

## Minireview: Ciliary filter feeding and bio-fluid mechanics— present understanding and unsolved problems

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### *Abstract*

The energy cost for various ciliary filter feeders shows that useful pump work constitutes 0.3–1.1% of the total metabolic expenditure. The ‘water processing potential’ (liters of water pumped per milliliter O<sub>2</sub> consumed by the animal) is a useful tool for characterizing filter feeding and adaptation to the environment. The six types of ciliary-capture mechanisms (collar sieving, cirral trapping, ciliary sieving, ciliary downstream collecting, ciliary upstream collecting, mucus-net sieving) are reviewed as well as the aerosol/hydrosol filtration theory. A brief overview of fluid mechanical principles and tools for studying ciliary functions is given.

Filter feeding (or suspension feeding) is widely represented among invertebrate taxa, and cilia-mediated feeding is particularly common in the marine environment. Ciliary filter feeders remove suspended food particles, mainly phytoplankton (2–200 μm), but in many cases also free-living bacteria (0.2–2 μm), from the water (Jørgensen 1966, 1975; Wotton 1994; Silverman et al. 1995, 1997; Riisgård and Larsen 1995, 2001; Gili and Coma 1998). These animals have adapted to life in a nutritionally dilute environment, and they show great variations in particle capture mechanisms and pump design (Foster-Smith 1976*a,b*, 1978; Jørgensen 1983, 1990; Jørgensen et al. 1984; LaBarbera 1984, 1990; Shimeta and Jumars 1991; Vogel 1994; Riisgård and Larsen 1995, 2001; Silverman et al. 1996). Because the animals have evolved to solve common basic problems, a great number of similarities exist between taxonomically distant species. Recent investigations of particle-capture mechanisms and properties of pumps include widely different groups such as sponges, bryozoans, polychaetes, bivalves, ascidians, and cephalochordates. Comparative studies have aimed to give more precise description of the particle-capture mechanisms and to characterize the pumps. Further, the studies have focused on assessment of energetic costs of filter feeding and adaptation to the environment.

An analysis of bio-fluid mechanical aspects of ciliary filter feeders at the level of the organism may begin with an examination of the “overall effects” (pump characteristic, energetics, particle retention efficiency, and adaptation to the

environment), then move on to the “internal flow system” (resistances to flow through the animal and type of pump in terms of functional morphology of pumping structures and kinematics of cilia), and finally give a complete analysis that may include the “particle-capture process” (encounter, capture, retention, and transfer to digestive system). The present review of ciliary filter feeding in marine invertebrates starts with the overall effects of ciliary pumps and energetics and adaptation to environment, and then focuses on a classification into the six known types of capture mechanisms. Then filter feeding and aerosol/hydrosol filtration theory is treated, and the review concludes with a brief overview of fluid mechanical principles that are being modeled by means of various analytical and computational tools, to understand ciliary pumps and the particle-capture process in ciliary filter feeders and by means of tools for studying ciliary functions, emphasizing the importance of improved experimental methods of observation.

### Ciliary pumps and energetics

For any ciliary filter-feeding organism it is possible to identify a pump, consisting of ciliary bands, and a system, consisting of canals, filters, siphons, and other devices through which water flows. Studied separately, the pump and the system can be described by the pump and system characteristics, respectively, which produce pressure change  $\Delta p$  (Pa) as a function of the volume flow,  $Q$  (m<sup>3</sup> s<sup>-1</sup>). Often the pressure change is given in terms of “head,”—that is, height of water column,  $\Delta H$  (m H<sub>2</sub>O), where  $\Delta p = \rho g \Delta H$ ,  $\rho$  = water density (kg m<sup>-3</sup>), and  $g$  = acceleration of gravity (m s<sup>-2</sup>).

The pump delivers a volume flow and maintains a pressure rise from suction side to pressure side. Because a ciliary pump is not watertight, this pressure difference causes backward leakage, and the delivered pump head ( $\Delta H_p$ ) decreases characteristically with increasing volume flow. Such “open”

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Table 1. Operating pressure of pump ( $\Delta H_0$ ), power output ( $P$ ), total metabolic rate of "standard" animal ( $R_t$ ), overall pump efficiency ( $P/R_t$ ), and liters of water filtered ( $F$ ) per milliliter  $O_2$  consumed at starvation ( $R_m$  = maintenance metabolism) for various ciliary filter-feeding invertebrates.

Taxonomic group and species	$\Delta H_0$ (mm H <sub>2</sub> O)	$P$ ( $\mu$ W)	$R_t$ ( $\mu$ W)	$P/R_t$ (%)	$F/R_m$ [L H <sub>2</sub> O (ml O <sub>2</sub> ) <sup>-1</sup> ]	Reference
Sponges						
<i>Haliclona urceolus</i>	0.673	0.677	80	0.85	—	Riisgård et al. (1993)
<i>Halichondria panicea</i>	—	—	—	—	2.7	Thomassen and Riisgård (1995)
<i>Mycale</i> sp.	—	—	—	—	19.6	Reiswig (1974)
<i>Verongia gigantea</i>	—	—	—	—	4.4	Reiswig (1974)
<i>Verongia fistularis</i>	—	—	—	—	9.7	Reiswig (1974)
<i>Tethya crypta</i>	—	—	—	—	22.8	Reiswig (1974)
Bryozoans						
<i>Crisia eburnea</i>	0.065	—	—	—	—	Nielsen and Riisgård (1998)
<i>Celleporella hyalina</i>	—	—	—	—	68	Riisgård and Manriquez (1997)
Polychaetes						
<i>Sabella penicillus</i>	0.022	0.451	112	0.403	354	Riisgård and Ivarsson (1990)
Bivalves						
<i>Mytilus edulis</i>	1.0	10	900	1.1	—	Jørgensen et al. (1986, 1988)
	—	—	—	—	15–50	Riisgård et al. (1980)
	—	—	—	—	18	Clausen and Riisgård (1996)
	—	—	—	—	15	Møhlenberg and Kiørboe (1981)
<i>Spisula subtruncata</i>	—	—	—	—	10	Møhlenberg and Kiørboe (1981)
Ascidians						
<i>Styela clava</i>	0.3	2.3	891	0.26	—	Riisgård (1988a)
<i>Ciona intestinalis</i>	—	—	—	—	82	Petersen et al. (1995)
	—	—	—	—	13	Jørgensen (1955)

pumps are found in, for example, bivalves, ascidians, and bryozoans. Geometries and motions of cilia in many pumps are known (e.g., Sleight 1974; Brennen and Winet 1977; Silvester and Sleight 1984; Nielsen 1987), and the pumping mechanism is understood in principle. A system characteristic is the total pressure drop ( $\Delta H_s$ ) as a function of flow through the system. It is the sum of frictional resistance ( $\Delta H_f$ ), inclusive of pressure drop across a filter, and kinetic pressure loss ( $\Delta H_k$ ) due to creation of an exhalant jet at the narrowing outlet of the animal, both of which increase with increasing volume flow. An additional hydrostatic back pressure ( $\Delta H_b$ ), which, under natural circumstances, is 0, may be imposed in an experimental setup, hence  $\Delta H_s = \Delta H_f + \Delta H_k + \Delta H_b$ . At the operating point (i.e., the conditions of flow rate and pressure rise at which the pump will operate) the flow has adjusted itself so that the pump-pressure rise exactly balances the total resistance of the pump system,  $\Delta H_p = \Delta H_s = \Delta H_o$ , hence

$$\Delta H_p = \Delta H_b + \Delta H_f + \Delta H_k. \quad (1)$$

The pump characteristic cannot be measured directly in ciliary filter feeders, but the back-pressure characteristic (i.e.,  $\Delta H_b$  vs.  $Q$ ) can be experimentally determined and, according to Eq. 1, used to calculate pump characteristics when the system characteristics are known. Such calculations can lead to satisfactory results by means of an assortment of standard fluid mechanical equations for pressure drop, caused by friction and kinetic energy loss, for water flowing through a pump system of known dimensions (Garby and Larsen 1995; Riisgård and Larsen 1995).

At the operating point, the useful power (energy per unit

time),  $P$  (W), received by the water can be calculated as (pump pressure)  $\times$  (volume flow):

$$P = \rho g \Delta H_o Q_o. \quad (2)$$

By using this approach, a number of ciliary filter-feeding invertebrates have been analyzed and characterized, to determine the operating point and the power output of their pumps. The normal operating pressure head in ciliary pumps has been found to be low, varying between 0.02 and 1.0 mm H<sub>2</sub>O among species (Table 1).

It appears that the above type of analysis applies for normal, nominal conditions; but clearly,  $\Delta H_f$  and  $\Delta H_k$  depend on the geometry of the system and deviations from the assumed geometry will influence the derived  $\Delta H_p$ . This was demonstrated by Jørgensen et al. (1988), who showed that the back pressure-flow characteristic varied with the valve gape of the blue mussel *Mytilus edulis*. A reduced valve gape results in shortening of the gill axes and thus of the width of the gill interfilament canals and, consequently, the distance between the opposing bands of water pumping lateral cilia. The change in gill geometry appeared to be the main factor in determining pump pressure and flow rate in the mussel. Because the fully open state (and maximum exploitation of the filtration rate potential) is typical of undisturbed mussels—and of other ciliary filter feeders—Jørgensen et al. (1988) concluded that the filtration rate constitutes an "emergent property of the spatial geometry of the interfilament canals and the mantle cavity, rather than a physiologically regulated process". For a discussion of reliable filtration rates and physiological regulation versus autonomous filtration in bivalves, see Riisgård (2001, in press).

The energy cost of filter feeding can be evaluated as the ratio of useful pumping power ( $P$ ) and total metabolic power expenditure,  $R_t$  (W). This ratio, the overall pump efficiency  $= P/R_p$ , has been estimated for various ciliary filter feeders and shows that useful pump work constitutes from 0.3% to 1.1% of the total metabolic expenditure (Table 1). It should be mentioned, however, that there will be metabolic costs associated with mucus secretions in the species that use mucociliary transport for either cleaning, feeding, or both.

Referring to powers estimated for the mussel *M. edulis* by Riisgård and Larsen (1995), it may be argued that measures of efficiency other than the overall pump efficiency may be appropriate when characterizing the energy cost of filter feeding. Denoting by  $R_p$  (W) the metabolic rate of the part of organism responsible for pumping action (i.e., bands of lateral cilia and the cells carrying those cilia) and denoting by  $R_g$  (W) the metabolic rate of all of the gill structures would lead to the much higher efficiencies  $R_p/R_t = 6.6\%$  and  $R_g/R_t = 19\%$ , respectively. Large, specialized gill structures are expensive to maintain irrespective of whether the mussel is pumping water. This line of reasoning supports the hypothesis of "minimal scaling," which implies that energy for functions other than pump work can be supported only when the part of the organism responsible for the pumping action is scaled appropriately for continuous feeding (Jørgensen 1975; Clausen and Riisgård 1996; Riisgård and Goldson 1997; Riisgård and Larsen 2001).

### Adaptation to environment

To assess the adaptation of a filter-feeding animal to a certain environment, it is of interest to know the minimum food energy uptake (ingestion) of the animal needed to cover its maintenance metabolic energy requirement. The maintenance metabolic need may conveniently be expressed as the respiration ( $R_m$ ) measured as the energy-equivalent amount of oxygen consumed per unit of time by the starving animal. Ingestion may be expressed as the energy per unit time obtained from the volume of water per unit of time that the animal pumps through the filter device ( $F$ ) times the food particle concentration and will thus also depend on phytoplankton concentration in the environment as well as the particle retention efficiency of the animal's filter (under the assumption of no postcapture loss or rejection). The ratio  $F/R_m$  expresses "the water processing potential" (Jørgensen 1952; Møhlenberg and Kiørboe 1981) and the traditional "unit" is liters of water pumped per milliliter  $O_2$  consumed ( $L H_2O [ml O_2]^{-1}$ ). For example, to balance a metabolic energy requirement equivalent to the consumption of 1 ml  $O_2$  (equivalent to 20 J, Gnaiger 1983), under the assumption of 100% particle retention efficiency of phytoplankton and 80% assimilation efficiency, a benthic filter feeder exposed to a realistic near-bottom phytoplankton concentration of  $1.5 \mu g$  chlorophyll *a*  $L^{-1}$  (equivalent to  $2.5 J L^{-1}$ ) must pump  $20 / (2.5 \times 0.8) = 10 L$  of water, or a ratio of  $F/R_m = 10 L H_2O (ml O_2)^{-1}$ . The water processing potential may be used as a tool to characterize filter feeding. Low values for most sponges (Table 1) reflect that they, apart from feeding on phytoplankton, also feed on free-living bacteria and colloidal

particles. Unfortunately, relevant field measurements of phytoplankton concentrations in the inhalant water, or in close proximity to benthic filter feeders, are still missing (but see Riisgård et al. 1996b; Vedel 1998; Dolmer 2000, 2001), although of great importance for understanding the adaptation of animals to the environment.

### Capture mechanisms

In ciliary filter feeders, extraction of suspended particles from the water is now believed to be based on six different capture mechanisms (collar sieving, cirral trapping, ciliary sieving, ciliary downstream collecting, ciliary upstream collecting, and mucus-net sieving—cf. Riisgård et al. 2000).

Collar sieving is restricted to sponges in which the basic element for both pumping and filtering is the choanocyte cell with a flagellum that pumps water through a collar of microvilli acting as a sieve that captures free-living bacteria and other particles down to  $\sim 0.1 \mu m$  diameter (Bidder 1923; Fjerdingsstad 1961a,b; Reiswig 1971, 1974, 1975; Bergquist 1978; Jørgensen 1983; Simpson 1984; Riisgård et al. 1993; Larsen and Riisgård 1994; Thomassen and Riisgård 1995). The striking similarity between choanoflagellates that feed on filter free-living bacteria in the sea (Fenchel 1982) and choanocytes has given rise to the assumption that sponges have evolved from choanoflagellates. One crucial difference between sponges and choanoflagellates is the ability of the former to feed also on phytoplankton, which is retained and digested (phagocytosis) in the extensive inhalant channel system before the water is finally filtered through the collar slits of the choanocytes.

Cirral trapping operates in suspension-feeding bivalves, such as mussels, cockles, oysters, and clams, where bands of lateral cilia produce the main water transport through interfilamentary canals of the gill. Near the entrance to the canals, particles are separated from the main currents and transferred onto the frontal surface by the action of the laterofrontal cirri (LFC) that have a fixed, alternating beat pattern. One detailed account (Riisgård et al. 1996a) reports that food particles carried with the through current are stopped for a while at the entrance to the interfilament gap. Then the path is reversed  $180^\circ$ , and the particles are transferred to the frontal side of the gill filament to be transported toward the marginal food groove by frontal cilia. Transfer of particles is accomplished by the compound LFC or by the water currents they generate as they beat against the current through an angle of  $90^\circ$ . Particles  $>4 \mu m$  are stopped and transferred to the frontal side, whereas smaller particles either follow the flow around the cirri or they are stopped by the cirri's branching cilia (Dral 1967; Owen and McCrae 1976; Silvester and Sleight 1984; Riisgård 1988b; Jørgensen 1990, 1996; Beninger et al. 1992, Nielsen and Larsen 1993; Nielsen et al. 1993; Riisgård et al. 1996a). A "new explanation" of particle capture in mussels, based on endoscopic observations of an apparent low angle ( $\approx 30^\circ$ ) of particles approaching the gill filaments and subsequent direct interception, has been proposed by Ward (1996) and Ward et al. (1998, 2000), but Riisgård and Larsen (2000) raised doubt about its bio-fluid mechanic foundation. Other objections,

including insufficient optical resolution and image quality of endoscopy, have been advanced against the new explanation by Silverman et al. (2000) and Beninger (2000). On the basis of estimates of pressure drop for flow through a LFC screen and fluid mechanical calculations of creeping flow, Riisgård et al. (1996a) found it plausible that, during normal beating of the LFC, the through current passes mainly around the LFC in an oscillatory, unsteady, three-dimensional pattern and that only little flow may leak through the branching cilia. It may provisionally be concluded that large particles ( $>4 \mu\text{m}$ ) are stopped and transferred to the frontal current, whereas smaller particles either follow the flow around the LFC and escape or they are stopped by the branching cilia with or without physical contact.

In mussels and other bivalves with compound LFC, particles  $>4 \mu\text{m}$  are retained with 100% efficiency by the gills (Møhlenberg and Riisgård 1978; Jørgensen et al. 1984; Riisgård 1988b). Large, compound LFC are widespread throughout the Bivalvia (the vast majority of species), with some notable exceptions, all occurring in the relatively few heterorhabdic taxa (Owen and McCrae 1976). The basic particle-capture mechanism in bivalves without LFC remains poorly known (*see also* Owen and McCrae 1976; Beninger and le Pennec 1988; Beninger et al. 1992; Silverman et al. 1995, 1996). Gill types with small or lacking LFC—for example, in pectinids and *Ostrea edulis*—have been found to be less retentive than gills with well developed cirri (Møhlenberg and Riisgård 1978; McHenry and Birkbeck 1985; Riisgård 1988b). *Monia squama*, which lacks the cirri, fits into this pattern (Jørgensen et al. 1984).

Ciliary sieving is found in bryozoans in which the feeding apparatus consists of a ring of extended ciliated tentacles that form a crown (lophophore), with the mouth at the center of its base (Bullivant 1968a,b; Ryland 1976; Winston 1978). In most bryozoans, three types of ciliary rows may be found on the tentacles: lateral, frontal, and laterofrontal. Lateral cilia produce the feeding currents of the lophophore (Gordon et al. 1987; Nielsen 1987, 1995). When the through currents pass between the tentacles, they form a relatively strong core current directed straight down the lophophore to the mouth. Particles in the through currents are retained by the stiff laterofrontal ciliary filter and are either transported downward on the tentacles by means of the frontal cilia or the particles are transferred to the core current by means of inward tentacle flicks triggered by the arrested particles. The extra drag force from an arrested particle on the 15- $\mu\text{m}$  long laterofrontal cilia seems to trigger a tentacle flick. (Strathmann 1982; Riisgård and Goldson 1997; Riisgård and Manríquez 1997; Grünbaum et al. 1998; Larsen et al. 1998; Nielsen and Riisgård 1998).

Strathmann and McEdward (1986) observed that bryozoan cyphonautes larvae filter particles with “a sieve of stationary cilia,” whereas “the adults respond to individual particles with an induced local reversal of the ciliary beat and concentrate particles without filtration” (Strathmann 1982). Strathmann observed a change of beat, interpreted as a reversal of beat. The observations of sieving in adult bryozoans provides an alternative to local ciliary reversals, and the roles of local responses of cilia and sieving in feeding bryozoans are not yet clear. In stenolaemates, which lack

frontal cilia, the particles captured by the laterofrontal cilia elicit a tentacle flick which transfers the particle to the core current; changes in the metachronal waves of the lateral cilia have not been observed (Nielsen and Riisgård 1998). Gymnolaemates may use the same flicking method, but the frontal cilia and a wider behavioral repertoire opens up for alternative methods (Riisgård and Manríquez 1997). The laterofrontal sieve prevents direct contact between particles and lateral cilia, and the function of the change in the metachronal wave (“local disruption”) of the lateral cilia associated with particle capture (Strathmann 1982) still remains to be explained.

Ciliary downstream collecting is a widespread basic feeding principle, used across taxonomic boundaries in spite of often great variation in functional morphology of the feeding organs (Strathmann et al. 1972). The ciliary bands show some generality in structure in all groups: a ciliary band of compound cilia constitute the pump, which generates a flow with suspended particles that enters the ciliary region. In this region the same cilia, during their power stroke, catch up with suspended particles and transfer the particles to a food groove or a mouth cavity (Riisgård et al. 2000).

Ciliary downstream particle collecting is found in varied taxonomic groups of invertebrates, including planktonic larvae of gastropods (Emlet 1990; Hansen 1991), bivalves (Strathmann and Leise 1979; Gallagher 1988), and polychaetes (Emlet 1990; Hansen 1993). Downstream collecting has been studied in adults of the polychaetes *Sabella penicillus* (Nicol 1931; Riisgård and Ivarsson 1990; Mayer 1994), *Spirorbis tridentatus*, the entoproct *Loxosoma pectinaricola*, and the cyclophore *Symbion pandora* (Riisgård et al. 2000). Metachronal waves have been observed in larvae and rotifers but not in adult polychaetes and entoprocts, in which Riisgård et al. (2000) assume that the compound lateral cilia beat in random phases. The interpretation of observations of structure and activity of the ciliary bands in *L. pectinaricola*, as summarized by Riisgård et al. (2000), may serve as a general description of ciliary downstream collecting. In *L. pectinaricola*, video observations of the paths and velocities of particles showed that suspended particles are accelerated with the water that enters the region swept by the compound lateral cilia and then caught up by one or several compound cilia in their power strokes. This element in the process, denoted “catch-up,” accelerates a particle and rapidly moves it in a curved path to the midline at the frontal side of the tentacle. In this phase of the power stroke, the particle is pushed out of the main water current that moves past the tentacle, and, as the compound lateral cilia come to rest in their angular motion, so does the particle. The opposed lateral cilia from the two sides of the tentacle prevent escape, and the frontal cilia carry the particle along the food groove to the mouth. The basic principle of particle catch-up, as observed in *Loxosoma* (and *Spirorbis*, *Sabella*, and others), also applies for the cyclophore *Symbion*, although the opposed ciliary bands have been replaced by a ciliated mouth ring and the frontal cilia by a ciliated mouth cavity. The present description of the catch-up principle further substantiates the hypothesis proposed by Strathmann and Leise (1979), who found that suspended particles are

concentrated when they are “overtaken” by cilia in their effective stroke and “pushed faster than the water.”

Ciliary upstream-collecting animals possess ciliary bands that divert suspended food particles from the main water current and concentrate them on the upstream side of the band (Bullivant 1968a; Strathmann 1971, 1973; Strathmann and Bonar 1976; Gilmour 1979, 1982, 1985; Nielsen 1987, 1995; Hart 1990, 1991; Hart and Strathmann 1994; for review, see Nielsen and Riisgård 1998). The capture mechanism is correlated with the presence of a single band of cilia, which appears to be responsible for both the water transport and particle retention. Ciliary upstream collecting has been described on the tentacles of adult brachiopods and in larvae of echinoderms. According to the trochaea theory (Nielsen 1987, 1995), the upstream particle-collecting mechanism is restricted to the deuterostomes—adult pteobranchs, larval and adult phoronids, and brachiopods, where the feeding structures of the adults are derived from those of the larvae—and larvae of echinoderms and enteropneusts. Sensory laterofrontal cilia (although not electrophysiologically confirmed) are found in phoronids, pterobranchs, and brachiopods, but their presence has not been reported in echinoderms and enteropneusts (Gilmour 1978, 1979, 1981; Nielsen 1987). The function of the laterofrontal cilia remains unknown, but a role in control of the lateral cilia may be suggested.

Suspension feeding by planktonic larvae of echinoderms has been described by several workers (Strathmann 1971, 1975; Strathman et al. 1972; Gilmour 1985, 1986, 1988a,b; Hart 1991). Early workers offered divergent opinion about the mechanism by which these larvae capture suspended food particles from the seawater, but apparently many of the conflicting descriptions were resolved by Strathmann (1971), Strathmann et al. (1972), and Hart (1991).

Strathmann et al. (1972) have suggested that local reversals of the ciliary beat of the neotroch in early echinoderm larvae may be responsible for the upstream-collecting function. High speed cinefilms of pluteus larvae indicate that a locally induced reversal of beat is the clearance mechanism operating at the band. Thus, according to Strathman et al. (1972), “In a feeding larva the beat is the same until a particle comes within reach of the cilia. Then an alternation of the beat of several cilia can be seen while the particle slows, changes direction, and finally pushed back in an arc suggesting a reversed effective stroke of the cilia.” Hart (1991) described particle captures and suspension feeding by the larvae from different echinoderm classes. The analysis of videotape recording is generally consistent with Strathmann’s description of the ciliary reversal suspension feeding mechanism, but Hart came up with several novel observations. Thus, the larvae appear to have two modes of particle capture: “most particles are caught by apparent ciliary reversal at the ciliated band, but a small proportion of particles are captured without contacting the peripheral band.”

Further studies of the ciliary structures and the particle upstream-collecting process are needed. Such more advanced studies should include the sensory laterofrontal cilia in the lophophorate phyla and their possible roles in the upstream particle-capture process.

Mucus-net sieving is characteristic of nonvertebrate chor-

dates. Ascidians pump water through the inhalant siphon into the pharyngeal chamber and through small slits (stigmata) into the atrium from which the water leaves the ascidian as a jet through the exhalant siphon. Ciliary tracts on either side of the stigmata create the feeding current. When water is pumped across the pharynx wall, suspended particles are trapped on the mucus net continuously produced by the endostyle. Cilia on the pharyngeal bars transport the mucus net with retained food particles to the dorsal side, where it is rolled into a cord that is passed downward into the esophagus as an unbroken string. Particles down to 2–3 in  $\mu\text{m}$  diameter are completely retained, and electron microscopic studies of the mucus net have revealed that, in the fixed state, it is composed of 10–40-nm thick fibers arranged in rectangular meshes that vary between 0.2 and 0.5  $\mu\text{m}$  in width and between 0.5 and 2.2  $\mu\text{m}$  in length (Millar 1971; Fiala-Médioni 1978; Randløv and Riisgård 1979; Flood and Fiala-Médioni 1981; Jørgensen et al. 1984; Holley 1986; Petersen and Riisgård 1992; Petersen et al. 1999).

The lancelet *Branchiostoma lanceolatum* (amphioxus) is a cephalochordate that lies buried in the sediment with the ventral side turned upward and with the mouth opening free of the bottom. A feeding current, maintained by the activity of the lateral cilia of the branchial bars, flows through the mouth, the branchial basket (pharynx) with a particle capturing mucus net produced by the endostyle, and via the atrium out of the exhalant opening (Orton 1913; Weel 1937; Barrington 1958; Welsch 1975; Baskin and Detmers 1976; Rähr 1982; Riisgård and Svane 1999). The lower size of suspended particles trapped by the mucus net is  $\sim 0.06 \mu\text{m}$ ; the upper size limit is determined by the oral cirri that prevent particles  $>100 \mu\text{m}$  to enter the pharynx (Ruppert et al. 2000).

The polychaete family Chaetopteridae is well known for using filter nets (Barnes 1964, 1965; Sendall et al. 1995). In *Spiochaetopterus oculatus*, *Telespavus costarum*, and *Phyllochaetopterus socialis*, the water current through the tube is generated by ciliary rings of the foliaceous notopodia. Another example is the small polychaete *Pygospio elegans*, which can build a mucus net within its tube (Hempel 1957). Finally, it can be mentioned that the gastropod *Crepidula fornicata* uses a ciliary pump and a mucus net covering the greatly enlarged gill (Werner 1959; Jørgensen et al. 1984).

#### Filter feeding and aerosol/hydrosol filtration theory

In a strict sense, aerosol (or hydrosol) filtration involves interception between a particle and a structure (usually a threadlike element), hence implying some relative motion between particle and structure. Further, the theory is concerned with the particle-encounter efficiency, which depends on path of approach and relative velocity and size of particle and filter element (Shimeta and Jumars 1991). For historical reasons, the topic is treated separately, although conceptually it has much in common with the preceding topics. In regard to classification of capture mechanisms, it has been claimed by Vogel (1994) that sieves may be relatively unusual biological filters and that the turning point in how the filtering process ought to be viewed came with the filtration theory

presented by Rubenstein and Koehl (1977), who made a number of theoretical considerations to illustrate that filter feeders need not be restricted to sieving. According to the filtration theory, five mechanisms were suggested by means of which a fiber may remove dispersed particles from a velocity field: direct interception, inertial impaction, gravitational deposition, diffusional deposition, and electrostatic attraction. Among these possibilities, it was found that direct interception was likely to be the main mode of capture. Later, LaBarbara (1984) suggested six distinct mechanisms of particle capture, being either biological (“scan and trap,” which involves active response for capture and therefore has to be conceived as an unsteady encounter mechanism under sensory feedback control) or physical (i.e., sieving, direct interception, inertial impaction, gravitational deposition, and diffusive deposition). Among these possibilities, LaBarbara claimed that the best evidence for the occurrence of the “scan and trap” mechanism in ciliary filter feeding animals comes from the work of Strathmann and coworkers (Strathmann 1971, 1973; Strathmann et al. 1972; Strathmann and Leise 1979) on upstream-collecting invertebrates. According to the “scan-and-trap” theory, a local ciliary reversal alters the flow so that a small parcel of water containing the particle is isolated on the upstream side of a band of simple cilia.

It is obvious that further investigations are needed to clarify whether alternative bio–fluid-mechanical principles may be at work in other groups of ciliary filter-feeding invertebrates (e.g., Jørgensen 1983; Silvester 1983; Jørgensen et al. 1984; Silvester and Sleight 1984; Shimeta and Jumars 1991; Hart and Strathmann 1994; Shimeta and Koehl 1997; Wildish and Kristmanson 1997), but sieving in groups other than sponges, bryozoans, and mucus-net filter feeders cannot be excluded. Shimeta and Jumars (1991) attempted to ferret out the reasons for the combination of “great promise and slow progress” of applying the aerosol filtration theory to suspension feeding (“hydrosol filtration”). So far, direct observations are missing, and aerosol/hydrosol filtration theory appears to lack scientifically based examples in ciliary filter feeding.

### Fluid mechanical principles

Much of the progress in the field of ciliary filter feeding until now—and that to come—relies on a thorough understanding of fluid mechanics and application of associated analytical and computational tools, as well as on good experiments. Only the most elementary and phenomenological analysis of the pump-system characteristics was included above. Good estimates can be made of the system characteristic, say from standard equations for pressure drop, caused by friction and kinetic energy loss for water flowing through a pump system with known dimensions (Garby and Larsen 1995; Riisgård and Larsen 1995). Pressure drop over a filter may be based on an estimate for infinite arrays of parallel cylinders (Tamada and Fujikawa 1957) or on a rectangular mesh (Silvester 1983). The flow between two parallel cylinders (Cheer and Koehl 1987) may be used to estimate how pairs of moving cilia may interact with a single

particle. Also, the drag on a spherical food particle has been used to determine the added force acting on a cilium and its deflection (Strathmann and McEdward 1986, using values of the flexural stiffness of a cilium; see Baba 1972, but also Hiramoto 1974) when a particle is intercepted. Since filter feeding generally occurs at low Reynolds numbers and in finite spaces, walls near moving cilia have a significant effect on the velocity field, and use of results derived for arrays of infinitely long cylinders should be treated with caution.

As a more important issue for particle capture, cilia-driven flow has been approached by several mathematical methods. In the envelope model (e.g., Taylor 1951; Blake 1971), a waving extensible surface of large extent is shown to drive fluid motion. Here, as in many other models, the ciliary motion, including metachronism, is prescribed a priori. It has been used as an approximation to determine the pump characteristic of an idealized pump consisting of a long, two-dimensional channel with ciliated walls (Nielsen and Larsen 1993). In the sublayer model (Blake 1972), each cilium is modeled by singularities appropriate for low Reynolds number Stokes flow. The method has been refined by many workers and used to model three-dimensional flows in complex, fixed geometries—for example, to determine the feeding currents in encrusting bryozoan colonies (Grünbaum 1995). Because of the size of this problem, cilia motion was not resolved, but its effect was included as a specified steady fluid velocity along tentacles. Singularities have also been used to approximately model unsteady ciliary action, bounding surfaces, and a finite-sized spherical particle (Mayer 2000).

In the immersed boundary method, first proposed by Peskin (1977), the governing equations are discretized on a computational mesh covering the domain in question. It has been used to model, for example, the ciliary pump in *M. edulis* (Grünbaum et al. 1998) for the simplified case of two-dimensional flow with specified motion of a small number of beating cilia, but it included the modeling of suspended particles being transported by the fluid. In another approach based on use of internal models (“engines”) of the cilia, their motion is not prescribed a priori but is a result of their interaction with fluid motion. Numerical simulations show multicilia flows, indicating metachronism to be a consequence of mutual interactions through the viscous fluid motion (Gueron and Liron 1992).

### Tools for studying ciliary functions

Theoretical models need experimental input for inspiration and ultimate verification. In principle, one needs simultaneous records of the motion of cilia, fluid, and suspended particles. Because of the geometric and kinematic complexities, scaled-up laboratory models are largely ruled out, and therefore in situ observations are needed. Available observation techniques include high-speed cinefilms recorded through microscopes (Nielsen and Rostgaard 1976; Strathmann 1982; Emler 1990), regular video microscopy (e.g., Gallager 1988; Nielsen et al. 1993; Hart 1996; Petersen et al. 1999), confocal laser microscopy (Silverman et al. 1996, 2000; Beninger et al. 1997a), and endoscopy (Beninger et

al. 1992., 1997b; Beninger and St-Jean 1997; Ward et al. 1996, 1998, 2000). Experimental physiological studies of water processing and particle retention, as well as morphological studies to describe cilia and structures, are important for theoretical modeling but ciliary mapping also may give pertinent information, especially when it is combined with endoscopy and mucocyte mapping (e.g., Beninger et al. 1999). Furthermore, advanced computational tools are needed to resolve, for example, the questions of the detailed mechanisms at play in particle capture. Here it is necessary to resolve three-dimensional, unsteady fluid motion in confined spaces driven by systems of moving cilia, as well as the resulting motion of at least a single spherical particle.

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