Predicting wave dislodgment of mussels: variation in attachment strength with body size, habitat, and season

Heather L. Hunt*, Robert E. Scheibling

Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada

ABSTRACT: Breaking waves impose large hydrodynamic forces which may dislodge mussels and other organisms living on exposed rocky shores. We examined the effect of variation in attachment strength with size, habitat and season on the predicted probability of wave dislodgment of mussels *Mytilus trossulus* and *M. edulis* on an exposed shore on the Atlantic coast of Nova Scotia, Canada. Mussels on this shore are exposed to maximum significant wave heights of at least 7 to 9 m each winter and to maximal water velocities of at least 12 m s\(^{-1}\). We used Denny’s (1995) mechanistic approach to predict probabilities of dislodgment from measures of attachment strength of mussels. Predicted probabilities of dislodgment indicated that mussels of 10 to 25 mm shell length are vulnerable to dislodgment by wave velocities of >7 m s\(^{-1}\). As a result of variation in dislodgment forces, probabilities of dislodgment did not differ consistently between tidepools and emergent rock, or with mussel size. Attachment strength increased from July to February as mussels were exposed to stronger wave action, reducing the probability of dislodgment by a given water velocity. This study indicates that knowledge of patterns of change in attachment strength are necessary for prediction of probabilities of dislodgment of mussels.

KEY WORDS: Disturbance · Wave forces · Mussels · Tide pools · Emergent rock · Seasonal variation · *Mytilus*
in pressure between the top and bottom of a mussel and act perpendicular to the direction of water motion, can potentially dislodge mussels (Denny 1987).

In addition to the hydrodynamic forces it experiences, a mussel’s risk of dislodgment varies with its strength of attachment to the substratum. Attachment strength of mussels depends on the number of byssal threads anchoring them to the substratum (Bell & Gosline 1997). These threads decay and must be replaced to maintain a constant attachment strength, which can be metabolically costly (Hawkins & Bayne 1985). Mussels respond to their flow environment by altering their attachment strength. In the laboratory, water agitation increases the number of byssal threads produced (Young 1985). In the field, attachment strength varies with location in a mussel bed (Witman & Suchanek 1984, Bell & Gosline 1997), and, seasonally with wind conditions (Price 1982). Because the attachment strength of mussels can vary seasonally, temporal variation in attachment strength must be incorporated in any assessment of dislodgment risk of mussels (Denny 1995).

Predicting the dynamics of communities on wave-exposed shores requires consideration of losses due to wave dislodgment. Denny (1995) developed a mechanistic approach for calculating the probability of wave dislodgment of an organism. In this study, we use Denny’s method to examine the effect of seasonal variation in water velocity and attachment strength on the probabilities of wave dislodgment of mussels (predominantly *Mytilus trossulus*, with some *M. edulis* and hybrids of the 2 species) of different sizes in tidepools and on emergent rock on a wave-exposed shore in Nova Scotia, Canada. Tidepools, apart from serving as a refuge from many of the stressful environmental conditions on emergent rock during low tide (Metaxas & Scheibling 1993), may provide some protection from wave forces because the overlying water column reduces the maximal horizontal water velocity experienced by benthic organisms (Denny 1995).

**METHODS**

This study was conducted on an exposed rocky shore at Cranberry Cove (44° 28’ N, 63° 56’ W) near Halifax, Nova Scotia, Canada. The shore is composed of granite platforms and outcrops with occasional large boulders (glacial erratics). There are numerous tidepools in irregular depressions along the shore, ranging from a few decimeters to over 10 m in maximum dimension. The shore is exposed to large southerly swells in fall and winter. We obtained records of significant wave heights (average height of the largest one third of all waves measured) for July 1994 to March 1998 from a buoy at the mouth of Halifax Harbour (44.483° N, 63.417° W, depth 56.7 m) ~40 km from the study site (Department of Fisheries and Oceans, Canada, unpubl. data). We measured maximum wave forces in tidepools and on emergent rock from November 1994 to April 1995 using wave meters based on the design of Bell & Denny (1994). Each meter consists of a practice golf ball attached to a spring in a plastic housing which is anchored to the substratum. The extension of the spring was converted to water velocity (Bell & Denny 1994). Three wave meters were deployed continuously in each habitat, and were checked and reset at 10 to 43 d intervals.

We measured the attachment strength of individual mussels *Mytilus* spp., at or near the edge of patches, as the force required to dislodge them from the substratum. In July, August, and November 1997, and February 1998, we measured dislodgment forces for 7 to 10 mussels from each of 2 (November), 3 (August, February), or 6 (July) tidepools and plots of emergent rock. Dislodgment force was measured perpendicular to the substratum because mussels are most strongly affected by hydrodynamic forces acting in this direction (Denny 1987). A thin multifilament fishing line was tied around each mussel and attached to a 250 or 2000 g spring scale (Ohaus). The dislodgment force was measured on the scale by pulling it at a right angle to the substratum until the mussel was detached. The shell length (SL, mm) of each detached mussel was measured and converted to cross-sectional, planform area (A, cm²) using the relationship: \( A = 0.003 \times SL^{1.833} \) (Hunt & Scheibling 1998), which approximates the cross-sectional area as an ellipse, with shell height and width as the axes. We were not able to measure dislodgment force for mussels in the center of patches, or for individuals <5 mm SL, because of difficulties in tying the line around these individuals. Because the dislodgment force of mussels in the center of patches is generally lower than that of individuals at the edge (Witman & Suchanek 1984), our measurements may overestimate the average dislodgment force of mussels in patches.

To examine the importance of wave dislodgment as a cause of loss and redistribution of mussels, we used Denny’s (1995) method to calculate probabilities of wave dislodgment using the measured dislodgment forces and estimates of hydrodynamic forces imposed on mussels. Firstly, the data relating dislodgment force \( f_d \) to \( A \) were fit to an allometric model: \( f_d = j \times m \times A^{q} \), where \( f_d \) is the predicted dislodgment force and \( j, m, q \) are constants fit to the power curve for each date using a nonlinear, simplex iterative procedure (SYSTAT: Wilkinson 1992). If the intercept \( j \) was negative, we fit a new curve with zero \( y \) intercept. To obtain relative dislodgment forces, each measured force was normalized by dividing it by the dislodgment force predicted by...
the allometric model. The variation in normalized dislodgment forces allows the estimation of the probability that a randomly selected mussel will have an attachment strength exceeding a given value. The normalized dislodgment forces \( f_i = f_i/f_p \) were ranked in ascending order and the probability \( (p) \) that an individual had a normalized dislodgment force less than a force of rank \( i \) was estimated as: \( p (f_i < f_p) = i/(n + 1) \), where \( n \) is the total number of individuals sampled. A mathematical description of the cumulative probability distribution of normalized dislodgment force \( \{f_i\} \) was then obtained by fitting a modified Weibull model: 

\[ p(f_i) = \exp\left\{-\left(\frac{a - bf_i}{(a - bc)}\right)^{1/b}\right\} \],

where \( a, b, \) and \( c \) are constants (Table 1). The Weibull model provided a good estimate of the cumulative probability distribution of the normalized dislodgment forces for each sampling date \( (r^2 > 0.99) \), Table 1.

We then predicted the hydrodynamic lift force imposed on mussels based on the relationship between lift \( (L) \) and maximal water velocity 

\[ (U): L = \left(\frac{1}{2\rho U}\right)\pi C_f A \]

where \( \rho \) is the density of seawater \( (1025 \text{ kg m}^{-3}) \), \( C_f \) is the coefficient of lift, and \( A \) is the cross-sectional area of a mussel \( (Denny 1987) \). Denny \( (1987) \) estimated that \( C_f \) for M. californianus is 0.88. Because the relationship between shell height, length, and width of M. trossulus is similar to that of M. californianus, 0.88 is also a reasonable estimate of the lift coefficient for M. trossulus \( (Bell \& Gosline 1997) \). Using this equation, we calculated lift forces imposed on mussels of 4 sizes \( (10, 15, 20, \text{ and } 25 \text{ mm SL}) \), which correspond to cross-sectional areas of \( 0.20, 0.43, 0.73, \text{ and } 1.1 \text{ cm}^2 \) respectively over a range of water velocities. Very few mussels at Cranberry Cove exceed 20 mm SL \( (Hunt \& Scheibling 1995, 1998) \). We did not calculate probabilities of dislodgment for mussels \( \leq 5 \text{ mm} \) because we did not have measurements of dislodgment forces for them. To estimate the probability of dislodgment of mussels of each size by water velocities of up to \( 15 \text{ m s}^{-1} \), we normalized the calculated lift force for each mussel size by dividing it by \( f_p \) for a mussel of that size, and used this as \( f_i \) in the Weibull model to obtain the probability of dislodgment.

### RESULTS

Significant wave heights recorded at a nearshore buoy were highest in fall and winter storms, reaching \( 9.4 \text{ m} \) in February 1995, \( 7.0 \text{ m} \) in December 1995, \( 8.7 \text{ m} \) in September 1996, and \( 8.2 \text{ m} \) in February 1998 (Fig. 1). Maximum wave-force meters deployed during winter 1994/95 recorded water velocities up to \( 12 \text{ m s}^{-1} \) (Fig. 2). Maximum water velocities were greater on emergent rock than in tidepools \( (F_{1,12} = 5.9, p = 0.032) \) and differed among dates \( (F_{3,12} = 15.4, p = <0.001) \); there was no interaction between habitat and date \( (F_{3,12} = 0.6, p = 0.69) \).

The force required to dislodge mussels Mytilus spp. ranged from 0.5 to \( 18 \text{ N} \), increasing with increasing mussel size (Fig. 3). ANCOVA showed that the relationship between dislodgment force and shell cross-sectional area differed between habitats and among months (Table 2). Therefore, we fitted the data to the allometric model separately for each habitat for each month. The relationship between dislodgment force and shell area

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Constants from cumulative probability distribution</th>
<th>( a )</th>
<th>( b )</th>
<th>( c )</th>
<th>( r^2 )</th>
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<td>July</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td>August</td>
<td></td>
<td></td>
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<td></td>
<td></td>
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<tr>
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<td></td>
<td>0.71</td>
<td>0.31</td>
<td>0.81</td>
<td>0.996</td>
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<tr>
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<td></td>
<td>0.20</td>
<td>-0.16</td>
<td>0.79</td>
<td>0.998</td>
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<tr>
<td>November</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tidepool</td>
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<td>0.63</td>
<td>0.991</td>
</tr>
<tr>
<td>Emergent Rock</td>
<td></td>
<td>-0.07</td>
<td>-0.49</td>
<td>0.74</td>
<td>0.992</td>
</tr>
<tr>
<td>February</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>0.08</td>
<td>0.73</td>
<td>0.999</td>
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Fig. 1. Maximum daily significant wave heights (average height of the largest one-third of all waves measured) for July 1994 to March 1998 from a buoy at the mouth of Halifax Harbour \( (44.483°N, 63.417°W, \text{ depth } 56.7 \text{ m}) \) – 40 km from the study site.
was exponential, with an exponent ranging from 0.53 to 3.51. Predicted dislodgment forces were lower in tidepools than on emergent rock for small mussels (ca 0.2 to ≤0.6 cm² shell area) but greater in tidepools than on emergent rock for the largest mussels. In tidepools, predicted dislodgment forces of mid-size mussels increased over time, while those of the smallest mussels remained relatively constant. On emergent rock, predicted dislodgment forces of mid-size mussels were similar in July and August, but greater in November and February than in the summer. These changes in dislodgment force (attachment strength of mussels) between sampling dates may have been a response to increased wave action between the measurement dates (Fig. 1). The maximum significant wave heights recorded at a wave buoy in the month preceding the July measurement and between the July and August measurements were <2 m, although higher waves were observed for at least 1 d in August when the wave buoy was disabled by a storm (T. Balch, Dalhousie University, pers. comm.). The maximum significant wave heights in the month preceding the November measurement were >2 m on 19 d and >4 m on 2 d, while those preceding the February measurement were >2 m on 20 d and >4 m on 6 d.

Predicted lift forces increased with increasing water velocity and mussel size (Fig. 4). For example, lift forces on 10 and 25 mm mussels were 0.3 and 1.8 N respectively at 6 m s⁻¹, and 2.1 and 11.1 N at 15 m s⁻¹. On average, velocities in tidepools were 87% of those on emergent rock at a given time, as indicated by the double x-axes in Figs. 4 & 5. Because of increasing lift forces, probabilities of dislodgment also increased with increasing water velocity.

### Table 2. *Mytilus*. Analysis of covariance of dislodgment force (N) of mussels. Factors are habitat (tidepools and emergent rock) and month (July, August, November, February) and the covariate is shell area (cm²). Sample size = 30 mussels per habitat (data from extra tidepools and plots excluded for balance), August and February, and 14 in tidepools and 17 on emergent rock in November. *p < 0.05; **p < 0.01; ***p < 0.001

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
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<td>17.0</td>
<td>0.001**</td>
</tr>
<tr>
<td>Month</td>
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<td>0.13</td>
<td>5.0</td>
<td>0.002**</td>
</tr>
<tr>
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<td>&lt;0.001</td>
<td>&lt;0.001***</td>
</tr>
<tr>
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<td>1.1</td>
<td>0.35</td>
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<td>4.2</td>
<td>0.04*</td>
</tr>
<tr>
<td>Month × Shell area</td>
<td>3</td>
<td>0.11</td>
<td>4.3</td>
<td>0.01*</td>
</tr>
<tr>
<td>Habitat × Month × Shell area</td>
<td>3</td>
<td>0.02</td>
<td>0.8</td>
<td>0.51</td>
</tr>
<tr>
<td>Residual</td>
<td>195</td>
<td>0.03</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### Fig. 2. Mean (+1 SD) maximum water velocities (m s⁻¹) in tidepools and on emergent rock (averaged across 1 to 3 wave meters per habitat) at Cranberry Cove between November 1994 and April 1995. No measurements were taken in tidepools during the period February 10 to March 12.

### Fig. 3. *Mytilus*. Relationship between force (N) required to dislodge a mussel and mussel cross-sectional area (cm²) in tidepools and on emergent rock in July (n = 60 per habitat), August (n = 30), and November (n = 14 in tidepools, n = 17 on emergent rock) 1997, and February 1998 (n = 30). Lines (dashed = tidepools; continuous = emergent rock) indicate dislodgment force predicted by the allometric model (r² = 0.85 and 0.78 on tidepools and in emergent rock respectively in July; r² = 0.81 and 0.88 respectively in August, 0.83 and 0.87 respectively in November, 0.86 and 0.91 respectively in February).
velocity (Fig. 5). Probabilities of dislodgment at a given water velocity generally were greater in tidepools than on emergent rock, except in August when larger mussels (20 and 25 mm) were more likely be dislodged on emergent rock than in tidepools at velocities >10 m s\(^{-1}\) (Fig. 5). Incorporating the between-habitat difference in water velocity reduced the differences in probabilities of dislodgment at a given time between tidepools and emergent rock. Thus, probabilities of dislodgment were predicted to be greater in tidepools than on emergent rock in about half of the cases, but greater on emergent rock or similar between habitats in the others.

Predicted probabilities of dislodgment suggest that mussels 10 to 25 mm SL are vulnerable to dislodgment by water velocities of >7 m s\(^{-1}\) (Fig. 5). For the attachment strengths we recorded, we would predict that maximal water velocities of 6 m s\(^{-1}\) (5.2 m s\(^{-1}\) in tidepools) would dislodge <9% of mussels in either habitat in any of the 4 mo sampled. By comparison, maximal water velocities of 9 m s\(^{-1}\) on emergent rock (7.8 m s\(^{-1}\) in tidepools) were predicted to dislodge 10 to 15% of large (20 to 25 mm SL) mussels on emergent rock and 12 to 35% in tidepools in July, but only 2 to 5% in February. Maximal water velocities of 12 m s\(^{-1}\) (10.4 m s\(^{-1}\) in tidepools) were predicted to dislodge 40 to 51% and 41 to 70% of large mussels on emergent rock and in tidepools respectively in July, and 11 to 15% of large mussels in February. Measurements of maximal water velocities at Cranberry Cove in 1995 (Fig. 2) can be used to examine the wave conditions (Fig. 1) under which different probabilities of dislodgment are predicted.

The relationship between mussel size and probability of dislodgment, which depends on the relationships between dislodgment force and size, and between lift force and size, varied with habitat and date (Fig. 6). Probability of dislodgment increased with increasing mussel size on emergent rock in August, November (only at velocities ≥10 m s\(^{-1}\)), and February, but decreased with mussel size in tidepools in February.

![Fig. 4. Mytilus. Relationship between the hydrodynamic force imposed on a mussel (lift) and maximal water velocity for mussels of 10, 15, 20, and 25 mm SL. The different scales for water velocity indicate that, at a given time, water velocities in tidepools are 87% of those on emergent rock](image)

![Fig. 5. Mytilus. Relationship between probability of dislodgment and water velocity in July, August, and November 1997 and February 1998 for mussels of 10, 15, 20, and 25 mm SL in tidepools (TP) and on emergent rock (ER). The different scales for water velocity indicate that, at a given time, water velocities in tidepools are 87% of those on emergent rock](image)
SL are vulnerable to dislodgment by water velocities at Cranberry Cove suggest that individuals of wave dislodgment of mussels particularly during fall and winter storms. Our predictions of wave dislodgment force, at Cranberry Cove during the winter of 1995 were comparable to those recorded by Blanchette (1997), with the same type of maximum wave force recorder, at an exposed shore in Oregon. The yearly average significant wave height at Cranberry Cove from 1995 to 1997 was 1.47 m, lower than the average (1.9 to 2.5 m) recorded at a number of sites along the west coast of North America (Denny 1995). However, *M. trossulus* and *M. edulis* have a much weaker byssal attachment (per unit cross-sectional area) than *M. californianus* (Harger 1970, Witman & Suchanek 1984, Bell & Gosline 1997), the dominant mussel on the west coast.

To understand how dislodgment by waves is influenced by mussel size, habitat, and season, we need to examine how these factors affect hydrodynamic forces and attachment strength. The hydrodynamic forces experienced by mussels increase with increasing mussel size (Denny 1987), and depend on whether an individual is solitary or in a patch (Bell & Gosline 1997), and on its position within a patch (Witman & Suchanek 1984). The force required to dislodge a mussel depends on the number of anchoring byssal threads (Bell & Gosline 1997). In our study and others (Harger 1970, Witman & Suchanek 1984), attachment strength increased with increasing mussel size. However, lift forces often increased faster with size than did attachment strength, resulting in a greater probability of dislodgment for larger mussels than smaller ones. The relationship between probability of dislodgment and mussel size varied with habitat and season. In contrast, Denny (1995) found that the attachment strength of *Mytilus californianus* increased faster than the area...
exposed to flow, resulting in large mussels being somewhat less susceptible to disturbance than small mussels. Bell & Gosline (1997) found that tenacity (dislodgment force/unit area) of *M. californianus* and *M. trossulus* was relatively constant with mussel size for individuals of 15 to 50 mm SL.

Because mussels in a patch are tightly bound together by their byssal threads, an individual mussel’s probability of dislodgment will be influenced by its neighbours, particularly for very small mussels. Dislodgment by waves of 1 or a few mussels in a patch would render the remaining mussels more vulnerable to hydrodynamic forces acting parallel to the substratum, drag and the acceleration reaction, and could lead to the dislodgment of many other mussels in the patch (Denny 1987). Wave action also may interact with other causes of mortality. For example, in an experiment examining whelk predation (Hunt & Scheibling 1998), predation could not entirely account for the decrease in mussel cover and abundance which occurred in unmanipulated plots. We attributed this discrepancy to wave action, as dislodgment of the shells of mussels eaten by predators would remove recruits associated with the drilled shells and weaken the surrounding mussel matrix.

We found seasonal variations in dislodgment forces and, therefore, in probabilities of dislodgment of mussels by a given water velocity. Similarly, Price (1980) found a seasonal cycle of attachment strength of *Mytilus edulis* in South Wales, UK, with a maximum in September and a minimum in May. Increases in the average attachment strength of a mussel population could result from the dislodgment of the most weakly attached individuals as well as from increases in the number of byssal threads produced. However, dislodgment of weakly attached individuals would result in a substantial shift in mean tenacity only if a large fraction of individuals were dislodged (Denny 1995). Price (1982) found that attachment strength decreased after 1 mo of weak wave action, which could only result from a decrease in the number of byssal threads. Seasonal variation in attachment strength may counteract seasonal changes in wave action to dampen any seasonality in the probability of wave dislodgment. For example, we estimate that <2% of 20 mm mussels on emergent rock in August (<6% in tidepools) were dislodged during the storm on September 29, 1997, when the significant wave height reached 3.9 m, and <7% of those on emergent rock in February (<10% in tidepools) were dislodged during the storm on February 25, 1998, when the significant wave height reached 8.2 m (Figs. 1 & 5).

Between-habitat differences in the probability of dislodgment of mussels at our site varied over time as a result of variations in dislodgment forces. Therefore, although wave forces were higher on emergent rock than in tidepools, probability of dislodgment did not necessarily mirror this pattern. We do not understand the factors influencing variation in the attachment strength of mussels well enough to be able to explain this temporal variation in between-habitat differences.

This type of mechanistic approach to prediction of probabilities of wave dislodgment (from Denny 1995) is powerful because it allows prediction of rates of disturbance. However, for organisms like mussels, whose dislodgment force is not constant, variation in attachment strength can affect relative probabilities of dislodgment between times, habitats, and sizes of individuals. Probability of dislodgment cannot be predicted from knowledge of hydrodynamic forces alone. We still have much to learn about the factors that control attachment strength. The mechanisms and response time of varying attachment strength in accordance with seasonal changes in wave action require further investigation.

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