Marine Biology 108, 255–261 (1991)

Marine Biology
International Journal on Life in Oceans and Coastal Waters

Mode of particle ingestion in five species of suspension-feeding bivalve molluscs

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Date of final manuscript acceptance: October 29, 1990. Communicated by R. O'Dor, Halifax

Abstract. In order to elucidate the mode of particle ingestion and the functional anatomy of the oesophagus in bivalves, a histological study was performed on *Mytilus edulis* (Mytilidae), *Crassostrea virginica* (Ostreidae), *Placopecten magellanicus*, *Chlamys varia*, and juvenile *Pecten maximus* (Pectinidae). Specimens were sampled from various sites in New Brunswick, Canada, and Brittany, France, from 1987 to 1989. The buccal, peribuccal, and oesophageal epithelia of all species contained a dense distribution of actively secreting mucocytes, although these were somewhat less abundant in *Crassostrea virginica*, which also has the shortest oesophagus. Mucocyte morphology, while constant within a family (Pectinidae), showed clear differences among families. Both acid and neutral mucopolysaccharides were secreted by the epithelial mucocytes of all species. Mucus and mucus-particle masses were observed in the peribuccal and buccal regions, as well as in the oesophageal lumina of all species, even in those specimens which had been maintained without feeding (*Placopecten magellanicus*) or held out of water for 48 h (*C. virginica*) prior to dissection and fixation. These results indicate that a basal level of mucus production and transport is continuous on the peribuccal, buccal, and oesophageal ciliated epithelia, regardless of the particle concentration in the external medium. Bucco-oesophageal glands, generally thought to be absent in the Bivalvia, were observed in one of the species examined (*M. edulis*). It is concluded that the mode of particle ingestion in these suspension-feeding bivalves is via cilia-transported mucus masses; the presence of bucco-oesophageal glands in *M. edulis* suggests a digestive role for the oesophagus in this species.

Introduction

As has recently been pointed out (Murakami and Sleigh 1989), much remains to be understood concerning the mechanisms of particle capture and subsequent treatment in suspension-feeding bivalves, even for the most thoroughly examined system (*Mytilus edulis* gill). The extensive literature on this subject may be divided into two radically different conceptions of particle capture and transport. Classically, particle capture and transport are thought to involve physical contact with the feeding epithelia. Different mechanisms have been proposed for different bivalve groups (or, more specifically, for different gill types), but all involve either a straining of particles from the water by gill cilia, or a combination of cilia-driven water currents at the gill and ultimate capture by mucus at some level of the feeding surface topography (Moore 1971, Owen 1974, Owen and McCrae 1976, Owen 1978, Sylvester and Sleigh 1984). Particles bound in mucus strings are subsequently transported to the buccal region by the continual beating of the dense ciliary cover of the feeding epithelia (Bernard 1974, Foster-Smith 1975, 1978), where they are ingested in mucus-bound masses and cords (Morton 1960). This mode of ingestion has since become part of the conventional wisdom of bivalve biology (Owen 1966, Bayne et al. 1976, Purchon 1977, Hickman et al. 1984, Barnes 1987, Pearse et al. 1987, Salvini-Plawen 1988).

A more recent model proposes that capture and transport of particles destined for ingestion occur wholly in water currents, from the pallial cavity to the stomach (Jørgensen 1981, Jørgensen et al. 1984). This model is supported by the work of Kiørboe and Møhlenberg (1981), who reported after visual observation of the pipetted contents that particles present in the oesophagus of *Mytilus edulis* were in free suspension. Similarly, Jørgensen (1981) based his suggestion of a completely hydromechanical mode of particle transport and ingestion largely on the visual observation of pipetted stomach contents in *M. edulis*.

As accurate knowledge of the mode of ingestion is important for paradigms of particle selection in suspension-feeding bivalves (see Beninger 1991 for review), it would appear to be of interest to examine the eventual distribution of mucocytes in the buccal and oesophageal regions of these organisms, as well as the presence or absence of mucus and mucus-bound particle masses using more direct observational techniques, thereby providing definitive data on the mode of particle ingestion. In addition, such observations would furnish anatomical bases necessary for the interpretation of feeding phenomena. Similar studies have been performed for the gills and peribuccal organs of scallops (Beninger et al. 1988, Le Pennec et al. 1988, Beninger et al. 1990a, b).

To the best of our knowledge, anatomical information concerning the mouth and oesophagus of bivalves is quite limited, being uncharacteristically absent from the classic treatises of Drew (1906), Dakin (1909) and Gutsell (1931). A single sentence or less is devoted to it in Galtsoff's (1964) extensive treatment of *Crassostrea virginica* and in Purchon's (1977) review of digestion in the Bivalvia, while Franc's (1960) general cursory description lacks any supporting photomicrographs. No histological or ultrastructural account is given in the reviews of Morton (1983) or Salvini-Plawen (1988). A single photomicrograph of a very small portion (15 to 20 cells) of the oesophageal epithelium of *Crassostrea virginica* may be found in the study by Shaw and Battle (1957).

The present study reports the data of a histological examination of the buccal and oesophageal regions of five species of suspension-feeding bivalves: *Mytilus edulis* (Mytilidae); *Crassostrea virginica* (Ostreidae); *Pecten maximus*, *Chlamys varia*, and *Placopecten magellanicus* (Pectinidae).

Materials and methods

Each species was sampled from a different location, and several treatment protocols were used, as outlined below.

Mytilus edulis

Seven adult specimens were sampled from the mouth of the Kouchibouguac River (Canada: 46°10′25″N, 64°20′10″W) on 11 September 1989, using snorkelling and breath-hold diving (depth 2 to 6 m). Only animals actively feeding were chosen (criteria: valves slightly gaping, both siphons visible, inhalent siphon guard tentacles fully deployed, natural seston observed entering inhalent siphon). The animals were detached either without rupturing the byssus (when the threads were attached to small stones), or by severing the byssus at the distal extremity. The animals were brought to shore and dissected on the beach. Several trial runs had previously been performed in order to ensure that the entire dissection procedure and immersion in fixative could be performed in 15 to 30 s. The oesophagus was dissected out and fixed in either Carnoy's or aqueous Bouin's solution for at least 3 d; this extended fixation period greatly reduced the problems of tearing upon sectioning previously encountered with the fragile epithelial tissue of the oesophagus.

Subsequent tissue processing and staining of paraffin-embedded sections was performed using the protocols described in Beninger et al. (1990a). Staining techniques included the modified Masson trichrome for general topology, as well as Alcian Blue for acid mucopolysaccharides and periodic acid-Schiff (PAS) for neutral mucopolysaccharides, counterstained with trioxyhematein.

The oesophagus of an additional *Mytilus edulis* sampled on 9 August 1989 was fixed in glutaraldehyde-cacodylate buffer, postfixed in osmic acid and dehydrated as in Le Pennec et al. (1988). The tissue was embedded in Epon resin, sectioned at 1 μm, and stained with toluidine blue.

Placopecten magellanicus

Several adult *Placopecten magellanicus* were captured from Passamoquoddy Bay (Canada: 45°00′50″N, 67°00′20″W) using a scallop drag on 16 August 1989. These animals were transported in ambient seawater to the Moncton laboratory, where they were placed in a refrigerated (6 °C) recirculating artificial seawater aquarium. The animals were not fed. Two individuals were dissected on 2 November 1989, and the oesophagus tissue was processed as for the paraffin-embedded *Mytilus edulis* tissue.

Pecten maximus

Juvenile *Pecten maximus* were produced in the Argenton bivalve hatchery (France) and were fed with unicellular algae using a continuous-feed system. In the course of a study on digestion several specimens were fixed whole in glutaraldehyde-cacodylate buffer, embedded in paraffin, sectioned and stained using the Mann-Dominici technique (Beninger et al. 1990a), which colors mucocytes blue and other secretory cells mauve.

Chlamys varia

Twelve *Chlamys varia* were sampled using a scallop drag in the Bay of Brest (France: 48°20′20″N, 4°20′30″W) in May 1987. The oesophagus and peribuccal organs of four specimens were dissected and immersed in aqueous Bouin's solution, embedded in paraffin and stained using a modified Masson trichrome technique (Beninger 1987) which stains ciliated epithelial cells but leaves mucocytes clear.

Crassostrea virginica

Seven adult *Crassostrea virginica* were harvested from a lease site in Caraquet Bay (Canada: 47°40′00″N, 64°40′20″W) on 30 September 1989. They were kept in cold storage (4 °C) for 2 d, and then transported on ice (6 h) to the laboratory in Moncton. As with *Mytilus edulis*, trial dissections had been performed on a previous batch of oysters, such that each oyster examined histologically was opened and the oesophagus dissected and immersed in aqueous Bouin's solution in less than 30 s. The tissue was then processed in the same manner as were the paraffin-embedded *M. edulis* specimens.

Results

Although generally similar, the epithelia of the peribuccal, buccal, and oesophagus regions showed some significant family-specific differences. Mucus and/or mucus-bound particle masses were found in these regions for all specimens examined.

Mytilus edulis

The peribuccal epithelium of *Mytilus edulis* merged into that of the mouth and oesophagus with relatively little modification, save that the anterior portion of the oesophagus presented significant folding and somewhat taller cells (Figs. 1: *1*, *2*; 2: *1*). The epithelium consisted of slender ciliated cells interspersed between numerous active mucocytes. Two different types of secretion were re-

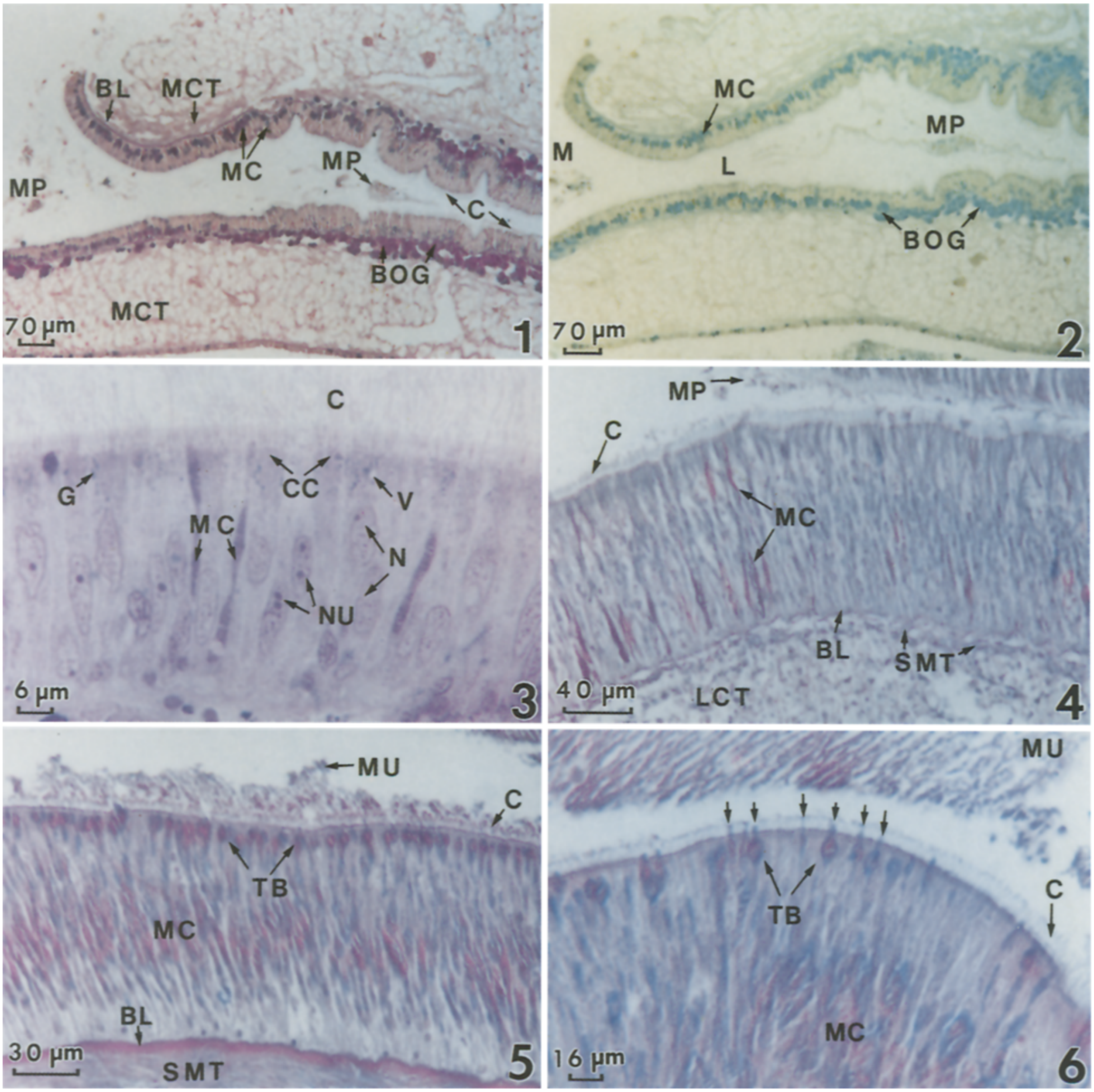
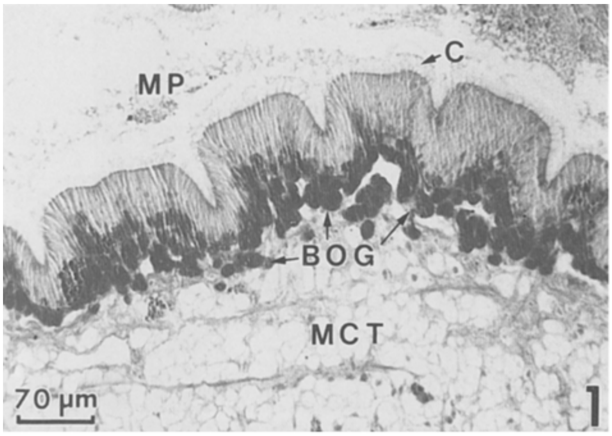


Fig. 1. *Mytilus edulis*, *Crassostrea virginica*, *Placopecten magellanicus*. Longitudinal histological sections of the peribuccal, buccal, and oesophageal regions. *1*: Paraffin-embedded section of *M. edulis*, showing mouth and anterior region of oesophagus. Note presence of mucus-particle masses (MP) entering mouth and in oesophageal lumen, and the dense distribution of mucocytes (MC) containing both acid and neutral mucopolysaccharides. Alcian Blue/PAS stain. *2*: Same as *1*, but stained with Alcian Blue only, showing acid mucopolysaccharides within mucocytes (MC). *3*: *M. edulis*, semi-fine resin section of the oesophageal epithelium, showing mucocyte (MC) morphology, as well as numerous granules (G) and vacuoles (V) in the ciliated cells, which contain prominent nucleoli (NU). Toluidine blue stain. *4*: Paraffin-embedded section of the buccal region in *Crassostrea virginica*. Note the slender mucocytes (MC) and mucus-particle masses (MP) in the buccal region. PAS/Alcian Blue stain. *5*: Paraffin-embedded section of oesophageal region in *Placopecten magellanicus*. Note typical shape of mucocytes (MC), with distinct terminal bulbs (TB). Mucus (MU) is present in the lumen and on top of the epithelial cilia (C). PAS/Alcian Blue stain. *6*: Detail of paraffin-embedded section of the apical region of the oesophageal epithelium in *P. magellanicus*. Note mucus secretions (arrows) of the terminal bulbs (TB), and abundant mucus (MU) in lumen

Abbreviations for Figs. 1 and 2. AV: apical vacuoles; BL: basal lamella; BOG: bucco-oesophageal glands; C: cilia; CC: ciliated cell; D: duct of bucco-oesophageal gland; DG: digestive gland; G: granules; L: lumen; LCT: loose connective tissue; M: mouth; MC: mucocyte; MCT: musculo-connective tissue; MP: mucus + particles; MU: mucus; N: nucleus; NU: nucleolus; PBE: peribuccal epithelium; SMT: smooth muscle tissue; TB: terminal bulb; V: vacuoles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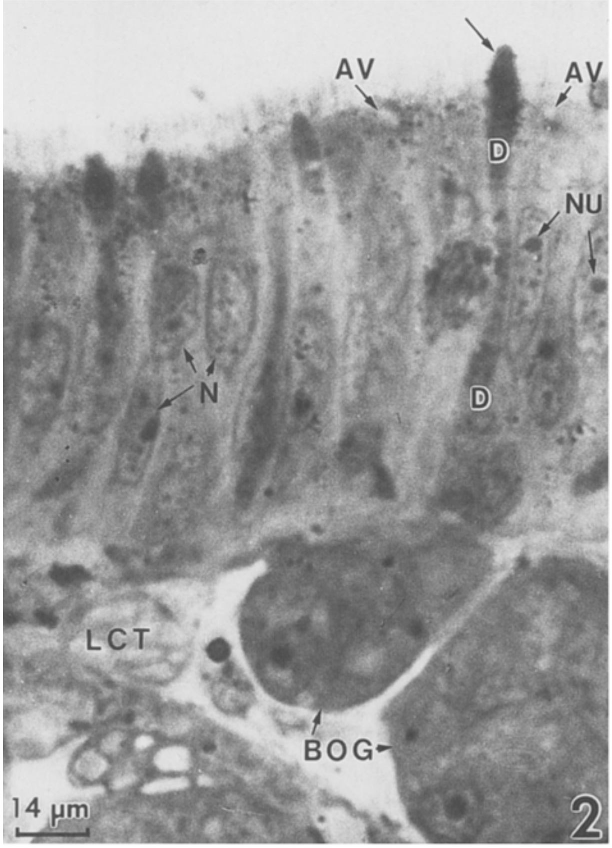
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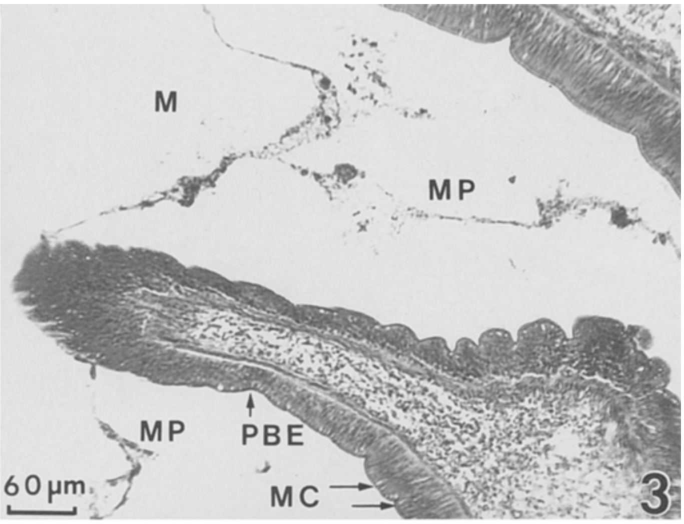
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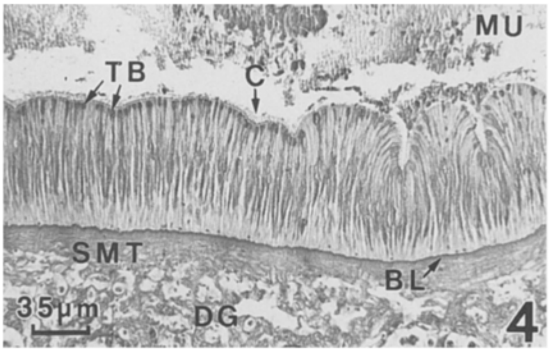
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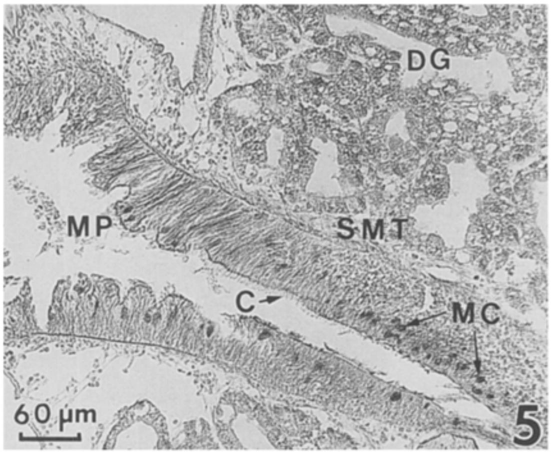
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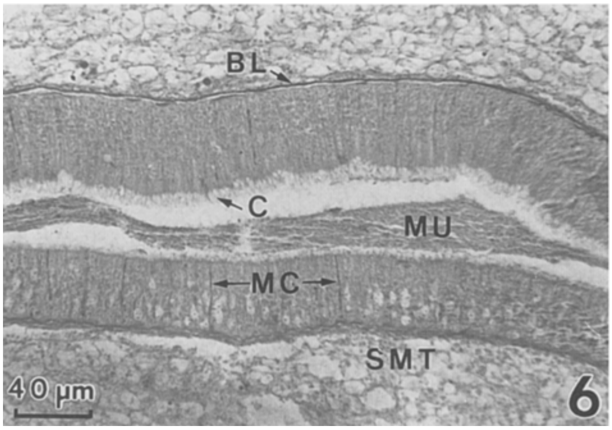
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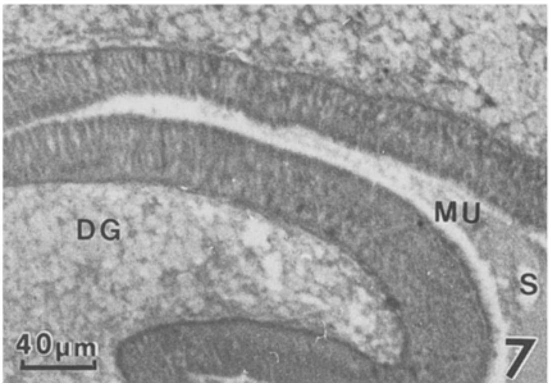
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vealed using the Alcian Blue and Alcian Blue/PAS techniques: acid and neutral mucopolysaccharides (Fig. 1: *1, 2*). Mucus and mucus-particle masses were found in the peribuccal and buccal regions and in the oesophageal lumen (Fig. 1: *1, 2*). The mucocytes were slender and lacked a pronounced terminal bulb (Figs. 1: *3*; 2: *2*). The ciliated cells had large nuclei with prominent nucleoli; their apical regions contained granules and vacuoles (Figs. 1: *3*; 2: *2*).

Secretion-rich cells were present in groups beneath the basal lamella (Figs. 1: *2*; 2: *1, 2*). These putative gland cells possessed prominent nucleoli and a basophyllic cytoplasm. The cell groups actively secreted into the lumen of the oesophagus via transepithelial ducts (Fig. 2: *2*). Their distribution in the buccal region and the anterior third of the oesophagus suggested that they were bucco-oesophageal glands. Immediately beneath the basal lamella and the gland cells was a loose network of musculo-connective tissue (Figs. 1: *1*; *2*; 2: *1*).

Placopecten magellanicus, *Chlamys varia*, and *Pecten maximus*

The buccal, peribuccal, and oesophageal epithelia of these three Pectinidae were histologically similar. In the two adult species examined (*Placopecten magellanicus* and *Chlamys varia*), the ciliated cells were interspersed between a very dense array of mucocytes (Figs. 1: *5, 6*; 2: *4*). The mucocytes were less numerous, but nonetheless quite evident, in the juvenile specimens of *Pecten maximus*. A distinguishing feature of the mucocytes of the two adult pectinid species was the presence of a very pronounced terminal bulb in the apical region (Figs. 1: *5, 6*; 2: *3, 4*). Beneath the terminal bulb, down to approximately one-third the length of the cell, little mucus was evident; this was followed by a central third in which mucus secretions were again evident, and a basal third which contained relatively little mucus. As in the *Mytilus edulis* mucocytes previously described, both neutral and acid mucopolysaccharides were contained within these cells, which were observed in active secretion (Fig. 1: *5, 6*).

Mucus-particle strands were observed in the peribuccal and buccal region of *Chlamys varia* and the juvenile *Pecten maximus*; these strands continued inward to the oesophagus (Fig. 2: *3, 5*). Abundant mucus was observed in the oesophageal lumen of the *Placopecten magellanicus* which had been held without feeding for over 2 mo (Figs. 1: *5, 6*; 2: *4*).

No associated gland cells were observed beneath the epithelium of any of the pectinids examined. The buccal, peribuccal, and oesophageal epithelia and their basal lamellae rested instead upon a well-developed smooth muscle layer, beneath which was situated the digestive gland tissue (Figs. 1: *5*; 2: *4*).

Fig. 2. *Mytilus edulis, Chlamys varia, Placopecten magellanicus, Pecten maximus, Crassostrea virginica*. Longitudinal histological sections of the peribuccal, buccal, and oesophageal regions. *1*: Paraffin-embedded section of the anterior oesophagal region of *M. edulis*, showing mucus-particle masses (MP), position of bucco-oesophageal glands (BOG) and subjacent musculo-connective tissue (MCT). PAS/Alcian Blue stain. *2*: Resin-embedded detail of the oesophageal epithelium and bucco-oesophageal glands of *M. edulis*. Note secretion (arrow) from gland duct (D) into the oesophageal lumen, and apical vesicles (AV) of ciliated cells. Toluidine blue stain. *3*: Paraffin-embedded section of the peribuccal and buccal regions of *C. varia*, showing mucus-particle masses (MP) from peribuccal region entering the mouth and oesophagus. Modified Masson trichrome stain. *4*: Paraffin-embedded section of the mid-oesophageal region of *P. magellanicus*. Note abundant mucus (MU) in lumen and adhering to cilia. PAS/Alcian Blue stain. *5*: Paraffin-embedded section of the buccal and oesophageal regions of juvenile *Pecten maximus*. Note mucus-particle masses (MP) in lumen and mucocytes (MC) in epithelium. Mann-Dominici stain. *6*: Paraffin-embedded section of the mid-oesophageal region in *C. virginica*, showing considerable mucus mass in lumen. PAS/Alcian Blue stain. *7*: Paraffin-embedded section of the junction between the oesophagus and the stomach (S) in *C. virginica*, showing mucus mass extending from oesophagus to stomach. PAS/Alcian Blue stain

Crassostrea virginica

Crassostrea virginica possesses a very short oesophagus (ca. one-fifth the length of the visceral mass, as reported by Shaw and Battle 1957), and a very narrow oesophageal lumen (<40 μm diameter for a 6-mm-long specimen). The mucocytes were less densely arranged than in the preceding species, and were distinctively characterized by their reduced width and lack of a terminal bulb. Both acid and neutral mucopolysaccharides were secreted (Fig. 1: *4*), and the oesophageal lumen of these dry-stored specimens contained significant amounts of mucus (Fig. 2: *6*) which could be seen entering the stomach (Fig. 2: *7*). Beneath the epithelial basal lamella was a thin smooth muscle layer, under which were a loose connective tissue and the digestive gland (Figs. 1: *4*; 2: *6, 7*).

Discussion

With the exception of a dense distribution of mucocytes, the peribuccal, buccal, and oesophageal epithelia of all five species are histologically similar to those of the ciliated surfaces of the palps and lips of *Placopecten magellanicus* and *Chlamys varia* (Beninger et al. 1990 a, b). The results for *Crassostrea virginica* agree with the observations of Shaw and Battle (1957) for this species.

The origin and significance of the presence of mucus on the feeding epithelia of bivalves have been the object of differing interpretations. Although the mucus has been ascribed a function in the capture or transport of particles destined for ingestion (Moore 1971, Owen 1974, Owen and McCrae 1976, Owen 1978, Sylvester and Sleigh 1984), an alternate paradigm maintains that it is only used to clean feeding surfaces under conditions of high particle concentration, and that particles to be ingested are transported in water currents from the gill to the stomach (Jørgensen et al. 1984). The presence of mucus on the feeding surfaces under normal particle concentrations has been attributed to the stress induced by dissection, this mucus being produced in <1 min following initial laceration (Jørgensen 1981). The apparent lack of mucus in oesophagus aspirates of *Mytilus edulis*, <30 s after sectioning the adductor muscles, seemed to support this interpretation (Kiørboe and Møhlenberg 1981). However, none of the animals in the present study were subjected to high particle concentrations prior to dissection (indeed, the concentrations were extremely low to nil for *Placopecten magellanicus* and *Crassostrea virginica*, respectively), and all dissections were performed in <30 s, yet copious amounts of mucus were observed in their oesophagi using the direct histological approach. Moreover, mucus/mucus-particle strands were observed in the peribuccal region and in the mouth, despite the probable physical and chemical removal of most of this material in these exposed regions due to histological processing. Detailed micrographs of the epithelia show the presence of abundant, actively secreting mucocytes, demonstrating that at least some of this mucus is produced locally. In addition, the combination of both acid and neutral mucopolysaccharide secretions is characteristic of surfaces involved in particle transport or handling, and contrasts with the wholly acid mucopolysaccharide secretions of surfaces not involved in such activities, such as the smooth surface of the labial palps (Beninger et al. 1990 a).

It is thus clear that mucus production in the peribuccal, buccal, and oesophageal epithelia is a normal phenomenon in these suspension-feeding bivalves. Particles included in the mucus are drawn down the oesophagus, probably as a result of ciliary beating. These results are at variance with the observations of Kiørboe and Møhlenberg (1981), who concluded that particles in the oesophagus of *Mytilus edulis* were in free suspension, rather than embedded in mucus. Moreover, since the oesophagus was not ligated at the entry to the stomach (admittedly a very difficult operation in light of the time constraints), it is possible that much of the aspirate was in fact stomach contents. Indeed, the approximate volume of the oesophagus of a 4-cm-long mussel is a mere 30 nl (assuming it to be roughly cylindrical, radius 30 μm and height 1 cm). Without strict precautions to limit the volume of aspirate of a non-ligated oesophagus, inclusion of stomach contents would be inevitable. Using a similar technique for the stomach contents, Jørgensen (1981) observed that particles in the stomach were predominantly in free suspension, whereas the examination of oesophagus aspirates in another species, *Crassostrea gigas*, showed that mucus was indeed present in the oesophagus (Bernard 1974).

The presence of active mucocytes and mucus in the peribuccal, buccal, and oesophageal regions of all five species studied including a juvenile specimen (*Pecten maximus*), representative of three bivalve families, suggests that the mucus-bound mode of ingestion is widespread among suspension-feeding bivalves, as has been classically assumed (Owen 1966, Bayne et al. 1976, Purchon 1977, Barnes 1987, Salvini-Plawen 1988). Furthermore, the presence of active mucocytes and abundant mucus in the peribuccal, buccal, and oesophageal regions of the *Placopecten magellanicus* specimens (which had been kept for over 2 mo in a refrigerated, recirculating artificial seawater system with no added algae) as well as in the *Crassostrea virginica* specimens (which were held out of water for 2 d) demonstrates a fundamental aspect of bivalve feeding. The only apparent explanation to account for these results is that a considerable basal amount of mucus is continually produced and transported on these feeding epithelia, regardless of particle concentration in the external medium. Under conditions of acute stress or high particle concentrations, this basal mucus secretion may well be increased, as originally shown by Jørgenson (1981). The energetic cost of a continuous basal production of mucus on these feeding epithelia is probably not very great, since the organic content of mucus is quite low (Prezant 1985), and the majority is re-absorbed by the animal in the alimentary tract.

Although the present study demonstrates the mucus-bound mode of particle ingestion, water currents appear to be important for particle capture at the gills of several bivalve species under normal particle concentrations (Owen 1978). Exactly what occurs between the gills and the peribuccal region in undisturbed animals under normal particle concentrations is still a matter of inference and conjecture. It is hoped that future careful observations using fiber optics will elucidate this part of the feeding pathway, upon which depends the understanding of such fundamental phenomena as ingestion volume control and particle selection.

The observation of bucco-oesophageal glands in *Mytilus edulis*, generally thought to be absent in the Bivalvia (Morton 1960, 1979, Owen 1966, Salvini-Plawen 1988), raises the possibility of a digestive function for this region of the alimentary tract of *M. edulis*. Further studies are needed to determine their role in the feeding process.

Acknowledgements. The authors thank Dr. K. Benhalima for assistance with histology and in the field, M. L. Blanchard and A. Le Mercier for their photographic work, and Dr. Y. Poussart for assistance in the field. Draft versions of the manuscript benefited from the comments of Drs. R. I. E. Newell and J. E. Ward. Help with word processing was kindly provided by Mad. L. Briard. This work represents a collaborative contribution in the context of the CNRS (France)-NRC (Canada) scientific exchange programme; it was financed by the Natural Sciences and Engineering Research Council of Canada operating grant number A3658, grant number 20-53221-54-12 from the Faculté d'études supérieures et de la Recherche de l'Université de Moncton, and CNRS-NRC travel awards (1987–1989).

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