, after exposure to serotonin capture, efficiency dropped significantly to a mean of 17% ± 12% SD (paired sample *t*-test, $n = 4$, $P < 0.01$). It was difficult to determine from the videotapes if this decline in capture efficiency was due to a reduction in encounter or retention efficiency because of the speed with which particles passed through the ctenidia. Nevertheless, the few particles that were retained by the ctenidia of serotonin-treated mussels were captured by direct interception on the frontal surface of the filaments.

Discussion

Analysis of flow—Flow through the infrabranchial chamber is induced by the combined action of cilia on several tracts, although primarily by lateral cilia of the ctenidium, which have an effective stroke directed from the frontal to the abfrontal surface (Fig. 2). Other tracts that contribute to flow include: (1) cilia that cover the dorsal tracts of the ctenidia, which direct water anteriorly, (2) cilia on the mantle, some of which beat anteriorly, and (3) in bivalves with heterorhabdic ctenidia, cilia on the frontal surface of the principal filaments, which have an effective stroke that is directed dorsally (Owen 1974; Jørgensen 1976; Beninger et al. 1992; Ward et al. 1994). In addition, the geometry of the pallial cavity organs and positioning of the inhalant aperture or siphons have a strong influence in directing flow across the ctenidial surface. The space between opposing ctenidial lamellae, or lamella and mantle tissue, is small relative to the length of the ctenidium. In many species, some, if not all, inhalant water enters the pallial cavity from a position that is near the posterior of the ctenidium. Consequently, inhalant water is pulled anteriorly along the ctenidium at a low angle (Fig. 1). On occasion, we observed that the anteriorly directed flow (Fig. 1, V_1) reversed and proceeded in a posterior direction. This reversal was ephemeral and might have been caused by contractions of the ctenidia or labial palps (Ward et al. 1994).

Flow speeds obtained with video endoscopy are similar to literature values calculated by indirect methods, but there are some differences. For example, our mean particle approach speed for *M. edulis* is 1.96×10^3 μm s^{-1} (Table 1). Assuming that the approach angle is 30° and that the interfilamentary spaces represent 37% of the ctenidial area (Jones et al. 1992), conservation of volume requires that the mean flow rate through these spaces be about 2.65×10^3 μm s^{-1}. This value is higher than those calculated by previous workers for *Mytilus* sp. (ca. 1.70×10^3 μm s^{-1}; *see* Nielsen et al. 1993) but falls within the tip speed of the lateral cilia, measured on isolated filaments, that drives this flow (ca. $2.0–3.0 \times 10^3$ μm s^{-1}; Sleigh and Aiello 1972; Jørgensen 1982; Silvester and Sleigh 1984). Theoretically, however, volume-averaged flow speed should be only 50% of the tip speed of the lateral cilia (Silvester 1988; Nielsen et al. 1993). Therefore, the tip speed of these cilia would have to be in the range of 5.3×10^3 μm s^{-1} to produce the particle approach velocity measured in vivo with the endoscope. A tip speed of this magnitude has never been measured for lateral cilia (*see* Nielsen et al. 1993). We suggest that the high approach velocities we measured in vivo, and the implied higher tip speeds of the lateral cilia, are due to lower drag on the ctenidium of whole, intact bivalves (*see below, New explanation of particle capture*).

Previous particle capture models—Our in vivo observations argue against aspects of prior explanations of particle capture in bivalves. For example, the laterofrontal cilia/cirri are often described as the "filtering mechanism" of the bivalve ctenidia (Tammes and Dral 1955; Dral 1967; Moore 1971; Ribelin and Collier 1977), and it is still being proposed that they function as mechanical sieves (Silverman et al. 1996*b*). Calculations of Reynolds number (Re) at the site of the laterofrontal cilia/cirri, however, range from 10^{-5} to 10^{-6} and do not support this mechanical sieving role (Ward 1996). Even if the velocities were two to three times higher because of streamline compression, Re values would still be $<<1$. Inertial impaction is not possible under such viscous flow, and it is unlikely that these structures can act as sieves. Instead, the cilia/cirri probably act as solid paddles and function in a manner similar to fine setules of other aquatic organisms (Koehl and Strickler 1981; Cheer and Koehl 1987).

Our endoscopic observations also indicate that particle capture does not occur exclusively by hydrodynamic processes, as has been proposed previously (Jørgensen 1981, 1990; Nielsen et al. 1993). One premise of particle entrainment by hydrodynamic processes is that there is a well-developed flow of water along the frontal surface of the ordinary filaments that carries particles toward ctenidial margins (Jørgensen 1981, 1982; Silvester and Sleigh 1984; Jørgensen 1990; Nielsen et al. 1993). A major component of inhalant flow, however, is perpendicular to, or often counter to, movement of particles on the frontal surface (Fig. 1, components V_1, V_3). Therefore, transport in a water current is not possible because particles would be swept off the frontal surface of the ordinary filaments. Other evidence, such as the short length of frontal cilia, the complex movement

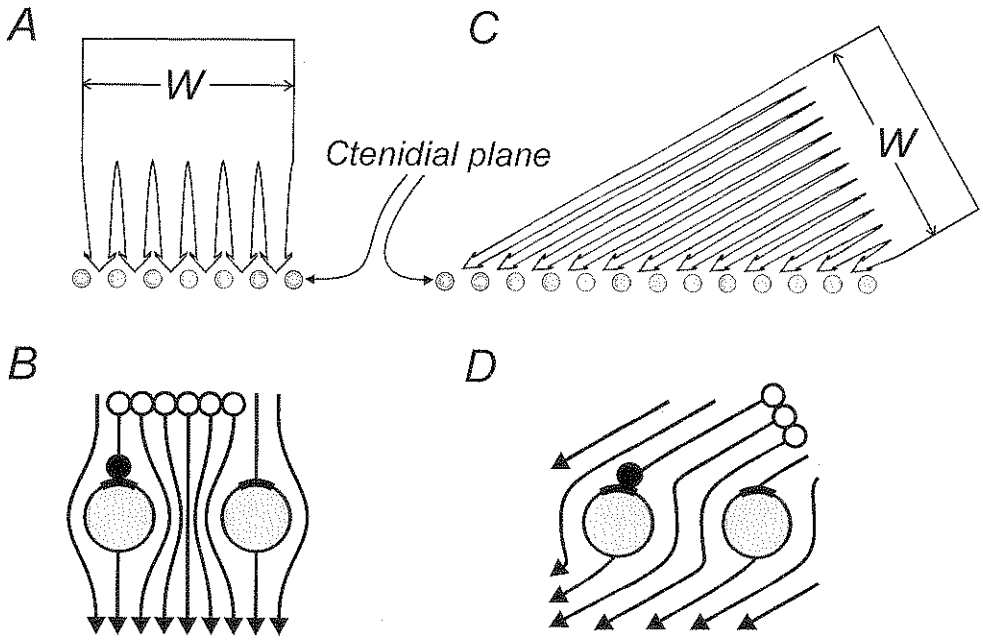

Fig. 4. Schematic diagrams of low Reynolds number flow forced through an infinite array of parallel cylinders with diameters equal to the gaps between cylinders, at two different approach angles. This is an approximate model for flow through the bivalve ctenidium. Small open and closed circles indicate preencounter and postencounter particles, respectively. Perpendicular approach: (A) An approaching flow of cross-sectional width W is forced through six interfilamentary gaps of total cross-section W/2, causing the flow to accelerate accordingly. (B) An enlargement of two filaments from (A), with streamlines drawn after Kirsch and Fuchs (1967). There is significant streamline compression in the center of the gaps. In this example, one out of six approaching particles encounters the frontal surface of a single filament. Approach angle of 30°: (C) An approaching flow of cross-sectional width W is forced through 12 interfilamentary gaps of total cross-section W, with no significant flow acceleration. (D) An enlargement of two filaments from (C), showing hypothetical streamlines. There is no significant streamline compression in the gaps. The flow turns after it passes through the ctenidium because space beneath the ctenidium is just as constrained as space above it. In this example, one out of three approaching particles encounters the frontal surface of a single filament.

of particles on these surfaces, and the velocity at which they are transported, argue against the existence of frontal-surface water currents on the ordinary filaments (Ward et al. 1993, 1994). It is more likely that particles are transported in a fine layer of mucus directly in contact with the frontal ciliary tracts. Particle transport in frontal-surface currents of ordinary filaments, described from surgically altered specimens and isolated filaments, is probably an artifact caused by dissection and isolation of ctenidia.

Although hydrodynamic entrainment does not seem to occur on the ordinary filaments of bivalves (*see* Silvester and Sleigh 1984), redirection of particles by hydrodynamic forces might operate on the principal filaments of those species with heterorhabdic ctenidia (e.g., oysters, scallops). Many of the conceptual mechanisms proposed by Jørgensen (1990) for ordinary filaments might apply to the principal filaments. Such entrainment has been proposed previously (Jørgensen 1976; Owen and McCrae 1976; Owen 1978) and would serve to concentrate particles in the principal filaments for subsequent transport to the food tracts at the ctenidial margins.

A new explanation of particle capture—Endoscopic observations, from this and previous studies (Beninger et al. 1992; Ward et al. 1993, 1994; Ward 1996), have allowed us to develop an alternate explanation for particle capture in suspension-feeding bivalves. Our explanation is consistent with the physical and biological constraints of the ctenidial system and mechanisms of hydrosol filtration. It also addresses species-specific differences in particle capture efficiency depending on the types of laterofrontal tracts and on the ctenidial form (heterorhabdic vs. homorhabdic).

We propose that particle encounter with the ordinary filaments occurs by direct interception with the frontal ciliary tracts when a particle comes within one particle radius of these tracts. This mechanism is the same as direct interception of particles in other suspension-feeding species that rely on hydrosol filtration (Rubenstein and Koehl 1977; LaBarbera 1984; Patterson 1991; Shimeta and Jumars 1991). Thus, in bivalves, the ctenidial filaments themselves are the capture units and not the laterofrontal cilia or cirri. Encounter is enhanced through two mechanisms. First, the low angle of approach observed in vivo increases the rate of contact

between particles and the frontal surface of filaments. Second, beating of the laterofrontal cilia/cirri produces vortices that redirect particles and flow away from interfilamentary spaces and toward the frontal surfaces of filaments.

Decreasing the approach angle to the ctenidial plane increases the percentage of approaching particles that encounter the frontal surface of filaments (Fig. 4). Flow through the ctenidial plane is presented conceptually as a low Reynolds number flow forced through an infinite array of parallel cylinders, spaced such that the intercylinder gaps are equal to the diameters of the cylinders. This arrangement is a suitable model for a planar ctenidium, such as that found in mytilids and *A. zebra,* with interfilamentary gaps and filaments of equal width (e.g., Jørgensen 1990).

A perpendicular approach angle (Fig. 4A) is similar to the models and experiments of Nielsen et al. (1993), although they examined an isolated filament rather than repeated parallel filaments. Streamlines in Fig. 4A are based on observations of low Re flow through a fibrous filter, with a geometry similar to that of the bivalve ctenidium (*see* Kirsch and Fuchs 1967, fig. 3). Streamlines that do not directly contact the frontal surface of a filament are forced through the interfilamentary gap with consequent streamline compression. Kirsch and Fuchs (1967) showed empirically that streamline compression is uneven across the gap, with maximum compression in the center. Thus, particles that approach a given filament more than one particle radius away from the streamline of direct interception are unlikely to come into contact with the filament, and the majority of particles that do contact the filament are more likely to contact a lateral surface than a frontal surface. Because the frontal surface is the only part of the filament involved in particle capture in bivalves, lateral encounters are lost. In the example shown in Fig. 4B, only one out of six approaching particles contacts the frontal surface of each filament.

The schematic diagram of flow at a 30° approach angle to the ctenidial plane (Fig. 4C) represents the situation we typically observed in actively pumping bivalves. The streamlines shown are not based on direct flow measurements or theory; to our knowledge, there have been no such measurements or theories reported in the literature, and they were beyond the scope of the present study. Rather, we have constructed streamlines based on our in vivo observations, on basic principles of low Re flow, and on observations such as those of Kirsch and Fuchs (1967). The most important consequences of a shallow approach angle are independent of the details of the flow field. Simple geometrical considerations indicate that the cross-sectional area available for flow through the ctenidium is the same as the cross-sectional area of the approaching flow for the filament spacing of Fig. 4 and an approach angle of 30°. Thus, no streamline compression is required in the interfilamentary gap (but note that there must be streamline expansion just upstream where the flow begins to turn toward the gap). In addition, the available frontal surface area for particle capture at an approach angle of 30° is twice that for a perpendicular approach angle, simply because the hypotenuse of a 30–60–90° triangle is twice the length of the short side. In the example shown in Fig. 4D, one out of three approaching particles encounters a frontal capture surface. This is twice as many as in Fig. 4B. We conclude that a shallow approach angle increases the likelihood that particles will encounter the frontal surface of a filament and decreases the likelihood that particles will be lost through interfilamentary gaps.

Reduced streamline compression in the interfilamentary gap likely reduces the drag of each ctenidial filament, although the magnitude of this effect cannot be determined without detailed experimentation and/or mathematical modeling. Tamada and Fujikawa (1957) formulated a low Re model for the drag on each cylinder in an infinite array at a perpendicular approach angle (e.g., Fig. 4A). They found that drag was greatly increased for a cylinder in an array relative to the drag of an isolated cylinder, and they attributed this effect to streamline compression in the gaps between cylinders. Kirsch and Fuchs (1967) results indicate that this streamline compression corresponds to greatly increased shear across the gap, which is the direct mechanism for increased drag. We hypothesize that a shallow approach angle decreases the drag of each filament relative to perpendicular approach by decreasing streamline compression. This does not mean that the drag of the entire ctenidium decreases, because the number of filaments per unit inflow is higher for a shallow approach angle than it is for perpendicular approach. Clearly, more research is needed.

Decreased drag on each filament at the shallow approach angles we observed in vivo would result in different flow characteristics from those observed by others at perpendicular approach angles. For example, it might result in a more rapid power stroke of the lateral cilia than has been previously reported for isolated ctenidia (e.g., Nielsen et al. 1993). Alternatively, lower drag might increase the efficiency of the power stroke of the lateral cilia so volume-averaged flow speed could attain 70% of the tip speed. Either mechanism would explain the higher mean flow rates through the interfilamentary spaces that we estimated above. Higher flow rates increase rates of particle encounter for a given particle concentration and hence, potentially increase feeding rates.

Although the ctenidial filaments are the capture units, the laterofrontal tracts play crucial roles in both particle encounter and particle retention. The cilia or cirri that form these laterofrontal tracts, however, affect particle capture by altering the pattern of flow around the ordinary filaments and not by physically intercepting particles. In the absence of beating by the lateral cilia, the action of the laterofrontal tracts would drive vortices above the laterofrontal edges of the filaments and possibly induce a backflow against the direction of pumping (Fig. 5A; *see* Jørgensen et al. 1986). When superimposed on the overall flow pattern produced by pumping, this vortical flow reduces or blocks direct flow through the interfilamentary spaces (Fig. 5A). Instead, water is redirected toward the filament's frontal surface, flows around the laterofrontal surface of each filament, and then enters the interfilamentary spaces (Figs. 5B,C, 6). As a result, the number of particles that encounter the frontal cilia is greatly increased and particle retention is aided by flow convergence over the frontal surface.

Vortices produced by laterofrontal cilia or cirri explain a number of our observations such as the trap-and-flip pattern of capture, "bouncing" of particles along filaments, circular movement of small particles at the lateral edges of filaments,

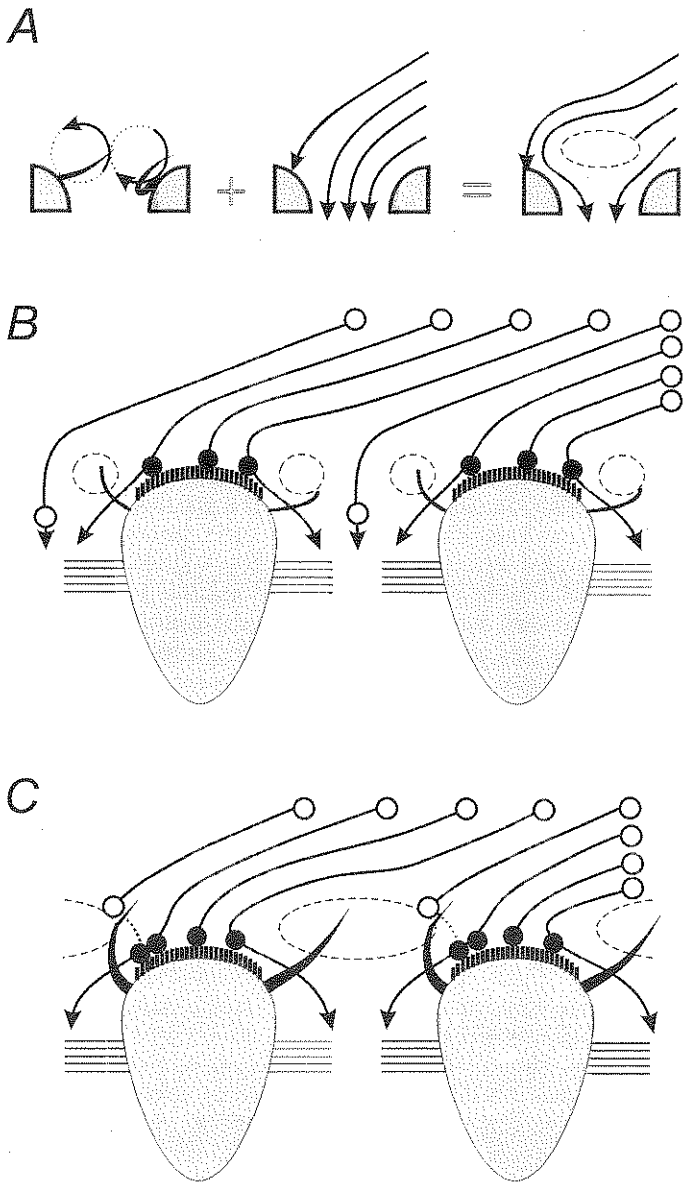

Fig. 5. Cross-sectional diagrams of ordinary filaments showing flow patterns and capture efficiencies due to beating of the laterofrontal cilia or cirri, based on our in vivo observations. Qualitative streamline patterns through the ctenidium are shown by solid arrows, and zones of blocked through-flow are shown by dashed ellipses. Open and closed circles indicate preencounter and postencounter particles, respectively. (A) Vortices produced by laterofrontal tracts, when superimposed on the mean flow through the ctenidium, generate zones of blocked through-flow with stagnation points directly above the interfilamentary spaces. Through-flow is redirected toward the frontal surface and passes along the laterofrontal surface of the filaments (*see Fig. 6*). (B) Version of model in which filaments possess simple laterofrontal cilia (e.g., *Arca zebra*). (C) Version of model in which filaments possess large laterofrontal cirri. This model produces the most restrictive flow paths, but highest encounter efficiency.

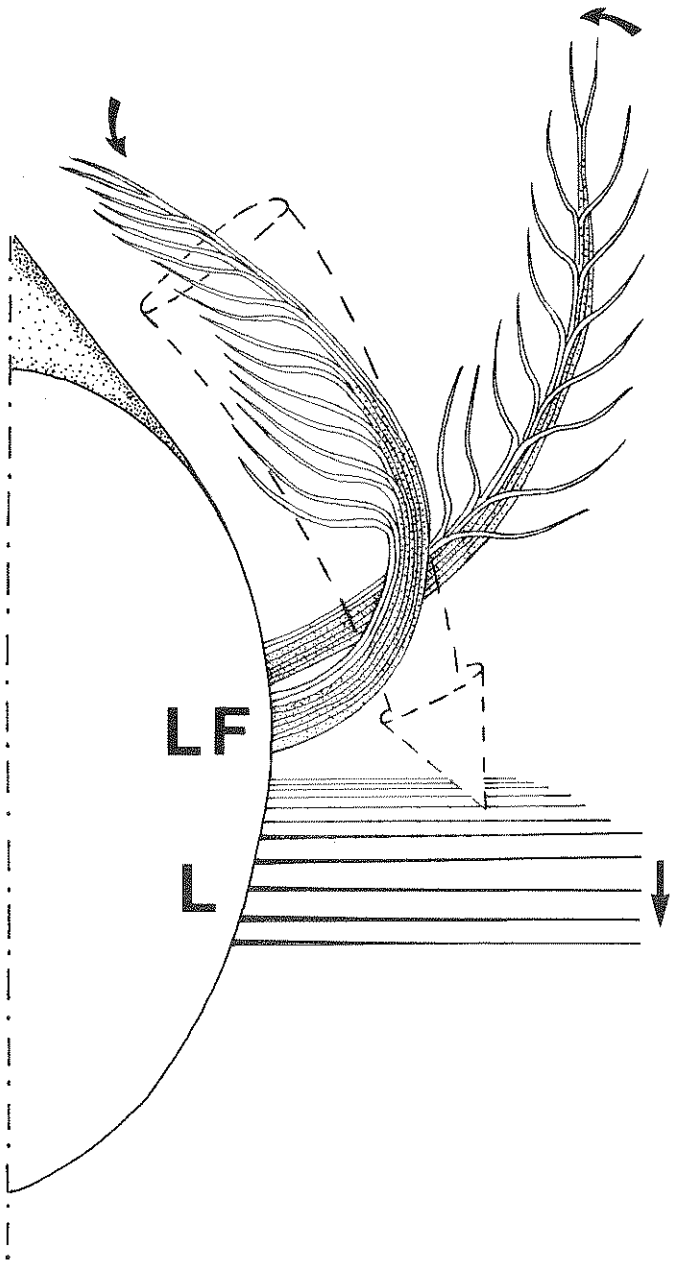

Fig. 6. Close-up drawing of the laterofrontal region of a filament of *Mytilus edulis,* showing hypothesized water flow (large, dashed arrow). Flow is directed across the laterofrontal surface of the filament, passes between the basal region of adjacent laterofrontal cirri (LF; proximal one-third of the length, ca. 10 μm), and then enters the interfilamentary space at the level of the lateral cilia (L). Small solid arrows indicate instantaneous movement of the cilia and cirri.

and lateral oscillations of particles that pass through the interfilamentary spaces. In addition, vortices produce stagnation points and zones of flow divergence directly above the interfilamentary spaces that act as barriers to flow. The magnitude of this barrier will vary among species of bivalves depending on the complexity of their laterofrontal tracts (Fig. 5B,C). These flow features explain our observation that

particles traverse interfilamentary spaces without being drawn through these spaces (skip pattern).

In bivalves with simple laterofrontal cilia, as opposed to cirri, the vortices are restricted to the edges of the frontal tracts (Fig. 5B). In *A. zebra,* for example, many particles were retained and transported dorsally along the laterofrontal edges of filaments instead of down the filament centerlines. Because of the short length of the laterofrontal cilia (10–17 μm), lateral flow produced by the vortices should be strongest in the laterofrontal region. Dorsal transport of particles can occur because the frontal ciliary tracts of *A. zebra* extend around to the laterofrontal edges of the filaments (Atkins 1937, 1938). Some water, however, should still be able to flow directly through the interfilamentary spaces, carrying some smaller particles with it (Fig. 5B).

In bivalves with laterofrontal cirri that extend across one-half of the interfilamentary space, the vortices created by opposing sets of cirri on adjacent filaments meet and completely block direct flow through the interfilamentary spaces (Fig. 5C). Consequently, almost all particles should encounter the frontal surface of a filament. Ctenidia with large laterofrontal cirri should produce the strongest lateral flows, as suggested by the more frequent trap-and-flip particle capture we observed in mytilids (*G. demissa, M. edulis, M. modiolus*), compared with nonmytilid species. The flow pattern produced by more extensive laterofrontal cirri might explain why particle capture efficiency has been correlated with the development of the laterofrontal tracts. Species with well-developed laterofrontal cirri capture particles below 7 μm at a higher efficiency than species with simple laterofrontal cilia (Mohlenberg and Riisgård 1978; Jørgensen et al. 1984; Riisgård 1988).

Particle capture by direct interception with the frontal cilia would occur in the absence of laterofrontal cilia or cirri (Fig. 4). Such a morphology would be inefficient, however, because many particles would not come within one particle radius of a filament and would pass directly through the interfilamentary spaces. Moreover, particles that encountered filaments would tend to slip over the filament edge and through the interfilamentary space, unless they remained on the centerline of a filament where there was no net lateral drag. We produced an approximation to this situation by exposing *M. edulis* to serotonin, thereby inactivating the laterofrontal cirri. During exposure, we observed a significant decrease in the percentage of particles captured. Nevertheless, some particles (17%) encountered the filaments and were retained on the frontal surfaces, suggesting that direct interception was still possible. Similar reduced particle capture efficiencies have been reported when 10^{-5} M serotonin is added to exposed and isolated ctenidia (e.g., Jørgensen 1976). It is of no small consequence, then, that all bivalves possess some type of cilia or cirri that form laterofrontal tracts on the ctenidium (Atkins 1938).

We propose that particles are retained on the frontal surfaces by a combination of mechanisms. As in other biological hydrosol filtration systems (Shimeta and Jumars 1991), an adhesive force produced by the fine layer of mucus associated with the frontal cilia is essential in holding particles on the frontal surface. The filament-directed component of drag induced by flow around the filament also serves to hold particles on the frontal surface. Inward beating of the laterofrontal cilia/cirri induces flow convergence over the frontal surface of the filament that returns particles toward the center of the filament when they begin to slip off. Finally, the alignment of the frontal cilia of some bivalve species serves to keep particles on the centerline of the filament during mucociliary transport (Ribelin and Collier 1977).

One of the novel aspects of our model is the idea that most of the water does not flow directly though the interfilamentary spaces. Instead, we hypothesize that water flows around each ordinary filament and across the laterofrontal surface, passing between the basal region (proximal one-third of length) of adjacent laterofrontal cilia or cirri (Fig. 6). Flow through the base of the laterofrontal tracts might be facilitated by the recovery stroke of the cilia/cirri, or the action of accessory laterofrontal cilia. Mucus produced by the ctenidial filaments of most bivalve species also could decrease resistance to flow at these sites through lowered viscosity (*see* Bernard and Noakes 1990). In addition, the pattern of activity of the laterofrontal tracts is such that adjacent cilia/cirri have effective strokes that are 180° out of phase, or 10–12 adjacent cilia/cirri have a synchronous beat that is 180° out of phase with the neighboring 10–12 cilia/cirri (Dral 1967; Silverman et al. 1996*b*). Such beat patterns produce larger instantaneous gaps in the laterofrontal tracts that might decrease flow resistance (Tamada and Fujikawa 1957). Finally, the proximal portion of a single laterofrontal cirrus possesses fused cilia that form a stalk aligned so as to present the least possible resistance to flow. The free tips of the compound cilia do not ramify from the cirrus until about one-third of the way along the length of the structure (Owen 1974; Ribelin and Collier 1977; Silverman et al. 1996*a,b*). These morphologies would minimize the extra drag caused by forcing flow through the narrowed gap between adjacent laterofrontal cirri.

Finally, our explanation provides a mechanism by which an individual bivalve might adjust feeding rate and efficiency. Bivalves can control the width of the interfilamentary spaces (Galtsoff 1964; Jørgensen 1990; Ward et al. 1994) and by doing so, might change the drag of the ctenidium so as to change pumping rate for a given level of pumping effort. Bivalves also might be able to control the spacing of the vortices produced by opposing rows of laterofrontal cilia/cirri, allowing more or less water to pass directly through the interfilamentary spaces to adjust capture efficiency.

Conclusions

Endoscopic observations of living, intact bivalves reveal that direct interception of particles by the surface of the ordinary filaments is the major encounter mechanism in suspension-feeding bivalves. In some species, particle concentration and redirection by hydrodynamic processes on the principal filaments (if present) also might be an important capture mechanism. Particles approach the ctenidium at a low angle, increasing the likelihood of particle encounters with frontal cilia and possibly decreasing the drag of the filaments. Laterofrontal cilia and cirri induce lateral flows that reduce or exclude direct flow through the interfilamen-

tary spaces and thereby increase particle encounter efficiency with frontal surfaces. Particles are retained on the frontal surfaces of ordinary filaments by a combination of mucus, drag, and flow convergence. Captured particles are then transported to the margins of the ctenidia by mucociliary action (ordinary filaments) and hydrodynamic forces (principal filaments).

Our model should be considered an overall principle for the mechanisms of particle capture in suspension-feeding, lamellibranchiate bivalves. The exact architecture of the ctenidium, together with the types of cilia and cirri present on the laterofrontal tracts, will affect the small-scale dynamics of particle encounter and retention. Further testing and quantitative modeling are needed to delimit these dynamics for the range of ctenidial types within the Bivalvia. We have described the general flow patterns responsible for particle capture, but a quantitative description of the actual time-dependent, complex flows remains to be developed.

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