

Mechanisms of suspension feeding in bivalves: Resolution of current controversies by means of endoscopy

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Abstract

Controversy concerning the mechanism of suspension feeding in bivalves centers around whether particle capture and transport on the gills (ctenidia) is accomplished via mucociliary or hydrodynamic action. Evidence for and against these fundamentally different processes has been based on examinations of isolated feeding structures and dissected specimens, techniques that may produce artifactual data owing to the trauma associated with the procedures. In the present study, *in vivo* observations of the ctenidia of undisturbed bivalves, made with a fiber-optic endoscope and video image-analysis system, revealed that the two mechanisms are not mutually exclusive. Both mucociliary and hydrodynamic mechanisms function concurrently at different sites on the ctenidia, thereby minimizing particle loss and optimizing particle transport efficiency. The importance of mucus in the normal feeding process of bivalves is confirmed. These findings refute results of previous studies that used surgically invasive techniques and emphasize the importance of making observations on morphologically intact specimens.

Suspension feeding is a common mode of food collection in several groups of aquatic organisms, including the Bivalvia. Bivalves are both ecologically and economically important; they can be dominant infaunal or epibenthic animals, influencing the surrounding environment through particle depletion, nutrient cycling, and biodeposition (Jørgensen 1990). Even so, the mechanisms of bivalve suspension feeding remain controversial and poorly understood. Feeding in bivalves involves pumping water through a set of ctenidia, removal of particles from suspension, and transport of collected material to the mouth. The traditional theory of particle removal by the ctenidia is based on a mucociliary concept (Kellogg 1915; Dral 1967; Foster-Smith 1975).

That is, suspended particles passing through ctenidial filaments are mechanically trapped by rows of laterofrontal cilia or cirri and transferred onto the frontal ciliary tracts of the filaments. Particles are then carried in mucus by the frontal cilia to the dorsal or ventral margins of the ctenidia, where they are incorporated into compact mucus strings and transported to the mouth for ingestion via ciliated food tracts.

This traditional theory of suspension feeding has been challenged by a hydrodynamic concept (Owen 1978; Jørgensen 1981, 1990; *but see* Silvester and Sleigh 1984). According to this theory, captured particles never physically contact cilia or cirri, but are transferred from water currents flowing through the ctenidia to frontal currents flowing along the ctenidia by shear forces arising at the interface of the two flows. Laterofrontal cirri are thought to facilitate water transport along the frontal surface. Particles in frontal surface currents are carried to the dorsal or ventral margins of the ctenidia, then transported in suspension directly to the mouth. Mucus is not normally used in the feeding process and is secreted only to "clean" particulate matter from the ctenidia when the capacity for ingestion or digestion is exceeded (Jørgensen 1990).

Resolution of the controversies regarding bi-

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valve suspension feeding would contribute significantly to an understanding of feeding dynamics, including capture, differential retention, selection, and preferential ingestion of particles. Previous research, however, has been hampered by difficulty in performing visual observations on bivalves due to the presence of a shell. Although many reports have been published concerning feeding mechanisms, observations on intact, undisturbed animals are lacking. Data concerning feeding processes have been collected primarily by morphological studies of preserved structures by means of light and electron microscopy, in vitro observations of isolated structures, in vivo observations of structures in surgically altered animals, and in vivo observations of structures in postmetamorphic specimens with transparent shells (see Ward et al. 1991).

In this study we use endoscopic examination and video image analysis to make direct, in vivo observations of feeding structures of intact animals. We examine and record suspension-feeding processes in three bivalve species representing three major types of ctenidia: the oyster *Crassostrea virginica* (pseudolamellibranch ctenidium, plicated, heterorhabdic; Galtsoff 1964); the mussel *Mytilus edulis* (filibranch ctenidium, nonplicated, homorhabdic; Owen 1978); and the clam *Mya arenaria* (eulamellibranch ctenidium, plicated, homorhabdic; Yonge 1923). These observations are then used to address questions central to the above two theories. After removal from suspension, are particles on the frontal surfaces of ctenidial filaments entrained in water currents? At low particle concentrations, is food material transported toward the mouth in water currents or in mucus strings? Is mucus produced only to remove excess material from the ctenidia?

Materials and methods

Endoscopy was performed with methods described by Ward et al. (1991). The rigid endoscope (optical insertion tube, 1.7-mm diam; Olympus Corp.) was connected to an optical zoom-adaptor (max magnification, $\sim 150\times$, Schölly Fiberoptic GmbH) and attached to a charge-coupled-device camera (Cohu, Inc.). Video signals were recorded on an 8-mm VCR (Hi8, Sony). Recorded images were then digitized with a TARGA digitizing board (True-

vision, Inc.) and analyzed with JAVA video analysis software (Jandel Sci.). Calibrations for morphometric measurements were obtained by dissecting the ctenidia of each species and measuring the width of filaments, interfilamentar spaces, and plicae with a compound microscope and calibrated ocular micrometer. Particle velocities on ctenidial surfaces were determined by counting the number of frames required for particles to traverse a known distance. Recording speed was 30 frames s^{-1} (NTSC).

During endoscopic examinations, mussels and clams were kept in flowing seawater, while oysters were held in an aerated, static seawater system. Animals were allowed to feed freely on natural seston or seston supplemented with a mixture of the diatom *Chaetoceros muelleri* ($\sim 6\text{-}\mu\text{m}$ diam) and light-reflective, red plastic particles ($\sim 5\text{-}\mu\text{m}$ diam, Radiant Color, Hercules, Inc.). Diatoms were cultured in f/2 medium and mixed with plastic particles in a ratio of 7:1. Individual bivalves were exposed to low, medium, and high concentrations of seston, diatoms, and plastic particles. Designated concentrations were: low = 5–7, medium = 11–13, high = 22–24 particles μl^{-1} ($\sim 1.5, 1.9,$ and $2.5 \text{ mg liter}^{-1}$). In experiments addressing the question of direct contact of particles with ctenidial filaments, we used polystyrene microspheres ($\sim 16\text{-}\mu\text{m}$ diam, Polysciences, Inc.).

The optical insertion tube (OIT) of the endoscope was introduced into the pallial cavity of a bivalve, and recordings were made after the animal was acclimated to experimental conditions and showed signs of normal feeding behavior. Bivalves that had extended mantle edges or siphons, and that were drawing particles into the pallial cavity, were considered to be feeding normally. A cannula, fitted onto the OIT, permitted removal of material from within the pallial cavity. The cannula, with attached Luer-Lok hub, was connected to a peristaltic pump via fine-bore surgical tubing. The pump was set to withdraw fluids at a flow rate of $300 \mu\text{l min}^{-1}$. The video camera with attached endoscope was mounted onto a micromanipulator, which allowed for precise three-dimensional adjustments. Manipulation of the endoscope was kept to a minimum during observations to reduce the chance of disturbing the experimental bivalve.

In one experiment we tested whether mucus-

Table 1. Summary of direct observations of particle transport on the ctenidia of bivalves exposed to a mixture of particles at three concentrations. Details concerning *Crassostrea virginica*, *Mytilus edulis*, and *Mya arenaria* given in text; details concerning *Placopecten magellanicus* given by Beninger et al. (1992). Particle velocity measurements ($\mu\text{m s}^{-1}$) were made at temperatures of 11–13°C for *C. virginica* and *P. magellanicus*, and 4–5°C for *M. edulis* and *M. arenaria*. Ten measurements were averaged for each mean velocity (\bar{x}). Error estimates are standard deviations. Dorsal ciliated tract of *M. arenaria* could not be examined (NE).

	Particle concn	Ventral ciliated groove		Dorsal ciliated tract	
		Particle transport mode	\bar{x} velocity (range)	Particle transport mode	\bar{x} velocity (range)
<i>C. virginica</i>	Low	Mucus string	101±9 (88–113)	Slurry	413±37 (366–462)
	Medium	Mucus string	258±54 (204–336)	Slurry	697±128 (490–907)
	High	Mucus string	193±34 (160–263)	Slurry	594±161 (408–907)
<i>M. edulis</i>	Low	Mucus string*	215±20 (185–250)	Slurry†	690±88 (582–850)
	Medium	Mucus string	224±11 (205–246)	Slurry†	698±102 (457–802)
	High	Mucus string	292±56 (232–363)	Slurry†	703±118 (552–904)
<i>M. arenaria</i>	Low	Mucus string	115±13 (107–150)	NE	—
	Medium	Mucus string	137±32 (102–177)	NE	—
	High	Mucus string	123±9 (117–138)	NE	—
<i>P. magellanicus</i>	Low	None‡	—	Slurry	8,115±1,561 (5,652–10,000)
	Medium	Sm mucus masses‡	380±95 (241–500)	Slurry	7,290±1,645 (5,652–10,000)
	High	Lg mucus masses‡	185±151 (0–433)	Slurry	5,890±943 (4,333–7,647)

* Material initially bound in mucus was ingested.

† Few particles naturally present, material artificially introduced.

‡ No "groove" present, most material on the ventral ciliated tract rejected as pseudofeces.

bound material, transported from the ctenidia to the labial palps, could be ingested. Three mussels were exposed to a low concentration of natural seston mixed with red plastic particles. The dorsal ciliated tracts and ventral ciliated grooves of each mussel were monitored during a 1–2-h feeding period, after which specimens were transferred to seawater without red particles. Feces were collected over the next 24 h and examined for the presence of red particles.

Results and discussion

In all three species, particles on the frontal ciliated surfaces moved in a manner consistent with maintaining direct contact with the filaments of the ctenidia (in *C. virginica*, these observations pertain to ordinary filaments only). On any given ctenidial filament, ventrally moving particles progressed uniformly, i.e. maintained their distance from one another, although occasionally a particle stopped moving and was overtaken by trailing particles on the same filament. We also observed particles hopping from the frontal surface of one filament to an adjacent filament. The distance between a given particle and the underlying filament could not be estimated because the

separation was smaller than the resolution of the endoscope ($<5 \mu\text{m}$ at $\sim 150\times$).

We detected no consistent difference between the manner in which large and small particles (~ 16 and $5 \mu\text{m}$) moved along the frontal surfaces of ctenidial filaments, and previously reported parabolic flow velocity profiles (Jørgensen 1975, 1981) were not observed. Furthermore, particle velocity on the frontal surface was more indicative of material transported in a mucus string than of that suspended in a slurry (*M. edulis*, 163 ± 22 SD $\mu\text{m s}^{-1}$, $n = 10$, cf. with velocities in Table 1), and the length of the frontal cilia is consistent with that of other mucus-propelling cilia ($5\text{--}7 \mu\text{m}$, Sleight 1982). These findings suggest that particles are transported by direct contact with frontal cilia or in a fine mucus layer covering these cilia.

In contrast to previous reports (Jørgensen 1990), under natural feeding conditions we never observed mucus strings being carried by the frontal cilia of two or more contiguous filaments. Injection of a concentrated suspension of polystyrene microspheres directly into the pallial cavity of mussels, however, induced the formation of particle-laden mucus strings that spanned 4–100 filaments and moved along

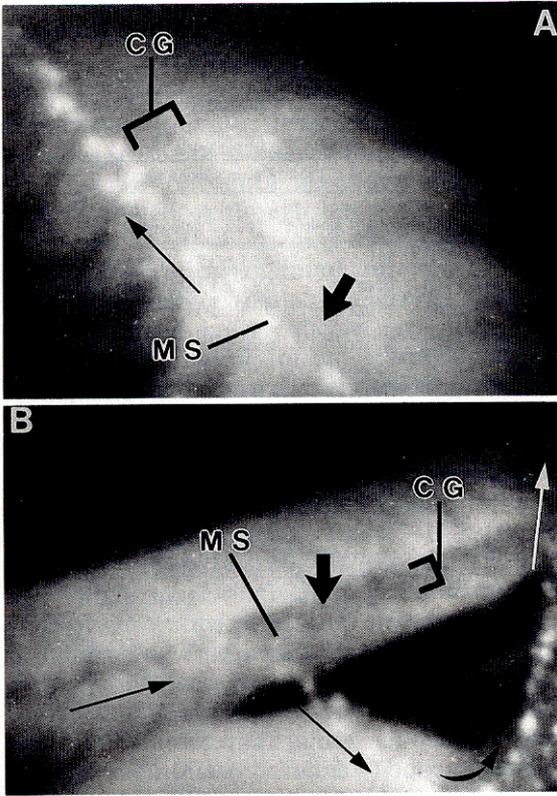


Fig. 1. Novel endoscope micrographs showing, in vivo, the ventral margins of ctenidia (1.5–1.7 mm long) at the ctenidium–palp interface. Micrographs were taken from digitized video images enhanced by contrast stretching and intensity smoothing. Compact mucus strings (MS), moving anteriorly in the ventral ciliated grooves (CG), are removed from the grooves and pulled onto the labial palps for further processing. Direction of movement is indicated by thin arrows. Notice that no material remains in the grooves after the point at which strings are removed (indicated by bold arrows). A. *Crassostrea virginica*. B. *Mytilus edulis*.

the frontal surface toward the ventral ciliated groove.

In all three species, material transferred to the ventral ciliated grooves travelled via previously described ciliated tracts (e.g. Foster-Smith 1975), and, on reaching the grooves, was immediately incorporated into mucus strings at all three particle concentrations (Table 1; Fig. 1). Material was never observed in suspension in the ventral grooves, even at the lowest particle concentration. This fact was confirmed by withdrawing particle-laden mucus strings from the grooves with the cannula, by observing strings occasionally dislodged

during rapid valve adductions, and by examining the ventral ctenidium–palp interface where mucus strings are normally removed from ciliated grooves by the labial palps (Fig. 1). Whereas some mucus clumps were carried on the outer margins of the ventral grooves, mucus strings were always transported inside the grooves. Slow motion and stop-frame analysis indicated that no material, in suspension or otherwise, remained in the ventral grooves after the point at which mucus strings were removed (Fig. 1). Our measured particle velocities in the ventral ciliated grooves of *M. edulis* correspond well with those made previously at the same temperature by different methods (cf. Jørgensen 1975 and Table 1). These particles, however, were in a mucus string, not in suspension as previously reported (Jørgensen 1975, 1990).

In contrast, material in the dorsal ciliated tracts was transported in a concentrated suspension or slurry (Table 1), not in mucus strings as previously suggested (e.g. Nelson 1923; Bernard 1974; Foster-Smith 1975). In *C. virginica*, material entered the dorsal tracts, via the principal filaments, as individual particles or small clumps and immediately joined the anteriorly moving slurry. These observations suggest that dorsward transport of material on the principal filaments is accomplished by cilia-generated currents, confirming previous hypotheses regarding this transport (Owen and McCrae 1976; Owen 1978). As particle concentration increased, larger and more numerous clumps were observed in the dorsal tracts, but these were still transported in the form of a slurry. Individual particles and clumps could be withdrawn from a dorsal tract, using the cannula, without disturbing the movement of other material in the tract. At the dorsal ctenidium–palp interface, we observed individual particles being directed either into the lateral groove or onto the ridged surface of the labial palps. In *M. edulis*, little material was transported along the dorsal tracts even at the highest particle concentration. However, the few particles that were observed and polystyrene microspheres that were injected directly into the dorsal tracts were all carried anteriorly by cilia-generated currents (Table 1). These observations suggest some vestigial function for the dorsal tracts in *M. edulis*. Due to the restricted space inside the pallial cavity of *M.*

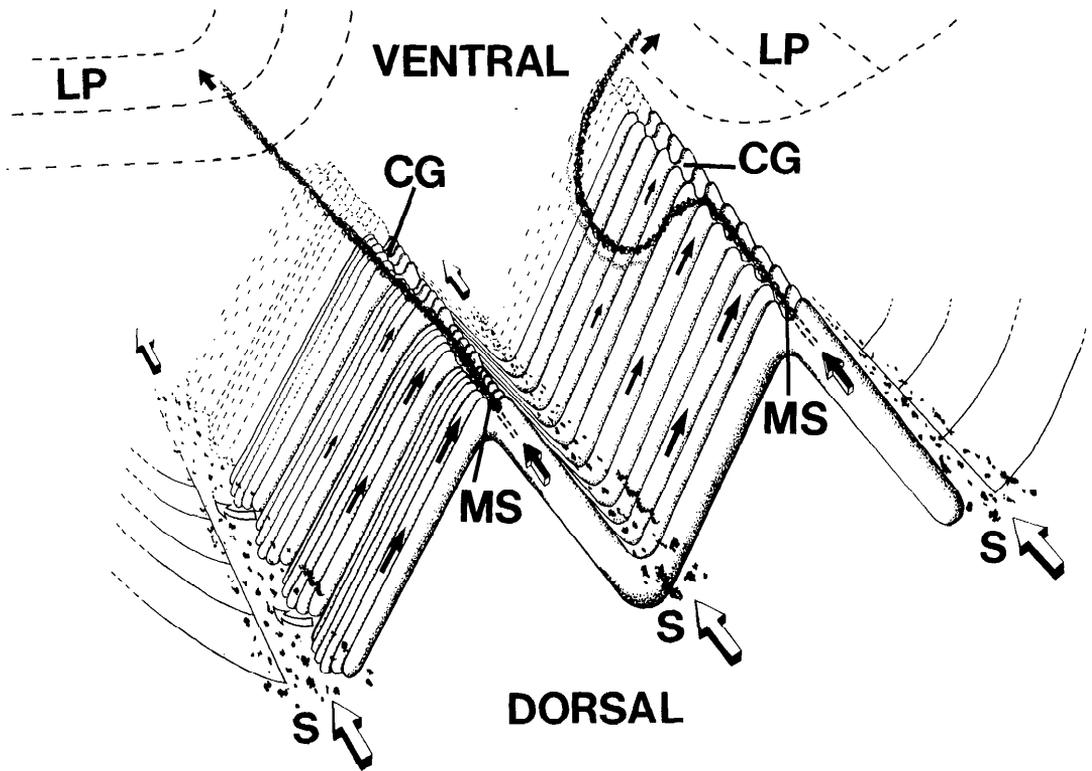


Fig. 2. Composite schematic of two demibranchs showing observed transport mechanisms on the lamellibranch ctenidium at all three particle concentrations. Left side of figure represents the plicated condition and the right side the non-plicated condition; direction of movement indicated by arrows. Solid arrows indicate movement of particles by mucociliary mechanisms, i.e. transport of material to the ventral margin and then along the ventral ciliated groove (CG) in a compact mucus string (MS). At the ctenidium–palp interface, mucus strings are removed from the ventral grooves and pulled onto the labial palps (LP) for further processing. Hollow arrows indicate movement of particles by hydrodynamic mechanisms, i.e. transport of material to the dorsal margin (via the principal filaments) and then along the dorsal ciliated tract in a slurry (S).

arenaria, we were unable to observe the dorsal ciliated tracts in this species.

Material transported from the ctenidia to the labial palps bound in mucus strings can be ingested. This finding was confirmed by examining the ctenidia of the three mussels exposed to a low concentration of natural seston and red particles. As before, all material was carried to the labial palps via the ventral ciliated grooves in the form of mucus strings, and no material was observed in the dorsal ciliated tracts. The following day all mussels produced red feces, indicating ingestion of the particles. The buccal regions of these specimens were not examined, so the actual form in which material was ingested—mucus strings or slurry—was not determined.

Endoscopic examination of intact bivalves

provides important information concerning postcapture particle processing and reveals that the two hypothesized mechanisms of bivalve suspension feeding are not mutually exclusive; both mechanisms can operate on the ctenidium and the two conflicting theories can be combined into a unifying model (Fig. 2). Particles removed from suspension are transported to ctenidial margins close to the frontal surface of the filaments. Ventrally moving particles are transported either in direct contact with the frontal cilia or are entrained in a fine layer of mucus covering these cilia. Material transferred to the ventral ciliated grooves is immediately incorporated into well-defined, compact mucus strings. Mucus is produced even at low seston concentrations, and material transported to the labial palps bound in

mucus is ingested, possibly after being dispersed by the palps (Newell and Jordan 1983). These observations indicate that mucociliary action is responsible for transporting material to the ventral margins of the ctenidia and then along the ciliated grooves.

At the ventral margins of the ctenidia, pallial water currents caused by normal pumping activities and rapid valve adductions are the strongest. Inclusion of particles in mucus at these sites may prevent resuspension of material by the pallial currents. Because most species can close the ventral groove by approximating the ventral margins of the lamellae, mucus binding may serve two functions. First, when the groove is open, mucus may increase transport efficiency and prevent the loss of food material. Second, when the groove is closed, mucus would facilitate rejection of excess material from the ventral margin and prevent dispersal and recollection by the animal. These functions may be important factors for individual energy balance. In some bivalve species, such as *M. edulis*, the ventral groove is the predominant route by which food material is carried to the labial palps for sorting and then ingestion. In other species, such as *C. virginica*, material in the ventral groove may be of lesser trophic importance, but it can be ingested. Taken together, our observations confirm the important role of mucus in the normal feeding process of undisturbed bivalves (see Beninger et al. 1991).

In contrast, dorsally directed particles in the principal filaments appear to be moved by cilia-generated currents. Material transferred to the dorsal ciliated tracts remains suspended and is carried in a slurry. These observations indicate that hydrodynamic mechanisms are important in transporting material to the dorsal margins of the ctenidia and then along the ciliated tracts.

The principal filaments form the base of each plical trough (see Galtsoff 1964). Currents moving along these troughs are probably created by the frontal cilia of the principal and, when present, the transitional filaments and are confined by the surrounding plicae. The dorsal tracts are situated at the base of the ctenidia. Currents moving along these tracts are probably generated by the heavily ciliated epithelium (see Galtsoff 1964; Beninger et al.

1988) and are confined by the surrounding ctenidial lamellae and viscera which form an arch that encloses each tract. Therefore, suspended particles on the principal filaments and in the dorsal tracts are protected by anatomical conduits that may prevent particle dispersion. Again, an efficient transport mechanism is critical because in some bivalve species, such as *C. virginica*, the dorsal tracts represent a major route for transporting food material to the labial palps for sorting and ingestion. It is important to realize, however, that hydrodynamic transport does not rule out the presence of low viscosity mucus. In the dorsal tracts of the scallop *Placopecten magellanicus*, low viscosity mucus and suspended particles are carried anteriorly in cilia-generated currents. The mechanism is hydrodynamic, but the medium is a mucus slurry (Beninger et al. 1992).

Some bivalve species, such as *P. magellanicus*, lack a ventral groove, but our model still applies. In this bivalve, material in the dorsal tract is transported in a slurry, while that on the ventral tract is transported in mucus masses and discrete strings (Table 1) and is usually rejected as pseudofeces. The ultimate fate (ingested or rejected) of material on the ctenidia, however, depends on particle concentration and gut fullness (see Beninger et al. 1992). When the ctenidia become overloaded with particles or when the ingestive capacity is exceeded, more material is directed toward the ventral margin for rejection. These observations are consistent with those made on the three bivalve species in the present study (Table 1).

Particle velocities measured in the ventral grooves and dorsal tracts support our model. The rate of particle transport in the dorsal slurry is more than twice that in the ventral mucus string (Table 1). These velocity differences are similar to those obtained from ciliated frog palate epithelium, where maximum particle transport rates one to two cilium lengths from the epithelium are 2 times higher in culture medium than in higher viscosity mucus (Winet and Blake 1980). We therefore suggest that, in bivalves, particles in the dorsal slurry are carried just above ciliated tracts in a high flow zone, whereas particles in the ventral mucus string are transported more slowly by direct contact with the tips of cilia. This model is consistent with fluid mechanical predictions of

mucociliary transport and with movement of particles at low Reynolds numbers, which is dominated by viscous forces (Sleigh 1982; Blake and Fulford 1984).

Finally, although our observations demonstrate that two different mechanisms are involved in transporting food particles to the labial palps, it is unclear why some species, such as *M. edulis*, predominantly carry material in the ventral grooves bound in a mucus string, whereas other species, such as *P. magellanicus*, predominantly move material in the dorsal tracts suspended in a slurry; and yet others, such as *C. virginica*, use both ventral mucus strings and dorsal slurries. Perhaps, one transport mechanism is more efficient than the other. Certainly, material in the dorsal tract is moving at a rate two to four times higher than that in the ventral groove. However, the mucus string is much more compact than the slurry, so the actual bulk transport rate may be the same. These questions need further study.

Our observations on intact bivalves refute many previous interpretations of the suspension-feeding mechanism, which were based on observations of isolated ctenidial fragments or on bivalves with severed adductor muscles, ablated mantle edges, or bisected pallial cavities (e.g. Jørgensen 1975, 1981). We suggest that much of the controversy surrounding suspension-feeding dynamics in bivalves is attributable to artifacts that have arisen when specimens have been prepared for observation. Surgery and dissection could destroy subtle hydrodynamic interactions between feeding structures and particles (Beninger et al. 1992), eliminate the control animals have over muscle and cilia movement, alter the normal flow of water through the pallial cavity, damage delicate feeding structures, and stress the animals, causing structures to function abnormally. These problems, together with difficulties in observing pallial structures with a dissecting microscope through the small valve gape or through holes drilled in the shell, have led to an incomplete picture of the feeding process (MacGinitie 1941; Morton 1983; Jørgensen 1990). Observations made under these conditions should be interpreted with caution. We suggest that endoscopic techniques should be used to observe feeding mechanisms in the diverse array of bivalve species, thus elimi-

nating anomalies caused by surgery and excessive manipulation.

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