Marine Biology 114, 281–288 (1992)

Marine Biology

Gill function and particle transport in *Placopecten magellanicus* (Mollusca: Bivalvia) as revealed using video endoscopy

Peter G. Beninger [1], J. Evan Ward [2], Bruce A. MacDonald [2] and Raymond J. Thompson [2]

[1] Département de Biologie, Faculté des Sciences, Université de Moncton, Moncton, New Brunswick, E1A 3E9, Canada
[2] Marine Sciences Research Laboratory, Memorial University of Newfoundland, St. John's, Newfoundland, A1C 5S7, Canada

Date of final manuscript acceptance: May 27, 1992. Communicated by J. Grassle, New Brunswick

Abstract. The technique of endoscopic video observation was used to study feeding processes of *Placopecten magellanicus* (Gmelin), collected from Bull Arm, Newfoundland in August 1991 and 1992, under near-natural feeding conditions. The fate of captured particles depended on the extent of ingestive or handling capacity saturation. Under low (1 to 10 particles μl^{-1}) to medium (10 to 20 particles μl^{-1}) particle concentrations, most particles were incorporated in continuous anteriorly directed slurries in the dorsal ciliated tracts of the gill arch and dorsal bends. As particle concentration or exposure time to the lower particle concentrations increased, four endogenous mechanisms of ingestion volume control were increasingly observed: (1) rejection of dense mucus-particle masses from the principal filament troughs onto the ventrally beating cilia and associated currents of the ordinary filament plicae, counter to and below the incoming pallial current maintained by the principal filament cilia; (2) intermittent stopping of the anteriorward flow in the dorsal ciliated tracts; (3) reduction or cessation of input from the principal filaments to the dorsal ciliated tracts; (4) detachment of the dorsal bends from the mantle to establish a shunt from the infrabranchial to the suprabranchial cavity. Chemical and histochemical tests of purified fluid withdrawn from the dorsal ciliated tracts indicate that mucus is present at all particle concentrations. Mucus therefore participates both in normal feeding and in ingestion volume control on the bivalve gill, although different mechanisms, and types of mucus, effect transport of material in the dorsal (feeding) and ventral (cleaning) ciliated tracts.

Introduction

Although the feeding mechanisms of most macroscopic metazoans are well known, the microphagous diet and presence of an opaque shell have imposed severe limitations on the study of these processes in adult suspension-feeding bivalve molluscs. A long-standing controversy centres around the exact mechanisms of particle capture and transport (see Beninger 1991 for review). One extreme position of this controversy is represented by MacGinitie (1941), who stated that all particles are trapped and transported in a mucus net on the bivalve gill. Although initially adhering to this idea (Jørgensen 1966), Jørgensen and his collaborators subsequently proposed an entirely hydrodynamic, cilia-driven mechanism for particle capture and transport from the gill to the stomach, while excess particles were said to be cleared from the gill via direct ciliary transport in mucus (Jørgensen 1981 a, b, 1990). Between these extreme positions a number of models have been proposed which involve either hydrodynamic or direct ciliary interception and transport in mucus at some level (Moore 1971, Owen 1974, Owen and McCrae 1976, Owen 1978, Sylvester and Sleigh 1984).

A recent histological study has demonstrated that mucus accompanies ingestion in the five bivalve species which have been examined, and arrival of mucus in the oral region appears to be continuous regardless of particle concentration (Beninger et al. 1991). With respect to the gill, anatomical and ultrastructural studies have provided some clues to functional correlates (Beninger et al. 1988, Le Pennec et al. 1988); however, only direct observation can unequivocally establish function in this organ. Although the elucidation of bivalve suspension feeding processes has long been hampered by the inaccessibility of the pallial organs to direct observation in undisturbed specimens, recent progress in the use of endoscopic video techniques has opened this field to investigation (Ward et al. 1991). The purpose of the present study was to describe the mechanisms involved in feeding at the gill in the giant scallop *Placopecten magellanicus*, using the technique of video endoscopy. The aspects of feeding addressed herein are particle trajectories, capture, and transport on the gill, as well as the regulation of ingestion volume and pseudofeces production.

Materials and methods

Video endoscopy

The apparatus and procedure used for endoscopic video observation has been described previously (Ward et al. 1991). Briefly, it consists of an endoscope fitted with a 1.7 mm diameter optical insertion tube (OIT), attached to a CCD video camera. The camera is fastened to a micromanipulator, allowing three-dimensional movement of the OIT within the mantle cavity. A video monitor and recorder are used for observation and storage of visual sequences.

Three adult *Placopecten magellanicus* (Gmelin) collected from Bull Arm, Newfoundland were used for endoscopic examination in August 1990 and four additional scallops collected form the same site on August 1991 were used both for chemical and histochemical tests of fluid withdrawn from the dorsal ciliated tracts in August 1991. The scallops were acclimated to laboratory open-circuit aquaria and fed daily with cultured *Chaetoceros muelleri* Lemmermann for at least 3 wk prior to observation. All were fitted with rubber stoppers on either side of the dorsal shell margin in order to attenuate valve-clap responses and mounted on an adjustable platform using velcro strips. The platform and scallop were then immersed in a holding chamber with flowing seawater (12 °C, 31‰). The inflow line was fitted with a sampling port.

The OIT was inserted between the shell valves in the anterior region of the gill. Observations of the frontal surfaces were made at three particle concentrations, based on values from the scallops' natural habitat, and monitored using a Multisizer 1 particle sizer (Coulter electronics): low (1 to 10 particles $\mu l^{-1} = 1.36 - 1.92$ mg ml^{-1}), medium (10 to 20 particles $\mu l^{-1} = 1.92 - 2.55$ mg ml^{-1}), and high (>20 particles $\mu l^{-1} = > 2.55$ mg ml^{-1}). Suspensions of particles consisting of the diatom *Chaetoceros muelleri* (4 to 7 µm diameter) and red reflective particles (2 to 5 µm, as tracers) were delivered to the holding chamber using a peristaltic pump. Observations always commenced at low particle concentrations, and recordings were made prior to and following changes in particle concentration, such that the total observation time for a given scallop varied from 3 to 6 h. Photographs were obtained using direct screen photography of images enhanced through video analysis (Ward et al. 1991). Particle speed was calculated from the number of frames (recording speed: 30 frames s^{-1}) required for a particle to traverse a known distance (average plical width, calculated from ordinary filament numbers, diameters, and interfilamentar spaces).

Chemical and histochemical analyses

In order to determine whether mucus was present in the dorsal ciliated tracts (mucus is transparent and therefore not visible), the contents of the gill arch were sampled at 1 to 3 mm from the gill surface using a cannula fitted to the endoscope and aspirated with a peristaltic pump at a rate of approximately 300 µl min^{-1}. Scallops were exposed to low and high particle concentrations. The aspirated fluid was centrifuged at 12 061 RCF (relative centrifugal force) for 10 min and the supernatant filtered through a 0.45 µm Nuclepore filter. The filtrate was dialysed against two changes of distilled water at 4 °C overnight to remove salts, then frozen in liquid nitrogen and lyophilized. The resulting powder was dissolved in a known volume of distilled water; a small amount of precipitate remained in some samples. Protein content was determined using the Lowry technique (Lawry et al. 1951), and carbohydrate was estimated using the method of Dubois et al. (1956). Controls were 1.0 µm Nuclepore filtered seawater and distilled water.

A second group of scallops was exposed to medium particle concentrations and used for histochemical analysis of ca. 50 ml of dorsal ciliated tract aspirate. The fluid was dialyzed as described above, lyophylized, re-dissolved in two drops of water, and centrifuged at 12 061 RCF for 10 min. Microscope slides were prepared for smears either by dipping in acetone or by coating with albumin. The fluid supernatant was applied to marked regions on the slides, concentrated on a slide warmer, fixed with Cytoprep aerosol (Fisher Scientific Co.), and stained in 1% alcian blue solution at pH 2.5 for 30 s. The slides were then quickly and gently dipped in four successive distilled water baths, allowed to dry, and examined under a light microscope. Positive controls were mucus from human nasal epithelium and from gill epithelium of dissected scallops; negative controls were albumin and sunflower seed oil (two clear, viscous, non-mucopolysaccharide fluids).

Results

The general morphology and anatomic terminology of the scallop gill have been presented in a previous study (Beninger et al. 1988); for consistency, this vocabulary will be used in the present work.

At all concentrations, particles drawn into the pallial cavity moved toward the dorsal region of the gill, and were progressively deflected into the plical troughs. Each plical trough is occupied by a gutter-shaped principal filament, and, unless there was a concertina response (Drew 1906, Dakin 1909, Owen and McCrae 1976), the particles disappeared from view when they reached these filaments. Particles on or close to the ordinary filament frontal surface were always transported ventrally; however, such phenomena were observed at high particle concentrations or after prolonged exposure to low-medium particle concentratios (i.e., when the scallop's ingestive/handling capacity was exceeded, hereafter referred to as overloaded).

Beyond these general observations, a distinct pattern of responses was observed in continuously feeding scallops with respect to particle concentrations and elapsed time since initation of feeding, as outlined below. In addition, particle transport on the gill was modulated by alterations of feeding activity; this will be described subsequently.

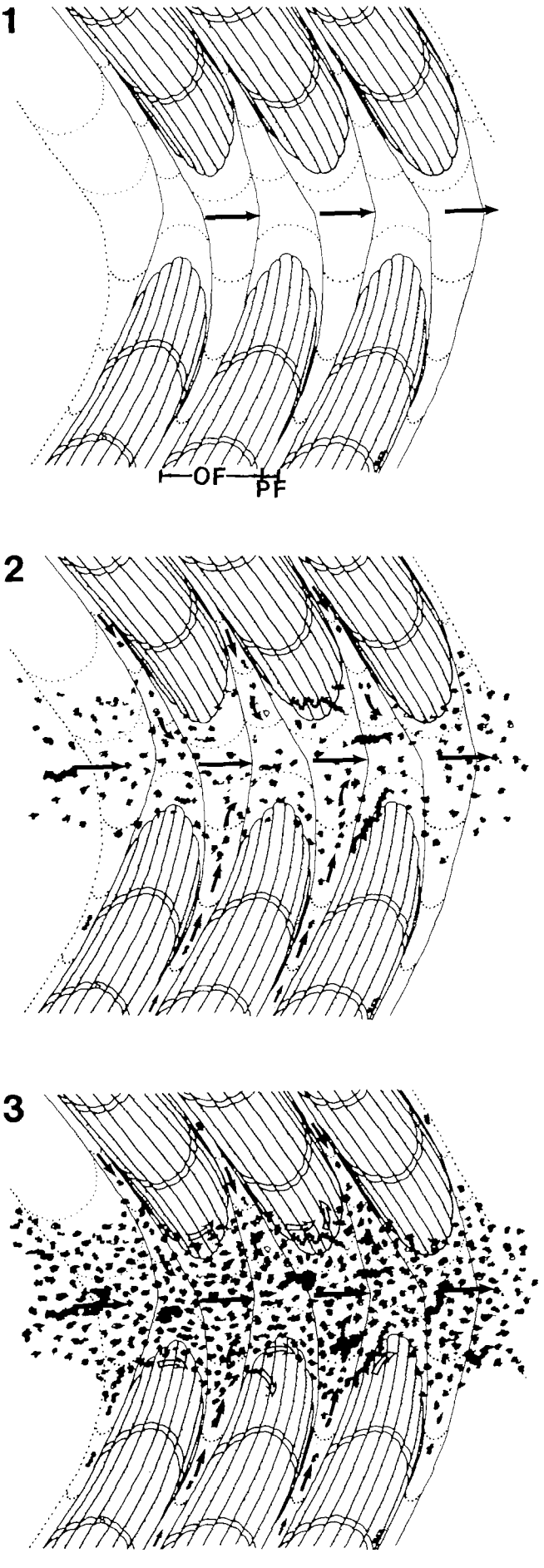
Low particle concentration (1 to 10 particles μl^{-1})

Material emerging from the dorsal-most regions of the principal filaments entered the semi-enclosed spaces of the dorsal bend and gill arch as individual particles (Fig. 1; *1*). These particles were then swept anteriorly in the gill arch at a speed ranging from 5.7 to 10 mm s^{-1}. The chemical analyses demonstrated the presence of a protein and carbohydrate-containing substance in the centrifuged aspirate of these regions.

Although particles were visible in the ventral bend region, they all travelled dorsally as described above. Very few particles were observed on the frontal surface or the ventral bend ciliated tract (Fig. 2: *1*).

Medium particle concentrations (10 to 20 particles μl^{-1})

As concentration increased, progressively more particles entering the dorsal ciliated tracts from the principal filaments were clumped, and the anteriorly directed current



of the gill arch and dorsal bend became opaque. The result was a flocculent slurry, which thickened as particle concentration increased. The shape of the anteriorly directed slurry conformed to the conduits formed by the gill arch and the dorsal bend. Velocities of this slurry were 5.7 to 9 mm s^{-1} (Fig. 1: *2*).

The characteristics and behavior of the slurry changed after a variable time interval (ca. 20 to 30 min after the start of feeding, depending on the specimen). The slurry became progressively opaque, and began to exhibit a more irregular anteriorward movement, punctuated by short intervals with no movement. In addition, as particle concentration increased, pulses of more opaque slurry were observed (time interval between pulses ranged from 10 to 115 s). These pulses were so thick that they occluded our view of the arch or bend. The periods of non-movement increased with time, or with particle concentration, or both. The slurry movement was more regular in the dorsal bend than in the gill arch. Chemical analysis again confirmed the presence of protein and carbohydrate in the dialysed, particle-free aspirate. This substance was alcian blue positive, indicative of acid mucopolysaccharides.

Some particles were observed travelling ventrally close to the frontal surface of the ordinary filaments, beneath the general dorsalward flow of particle-laden water arriving from the pallial cavity (Fig. 3). Although the net movement of these particles was toward the ventral bend, individual particles usually "bounced" obliquely across the ordinary filaments and often descended into the troughs of the principal filaments, where they again moved dorsally. Occasionally, these particles were ejected from the principal filaments and continued ventrally on the ordinary filaments. Such a sequence could occur several times before a given particle reached the ventral bend and began moving anteriorly (Fig. 3). As particle concentration increased, many of the dorsally moving particles in the principal filament gutters (as revealed during concertina responses, see Fig. 5) tended to aggregate, and these clumps were usually ejected onto the ordinary filaments and thence to the ventral bend.

High particle concentrations (>20 particles μl^{-1})

At high concentrations particle movement and gill behaviour were similar to those described above for scal-

Fig. 1. *Placopecten magellanicus*. Gill arch (ventral view). Dorsal portions of ordinary filament plicae (OF) and principal filaments (PF) fuse dorsally to form gill arch. *1*: Low particle concentration (1 to 10 particles μl^{-1}). No mucus-particle masses visible, and only general anteriorward flow of fluid evident from occasional passage of reflective particles (filled arrows). Few reflective particles seen exiting the PF to join anteriorward flow. *2*: Medium particle concentrations (10 to 20 particles μl^{-1}). Small mucus-particle masses exit principal filament troughs to join general anteriorward flow, in which some larger clumps are visible. *3*: High particle concentrations (>20 particles μl^{-1}). The gill arch filled with anteriorly directed mucus-particle masses of various sizes. Many particle masses at margins of the gill arch and existing principal filament troughs are dragged onto the ordinary filament plicae and moved ventrally (open arrows)

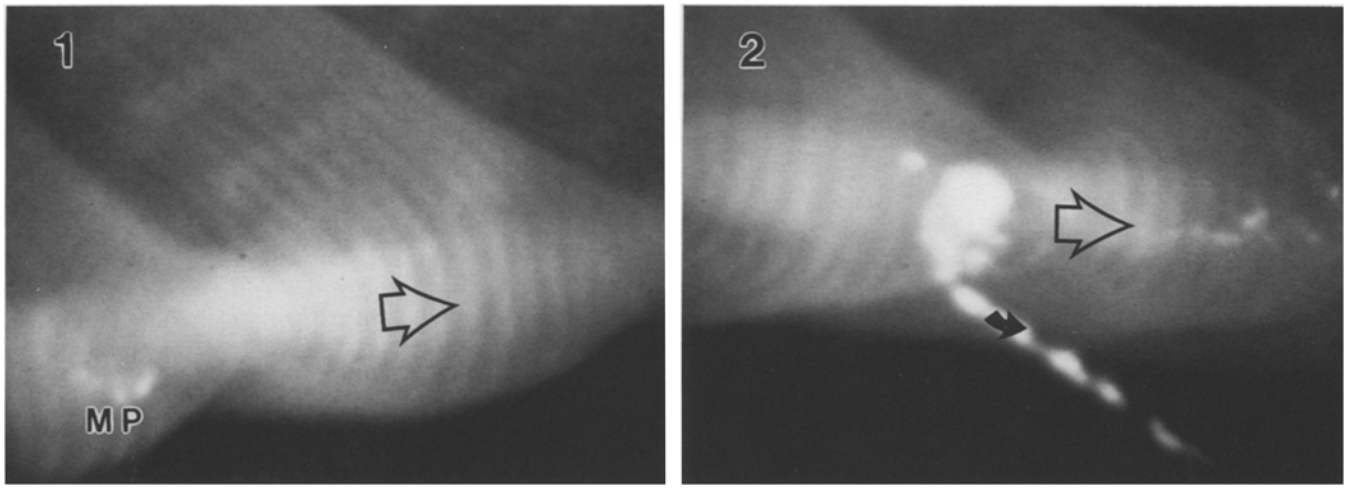


Fig. 2. *Placopecten magellanicus*. Photographs of gill ventral bend as seen on endoscope monitor. *1*: Low particle concentration. Note paucity of mucus-particle masses (MP). *2*: High particle concentration or after prolonged (≥ 1 h) exposure to lower particle concentrations. Note distinct mucus-particle string in process of detaching and floating into pallial cavity. Open arrows indicate mucus-particle movement on ventral bend; filled arrow indicates direction of movement of mucus-particle mass

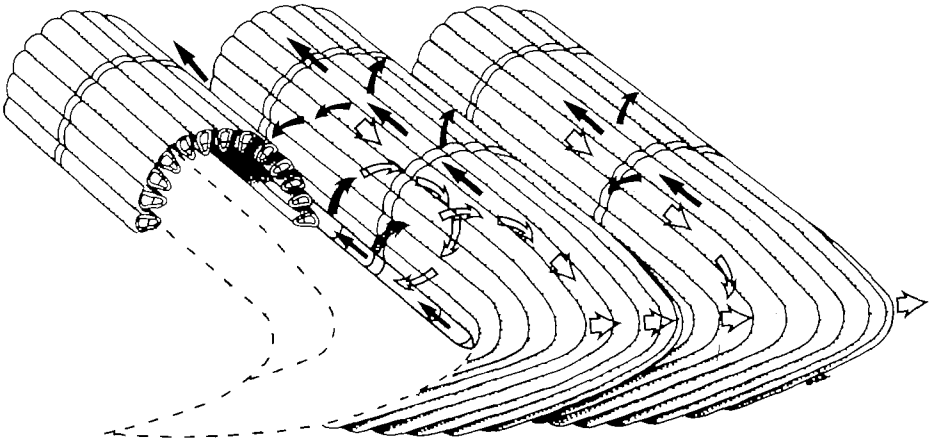


Fig. 3. *Placopecten magellanicus*. Gill ventral bend, high particle concentration or prolonged (≥ 1 hr) exposure to lower particle concentration. General flow of water and particles is dorsal, as water is drawn into principal filament troughs (solid filled arrows). Particle masses destined for rejection move beneath and counter to this flow, becoming incorporated into the anteriorly moving mucus-particle string (open arrows, particles and string not shown). Such particle masses often bounce obliquely across ordinary filaments and re-enter principal filament troughs, to be ejected after a short dorsal displacement (stippled arrows). Dorsal displacement is accompanied by an increase in volume of the particle mass. Through currents not shown

lops held for extended periods at medium concentrations. The slurry in the gill arch and dorsal bend was most opaque at high concentrations, and once again the slurry movement was more regular in the dorsal bend than in the gill arch. Velocities of the slurry were 4.3 to 6.5 mm s^{-1}. The appearance of slurry pulses was also more frequent, and tightly bound mucus masses were more prevalent and voluminous than at the lower concentrations. At the highest particle concentrations tested (28 to 32 particles μl^{-1}), some tightly-bound material also accumulated on the gill arch and plicae around the arch. These masses continuously dissociated and descended toward the ventral bend (Fig. 1: *3*). Upon arriving at the ventral bend, the particles and masses were included in dense, slowly anteriorward-moving strings and clumps which often broke away and floated off into the pallial cavity, presumably as pseudofeces (Fig. 2: *2*).

Although the above behaviour was typical at high particle concentrations, it was also observed after a scallop had been exposed to low particle concentrations for several hours, suggesting that it was not induced by the particle concentration *per se*, but rather by the scallop's capacity to process or ingest the particle slurry. In one individual scallop exposed to high particle concentrations followed by a "purge" of low concentration (3 μl^{-1} for 4 h), the particle slurry in the gill arch and dorsal bend behaved first as described above, and then as described for low particle concentrations (steady anteriorward stream in gill arch and dorsal bend, sparse particle distribution).

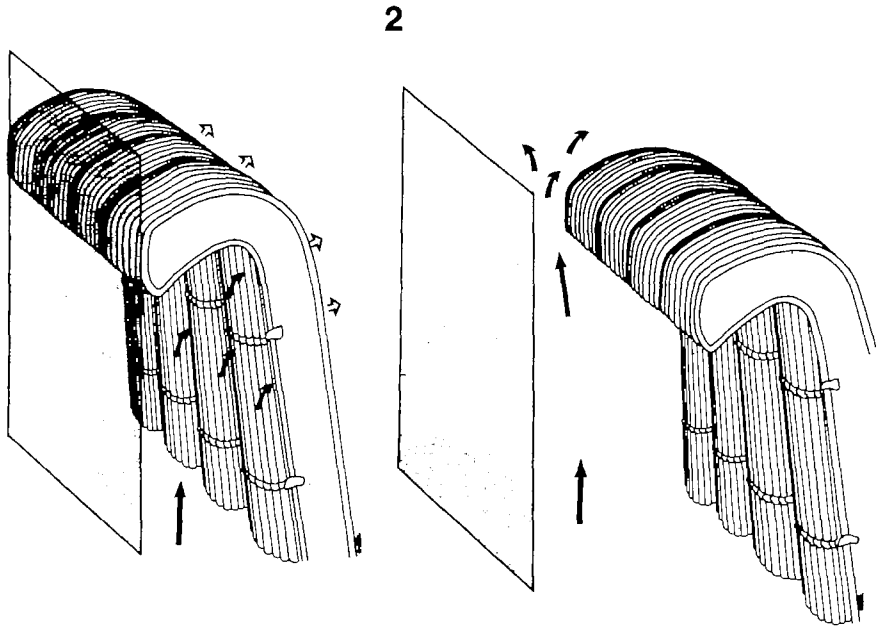


Fig. 4. *Placopecten magellanicus*. Gill, dorsal bend of lateralmost ascending lamella. *1*: Normal position in contact with mantle, low to medium particle concentrations. Incoming water and particles (filled arrows) are intercepted by gill and cleared water exits via through currents (open arrows). *2*: At high particle concentrations or after prolonged ($\geq$1 h) exposure to lower particle concentrations, dorsal bend detaches from mantle, allowing incoming particle-laden water to be shunted directly into the suprabranchial cavity (filled arrows), bypassing the clearing activity of the gill

Modifications of feeding behaviour

Superimposed upon the sequence described above were several modulatory behaviors which could occur during exposure to a constant particle concentration. These were most evident at high particle concentrations. The movement of the anteriorly directed mucus-particle slurry could either increase in velocity, decrease in velocity, or momentarily cease completely. Cessation was associated with a slight reversal of direction ("sloshing"), resulting in the dissociation of the discrete slurry and causing the particles to leave the dorsal tract and swirl within the semi-enclosed spaces of the gill arch and dorsal bend. Forward motion would then suddenly recommence, drawing material back into the dorsal tracts and re-forming the mucus-particle slurry.

Specimens were also able to reduce and even cease channeling of material from the principal filament troughs to the dorsal ciliated transport tracts, resulting in a clearing of the tracts as anterior currents continued to transport existing material. Complete clearing of a continuous, thick particle slurry could be achieved in 30 to 60 s. Following such a clearing event (generally within 1 min), input from the principal filament troughs recommenced, with a consequent reformation of the particle slurry.

Finally, at high particle concentrations or after prolonged (ca. 1 h) exposure to medium concentrations, the dorsal bend intermittently detached from the mantle. This allowed the particle slurry to escape into the excurrent flow of the suprabranchial chamber (Fig. 4).

Discussion

Endoscopic examination clearly showed that the appearance of the mucus is quite different in the dorsal cilitated (feeding) and ventral (cleaning) tracts, being much more dense in the latter. The existence of two visually distinct types of mucus on the bivalve gill has previously been reported (Bernard 1974), and histochemical differences between mucocytes on feeding and nonfeeding epithelia have also been observed (Beninger et al. 1990a, b, Beninger et al. 1991). Histochemical studies currently underway also indicate that chemically different types of mucus are secreted by the ordinary filament plicae (which send material ventrally for rejection) and the principal filament troughs (which send material to the dorsal ciliated tract, Beninger et al. in preparation). The importance of this point will be discussed below.

Particle capture and dorsalward transport

Direct observations of particles arriving at the scallop gill confirm *in vivo* the previously proposed mechanism of particle capture (Owen 1978, Beninger et al. 1988, Beninger 1991). The incurrent flow is parallel to the gill filaments, proceeding dorsally while being deflected into the gutters of the principal filaments. This current appears to be created chiefly by the heavily ciliated frontal surfaces of the principal filaments and the lateral cilia of the ordinary filaments (Jørgensen 1981a). It was seen to operate even under high particle concentrations, when the frontal cilia of the ordinary filaments were moving particles in the opposite direction toward the ventral bend.

At low particle concentrations or after short (i.e., 10 to 30 min) exposure to medium concentrations, captured individual particles arriving in the anteriorly directed currents of the gill arch and dorsal bend were observed exiting the principal filament troughs. Although it was not possible to determine whether these particles were coated in mucus, they were frequently observed to adhere together when two or more particles collided. If particle capture is defined as the extraction of particles from the

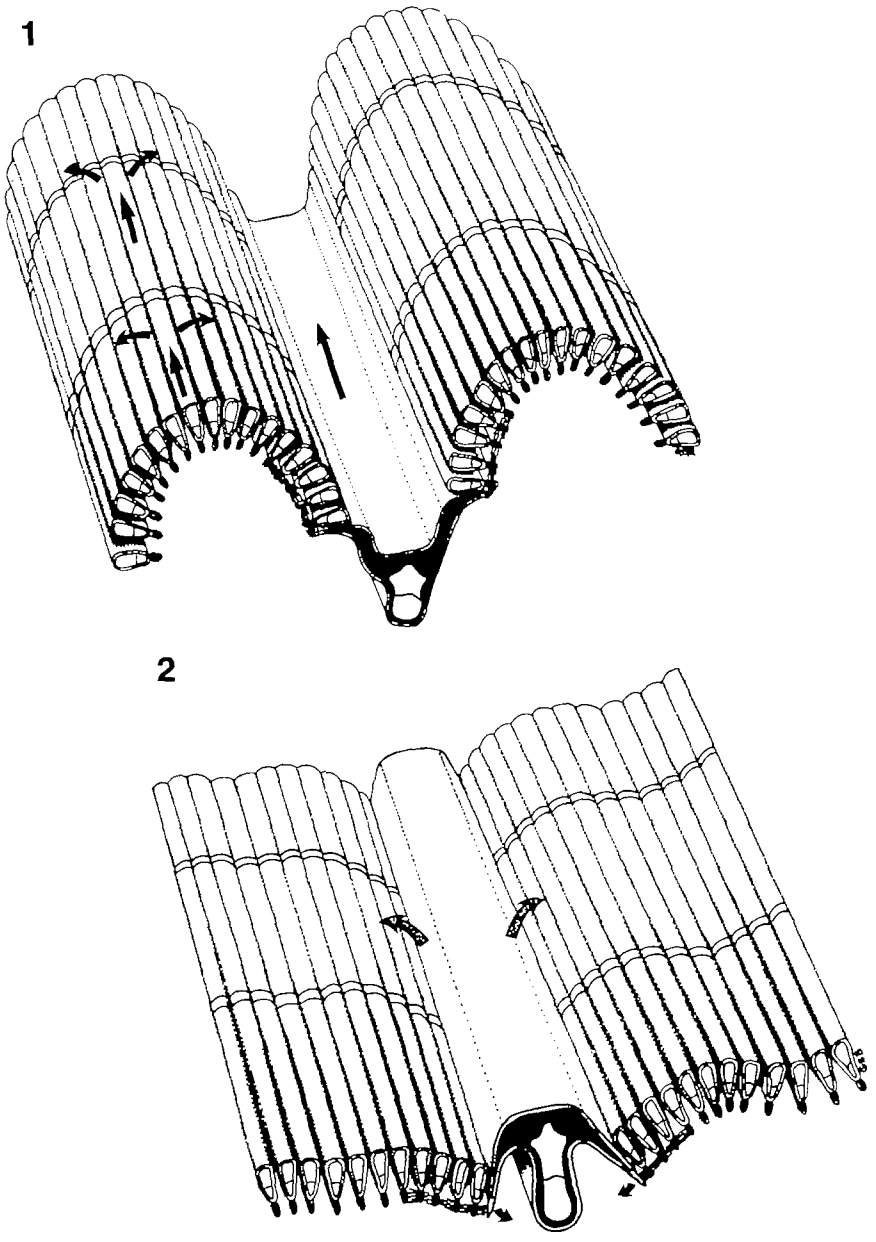


Fig. 5. *Placopecten magellanicus*. Segment of gill. *1*: normal plicate configuration, showing general movement of incoming particle-laden water. For clarity, principal filament trough shown here much wider open than in real life. *2*: At high particle concentration or after prolonged (≥ 1 h) exposure to lower particle concentration, a concertina response may occur: lateral walls of principal filament retract (filled arrows), ejecting matter contained in trough onto ordinary filament plicae (stippled arrows)

through currents, then capture is effected hydrodynamically in an aqueous medium by the strong currents produced by the principal filament through cilia. This hydrodynamic mechanism continues to act as particles move dorsalward in the principal filament trough, although the medium is altered by the addition of mucus.

Oralward transport

Upon leaving the principal filament gutters, particles are incorporated into mucus in the anteriorly directed particle slurry which was present at all particle concentrations, as unequivocally demonstrated by the chemical and histochemical tests performed on samples taken from these tracts. At all particle concentrations, prior to saturation of ingestive/handling capacity, particles are incorporated into an anteriorly directed mucus slurry in the dorsal ciliated tracts. Particle transport oralward in the dorsal tract is thus not strictly in water currents, as proposed by Jørgensen (1981 b, Jørgensen et al. 1984) nor is it entirely dependent on mucus directly moved by cilia, as postulated by Beninger (1991). Rather, mucus appears to accompany particles at all concentrations, and this mucus is swept along as a continuous slurry in the dorsal transport tracts in what appears to be a cilia-generated current. The mechanism is therefore hydrodynamic, but the medium is a mucus slurry.

At high particle concentrations, or when overloaded, the ventral ciliated tract transports particles anteriorly in mucus strings and clumps. As described above, this ventral tract appears to be a rejection route which is activated when the ingestive or handling capacity of the scallop is saturated. Although mucus is involved in "cleaning" (*sensu* Jørgensen 1981 b, 1990) the scallop gill, it is also involved in normal oralward particle transport. These

observations are at variance with those of Jørgensen (1981 b, 1990) in which mucus was only ascribed a role in cleaning the gill of excess particle material, whereas particle capture and transport was considered purely hydromechanical. Furthermore, endoscopic observations on *Mytilus edulis*, *Mya arenaria*, and *Crassostrea virginica* feeding also show that particles are transported in mucus strings in the ventral food groove, even at low concentrations (Ward et al. in press) Taken together, these data indicate that although mucus is always involved in particle transport, different types of mucus are used in feeding and in cleaning – and in the scallop these functions are ultimately carried out on different ciliated tracts.

Particle selection

Understanding of the mechanisms involved in particle selection has been hindered by a lack of knowledge concerning the state in which particles are captured and transported to the oral region. To date it has been demonstrated that particles are ingested as mucus-particle masses (Beninger et al. 1991) and, in the present study, that particle transport oralward from the gill is also in either a flocculent mucus "slurry" (low particle concentrations) or in a denser mucus slurry (higher particle concentrations). Studies in the near future should focus on the handling of particles in the oral groove, and the roles of the lips and palps. Attempts to examine these structures using endoscopy in *Placopecten magellanicus* were repeatedly frustrated by the extreme sensitivity of the palps and lips, and by the voluminous nature of the ramified lips typical of pectinids, which obscured the oral region from view. Although lip excision was attempted, none of the excised scallops recovered.

The ability of some bivalves to feed selectively is well-documented (Newell and Jordan 1983, Shumway et al. 1985, Newell et al. 1989, Ward and Targett 1989); however, the sites and mechanisms of particle selection are as yet unknown. Although the labial palps have been assigned such a role, incontrovertible evidence is lacking (Beninger et al. 1990 a, Beninger 1991). A major conceptual obstracle is the problem of selection based on individual particle characteristics, given that particles have been assumed to arrive in the oral groove or on the palps in a mucus cord (see Beninger 1991 for review). The observations of the present study clearly show that in scallops, at all concentrations, particles are transported oralward in the dorsal ciliated tracts in a mucus slurry; the implications of this finding for particle selection should be explored in future studies. It should be noted that this situation contrasts with that in other species, in which mucus-bound strings can be clearly seen passing onto the palps (Ward et al. in press).

Ingestion volume control

At high particle concentrations, or after prolonged (ca. $\geq$1 h) exposure to low-medium particle concentrations, the scallop gill exhibits several behaviors which act to clear particles from the gill. The well-known concertina response (Drew 1906, Dakin 1909, Kellogg 1915, Owen and McCrae 1976) becomes increasingly frequent, ejecting particles from the principal filament troughs (Fig. 5). The spreading of the principal filaments allows direct observation of their contents, which comprise increasing amounts of mucus-bound particle masses. These aggregates appear to be caught by the cilia of the lateral walls of the principal filament, are dragged onto the surface of the ordinary filament plicae, and then directed toward the ventral rejection tract. Such behavior shows that: (1) the ordinary filament plicae are responsible for transporting particles to the ventral rejection tract; (2) regardless of particle concentration or ingestive capacity, the net movement of particles and water in the principal filament troughs is dorsal; (3) at high particle concentrations or when the ingestive/handling capacity is saturated, dorsally moving particles or mucus-bound particle masses in the principal filament troughs are often ejected onto the ordinary filament plicae, either via a concertina response or by ciliary beating; and (4) at least in the case of rejected individual particles, a feedback mechanism functions to initiate this rejection behavior in the principal filaments.

The volume control mechanism described above reconciles the need for maintaining a water current over the gill (due to the dorsally beating principal filament cilia and the through currents created by the ordinary filament lateral cilia) for both respiration and feeding, while at the same time allowing particles to be extracted and rejected when either the ingestive or handling capacity become overloaded. As the primitive function of the bivalve gill was gas exchange, it is probable that the volume control mechanism for the feeding function evolved later in compatibility with the basic respiratory function. These observations explain the bidirectional movement of particles on the gills, which is related to ingestion volume control rather than to particle selection (Beninger 1991).

Particle and gill behavior at high particle concentrations (or after exposure for several hours to low-medium particle concentrations) suggest three additional mechanisms for ingestion volume control. The frequently observed detachment of the dorsal bends from their points of attachment under such conditions provides not only a shunt for water to pass through unfiltered, as postulated by Wildish et al. (1987), but also an escape site for accumulations of particle-laden slurry in these regions. The second mechanism is the intermittent abrupt stopping of the anteriorly moving slurry in the dorsal ciliated tracts. The third mechanism involves the rapid clearing of the dorsal ciliated tracts following the reduction or cessation of input from the principal filaments. Such behavior suggests a neuronally controlled feedback mechanism.

The above observations allow us to summarize the four mechanisms which allow the scallop to regulate the amount of material arriving in the buccal region: (1) ejection onto the ventrally beating cilia of the ordinary filament plicae; (2) intermittent stopping of the anteriorward flow in the dorsal ciliated tracts; (3) detachment of the dorsal bends to create a shunt; and (4) momentary reduction or cessation of the input from the principal fila-

ments. As this last phenomenon is of short duration, it is compatible with the complementary respiratory role of the gill. This demonstration of regulatory feeding behavior is at variance with recent assertions that bivalve feeding is not subject to endogenous regulation (Jørgensen 1990).

The considerable volume of the slurries observed in the dorsal ciliated tracts is consistent with the properties of secreted mucus, which rapidly hydrates in the presence of water, extending to create a loose network which forms a visco-elastic gel (Sleigh 1989). Although correct in representations of position and continuity, previous reports of compact mucus cords or strings in the dorsal tracts of the gill (Beninger et al. 1990a) are artifactual. This material is really a much more voluminous, flocculent slurry of variable thickness, depending on particle concentration. However, when present, the dense mucus-particle masses on the ventral bend (rejection tract) do assume the form of strings which approach that of a mucus cord.

Although endoscopic examination only allows the detection of mucus when particles are trapped in it, complementary techniques such as fluid aspiration and subsequent analysis can confirm its presence or absence even at extremely low particle concentrations. Ongoing histological studies, such as the exact distrubtion of mucocytes on the gill epithelia, could also contribute information essential to the elucidation of the details of particle capture and transport.

Acknowledgements. The authors thank Ms. E. Hatfield for technical assistance with the chemical analyses, Mr. G. Bacon for providing the drawings, and Mad. L. Briard for assistance with word processing. Dr. S. Shumway played a crucial catalytic role in bringing together P.G.B. and J.E.W. Helpful comments were provided by C. A. Fesefeldt and Dr. J. Grassle. This work was funded by Natural Sciences and Engineering Research Council of Canada operating grants and by the Ocean Production Enhancement Network (OPEN), one of fifteen national Networks of Centres of Excellence.

Literature cited

Beninger, P. G. (1991). Structures and mechanisms of feeding in scallops: paradigms and paradoxes. In: Shumway, S. E., Sandifer, P. A. (eds.) An international compendium of scallop biology and culture. Wld Aquaculture Workshops 1: 331–340

Beninger, P. G., Auffrett, M., Le Pennec, M. (1990a). Peribuccal organs of *Placopecten magellanicus* and *Chlamys varia* (Mollusca: Bivalvia): structure, ultrastructure, and implications for feeding. I. The labial palps. Mar. Biol. 107: 215–223

Beninger, P. G., Le Pennec, M., Auffrett, M. (1990b). Peribuccal organs of *Placopecten magellanicus* and *Chlamys varia* (Mollusca: Bivalvia): structure, ultrastructure, and implications for feeding. II. The lips. Mar. Biol. 107: 225–233

Beninger, P. G., Le Pennec, M., Donval, A. (1991). Mode of particle ingestion in five species of suspension-feeding bivalve molluscs. Mar. Biol. 108: 255–261

Beninger, P. G., Le Pennec, M., Salaün, M. (1988). New observations of the gills of *Placopecten magellanicus* (Mollusca: Bivalvia), and implications for nutrition. I. General anatomy and surface microanatomy. Mar. Biol. 98: 61–70

Bernard, F. R. (1974). Particle sorting and labial palp function in the Pacific oyster *Crassostrea gigas* (Thunberg, 1795). Biol. Bull. mar. biol. Lab., Woods Hole 146: 1–10

Dakin, W. J. (1909). Pecten. L.M.B.C. Mem. typ. Br. mar. Pl. Anim. 17: 1–36

Drew, G. A. (1906). The habits, anatomy, and embryology of the giant scallop (*Pecten tenuicostatus*, Mighels). Univ. Maine Stud. 6: 1–71

Dubois, M., Gilles, K. A., Hamilton, J. K., Rebers, P. A., Smith, F. (1956). A colorimetric method for the determination of sugars and related substances. Analyt. Chem. 28: 350–356

Jørgensen, C. B. (1966). The biology of suspension feeding. Pergamon Press, Oxford

Jørgensen, C. B. (1981a). A hydromechanical principle for particle retention in *Mytilus edulis* and other ciliary suspension feeders. Mar. Biol. 61: 277–282

Jørgensen, C. B. (1981b). Feeding and cleaning mechanisms in the suspension feeding bivalve *Mytilus edulis*. Mar. Biol. 65: 159–163

Jørgensen, C. B. (1990). Bivalve filter feeding: hydrodynamics, bioenergetics, physiology and ecology. Olsen and Olsen Press, Fredensborg, Denmark

Jørgensen, C. B., Kiørboe, T., Møhlenberg, F., Riisgard, H. U. (1984). Ciliary and mucus-net filter feeding, with special reference to fluid mechanical characteristics. Mar. Ecol. Prog. Ser. 15: 283–292

Kellogg, J. L. (1915). Ciliary mechanisms of lamellibranchs with descriptions of anatomy. J. Morph. 26: 625–701

Le Pennec, M., Beninger, P. G, Herry, A. (1988). New observations of the gills of *Placopecten magellanicus* (Mollusca: Bivalvia), and implications for nutrition. II. Internal anatomy and microanatomy. Mar. Biol. 98: 229–237

Lowry, O. H., Rosebrough, N. J., Farr, A. L., Randall, R. J. (1951). Protein measurement with the folin phenol reagent. J. biol. Chem. 193: 265–275

McGinitie, G. E. (1941). On the method of feeding in four Pelecypods. Biol. Bull. mar. biol. Lab., Woods Hole 80: 18–25

Moore, H. J. (1971). The structure of the latero-frontal cirri on the gills of certain lamellibranch molluscs and their role in suspension feeding. Mar. Biol. 11: 23–27

Newell, C. R., Shumway, S. E., Cucci, T. L., Selvin, R. (1989). The effects of natural seston particle size and type on feeding rates, feeding selectivity and food resource availability for the mussel *Mytilus edulis* Linnaeus, 1758 at bottom culture sites in Maine. J. Shellfish Res. 8: 187–196

Newell, R. I. E., Jordan, S. J. (1983). Preferential ingestion of organic material by the American oyster *Crassostrea viriginica*. Mar. Ecol. Prog. Ser. 13: 47–53

Owen, G. (1974). Studies on the gill of *Mytilus edulis*: the eulaterofrontal cirri. Proc. R. Soc. (Ser. B) 194: 527–544

Owen, G. (1978). Classification and the bivalve gill. Phil. Trans. R. Soc. (Ser. B) 284: 377–385

Owen, G., McCrae, J. M. (1976). Further studies on the latero-frontal tracts of bivalves. Proc. R. Soc. (Ser. B) 194: 527–544

Shumway, S. E., Cucci, T. L., Newell, R. C., Yentsch, C. M. (1985). Particle selection, ingestion, and absorption in filter-feeding bivalves. J. exp. mar. Biol. Ecol. 91: 77–92

Sleigh, M. A. (1989). Adaptation of ciliary systems for the propulsion of water and mucus. Comp. Biochem. Physiol. 94A: 359–364

Sylvester, N. R, Sleigh, M. A. (1984). Hydrodynamic aspects of particle capture of *Mytilus edulis*. J. mar. biol. Ass. U.K. 64: 859–879

Ward, J. E., Beninger, P. G., MacDonald, B. A., Thompson, R. J. (1991). A new technique for direct observations of feeding structures and mechanisms in bivalve molluscs using endoscopic examination and video image analysis. Mar. Biol. 111: 287–291

Ward, J. E., MacDonald, B. A., Thompson, R. S., Beninger, P. G. (1992) Mechanisms of suspension-feeding in bivalves: resolution of current controversies using endoscopy. Limnol. Oceanogr. (in press)

Ward, J. E., Targett, N. M. (1989). Influence of marine microalgal metabolites on the feeding behavior of the blue mussel *Mytilus edulis*. Mar. Biol. 101: 313–321

Wildish, D. J., Kristmanson, D. D., Hoar, R. L., De Coste, A. M., McCormick, S. D. (1987). Giant scallop feeding and growth responses to flow. J. exp. mar. Biol. Ecol. 113: 207–220