Research Note

Comparative Morphology of the Byssi of *Dreissena polymorpha* and *Mytilus edulis*

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Abstract. Scanning electron micrographs reveal differences in byssal stems, threads and plaques of two common biofouling mussels, the zebra mussel *Dreissena polymorpha* (Pallas), and the blue mussel *Mytilus edulis* (Linnaeus). These differences include anchorage of the stem, the pattern in which threads branch from the growing stem, thread surface topography, plaque orientation, and the morphology of the region of the thread that extends into the plaque. Morphological dissimilarities are likely to be related to differences in the mechanics of byssus formation and to differences in the surface texture and length of the ventral groove. Morphological differences between byssi of various biofouling mussels should be considered as researchers develop and adapt mechanisms of control.

The post-larvae of most bivalve molluscs possess byssal structures by which they are secured to the substratum as they undergo metamorphosis (Yonge, 1962). Some bivalves retain a byssal apparatus into the adult stage. For example, the marine blue mussel *Mytilus edulis* (Linnaeus), which is well known for its commercial importance, and the freshwater zebra mussel *Dreissena polymorpha* (Pallas), a recent invader of the Great Lakes (see Mackie *et al.*, 1989 for a review of the zoogeography of *D. polymorpha*), are two species that retain a byssus as juveniles. Thus, the byssus plays a major role early in the lives of most bivalves and is important throughout the lives of some species.

Purchon (1977) lists two major advantages to the presence of a byssal attachment. First, by forming a byssal attachment, molluscs do not expend energy unnecessarily to maintain position on a substratum. In addition, when the tide ebbs or the water level falls, a byssate mollusc can withdraw its foot and close its shell valves to prevent desiccation. Mussels are, therefore, regarded as being among the most difficult fouling organisms to control because they are capable of withstanding conditions that eliminate most other species. For instance, chlorination has been used in attempts to control both *Mytilus edulis* and *Dreissena polymorpha*. Holmes (1970) reports that in *M. edulis*, one of the most serious offenders in fouling marine intake systems (Clapp, 1950), the principal effect of chlorination was a depression in the activity of the foot, leading to a reduction in the number of threads formed. In addition, chlorination interfered with the quinone tanning process of thread formation, so that the threads formed were weaker than those of unchlorinated animals (Holmes, 1970). Therefore, although chlorination created a flow dependent distribution of mussels due to weakening of their byssus attachment systems, chlorination failed to suppress fouling by *M. edulis* in areas of low water flow. In *D. polymorpha*, chlorination is effective in controlling zebra mussel larvae, but adult mussels are able to protect themselves from intermittent doses of chlorine by adduction (Anon., 1991).

Since zebra mussels were first identified in the Great Lakes as a two-year-old age class in 1988 (Hebert *et al.*, 1989), they have been causing fouling problems for users of raw water by accumulating on exposed surfaces and physically blocking intake pipes by attaching to one another to form layers as thick as 0.3 m (Clarke, 1952; Griffiths *et al.*, 1989). Because the zebra mussel contributes to the biofouling of water supplies primarily by forming byssal attachments, the study of byssus morphology could lead to the development of a method of controlling this mollusc.

It has been reported that the byssus of *Dreissena polymorpha* is similar to the byssal apparatus found in *Mytilus edulis* and other marine bivalves (Moore, 1991). In previous studies, however, the authors (Steele, 1991; Eckroat *et al.*, 1992) observed that the structure of the byssus of *D. polymorpha* differed from the byssal structure of *M. edulis* that had been described in the literature (Brown, 1952; Smeathers and Vincent, 1979). Therefore, the current study was undertaken to clearly delineate differences between the byssi of *D. polymorpha* and *M. edulis* by making morphological

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comparisons of their stems, threads, and plaques. Accurate comparisons are especially important because morphological differences between the byssi of various biofouling mussels should be recognized as researchers develop and adapt control mechanisms that affect the byssus.

MATERIALS AND METHODS

Live specimens of *Dreissena polymorpha*, 2.1-2.5 cm in length, were collected at Lampe Marina on Presque Isle, Erie, Pennsylvania, during October 1990 and maintained in a 15°C freshwater aquarium for approximately one month, where they were fed 200 ml of an alga mixture (3 g of *Chlorella* spp. blended in 1 L of water) daily. Additional live specimens of *D. polymorpha*, 1.5-2.3 cm in length, were collected in Thompson's Bay on Presque Isle, Erie, Pennsylvania, during May 1991 and maintained in a 15°C freshwater aquarium overnight before their byssal threads were prepared for examination. Live specimens of *Mytilus edulis* measuring approximatelyt 1.0 cm and 5.0-6.5 cm were collected at Wachapreague, Virginia, and at Rye, New Hampshire, respectively, and maintained in a 24°C saltwater aquarium (31 ppt) for 14 days and fed marine *Chlorella* spp. daily as described above.

To prepare specimens for scanning electron microscopy, either the byssi were removed, or the mussels' shells were opened so that the byssi could be studied intact. Specimens were fixed in 5% glutaraldehyde in sodium phosphate buffer (pH 7.2) for 24-48 hours at 5°C, washed in buffer alone for 15 minutes, and dehydrated in a graded ethanol series. After specimens were critical point dried using carbon dioxide as the transitional fluid, they were mounted on aluminum stubs and sputter coated with gold-palladium. Specimens were examined and photographed with a Hitachi S-570 scanning electron microscope.

RESULTS

Scanning electron micrographs provided more detailed views of byssal structures that have been diagrammatically represented by other workers (Brown, 1952; Smeathers and Vincent, 1979). Comparisons between the byssi of *Dreissena polymorpha* and *Mytilus edulis* were limited to noting morphological differences because age differences of specimens make size comparisons of structures meaningless.

In intact specimens of *Dreissena polymorpha*, the byssal stem was concealed inside a collar-like structure that was continuous with the foot, and the region where the byssal threads branched from the stem was not visible (Fig. 1). The stem of *Mytilus edulis*, which emerged from a raised area at the base of the foot was, however, visible in intact specimens, and the locations at which the threads branched from the stem were exposed (Fig. 2). Additional observations showed that the ventral groove extended to the distal tip of the foot of *M. edulis*, but extended only about half the length of the foot in *D. polymorpha*.

Removal of the byssus from specimens of *Dreissena polymorpha* revealed that most of their byssal threads branched from one linear location of the stem and from all around the stem's circumference (Fig. 3). Cuffs or sheaths, formed by the outer laminae, were observed at the bases of the threads in some specimens (Eckroat *et al.*, 1992). Examination of intact specimens of *Mytilus edulis* showed that threads, attached to the stem by overlapping rings, branched from progressively more distal locations along two opposite edges of the stem (Fig. 4).

In the proximal region, threads of *Dreissena polymorpha* were cylindrical and smooth (Fig. 5), but the proximal portions of threads of *Mytilus edulis* were flattened with a crimped edge and had corrugations or folds around their circumferences (Fig. 6). The distal half of threads of *D. polymorpha* became increasingly rough with longitudinal ridges that were most pronounced at the distal ends of the threads (Fig. 7). Threads of *M. edulis*, however, were smooth in the distal region (Fig. 8).

Threads of *Dreissena polymorpha* and *Mytilus edulis* formed oblique angles with the substratum and ended distally in thin, oval plaques (bottom portions of Figs. 9 and 10). In *D. polymorpha*, threads became broader, flattened, and bifurcated as they expanded along the plaque's wide axis (Fig. 9, near top), which was oriented perpendicular to the longitudinal axis of the thread (bottom portion of Fig. 9). Threads of *M. edulis*, however, trifurcated and formed thin, root-like extensions that continued into the plaque (top portion of Fig. 10). The narrow axis of the plaque was oriented perpendicular to the longitudinal axis of the thread (Fig. 10).

DISCUSSION

Byssus morphology is related to the mechanical events that occur during byssus formation. One of the first mechanical events involves the movement of the foot tightly against the substratum so that the mussel can secrete a plaque (Waite, 1983; Eckroat *et al.*, 1992), which is molded by the distal depression of the ventral groove of the foot (Brown, 1952; Waite, 1983). After a plaque has been formed, an individual thread, which is of a fluid consistency, is extruded from the ventral groove (Smyth, 1954; Waite, 1983). The plaques of *Mytilus edulis* and *Dreissena polymorpha* are very thin at their peripheral regions, but their orientations on the substratum differ. In addition, the structure of the portion of the thread that continues into the plaque is dissimilar in the two species. These differences in plaque orientation and distal thread morphology could result because the ventral groove does not extend to the distal tip of the foot in *D. polymorpha* as it does in *M. edulis*, which could affect the

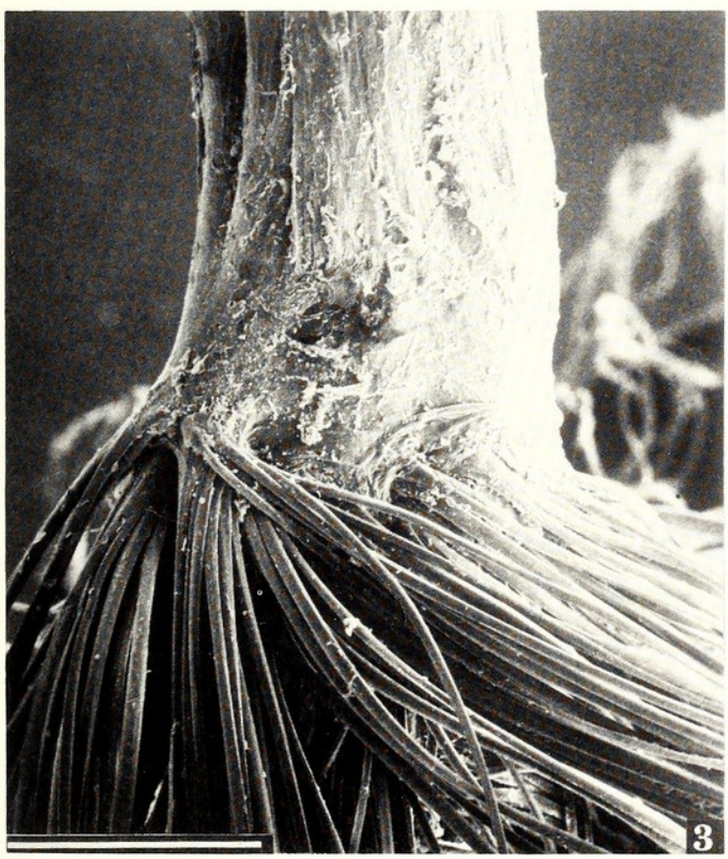

Fig. 1. Intact byssus of *Dreissena polymorpha* with threads emerging from a collar-like structure that conceals the stem (scale bar = 1.00 mm). **Fig. 2.** Intact byssus of *Mytilus edulis* with the stem emerging from a raised structure near the base of the foot (scale bar = 0.30 mm). **Fig. 3.** Stem of *D. polymorpha*. Threads branch from around the circumference of one proximal-distal location of the stem (scale bar = 0.60 mm). **Fig. 4.** Stem of *M. edulis*. Threads branch from progressively distal regions along two opposite sides of the stem and are attached by overlapping rings (scale bar = 0.50 mm).

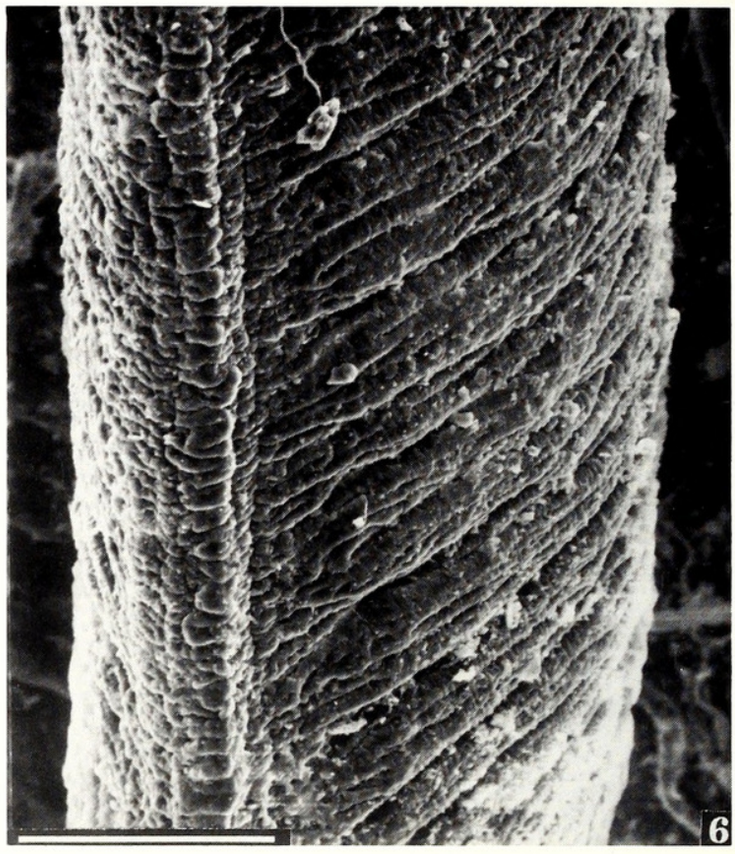

Fig. 5. Smooth, proximal portion of thread of *Dreissena polymorpha* (scale bar = 10.0 μm). **Fig. 6.** Flattened proximal portion of thread of *Mytilus edulis* with crimped edge and folds around circumference (scale bar = 43.0 μm). **Fig. 7.** Distal portion of thread of *D. polymorpha* with longitudinal ridges (scale bar = 23.1 μm). **Fig. 8.** Smooth, distal portion of thread of *M. edulis* (scale bar = 38.0 μm).

shape of the distal depression as the foot is pressed against a substratum. In addition, differences could arise in the shape of the distal depression that could affect the morphology of the distal ends of the threads if the muscle action of the foot differs in the two species.

As threads are secreted as a liquid, they are molded to the walls of the ventral groove (Brown, 1952; Smyth, 1954; Bairati and Vitellaro-Zuccarello, 1974; Waite, 1983). Our results, which agree with those of other workers (Brown, 1952; Smeathers and Vincent, 1979), show that the threads of *Mytilus edulis* are corrugated in the proximal third and smooth in the distal two-thirds. The threads of *Dreissena polymorpha*, which are smooth in the proximal half and rough with longitudinal ridges in the distal half, therefore, differ from those of *M. edulis*. These thread surface differences suggest that the walls of the ventral groove of *D. polymorpha* have a different surface topography than those of *M. edulis*.

Once a thread has been completed, specimens of *Mytilus edulis* change position and repeat the process to form another thread (Clapp, 1950). The changes in position made by *Dreissena polymorpha* and *M. edulis* could differ because in the two species, the patterns in which the threads branch from the stem differ. In *D. polymorpha*, threads branch from around the circumference of the stem, but in *M. edulis*, threads branch from two opposite sides.

The ways in which the threads of the two species are attached to the stem are dissimilar. Our observations agree with those of Brown (1952), who reported that the threads of *Mytilus edulis* are attached to the byssus with overlapping rings that are fused with the fibrous laminae of the byssal root, while the threads of some *Dreissena polymorpha* specimens have cuffs at their bases (Eckroat *et al.*, 1992). Unlike the threads of *M. edulis*, which branch from progressively distal locations along the stem, threads of *D. polymorpha* branch from the stem at one linear location. Brown (1952) explained that in *M. edulis*, as the fibrous laminae of the root increase in length, the stem lengthens and older threads are carried farther from the body of the organism. The thread branching pattern observed in *D. polymorpha*, however, suggests that as threads are added to the byssus, the stem does not lengthen in the region where the threads branch. New threads are attached to the outside of the stem, which increases stem diameter but not stem length.

The byssi of *Dreissena polymorpha* and *Mytilus edulis* differ in the anchorage of the stem, the pattern in which threads branch from the growing stem, thread surface topography, plaque orientation, and the morphology of the region of the thread that extends into the plaque. Therefore, although previous reports (Moore, 1991) stated that the byssi of these molluscs were similar, marked structural differences exist. Because byssal attachment is fundamental to the success of mussels that colonize hard substrata, information concerning structural characteristics of the byssus could be used together with knowledge of thread formation and attachment to develop or adapt mechanisms of controlling biofouling mussels. It is therefore important to realize that among different molluscan species, the byssal apparatus has diverse designs. As control mechanisms are proposed, researchers should recognize such morphological dissimilarities and the possible differences in the mechanics of byssus formation that they could reflect.

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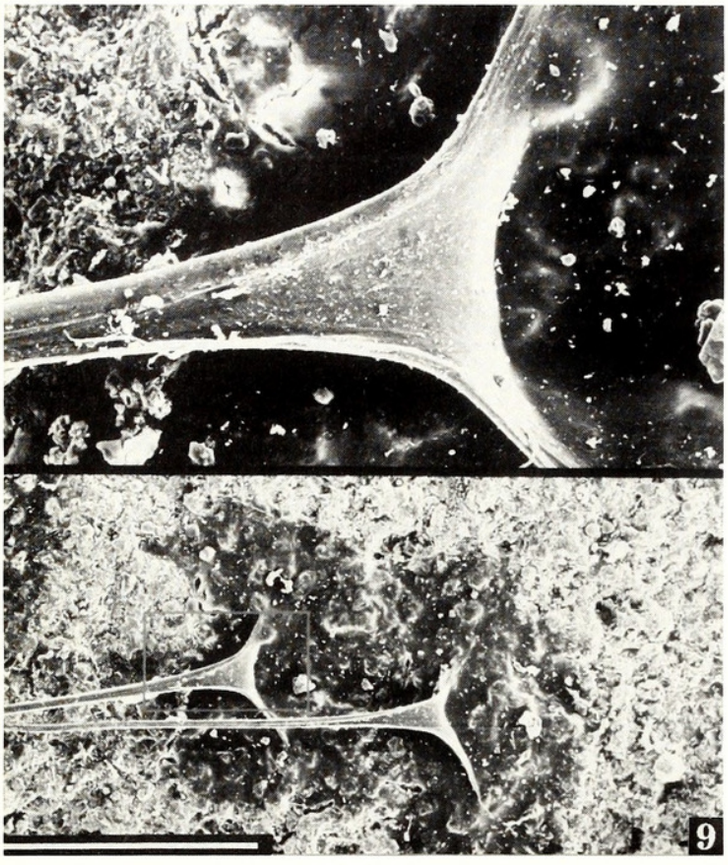

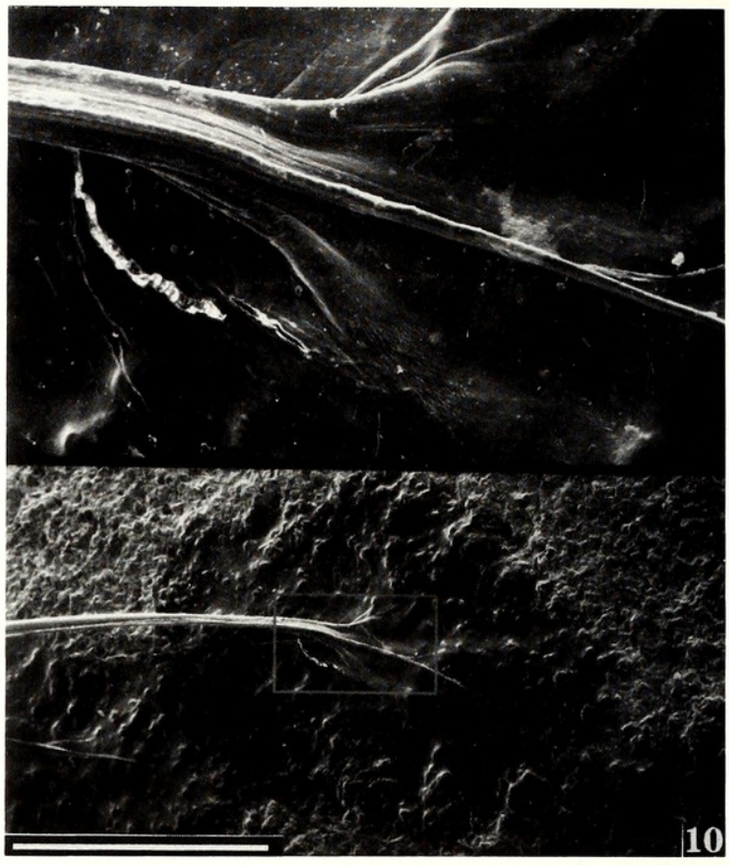

Fig. 9. Plaque of *Dreissena polymorpha* oriented with its wide axis perpendicular to the longitudinal axis of the thread in perpendicular vertical planes (bottom - scale bar = 0.43 mm). Broad, flattened portion of thread expanding along wide axis of plaque (top - scale bar = 86.0 nm). **Fig. 10.** Plaques of *Mytilus edulis*. The narrow axis of each plaque is perpendicular to the longitudinal axis of the thread to which it is attached (bottom - scale bar = 1.0 mm). Thin, root-like extensions spreading into plaque (top - scale bar = 0.20 mm).

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