



Effects of injured conspecifics and predators on byssogenesis, attachment strength and movement in the blue mussel, *Mytilus edulis*



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ABSTRACT

Mussels respond to threats from predators by increasing anti-predator traits, which include a suite of inducible defenses. Blue mussels (*Mytilus edulis*) can modify the strength, number and attachment site of byssal threads in response to water borne cues from predators and injured conspecifics. We quantified byssal thread production, attachment strength and movement in blue mussels of two size classes in response to effluent from the American lobster *Homarus americanus*, the rock crab *Cancer irroratus*, the sea star *Asterias rubens*, and injured conspecific mussels. In a factorial laboratory experiment, effluent from the predatory crab, *C. irroratus*, resulted in higher numbers of functional byssal threads compared only to exposure to injured conspecific mussels, and not to any other treatment group. Large mussels produced stronger byssal attachments than small mussels. Over 24 h, small mussels formed and released more byssus bundles than large mussels, an indication of increased movement. Small mussels started producing byssal threads sooner than large mussels. Mussels exposed to effluent from injured conspecific mussels began producing byssal threads earlier, compared to the control and not to any other treatment group. Our results show that byssogenesis was influenced by predator type and mussel size, whereas attachment strength and movement depended on mussel size. This study highlights the ability of two size classes of blue mussels to selectively alter byssal thread production and movement in the presence of injured conspecifics and potential predators.

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1. Introduction

Chemical cues are essential for guiding behavioral responses and decision-making processes of an organism (Vickers, 2000), especially in the case of predator–prey dynamics in aquatic habitats (Czarnoleski et al., 2010). Inducible anti-predator responses are phenotypically plastic traits that result from unpredictable predation pressure and are important in reducing successive damage to an organism (Harvell, 1990). These responses enable prey to reduce the likelihood of injury or death while minimizing energy allocated to anti-predator defenses (Harvell, 1990).

Blue mussels, *Mytilus edulis* are dominant organisms in many near-shore environments, comprising extensive mussel beds on both soft and hard substrata and are important in structuring intertidal and subtidal communities (Suchanek, 1985). Mussels suffer intensive predation threats by a wide variety of carnivores (Seed and Suchanek, 1992) to which they have evolved specific behavioral and morphological defenses (Cheung et al., 2004). Inducible responses include greater strength of byssal attachment in the presence of starfish and crabs (Côté, 1995; Leonard et al., 1999; Reimer and Harms-Ringdahl, 2001; Reimer and Tedengren, 1997), increased byssogenesis when exposed

to crabs feeding on conspecific mussels (Fässler and Kaiser, 2008), and rapid clumping behavior when exposed to lobsters (Côté and Jelnikar, 1999).

Damaged conspecifics may have a greater influence on defense mechanisms than predators alone. For example, upon exposure to damaged conspecifics, feeding and growth in the Atlantic dogwhelk, *Nucella lapillus* was reduced (Palmer, 1990), and *M. edulis* and the green-lipped mussel, *Perna viridis*, exhibited enhanced byssal thread production (Cheung et al., 2004; Chiu et al., 2011; Fässler and Kaiser, 2008). Additionally, *P. viridis* also increased mean byssal thread length and thickness, were less mobile, and less readily shed their byssal thread stalks (Cheung et al., 2004).

The ability to remain anchored to the substrate during predation events depends on the attachment strength of byssal threads. According to Côté (1995), byssal threads of mussels become more numerous, thicker and shorter in the presence of the crab *Cancer pagurus*. Stronger byssal attachment in predator-exposed mussels is significant after 24 h and doubles in strength after 4 days (Reimer and Tedengren, 1997). Furthermore, mussel movement can also be influenced by predator presence with increased movement towards clumping in *M. edulis* (Côté, 1995; Côté and Jelnikar, 1999). When moving to a new attachment site, mussels sever existing byssal threads (Wiegemann, 2005). Hence, any bundles left behind can be used as a proxy for mussel movement, with large numbers of abandoned bundles indicating a higher degree of locomotion (Ishida and Iwasaki, 2003). Furthermore,

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movement ability appears to be size dependent, with smaller mussels able to move more often than larger individuals (Wiegemann, 2005).

The goals of this study were to examine changes to byssal thread production and mussel movement in relation to mussel size and simulated risk of predation by exposure to effluent from the American lobster *Homarus americanus*, the rock crab *Cancer irroratus*, the sea star *Asterias rubens*, and injured conspecific mussels. Byssogenesis was measured by adhesive plaque areas, as well as number, strength, and diameter of threads. Mussel movement was quantified by the number of abandoned byssus bundles.

2. Materials and methods

2.1. Experimental setup

Mussels of 20–45 mm ($n = 90$) and 45–70 mm ($n = 90$) size classes were collected from the UNH Coastal Marine Laboratory Pier, New Castle, NH (43.071971° N, 70.711465° W). After manual removal of all epibionts, mussels were measured for length, depth and height using digital calipers (General Tools and Instruments, New York, NY, USA), weighed, labeled with queen bee tags (The Bee Works, Orillia, Ontario, Canada) and maintained in unfiltered flowing seawater at the UNH Coastal Marine Lab, New Castle, NH.

The rock crab, *C. irroratus*, and the sea star, *A. rubens* were collected from the UNH Coastal Marine Lab Pier, and the American lobster, *H. americanus* was obtained from the UNH Coastal Marine Lab. Additional mussels, whose posterior adductor muscles were cut with a scalpel immediately prior to the experiment, were used for the injured conspecifics treatment. Whole live predators and injured mussels (with a combined weight of 40 g per treatment, respectively) were separately soaked in 3.5-l containers filled with unfiltered, aerated sea water for 36 h to produce effluent to be used in the experimental setups. The control consisted of 3.5-l of unfiltered sea water, aerated for 36 h.

All byssal threads protruding from the shells were trimmed and mussels were placed individually into sixty 150-ml glass bowls (30 bowls with small mussels, 30 bowls with large mussels) that were randomly arranged in a sea water table. Each bowl was filled with sea water containing effluent from one of four predator treatments or with control seawater. The waterline of the seawater table was 1 cm below the top lip of the glass bowls to avoid mixing with treatment water and to keep temperatures of all bowls constant. After the experiment began, treatment bowls were static systems to avoid the addition of confounding variables such as agitation or water velocity, which have been shown to influence byssal thread production (Moeser et al., 2006; Young, 1985).

After 1.5, 3, 4.5, 6, 9 and 24 h, the number of byssal threads attached to the glass bowls was counted. Additionally, after 24 h, byssal threads were photographed under a dissecting microscope, numbers of abandoned byssus bundles were noted, and byssal thread attachment strength was measured using a dual range force sensor (Vernier Software and Technology, Beaverton, OR, USA). To test for attachment strength, a piece of monofilament line was secured around each mussel and onto the force sensor and a steady force was applied normal to the substrate until byssal thread failure occurred. The point of maximum force required (N) to break the threads was noted. Adhesive plaque areas and byssal thread widths at 1–1.5 mm from the adhesive plaque were measured using ImageJ (NIH). Trials were repeated three times using fresh mussels and predator treatments.

2.2. Data analysis

A two-way randomized complete block ANOVA, with trial as the blocking factor, was utilized to test the effects of mussel size and predator type on byssal thread counts, number of abandoned byssus bundles, time to thread production start, average adhesive plaque area, and average byssal thread diameter (SYSTAT, Richmond, CA, USA).

Mussel size was a fixed factor with two levels (small vs. large mussels), predator type was a fixed factor with five levels (crab, sea star, lobster, injured conspecific mussels, and control) and trial was a random factor with three levels. Significant differences between treatments were evaluated with Tukey's honest significant difference post hoc analysis of variance in SYSTAT. After byssal thread strength data were log transformed, a multiple linear regression was utilized (Microsoft Excel 2007).

3. Results

After 24 h, more functional byssal threads were present for both large and small mussels exposed to effluent from the predatory crab (average number 9.86 ± 1.16 S.E.) compared only to mussels in the injured conspecific treatment (average number 5.22 ± 1.16 S.E.), and not to any other treatment group (Fig. 1; $n = 34$ control, 35 lobster, and 36 crab, injured mussel and sea star, $p = 0.031$; Table 1). Small mussels (average number 2.72 ± 0.22 S.E.) formed and released more byssus bundles compared to large mussels (average number 0.37 ± 0.22 S.E.) ($n = 90$ small and 89 large, $p < 0.001$; Table 1). Exposure to effluent from predators or injured conspecifics did not influence the amount of byssus bundles released (n.s., $p = 0.903$; Table 1). Large mussels had greater average byssal thread diameters (average diameter 0.09 mm \pm 0.002 S.E.) ($n = 66$ small and 68 large, $p < 0.001$; Table 1) and greater average byssal thread plaque areas (average area 1.60 mm² \pm 0.08 S.E.) ($n = 65$ small and 68 large, $p < 0.001$; Table 1) than small mussels (average diameter 0.06 ± 0.002 S.E.) (average area 0.79 mm² \pm 0.08 S.E.). Largest average plaque areas were found during the second trial (1.41 mm² \pm 0.10 S.E.) when compared to the first (0.97 mm² \pm 0.10 S.E.) ($n = 43$ trial one, 46 trial two and 44 trial three, $p = 0.006$; Table 1).

Small mussels (average time 12.04 h \pm 1.17 S.E.) started producing byssal threads sooner than large mussels (average time 16.33 h \pm 1.25 S.E.) ($n = 78$ small and 72 large, $p = 0.014$; Table 1). Mussels exposed to effluent from injured conspecific mussels began producing byssal threads earlier (average time 10.24 h \pm 2.24 S.E.), compared to the control, (average time 18.64 h \pm 1.77 S.E.) (n.s., $p = 0.053$; Table 1) although the trend was not significant.

Using multiple regression, a 2.9% relative increase in byssal thread attachment strength was found with each additional byssal thread produced ($n = 134$, $p < 0.001$; Table 2), an increase in strength of 15% occurred with each 1 mm² increase in average byssal thread

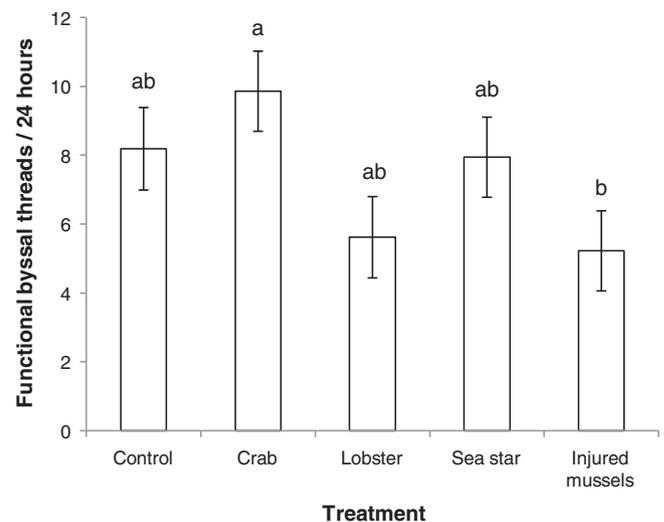


Fig. 1. Mean (\pm S.E.) number of functional byssal threads produced after 24 h for all mussels exposed to different predator treatments; $p = 0.031$. The characters above the error bars denote significant differences between the treatment means based on Tukey's honest significant difference post hoc analysis of variance.

Table 1

Results of 2-way randomized complete block ANOVA for functional byssal threads produced after 24 h (FBT), number of abandoned byssus bundles after 24 h (ABB), average byssal thread diameter after 24 h (BTD), average byssal thread plaque area after 24 h (BTPA), and time to start byssal thread production (TSBT), with trial as a blocking factor and mussel size and predator type as fixed factors (df = degrees of freedom, MS = mean square, F = value of the F -statistics, p = p -value).

| Source of variation | FBT | | | | BTD | | | | TSBT | | | |
|-------------------------------|------|--------|------|------|------|------|-------|--------|------|--------|------|-------|
| | df | MS | F | p | df | MS | F | p | df | MS | F | p |
| Trial | 2 | 97.38 | 2.0 | 0.14 | 2 | 0.00 | 0.45 | 0.64 | 2 | 140.44 | 1.33 | 0.27 |
| Mussel size | 1 | 0.00 | 0.00 | 0.99 | 1 | 0.03 | 96.78 | <0.001 | 1 | 662.99 | 6.26 | 0.01 |
| Predator | 4 | 132.86 | 2.72 | 0.03 | 4 | 0.00 | 1.21 | 0.31 | 4 | 254.14 | 2.40 | 0.053 |
| Predator \times mussel size | 4 | 22.03 | 0.45 | 0.77 | 4 | 0.00 | 1.32 | 0.27 | 4 | 107.64 | 1.02 | 0.40 |
| Error | 165 | 48.77 | | | 122 | 0.00 | | | 138 | 106.0 | | |

| Source of variation | ABB | | | | BTPA | | | |
|-------------------------------|------|--------|-------|--------|------|-------|-------|--------|
| | df | MS | F | p | df | MS | F | p |
| Trial | 2 | 4.00 | 0.90 | 0.41 | 2 | 2.17 | 5.34 | 0.01 |
| Mussel size | 1 | 246.57 | 55.36 | <0.001 | 1 | 21.35 | 52.42 | <0.001 |
| Predator | 4 | 1.16 | 0.26 | 0.90 | 4 | 0.80 | 1.97 | 0.10 |
| Predator \times mussel size | 4 | 4.57 | 1.03 | 0.40 | 4 | 0.37 | 0.90 | 0.46 |
| Error | 167 | 4.45 | | | 121 | 0.41 | | |

plaque area ($p < 0.001$; Table 2), a 2.3% increase in thread strength resulted with each 0.01 mm increase of average thread diameter ($p = 0.039$; Table 2), while large mussels produced a 16.9% stronger attachment than small mussels ($p = 0.010$; Table 2). Conversely, a relative decrease in byssal thread strength was observed with increased byssus bundles shed, although it was not significant (n.s., $p = 0.073$; Table 2). A trend of increased attachment strength was found with exposure to crustacean predators and injured conspecifics compared to the control treatment (n.s., Table 2). Conversely, a relative decrease in strength was found with exposure to effluent from sea stars, although it was not significant (n.s., $p = 0.557$; Table 2).

4. Discussion

Mussels face a variety of active predators which has resulted in the evolution of predator-specific defense mechanisms capable of rapid response, including an increase in byssogenesis which translates into a stronger attachment and an increase in movement towards clumping to avoid predation (Beadman et al., 2003; Côté, 1995; Côté and Jelnikar, 1999). In addition to direct exposure and contact with predators, water borne chemical cues from live predatory invertebrates are also known to result in dramatic changes to the behavior and morphology of intertidal mussels (Côté, 1995; Côté and Jelnikar, 1999; Ishida and Iwasaki, 2003; Leonard et al., 1999). Testing mussel responses against effluent from one echinoderm and two crustacean predators, we found increased byssal thread production for all mussel

Table 2

Results of multiple regression assessing relative changes in byssus attachment strength in relation to average byssal thread plaque area, average byssal thread width, mussel size, the addition of individual byssal threads, number of abandoned byssus bundles, and exposure to effluent from lobster, crab, and sea star predators and injured conspecific mussels; $p < 0.001$, $r^2 = 0.70$. Equation: $\log(\text{attachment strength}) = B_0 + B_1 \cdot \text{plaque area} + B_2 \cdot \text{thread width} + B_3 \cdot \text{mussel size} + B_4 \cdot \text{byssal thread} + B_5 \cdot \text{byssus bundle} + B_6 \cdot \text{lobster} + B_7 \cdot \text{crab} + B_8 \cdot \text{sea star} + B_9 \cdot \text{injured conspecific}$.

| | Coefficients | Standard error | p -value | Exponentiated coefficients |
|---------------------|--------------|----------------|------------|----------------------------|
| Intercept | -1.00681 | 0.09125 | <0.001 | 0.36538 |
| Plaque area | 0.13961 | 0.03859 | <0.001 | 1.14982 |
| Thread width | 2.25500 | 1.08264 | 0.039 | 1.02281 |
| Mussel size | 0.15587 | 0.05936 | 0.010 | 1.16867 |
| Byssal thread | 0.02883 | 0.00263 | <0.001 | 1.02925 |
| Byssus bundle | -0.01770 | 0.00978 | 0.073 | 0.98245 |
| Lobster | 0.07319 | 0.05343 | 0.173 | 1.07593 |
| Crab | 0.02441 | 0.05219 | 0.641 | 1.02471 |
| Sea star | -0.03172 | 0.05390 | 0.557 | 0.96878 |
| Injured conspecific | 0.05058 | 0.05799 | 0.385 | 1.05189 |

sizes when exposed to effluent from the crab, *C. irroratus*, but not to sea star or lobster effluent. Similar results for *M. edulis* exposed to the scent of crab predators have been reported previously (Côté, 1995; Leonard et al., 1999; Reimer and Harms-Ringdahl, 2001; Reimer and Tedengren, 1997). Because crabs must remove mussels from the substrate prior to consumption, producing more threads and increasing the strength of attachment reduce the chances of dislodgement for the mussel, and increase likelihood of survival (Hughes and Seed, 1995; Lin, 1991). Even though mussels did not produce increased numbers of byssal threads in response to effluent from lobster predators, we did find a trend of increased attachment strength compared to the control treatment. We attribute the difference in byssus response to differences in handling by the predator. Both crabs and lobsters are shell crushing predators; however, crabs employ a wider range of shell opening tactics and are quicker and more dexterous than lobsters (Moody and Steneck, 1993).

Allen et al. (1976) found that adhesive plaque size was highly variable among mussels and that plaques with the smallest area had the strongest byssal attachment due to thicker adhesive layers. Côté (1995) hypothesized that mussels exposed to predators would be expected to reduce plaque area which would presumably increase attachment strength as suggested by Allen et al. (1976). The present study, however, found that increasing plaque area resulted in a stronger byssal attachment. Despite trends suggesting that effluent from crustacean predators and injured conspecifics resulted in a stronger byssal attachment compared to controls, plaque area itself was not influenced by predator presence in this study. However, differences in plaque area occurred between the first and second trial of the experiment, which are puzzling since mussels and predators in all treatments were exposed to the same conditions before and during all trials.

Reduced byssogenesis by mussels exposed to effluent from injured conspecifics may be attributed to a "clamming up" response of mussels when a predatory threat is imminent (Czarnoleski et al., 2010; Ishida and Iwasaki, 2003). During byssal thread formation, the mussel's soft foot is exposed to predators, drawing visual attention and enabling chemical cues to dissipate in the water (Ishida and Iwasaki, 2003). Closed valves and feet contained within shells reduce the chances of predators detecting the presence of mussels (Czarnoleski et al., 2010; Ishida and Iwasaki, 2003). Ishida and Iwasaki (2003) suggest that reduced movement and byssal thread production are protective behaviors, by which solitary mussels provide predators with fewer visual and chemical cues.

Although exposure to injured mussels resulted in lowest byssal thread counts, we found that mussels began depositing threads sooner when exposed to chemical signals from damaged conspecifics as

compared to the control group, which support findings by Czarnoleski et al. (2010). Fässler and Kaiser (2008), on the other hand, found that mussels exposed to effluent from the crab, *Carcinus maenas* feeding on mussels produced more byssal threads compared to mussels in a control treatment containing unaltered sea water. Similarly, Cheung et al. (2004, 2009) report increases in byssal thread production in the green-lipped mussel, *P. viridis*, when exposed to effluent from injured conspecifics.

In this experiment, time to begin byssal thread production could have been delayed due to potential reduced dissolved oxygen levels since treatments were not aerated after the study began. Other variables such as increased agitation and water velocity have been shown to influence byssal thread production rates and were avoided in this study to focus solely on influences of predators and injured conspecifics (Mooser et al., 2006; Young, 1985). Studies by Wang et al. (2010) have shown that green-lipped mussels (*P. viridis*) exhibit decreases to overall byssus performance in environments with reduced oxygen levels, even though the presence of predators still resulted in increased byssal thread production at all oxygen levels.

While effluent of damaged conspecifics may signal predation risk, it also could indicate non-predation mortality (Cheung et al., 2004). For example, mussels experience strong hydrodynamic forces from breaking waves which require a strong attachment to the substrate to prevent dislodgement (Bell and Gosline, 1997). Studies suggest that *M. edulis* exposed to high wave action deposit fewer threads and possess an overall weaker attachment compared to mussels in protected sites which produce more threads with an overall stronger attachment (Garner and Litvaitis, 2013; Mooser et al., 2006), which is contrary to previous work (Bell and Gosline, 1997; Carrington, 2002). The decreased thread production at sites with high wave activity could be attributed to the inability of mussels to extend their fleshy foot to the substrate, a process that is necessary for thread deposition to occur (Mooser et al., 2006). The presence of predators, which are known to inhabit sheltered sites in the Gulf of Maine, could be the reason behind the increased threads produced in the low wave energy environment (Garner and Litvaitis, 2013; Leonard et al., 1999). Although the results are not significant in this study, the trend of increased attachment strength with exposure to chemical cues from injured conspecific mussels suggests that mussels produced fewer, but stronger threads over 24 h. Such a response then not only reduces predation risk but also non-predation mortality due to dislodgement which occurs upon exposure to high wave action. Field studies investigating the presence of predators and conspecifics at exposed and protected sites would be necessary to further tease apart the factors which influence the attachment strength and byssal thread production in blue mussels.

Prior studies examining predation of mytilid mussels by the sea stars, *Coscinasterias acutispina*, *A. rubens* and *Heliaster helianthus*, suggest that increasing byssal thread numbers and attachment strength has little effect on preventing predation, and that the presence of sea stars does not elicit changes in byssogenesis (Caro et al., 2008; Ishida and Iwasaki, 2003; Reimer and Harms-Ringdahl, 2001). Mussels are capable of differentiating between chemical cues of various predator types and accordingly elicit a differential response. Specifically, predators that employ crushing methods after removing mussels from the substrate (i.e., crabs) affect byssal thread strength, resulting in improved attachment. On the other hand, predators that pull apart valves (i.e., sea stars) do not affect attachment strength (Reimer and Harms-Ringdahl, 2001; Reimer and Tedengren, 1997). Our results further support these findings. Because sea stars do not remove mussels from the substrate prior to consumption, but rather pry open the valves to digest the soft tissues in situ, increased attachment strength does not provide an effective defense. It is possible that mussels respond to sea star predators by increasing the size of their adductor muscles rather than by increasing byssal attachment strength (Freeman, 2007; Reimer

and Harms-Ringdahl, 2001). However, we did not quantify changes in adductor muscles in our study.

Previous studies have shown that within the first few hours of exposure to a predation threat, mussels initially reduce movement, but after a day they actively form aggregations, seek structural refuges and attach firmly (Reimer and Tedengren, 1997; Reimer et al., 1995). In dense mussel beds in the intertidal or subtidal environment, movement is limited because individuals are retained by a network of byssal threads from neighboring mussels, which presumably also limits the degree to which mussels can be dislodged by predators and wave action (Bell and Gosline, 1997; Côté and Jelnikar, 1999). We found no relationship between the presence of predators or injured conspecifics and movement of mussels as indicated by abandoned byssus bundles.

Small mussels formed and abandoned more byssus bundles than large mussels, which is an indication of increased movement. Support for our observations also comes from studies showing small mussels capable of changing their byssal attachment sites and moving longer distances than large mussels (Uryu et al., 1996; Wiegemann, 2005). Additionally, small mussels formed byssal threads sooner than large mussels. It is possible that large mussels invest their energy into the production of stronger attachments rather than into the continued formation and release of threads.

Alternatively, size-related differences of byssal attachment and movement could be due to an apparent size refuge from crab predators for individuals above 40 mm shell length (Davies, 1966). The small size class used in this study was 20–45 mm, which is the target size range for predatory crabs. Mussels within that size range suffer exceedingly high mortality from crabs (Elner and Hughes, 1978; Seed, 1976). Hence, the observed increase in mobility may be due to mussels seeking refuge in aggregations, which have been shown to reduce the rate of predation (Côté and Jelnikar, 1999; Reimer and Tedengren, 1997).

Our results and those of other studies suggest that *M. edulis* are capable of exhibiting inducible defenses based on the presence of an array of predators or injured conspecifics. These responses are varied and depend on the particular environment, predator type, and foraging behavior of the predator. In the intertidal environment, which is a dynamic system of predators and prey, mussels are presumably able to alter their movement patterns and byssogenesis in response to a wide variety of predators with different attack modes, although further field studies are necessary to validate those claims.

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