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The role of mucus in particle processing by suspension-feeding marine bivalves: unifying principles

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Abstract Contemporary research on bivalve suspension-feeding has revealed a diversity of particle processing mechanisms depending on the anatomy and functioning of the pallial organs involved. On the biochemical level, however, some evidence of homogeneity has emerged concerning the types of mucopolysaccharide associated with particle processing. The present study uses both previous data and original research combining video endoscopy and mucocyte mapping to further explore the relationships between pallial organ topography, functional correlates, direction of current flow, and mucocyte secretion type. Five species representing five different families and all four major gill types are represented: *Mytilus edulis*, *Placopecten magellanicus*, *Crassostrea virginica*, *Mya arenaria*, and *Spisula solidissima*. Viscous acid or acid-dominant mucopolysaccharides are used when particle transport occurs on an exposed surface, or on a structure leading directly to such a surface, counter to the prevailing current flow. Associated functions are indiscriminate transport in gill ventral particle grooves and rejection of pseudofeces. Lower-viscosity mixed mucopolysaccharides are used when particle transport is on an enclosed or semi-enclosed surface, leading to other such surfaces, and with the current flow. Associated functions are transport of particles destined for ingestion, and ingestion itself. Low-viscosity neutral mucopolysaccharides are found in regions where reduction of mucus viscosity is important, such as the areas of the labial palps responsible for fluidization of the high-viscosity mucus-particle cord of the gill ventral particle groove prior to particle extraction. There thus appears to be a specialization of mucus type corresponding to functional specialization of the various pallial organs in suspension-feeding marine bivalves.

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Introduction

Recent advances in investigate techniques have led to a re-examination of previous paradigms concerning the mechanisms of suspension-feeding in bivalves (see Beninger et al. 1992, 1993; Ward et al. 1993, 1994). In particular, the role of mucus has been debated for decades, with protagonists sometimes adopting completely contradictory positions (MacGinitie 1941; Jørgensen 1966, 1990). Notwithstanding recent assertions to the contrary (Jørgensen 1996), it is now clear that mucus secreted by the epithelia of the pallial organs plays a key role in all aspects of particle processing (Beninger et al. 1991, 1993, 1997a, b; Beninger and Le Pennec 1993; Beninger and Dufour 1996; Beninger and St-Jean 1997). Reports that specific types of mucopolysaccharide are associated with certain anatomical configurations and mediate distinct functions on the bivalve gill (Beninger et al. 1993; Beninger and Dufour 1996) have been extended to the labial palps (Beninger and St-Jean 1997). It is thus pertinent to examine the role of mucus in bivalve particle processing to determine whether a uniform set of principles applies regardless of species, gill type, or pallial organ involved. Indeed, behavioral observations to date have revealed a multiplicity of transport characteristics according to gill and palp type; the eventual existence of a common underlying thread would greatly facilitate the understanding of bivalve particle processing.

The present study draws upon both original research using video endoscopy and mucocyte mapping, as well as previous data from various sources, to outline common features of mucus involvement in particle processing on the pallial surfaces of five species of sus-

pension-feeding bivalves, representing five different families and all four major gill types.

Materials and methods

Data base

The data for the present study were derived from three sources: (1) previous reports of organ function and/or mucocyte distribution for the gills and labial palps of *Mytilus edulis*, *Placopecten magellanicus*, *Mya arenaria*, and *Spisula solidissima* (Beninger et al. 1993, 1997a; Beninger and St-Jean 1997), (2) current investigations of these characteristics for the mantle and lips of *M. edulis* and *P. magellanicus* and (3) previous reports of mucocyte distribution and function of the gills of *Crassostrea virginica* (Ward et al. 1994; Beninger and Dufour 1996). Details of data type and sources are summarized in Table 1.

Sampling of *Mytilus edulis* and *Placopecten magellanicus*

A total of 11 *Mytilus edulis* were sampled from lease sites in Mahone Bay (44°32′N; 64°13′W) and from the intertidal in Passamaquoddy Bay (45°00′N; 67°05′W) in May and November 1992. Three specimens were used for histological preparation and eight for in vivo observations. A total of seven adult *Placopecten magellanicus* were taken from drag samples at Digby Bank (44°40′N; 65°50′W) and Passamaquoddy Bay in May and June 1992. Three of these were used for histological preparation, while four were used for in vivo observations. All specimens destined for histological preparation were maintained in a recirculating seawater system (5 °C, 31‰S) for 30 d prior to dissection. They were fed weekly with 2 g of spray-dried *Tetraselmis* sp. (Algal 161, Celsys Inc.) suspended in 1 litre of seawater. Individuals destined for in vivo observations were maintained for several days either in an open ambient seawater circulating system at the Huntsman Marine Laboratory or in a recirculating seawater system at University of New Brunswick (St. John, New Brunswick, Canada), where they were fed a mixture of the unicellular algae *Isochrysis* (Tahitian strain), *Chaetoceros muelleri*, and *Dunaliella tertiolecta* at 10 000 cells ml^{-1} final volume (15 to 16 °C, 33‰ S).

In vivo observations

The technique of video endoscopy (Ward et al. 1991) was used to observe pseudofeces transport from the labial palps to the external medium in two *Mytilus edulis*. The mussels were presented with the unicellular algal mixture, to which was added dropwise a suspension of reflective paint particles. Using a dissecting microscope this was compared to transport of carmine particles in six specimens, in which one valve had been removed. As no differences were observed in particle treatment, only the latter technique was used for *Placopecten magellanicus*.

Mucocyte staining and counting

The combined periodic acid–Schiff (PAS) and Alcian-blue technique was used for staining mucocytes (Beninger et al. 1993). Because of the nature of the tissues (thickness, mucocyte density), the mantle was stained in toto, while the lips and anterior part of the oesophagus were embedded in paraffin and sectioned at 10 μm (mean mucocyte diameter) prior to counting.

The lips of *Mytilus edulis* and *Placopecten magellanicus* were divided into counting zones representing regions from the distal to the proximal extremities, as shown in Fig. 1.2 and 1.4. The mucocytes of *M. edulis* were situated both within and beneath the epithelium. All mucocytes within a 100 μm length of epithelium were counted first in one direction, then in the opposite direction. In order to maintain an error of less than 5%, a third count was performed if a difference of >2 was found for counts between 30 and 50, or if a difference of >3 was found for counts between 51 and 100. The means of these counts all then had ranges of 5% or less. Above 100, a 5% range was maintained in a similar manner. This procedure was repeated for each of three individuals. Since the subepithelial mucocytes were often arranged in poorly defined, dense clusters, a semiquantitative visual scale of their density was adopted, with the following values: 4 = cells indistinguishable; 3 = cells barely distinguishable; 2 = cells easily distinguished; 1 = few mucocytes. Nine histological sections were counted as described for the lips of each of three specimens. Mean values and standard deviations were calculated for each region. The lip mucocytes of *P. magellanicus* were exclusively epithelial, and were counted as for the epithelial mucocytes of *M. edulis*.

The pallial surface of *Mytilus edulis* was divided by three transects perpendicular to the dorsal margin, across the anterior, median, and posterior regions, as shown in Fig. 2.2; the pallial surface of the mantle of *Placopecten magellanicus* was similarly divided by seven transects as shown in Fig. 2.4, because of its more circular shape compared to the mussel. Counts were performed in toto at intervals corresponding to 1/3 of each transect length, to the ventral margin (Fig. 2.4). All mucocytes within a 100× field (170 μm diameter) were counted once in a clockwise direction and once in a counter-clockwise direction using a hand-held haemocyte counter. The counts were standardized to a 1-mm-diameter circle. An error of 5% was maintained as described above.

Table 1 Data sources for particle transport observations and mucocyte mapping of pallial organs in representatives of five bivalve families [*1* Beninger et al. (1992); *2* Beninger et al. (1993); *3* Ward et al. (1993); *4* Ward et al. (1994); *5* Beninger and Dufour (1996); *6* Beninger and St-Jean (1997); *7* Beninger et al. (1997a); *8* Present study; – no known study]

Family, species	Gill		Palp		Lips		Mantle	
	Endoscopy	Mucocyte mapping	Endoscopy (E)/ Carmine (C)	Mucocyte mapping	Endoscopy	Mucocyte mapping	Endoscopy	Mucocyte mapping
Mytilidae *Mytilus edulis*	3	2	6 (E + C)	6	8	8	8	8
Pectinidae *Placopecten magellanicus*	1	2	6 (E + C)	6	–	8	8	8
Myacidae *Mya arenaria*	3, 7	7[a]	6 (E + C)	–	7	–	7	–
Mactridae *Spisula solidissima*	7	7[a]	7 (E + C)	–	–	–	–	–
Ostreidae *Crassostrea virginica*	4	5	4 (E)	–	4	–	–	–

[a] Quantitative mapping not possible

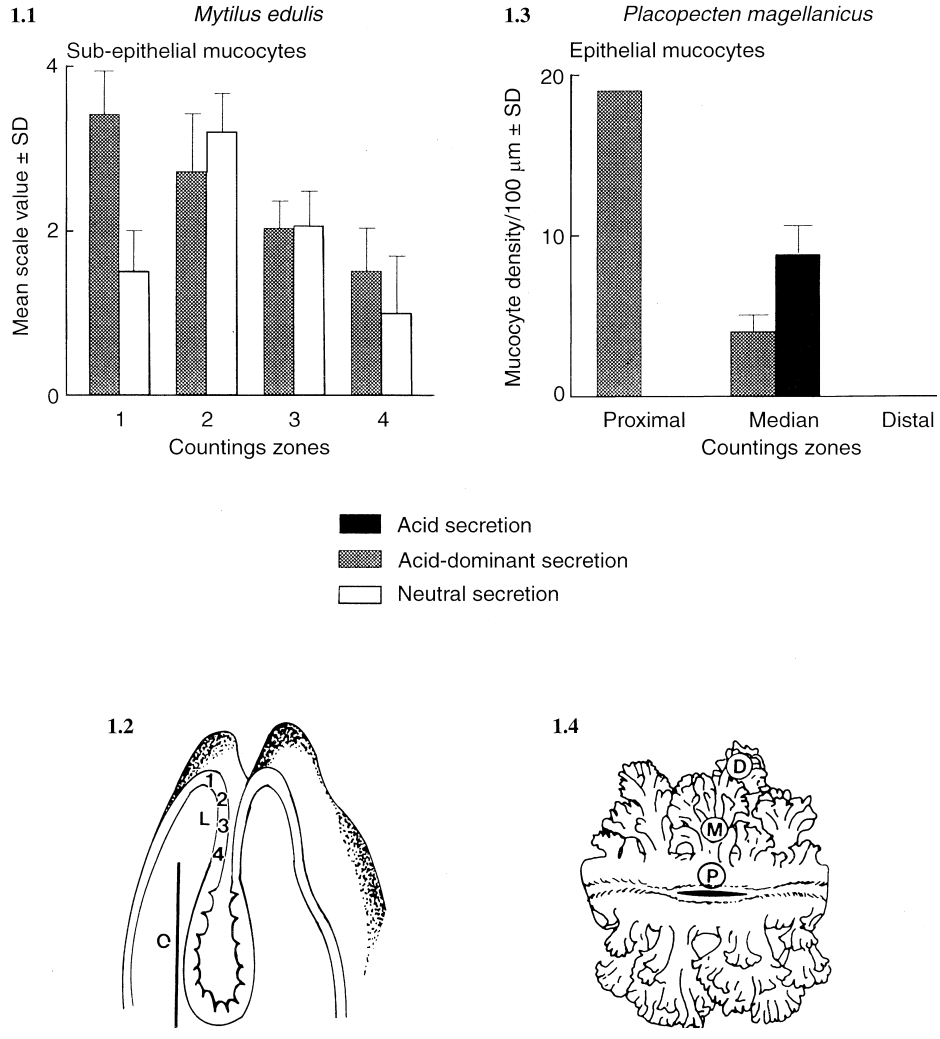

Fig. 1 *Mytilus edulis* and *Placopecten magellanicus*. Mucocyte densities on lips. **1.1** Mean semi-quantitative scale values for *M. edulis* sub-epithelial mucocytes in counting zones represented in **1.2** (*L* lip; *O* oesophagus). **1.3** Mean counts ± standard deviation for epithelial mucocytes in three counting zones indicated in **1.4** (*D* distal; *M* median; *P* proximal to mouth). Standard deviation for proximal zone negligible

Results and discussion

Current flow

The direction of current flow in the bivalve pallial cavity should be kept in mind when considering the pathways and mechanisms of particle transport. Since current flow in the various regions of the pallial organs can only be observed in intact animals, such data is derived from the endoscopic studies cited in Table 1, to which the reader is referred for detailed information. The general features of current flow are summarized in Fig. 3. These movements reflect the direction of water flow above the zone of influence of the transporting cilia beats (Sleigh 1989).

Composition and characteristics of mucus

Mucus is the hydrated form of secretions produced by mucocytes within epithelia, notably those of the pallial organs. The secretions consist of polysaccharide units with associated protein moieties. Classically (i.e. in vertebrates) these secretions are termed either mucopolysaccharides (synonym glycosaminoglycans) when the polysaccharide component consists of long, usually linear chains and the protein component is very small, whereas they are termed glycoproteins when the polysaccharide component consists of short, mainly branched chains and the protein component is relatively high. In invertebrates, these distinctions are not clear-cut, and mucocytes may contain a mixture of secretions (Denny 1983). In the present work, we adopt the standard histochemical classification of mucus secretions (Vacca 1985; Cook 1990), wherein all mucocyte secretions are termed mucopolysaccharides (MPS), and are classed according to their degree of acidity (a result of acid groups on the saccharide units). Neutral mucopolysaccharides (NMPS) are PAS positive, Alcian-blue negative, and present low viscosity. Acid mucopolysaccharides (AMPS) are PAS negative, Alcian-blue positive, and present high viscosity. Between these two endpoints we distinguish mixed mucopolysaccharides (MMPS), containing roughly equal proportions of NMPS and AMPS, and acid-dominant

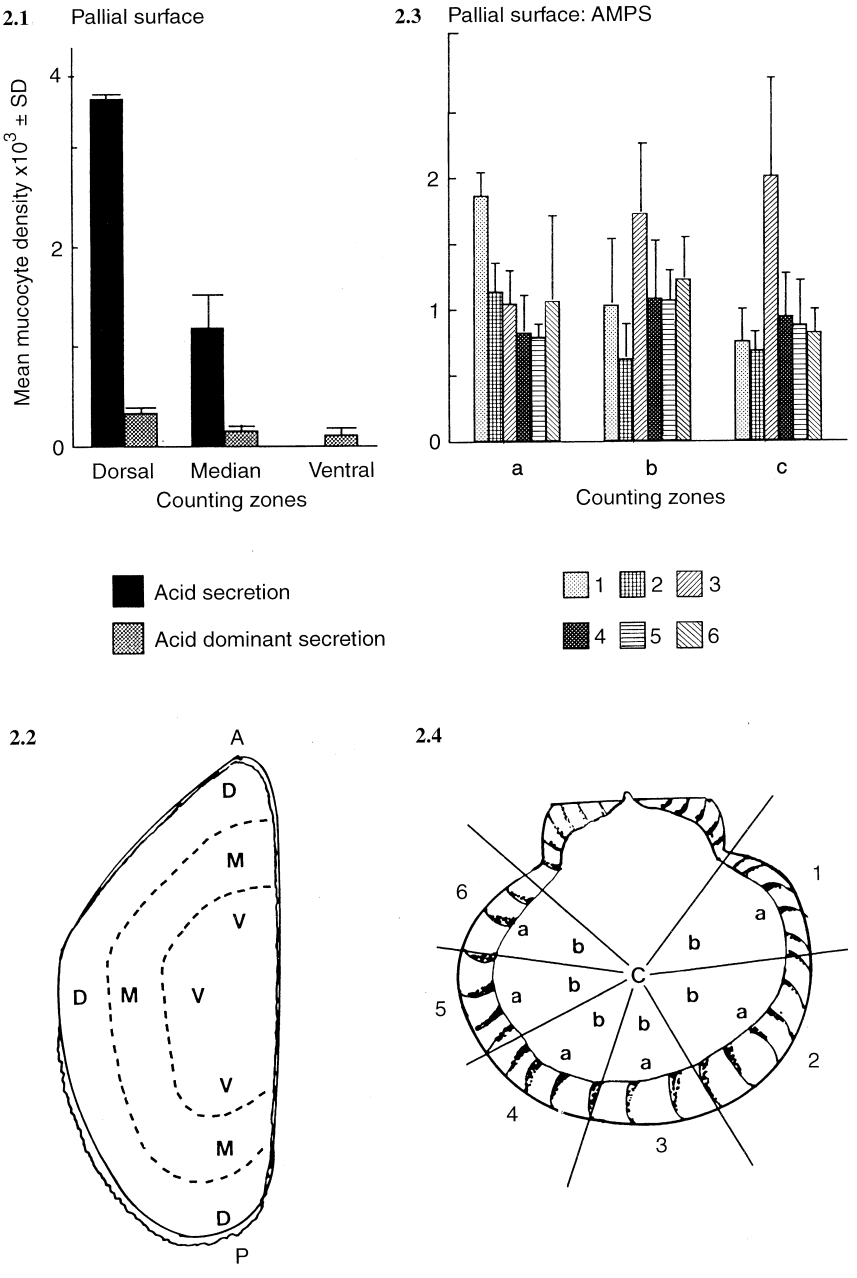

Fig. 2 *Mytilus edulis* and *Placopecten magellanicus*. Mean mucocyte densities for the pallial surface. **2.1** Mean mucocyte densities for *M. edulis* counting zones depicted in **2.2** (*A* anterior; *P* posterior; *D* dorsal; *M* median; *V* ventral zones). **2.3** Mean mucocyte densities for *P. magellanicus* counting zones depicted in **2.4**. Only AMPS mucocytes were found on this surface in this species

mucopolysaccharides (ADMPS), which contain a majority of AMPS (see Table 5).

Participation of mucus in particle processing

In recent years, a considerable body of data using a variety of different techniques has both confirmed the participation of mucus in all aspects of particle processing and elucidated which types of mucus are used for which functions on which pallial organs (Beninger et al. 1991, 1992, 1993, 1997b; Ward et al. 1991, 1993, 1994; Tankersley and Dimock 1993; Beninger and Dufour 1996; Silverman et al. 1996; Beninger and St-Jean 1997). This body of data has recently been peremptorily dismissed (Jørgensen 1996), ostensibly on the grounds that in those studies using endoscopy, prolonged observation results in enhanced mucus production. This interpretation of the endoscopic work is fundamentally incorrect, as it confuses increased mucus production following prolonged exposure to low or medium particle concentrations (i.e. normal ingestion volume control, see Beninger et al. 1992) with artefactual mucus production due to the presence of the optical insertion tube (OIT). Such artefactual mucus production has never been observed with a properly positioned OIT.

To our knowledge, the only datum which has been interpreted to support the contention that mucus is not involved in normal feeding of marine suspension-feeding bivalves is the single visual observation of apparent lack

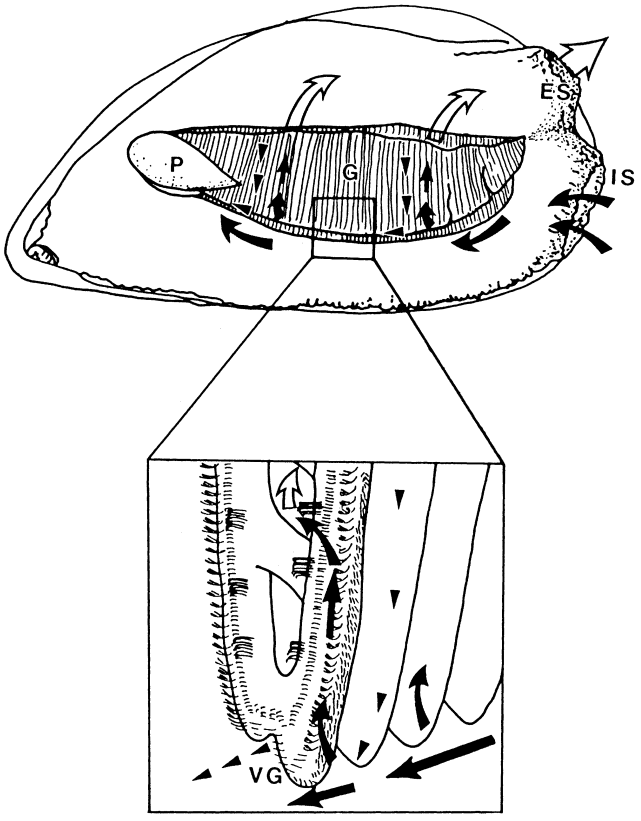

Fig. 3 Principal pathways of current flow and particle transport in a representative bivalve, *Mytilus edulis*. Water arrives via the incurrent siphon (*IS*), and the frontal surface of the gill (*G*) is exposed to a postero-anterior flow at the ventral margin, while the rest of the frontal surface is swept by a ventro-dorsal flow, with a progressive through component to the abfrontal region and out the exhalent siphon (*ES*). *Solid arrows* indicate current flow prior to passage across gills; *open arrows* show current flow after crossing through to abfrontal region and on to exhalent siphon. *Arrowheads* represent particle transport typical of the many species which possess homorhabdic gills and a ventral particle groove (*VG*) (*P* labial palp)

of particle cohesiveness in alimentary tract aspirates (Kiørboe and Møhlenberg 1981). Using a similar technique, Bernard (1974) concluded the exact opposite; moreover, we now know that the mucus which accompanies ingestion is of relatively low viscosity (Beninger et al. 1992; Ward et al. 1994, Beninger and St-Jean 1997; present paper), such that it may not engender particle cohesiveness. Observations of this type are thus not appropriate for determining the presence of mucus. The overwhelming weight of data therefore supports the participation of mucus in all aspects of particle processing.

Lips and buccal region – *Mytilus edulis* and *Placopecten magellanicus*

Mytilus edulis possesses small, simple lips in contrast to the hypertrophied arborescent lips of *Placopecten magellanicus*. In the *M. edulis* lips, only ADMPS were found in the epithelial mucocytes, whereas in the much more extensive subepithelial network, both ADMPS and NMPS mucocytes were present. A clear preponderance of subepithelial ADMPS (relatively high viscosity) was observed in the distalmost regions of the lips, compared to NMPS (Fig. 1.1, 1.2). This difference tended to even out toward the mouth and oesophagus, where the secretions would thus present a lower viscosity. In *P. magellanicus*, no mucocytes were found in the distalmost regions of the lips, but the middle region was characterized by a preponderance of AMPS and ADMPS (Fig. 1.3, 1.4), which would result in a relatively high-viscosity mucus on these epithelial surfaces. One of the proposed functions of the arborescent pectinid lips is to prevent the removal of material to be ingested by the strong currents produced by valve clapping, a characteristic defense response and the routine method of clearing the pallial cavity of detritus and pseudofeces. Food particles lifted out of the buccal region would thus tend to adhere to the lip epithelia and be more readily returned to the mouth via the amply ciliated lip tracts (Beninger et al. 1990).

Mantle – *Mytilus edulis* and *Placopecten magellanicus*

The dorsal region of the mantle in *Mytilus edulis* was characterized by a marked dominance of AMPS, which declined sharply in the median region and disappeared altogether in the ventral region. This corresponded to the observed behavior of particles transported as pseudofeces from the gill particle groove to the palp (Fig. 4.1), then ventrally and posteriorly along the palp ventral margin (Fig. 4.2) to the mantle. Pseudofeces followed a very discrete pathway along the mantle just ventral to the dorsal bend of the gill, through to the inhalent siphon, where they were ejected (Fig. 4.3 to 4.6). This is in fact the only possible trajectory, since pseudofeces must be (and is) deposited in the infrabranchial chamber of the pallial cavity. Access to the exhalent siphon is blocked by the gill lamella itself, so the only possible exit is the inhalent siphon. It should be noted that the transport of pseudofeces on the *M. edulis* mantle is therefore almost entirely counter to the strong pallial current; the prevalence of AMPS along the rejection pathway thus corresponds to the requirement to anchor pseudofeces to the epithelium and prevent its resuspension in the pallial cavity, where it would again impinge upon the frontal surface of the gill filaments. The dorsal route of the rejection pathway corresponds to the location of the posteriormost tips of the labial palps and the very dorsal position of the gill dorsal bends (Beninger et al. 1995).

In contrast to the siphonal voidance of pseudofeces seen in *Mytilus edulis*, the Pectinidae reject pseudofeces via valve clapping, which periodically flushes out the mantle cavity (Yonge 1967; Morton 1979). There is thus no specific rejection pathway on the mantle, and this is

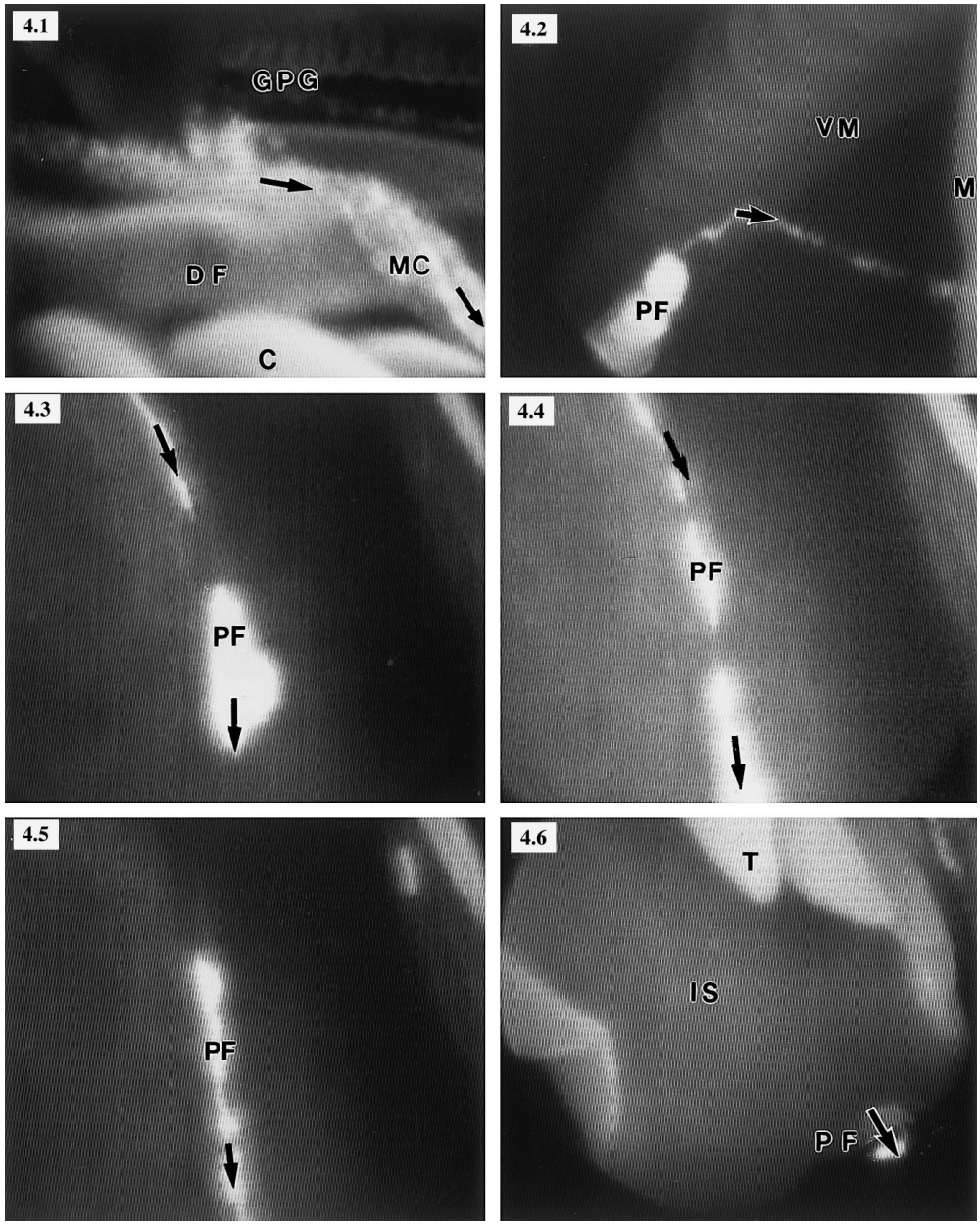

Fig. 4 *Mytilus edulis*. Still images from Hi-8 video endoscopic recordings of particle processing. *Arrows* indicate direction of movement. **4.1** Mucus-particle cord (*MC*) exiting gill particle groove (*GPG*) and being drawn onto palp dorsal fold (*DF*), and then onto the palp crests (*C*). Note that mucus-particle cord is transported parallel to palp ridges. **4.2** Pseudofeces (*PF*) exiting palp ventral margin (*VM*) and being transported as a mucus-particle bridge to the mantle (*M*). **4.3**, **4.4**, **4.5** Pseudofeces transported on a distinct mantle tract toward inhalent siphon. **4.6** Pseudofeces exiting inhalent siphon (*IS*) (*T* siphon tentacles). Scales are not indicated due to large depth of field

reflected in the mucocyte distribution (Fig. 2.3, 2.4). The greatest AMPS densities are found in the region where the palps are situated (Zone 1a) and near the centre of the mantle (Zones 3b, c), indicating that this may be where pseudofeces collect prior to expulsion radially during valve clapping.

Although in the case of both species, AMPS are used almost exclusively in the transport of particles (pseudofeces) on the mantle, the presence of siphons in *Mytilus edulis* is correlated with a very precise rejection pathway, which is not seen in the siphonless *Placopecten magellanicus*. Studies underway in our laboratory show that a discrete mantle rejection pathway appears typical of siphon-bearing bivalves.

Patterns in bivalve particle transport and associated mucus types

Despite considerable differences in pallial organ structure and particle processing, certain common features characterize the involvement of mucus in the representatives of all five families examined here. In all cases where particle transport occurs on an exposed surface, or on an enclosed surface leading directly to an exposed surface, the accompanying mucus secretion is either ADMPS or AMPS, i.e. very viscous (Tables 2 to 4). In all these cases, particle transport is counter to the current flow (here counter is defined as an angle approximately 0 to 90° with the current flow), indicating that viscous MPS is essential for particle transport under

Table 2 *Mytilus edulis*. Mucus secretion type in relation to organ topography, function and current flow relative to particle movement

Site	Surface type	Current flow	Function	Dominant secretion	Source
Gill (frontal)	Open	Counter	Indiscriminate transport	Acid-dominant	Beninger et al. (1993)
Palp (dorsal fold)	Open	Counter	Indiscriminate transport	Acid-dominant	Beninger and St-Jean (1997)
Mantle (dorsal)	Open	Counter	Rejection (pseudofeces)	Acid	Present study
Palp (trough rejection tracts)	Enclosed[a]	Forward	Rejection (pseudofeces)	Acid	Beninger and St-Jean (1997)
Palp (postero-ventral margin)	Open	Counter	Rejection (pseudofeces)	Acid	
Palp (oral tract)	Semi-enclosed	Forward	Ingestion	Mixed	
Oesophagus	Enclosed	Forward	Ingestion	Mixed	Present study

[a] Enclosed surface leading directly to open surface (labial palp ventral margin)

Table 3 *Placopecten magellanicus*. Mucus secretion type in relation to organ topography, function and current flow relative to particle movement

Site	Surface type	Current flow	Function	Dominant secretion	Source
Gill (ordinary filament)	Open	Counter	Rejection (pseudofeces)	Acid	Beninger et al. (1993)
Palp (postero-ventral margin)	Open	Counter	Rejection (pseudofeces)	Acid	Beninger and St-Jean (1997)
Gill (principal filament)	Semi-enclosed	Forward	Transport for ingestion	Mixed	Beninger et al. (1993)
Palp (oral tract)	Semi-enclosed	Forward	Transport for ingestion	Mixed	Beninger and St-Jean (1997)
Palp (ridged surface)	Semi-enclosed	Uncertain	Uncertain	Mixed	
Lips (proximal)	Enclosed	Forward	Transport for ingestion	Mixed	Present study
Oesophagus	Enclosed	Forward	Transport for ingestion	Mixed	

Table 4 *Crassostrea virginica*, *Spisula solidissima*, *Mya arenaria*. Mucus secretion type in relation to gill topography, function and current flow relative to particle movement

Species, site	Surface type	Current flow	Function	Dominant secretion	Source
Crassostrea virginica					
Gill ordinary filament crest	Open	Counter	Indiscriminate transport	Acid-dominant	Beninger and Dufour (1996)
Gill principal filament trough	Semi-enclosed	Forward	Transport for ingestion	Mixed	
Spisula solidissima					
Homorhabdic filaments	Open	Counter	Indiscriminate transport	Acid	Beninger et al. (1997a)
Gill particle groove	Semi-enclosed[a]	Forward	Indiscriminate transport	Acid	
Mya arenaria					
Homorhabdic filaments	Open	Counter	Indiscriminate transport	Acid	
Gill particle groove	Semi-enclosed[a]	Forward	Indiscriminate transport	Acid	

[a] Semi-enclosed surface leading directly to exposed surface (palp ridged surface)

such conditions. The functions associated with particle transport accompanied by viscous MPS are rejection, as well as initial particle transport on the gill for a later "decision" (i.e. selection, ingestion volume regulation – see Beninger and Dufour 1996; Beninger and St-Jean 1997) by the other pallial organs. This latter function is found only in bivalves possessing a single ventral gill particle groove (Mytilidae, Myacidae, Mactridae, etc.).

Table 5 Summary of mucus secretion types used in particle processing on bivalve pallial cavity organs (*NMPS* neutral mucopolysaccharides; *MMPS* mixed mucopolysaccharides; *ADMPS* acid-dominant mucopolysaccharides; *AMPS* acid mucopolysaccharides)

	Viscosity:			
	Low	→	→	High
Secretion type	NMPS	MMPS	ADMPS	AMPS
Surface type	Various	Enclosed/ semi-enclosed	Open	Open
Current flow	Forward	Forward	Counter	Counter
Function	Dilution of AMPS and ADMPS to reduce viscosity	Ingestion	– Indiscriminate transport for later "decision" – Rejection of pseudofeces	

Bivalves which possess both a ventral and a dorsal tract use the ventral tract mainly for rejection (Atkins 1937; Beninger et al. 1992).

In all cases where particle transport is on an enclosed or semi-enclosed surface, leading to other such surfaces, the accompanying mucus is a lower-viscosity MMPS (Tables 2, 3). This is also associated with forward current flow. Although the mucus-particle cord in the gill ventral particle groove is composed of either AMPS (among *Mya*, *Spisula* species) or ADMPS (among *Mytilus*, *Crassostrea* species), this is not really an exception to the rule, since the preceding surface (gill frontal surface) is exposed, and transfer of the cord to the palps usually occurs in an extremely exposed context; the subsequent surfaces are also exposed, and current flow is counter or perpendicular. The data to this point thus indicates a set of constants in the participation of mucus in particle processing, regardless of the pallial organ or the species considered (Table 5). Hence, in spite of the diversity of structure and processing function of bivalve pallial organs, an underlying common thread now appears evident.

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