

Mussel attachment on rocky shores: the effect of flow on byssus production

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Synopsis Mussels rely on a strong byssal attachment to persist in a range of habitats with differing rates of water flow. Recent studies, however, suggest that the ability of one mussel species to sense and respond adaptively to the flow in its environment is limited under even modest flow conditions because the process of byssal thread formation is disrupted. This study extends these findings to four mussel species, *Mytilus trossulus*, *M. galloprovincialis*, *M. californianus*, and *Modiolus modiolus*. Collectively, the response of byssal thread formation decreased with rates of flow above ~25 cm/s and the critical flow threshold was estimated to be <50 cm/s. How can mussels persist on shores where flow is an order of magnitude higher? Using a combination of techniques for measuring flow, velocity profiles were obtained above and within mussel aggregations in the laboratory and in the field. Flow was greatly reduced within mussel aggregations, ranging from 0.1% to 10% of free-stream velocity. These results suggest one key to the success of mussels in habitats with high rates of flow is the ability to form aggregations that ameliorate flows to a level that is conducive to byssal thread formation.

Introduction

Byssal threads are the lifelines of marine mussels. The extensible fibers tether the animal firmly to hard substrates and play a critical role in the ability of mussels to dominate space on many temperate shores worldwide. Each thread is molded within a groove in the extended foot, a process that takes ~3 min (Waite 1992). Members of the family Mytilidae, the “true” mussels, differ from their burrowing bivalve ancestors in their ability to produce byssal threads beyond the post-larval stage, thereby enabling adults to adopt an epibenthic lifestyle (Yonge 1960; Stanley 1972). Mussels form dense aggregations, or beds, which can exclude occupiers of primary space but can also provide structure for a diverse assemblage of organisms (Paine and Levin 1981; Suchanek 1986; Tsuchiya and Nishihira 1986).

Mussels live in a wide range of habitats that vary with respect to water motion. Many species are found subtidally, where water velocities are typically well below 1 m/s (Suchanek 1986; Koehl 1977; Gaylord et al. 2003). Several species are common to intertidal shores, where they may be subjected to high velocities of water from breaking waves. These velocities can be on the order of 1 m/s on protected shores and bays, but routinely exceed 10 m/s on

wave-exposed outer coasts (Bell and Denny 1994; Gaylord 1999). Moving water generates forces on mussels; a mussel must maintain a strong byssal attachment that withstands hydrodynamic challenges in order to persist (Denny 1987; Carrington 2002a).

Several studies have suggested that mussels “go with the flow,” producing more byssal threads that increase the strength of attachment when higher water velocities are encountered (Price 1982; Bell and Gosline 1997; Carrington 2002a). A recent study by Moeser et al. (2006), however, suggests that there is a limit to this potentially adaptive response. In flume studies with *Mytilus edulis*, the response of byssal thread production to flow was curvilinear, peaking at 11 cm/s. Flows above 18 cm/s hindered thread production because the animal was unable to maintain the extended posture of its soft foot long enough to complete the molding process. These results are surprising, given that *M. edulis* commonly occurs on shores exposed to flows that are over an order of magnitude >18 cm/s (Carrington 2002a).

The purpose of this study is 2-fold. First, we extend the findings of Moeser et al. (2006) by evaluating the tolerance to flow of several other species found locally in Washington State in a range of habitats. We did not examine the effects of two other

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aspects of water motion, agitation and loading of the byssus retractor mussel, because these potential cues failed to stimulate byssal thread production in *M. edulis* (Moeser et al. 2006). Specifically, we examined two sibling species of *M. edulis*, *M. trossulus*, and *M. galloprovincialis* (MacDonald and Koehn 1988), all of which inhabit calm to moderately exposed shores (Suchanek 1986). We also evaluated *Modiolus modiolus* (hereafter, *Modiolus*), a species found in relatively calmer subtidal habitats, and *M. californianus*, a species common to wave-exposed shores. Second, we evaluate the ability of mussels to modulate the flow in their environment by forming aggregations, as has been observed by others (Koehl 2000; Gaylord et al. 2003; O'Donnell 2008). Specifically, we provide quantitative and qualitative measures of the flow within mussel beds, with special attention to flows near the substrate, where byssal thread production occurs.

Methods and materials

This study comprises two sets of experiments, one of which examines the ability of mussels to produce threads under a range of water velocities in the laboratory and another which measures water velocity within mussel beds in both the laboratory and in the field. The laboratory experiments were performed at the University of Washington's Friday Harbor Laboratories on San Juan Island, Washington, USA over summer and early fall 2006. The field studies were also performed on San Juan Island, at Argyle Creek (a marine research preserve, 48.52° N, 123.01° W) in summer 2006, and at Cattle Point (48.45° N, 122.96° W) in summer 2007. Four species of mytilid mussels were used in the laboratory experiments: *M. trossulus* collected from Argyle Creek, *M. galloprovincialis* collected from Westcott Bay Sea Farms on San Juan Island, *M. californianus* collected from Tatoosh Island, WA (48.39° N, 124.74° W) and *Modiolus* collected by trawl from Mosquito Pass (48.58° N, 123.17° W).

Thread production as a function of water velocity

Laboratory studies were conducted to evaluate thread production by the four mussel species over a range of unidirectional water velocities, nominally 0–60 cm/s, following the protocol used by Moeser et al. (2006) for *M. edulis*. A circulating flume was used to expose solitary mussels to a constant water velocity for 24 h and the subsequent number of byssal threads produced was assessed. Using 5-min epoxy (Devcon, Riviera Beach, FL, USA), each mussel was fixed to a vertical plastic post and

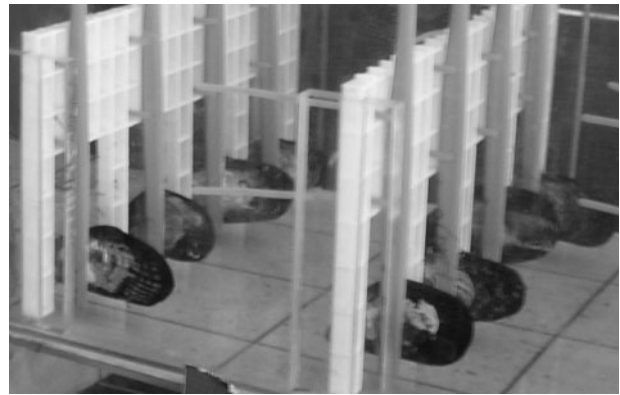


Fig. 1 A portion of the flume used in the assays of byssal thread production. Mussels (in this case *M. californianus*) are attached to racks placed in the working section of the flume. Flow is from left to right (see text for details).

suspended 6.5 mm above the substrate with the posterior end facing upstream (Figs. 1 and 2). Each post was mounted to a rack constructed from plastic egg crate lighting panel (1.5 cm grate size) mounted flush with the floor of the flume's working section (L × W × H; 100 cm × 37 cm × 36 cm). Mussels were mounted in the center of 6 cm × 6 cm square gaps cut into the rack, thereby reducing the obstruction of flow caused by the rack itself. A total of 16 mussels, distributed evenly among four racks, were mounted in the working section for each experiment. Mussels were separated by at least one shell length. The seawater in the flume was aerated and continually replenished by a flow-through system, maintained at a temperature of $15 \pm 2^\circ\text{C}$.

After each 24-h trial, threads produced by each mussel were counted and cut. The mussels were then returned to the flume for another trial. Thread production was monitored at 6–7 velocities for each species; the order of velocities was randomized among trials. Sample size was 7–16 mussels for each species; the lower values were due to limited availability of specimens. The range of sizes (shell length) varied among the species as follows: *M. trossulus* was 57–69 mm, *M. galloprovincialis* was 57–63 mm, *Modiolus* was 68–83 mm, and the two size classes of *M. californianus* tested were 57–74 mm and 87–112 mm. For the ensuing data analyses, the mean shell length was used to characterize each group: 60, 60, 75, 65, and 97 mm, respectively.

The racks with mussels obstructed the flow through the working section of the flume, altering velocities from the nominal values reported above. To determine the velocity in the vicinity of the mussel's foot for each trial, video analysis was used to track particles passing through the gaps in the racks and within 1 cm of the bottom of the working section.

Neutrally buoyant, rehydrated *Artemia* sp. cysts were carefully pipetted into the flume and filmed through the side of the working section using a Sony Digital Handycam (Sony Electron. Inc., San Diego, CA, USA). The digital video was imported into iMovieHD (Apple Computer Inc., Cupertino, CA, USA) and separated into short clips (2–3 s) for analysis. The video clips were analyzed using two programs written for MatLab (The MathWorks Inc., Natick, MA, USA) to track points and determine velocities. Mean values were calculated for each velocity trial and used in all subsequent analyses.

Nonlinear regression analysis was used to evaluate the effect of water velocity on mean byssal thread production for each species and size class. A quadratic equation (second-order polynomial) was fit to the data using TableCurve2D (Systat, Richmond, CA, USA). U_{crit} or the velocity at which thread production equals zero (in centimeter per second), was calculated as the x -axis intercept of each curve.

Flow within mussel beds

Water velocity above and within a mussel bed was quantified in the laboratory separately for two species, *M. galloprovincialis* and *M. trossulus*; shell length ranges were 40–60 and 20–30 mm, respectively. A monospecific bed was created in the working section of a flume originally described by Boller and Carrington (2006), but modified by removing the flow reducer (to create a larger working section; $L \times W \times H$; 160 cm \times 32 cm \times 25 cm) and adding several upstream flow straighteners (to remove large vortices). Mussels were carefully positioned 40 cm downstream from the flow straighteners in a dense monolayer on the bottom of the working section with the posterior end down, as they occur in nature. The flume was then filled with 15–16°C seawater and constantly aerated while the velocity was increased to ~ 10 cm/s for 24 h to allow mussels to attach and reposition. The resultant mussel bed measured 50–60 cm in length and spanned the width of the working section.

Vertical profiles of water velocity were measured for a range of free-stream velocities (U_{fs} , measured >15 cm above the mussels) at several positions spanning the length of the mussel bed using a 16 MHz Acoustic Doppler Velocimeter (ADV; Sontek/YSI Inc., San Diego, CA, USA). The ADV reported velocity in three dimensions at 25 Hz, and approximately 300 samples were processed and averaged for each measurement using WinADV software (Sontek/YSI Inc., San Diego, CA, USA). To measure velocities within the mussel bed, individuals were carefully removed to create a 3 cm

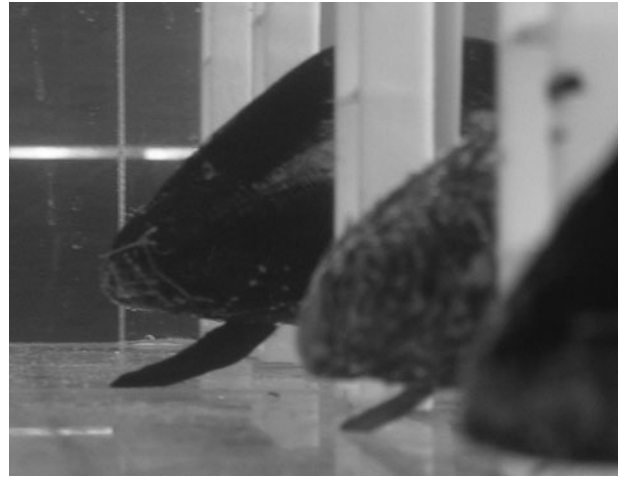


Fig. 2 Side view of a single rack used in the assays of byssal thread production. Two mussels have their foot extended upstream and are in the process of molding a single byssal thread.

diameter gap to accommodate the ADV probe. The size of this opening is small relative to mussel height, thus it likely has a negligible effect on the pattern of water flow in the bed (O'Donnell 2008). To minimize disruption to the bed, gaps were first formed on the downstream end of the bed and refilled before progressing to locations upstream. Flow <1 cm above the substrate could not be accurately measured with the ADV; velocities in this region were quantified by tracking particles filmed through the transparent floor of the working section, as described above.

Because laboratory-made mussel beds lack the sediment and organic material commonly found in established mussel beds, vertical velocity profiles were also measured in a naturally occurring bed of *M. trossulus* at Argyle Creek. This shallow saline corridor (~ 10 m across) connects a lagoon to a bay, and a steady unidirectional current is generated in the creek as the lagoon fills and drains during large tidal exchanges. Measurements were taken at the onset of an ebbing tide on July 25, 2006, and the height of the water column was ~ 14 cm above the mussel bed. Mussels were ~ 25 mm in length and the monolayered aggregation lined the creek for several meters. The ADV probe was placed 40 cm downstream from the upstream edge of the bed, and a vertical velocity profile was measured every 1 cm from the substrate, as in the laboratory measurements. The procedure was repeated three times during the ebbing tide and mean values for each height were calculated.

A different approach was used to characterize the pattern of flow within *M. californianus* beds at Cattle Point, a site exposed to moderate wave action that precludes the use of the ADV. Instead, the dissolution pattern of plaster rods was used to

provide a simple, qualitative measure of water motion. No attempt was made to convert the dissolution rates to flow values because the rate of plaster dissolution depends on several aspects of water motion, such as current speed, turbulence, and frequency of oscillation (Porter et al. 2000; Falter et al. 2005). Plaster of Paris rods of 1.5 cm × 12 cm (diameter × length) were molded in PVC tubes lined with plastic laminating sheet, following the manufacturer's directions. In the field, each rod was affixed to the substrate using marine epoxy during low tide on July 25, 2007. Three rods were embedded in each of three small mussel beds (monolayered, ~1 m²) and an additional three rods were mounted on emergent rock adjacent to each bed. The rods were retrieved after 24 h and the dissolution patterns were compared between treatments.

Results

Mean thread production by solitary mussels in the flume generally decreased with water velocity (Fig. 3). In *M. californianus*, declining thread production was observed only at higher velocities (>25 cm/s). No threads were produced by *Modiolus* exposed to 16 cm/s, or by *M. trossulus* exposed to

30 cm/s. Overall, the quadratic equation described these relationships well ($r^2 = 0.53\text{--}0.94$), although the fits for the two size classes of *M. californianus* were not significant (Table 1). With respect to U_{crit} , the main pattern that emerges is a low-flow threshold for *Modiolus*, and similar, but modest, flow thresholds for the remaining species (22–48 cm/s). Due to small sample size and differences in shell length, no further interspecific comparisons of thread production were made.

The velocity profiles measured in flumes indicate mussel beds substantially reduce flow. Reductions to 0.1–10% of free-stream velocity were observed along the entire length of the *M. galloprovincialis* bed and even extended beyond the height of the mussels (Figs. 4 and 5). Similar trends were observed with *M. trossulus* in the laboratory (data not shown). Even more dramatic flow reduction (0.2–0.5% of free-stream velocity) was observed in an established bed of *M. trossulus* at Argyle Creek (Fig. 6). In all cases, flow in the vicinity of the mussel's foot (<1 cm) never exceeded 10 cm/s, even when free-stream velocity approached 1 m/s.

Several of the plaster rods deployed at Cattle Point washed away after 24 h, particularly those

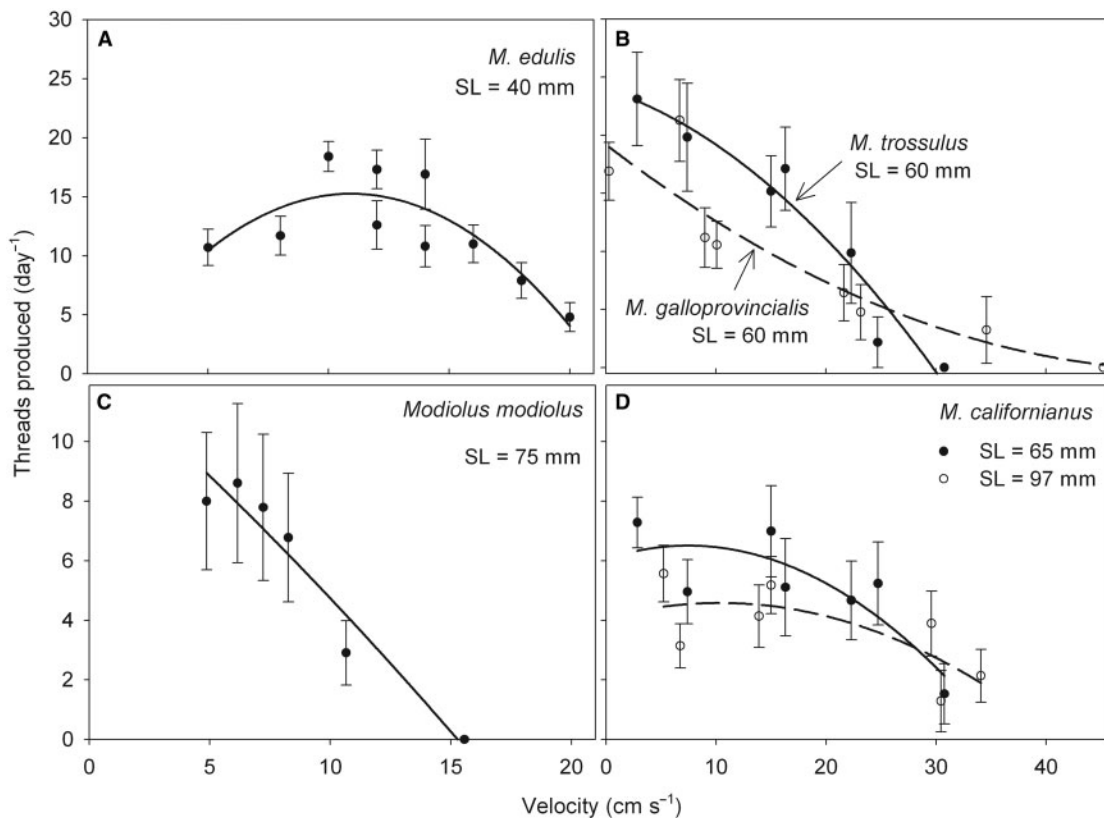


Fig. 3 Mean thread production over 24 h as a function of water velocity in a circulating flume. Symbols are means \pm standard errors, curves are best-fit quadratic equations. Mean shell length (SL, in centimeter) is indicated for each species. (A) *M. edulis* (data replotted from Moeser et al. 2006). (B) *M. trossulus* and *M. galloprovincialis*. (C) *Modiolus*. (D) Two size classes of *M. californianus*.

Table 1 Summary of nonlinear regression analysis of byssal thread production as a function of water velocity for each species and size class

Species	Shell length (mm)	r^2	N	P	$U_{crit} \pm 95\% \text{ CL}$ (cm/s)
<i>Modiolus</i>	75	0.934	6	0.017	15.3 ± 3.3
<i>M. californianus</i>	65	0.700	7	0.091	35.9 ± 5.9
<i>M. californianus</i>	97	0.526	7	0.225	41.3 ± 7.4
<i>M. edulis</i>	40	0.713	10	0.013	21.5 ± 7.2
<i>M. galloprovincialis</i>	60	0.834	8	0.011	47.5 ± 9.8
<i>M. trossulus</i>	60	0.943	7	0.003	29.7 ± 5.7

The resulting quadratic equations are plotted in Fig. 3. N is the number of velocities, U_{crit} is the x-axis intercept of the regression line, and CL is the confidence limit. Data for *M. edulis* are from Moeser et al. (2006).

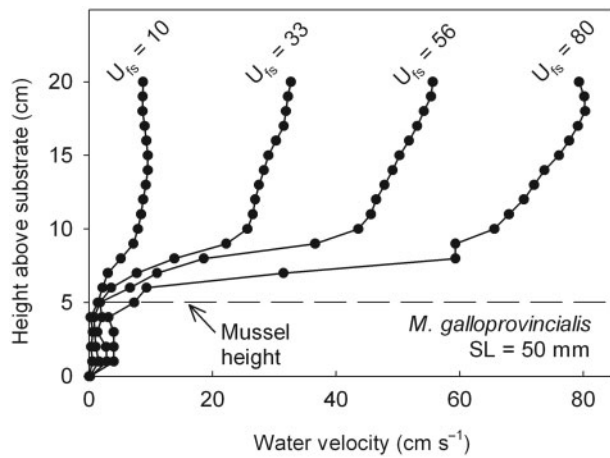


Fig. 4 Velocity profiles above and within a *M. galloprovincialis* bed in a flume. All measurements were taken in the center of the bed, 40 cm from the upstream end. Mean downstream flow was measured every 1 cm above the substrate for each of four free-stream velocities, U_{fs} : 10, 33, 56, and 80 cm/s. Note how flow is greatly reduced (<7 cm/s; 0.1–9% of U_{fs}) in the region occupied by mussels.

on emergent rock. The few that did remain, however, displayed distinct patterns of dissolution (Figs. 7 and 8). Rods on emergent rock were uniformly eroded along their entire length, while those within mussel beds were tapered. In the latter case, the tip of the rod was $\sim 40\%$ thinner than the base.

Discussion

This study extends the findings of Moeser et al. (2006) to show that byssal thread production by mussels is limited, not stimulated, by high flow. In all four of the species examined in the flume assays, velocities above 20 cm/s visibly hindered the mussel's ability to extend its soft muscular foot beyond the margin of the shell, a posture that must be maintained for several minutes to mold and attach a new thread to a substrate. Even in *M. californianus*, the species common to outer coast (wave exposed)

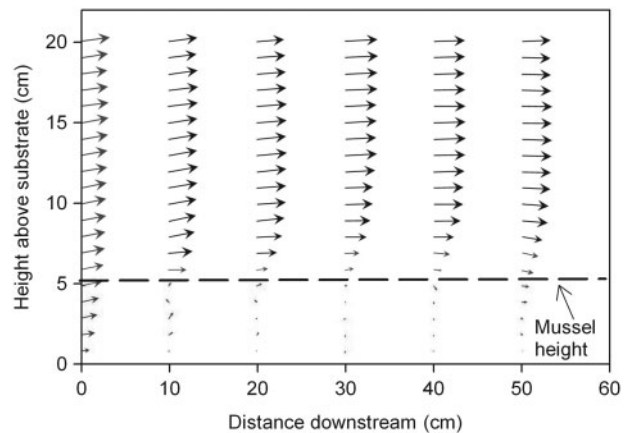


Fig. 5 Vector plot of velocity above and within a *M. galloprovincialis* bed in a flume. All measurements were taken at a free-stream velocity of 30 cm/s along a transect down the middle of the bed. Velocity was measured every 1 cm above the substrate for each of six distances (0–50 cm) from the upstream edge of the bed. Each arrow represents the vector-averaged magnitude and direction of flow at that location. Note the strong reduction in flow within the mussel bed (<3 cm/s; 0.8–10% of U_{fs}).

shores, flows on the order of 30 cm/s deflected the foot downstream and precluded thread formation. The subtidal species *Modiolus* was the clear weakling of the group, with thread production curtailed at only 16 cm/s. Altogether, these studies establish 50 cm/s as a reasonable threshold limiting byssal thread production in solitary mussels.

How then, do mussels persist in habitats where flows routinely exceed their physiological limits? The answer lies in their aggregative behavior. Dense mussel beds modulate flow, creating microhabitats that are conducive to thread production. The magnitude of flow reduction observed in the laboratory and field studies presented here ranged from 0.1% to 10% of free-stream velocity. Applying this reduction to a 10 m/s wave, a velocity common in intertidal habitats of the outer coast, flow inside a mussel bed would range 1–100 cm/s and thread production would likely be possible. Note that this

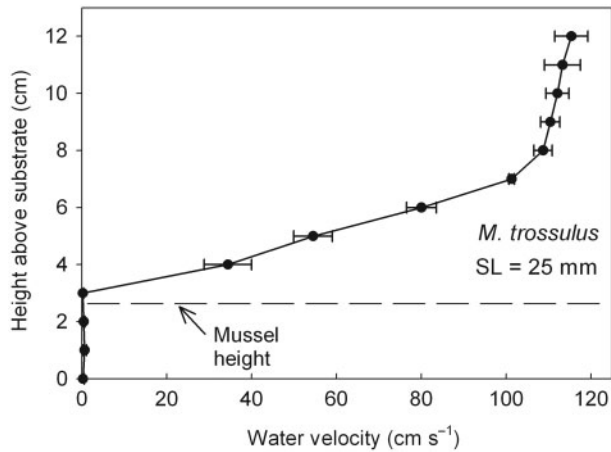


Fig. 6 Mean velocity profile above and within a *M. trossulus* bed at Argyle Creek. Symbols are mean and standard error of the three measurement sessions. Flow within the mussel bed is <1 cm/s, or 0.2–0.5% of free-stream velocity, U_f .

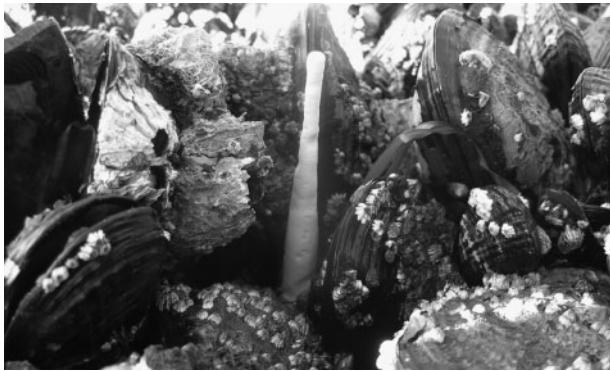


Fig. 7 A plaster rod 24h after deployment within a mussel bed at Cattle Point, WA. Note the tapered pattern of dissolution. Height of the rod is 8 cm.

rough calculation is based on only a few measurements in small, monolayer mussel beds in unidirectional flow; the magnitude of flow reduction in mussel aggregations likely reflects a complex interaction of factors such as mussel size, bed density, and flow characteristics. Nonetheless, these findings are consistent with those of O'Donnell (2008), who elegantly demonstrated dramatic reductions in force adjacent to mussel beds on wave-exposed shores. Modulation of flow has also been observed in many other benthic marine species, such as seaweeds and corals (e.g., Sebens et al. 1997; Koehl 2000) and complex-surface topography can also offer microhabitats of reduced flow (O'Donnell and Denny 2008). This underscores the importance of evaluating physiological tolerances relative to environmental conditions at a scale that is relevant to the organism, a point that has been argued convincingly by Koehl (1999) and others.

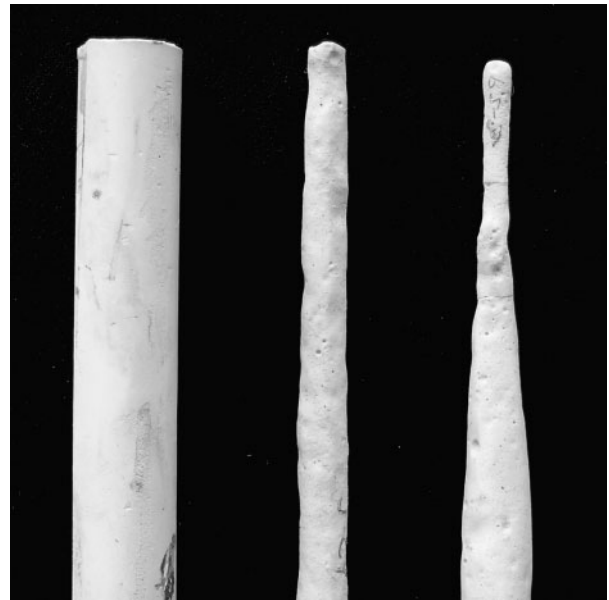


Fig. 8 Comparison of three plaster rods. The initial rod size is shown on the left (1.5 cm diameter; 8 cm height). The two other rods were deployed at Cattle Point and recovered after 24h. On an emergent rock (center), the pattern of dissolution is uniform (diameter = 5.8–6.6 mm). Within the mussel bed (right), dissolution decreases with proximity to the substrate (diameter = 3.7–10.1 mm).

Another behavioral tactic available to mussels is to fine-tune their production of threads. Extreme flows are, by definition, not the norm. Mussels with sufficiently strong attachment can wait out stormy episodes and produce threads when more benign conditions return. The timing of these “windows of calm” relative to the durability of the threads could be an important consideration in evaluating the ability of mussels to persist on wave-exposed shores. A similar argument has been made convincingly for barnacles feeding on wave-swept rocky shores by Miller (2007). An unusual version of this scenario may be employed by *M. californianus*, which thrives on shores pounded by surf. During the assays of thread production in the present study, individuals were observed making several byssal threads while exposed to air between trials in the flume. This behavior was not observed in any of the other species. The ability of *M. californianus* to produce threads during low tide may represent an important adaptation for survival on outer coast habitats.

In summary, the ability of mussels to produce a strong attachment on wave-swept shores is not due to the provision of a strong foot, but rather to their aggregative behavior which ameliorates flows to levels at which their relatively weak foot can function. The extent to which mussels tune their attachment strength to their hydrodynamic environment is,

at this point, unclear. Indeed, a temporal mismatch between attachment strength and wave conditions is often observed, rendering mussels prone to dislodgment (Carrington 2002a). As discussed by Carrington (2002a, 2002b) and Moeser et al. (2006), the strength of byssal attachment likely depends on a suite of factors other than flow, such as temperature, water chemistry, abundance of predators, reproductive cycles, and physiological condition.

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