

Seasonal variation in the attachment strength of blue mussels: Causes and consequences

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Abstract

The midintertidal zone of temperate rocky coasts is often dominated by mussels that form dense beds and exclude other primary space holders. The rate at which storms remove mussels from their substrate consequently has a controlling influence on intertidal community structure. The rate of disturbance by waves can be predicted mechanistically by comparing the attachment strength of an organism to the force it encounters. One simplifying assumption often implemented with this approach is that organismal strength is temporally constant. This study demonstrates that such an assumption is not valid for *Mytilus edulis* in Rhode Island, where byssal attachment strength (tenacity) increases twofold in winter compared to summer. Time series analysis of monthly samples (1998–2000) indicates tenacity generally tracks seasonal fluctuations in wave height, which suggests that mussels sense and respond to changes in their flow environment. However, the ability of mussels to respond to wave climate is not precise; during September and October (hurricane season), mussels remain weakly attached and are prone to major mortalities. Mussel reproductive condition also displays seasonal cycles, peaking 3–4 months after attachment strength. This suggests a possible energetic constraint on the ability of mussels to respond to their flow environment, as mussels trade byssal thread production for gonad development. This study demonstrates that accurate predictions of disturbance events must consider not only a storm's magnitude, but its timing relative to the cycle in attachment strength. Given the recent shift to increased hurricane activity in the North Atlantic, it is likely that mussels will begin to suffer more frequent and more severe disturbances compared to those that occurred during 1971–1994.

Investigations of the rocky intertidal zone have made important contributions to our understanding of how disturbance and patch dynamics influence nonequilibrium communities (e.g., Menge 1976; Lubchenco and Menge 1978; Paine and Levin 1981; Sousa 1985). Disturbance in the rocky intertidal zone is often dominated by a single physical factor, the hydrodynamic forces generated by breaking waves. In recent years, a number of studies have detailed the mechanisms by which moving water interacts with intertidal plants and animals (e.g., Denny et al. 1985; Carrington 1990; Gaylord et al. 1994; Denny 1995), contributing to the development of a mechanistic approach to the prediction of disturbance in marine communities by Denny (1995). Denny's six-step approach couples wave statistics and hydrodynamics with measurements of organismal attachment strength to predict disturbance as a function of time and the waviness of the sea offshore. Preliminary tests of Denny's approach are promising; it correctly predicts the survivorship of a variety of organisms along an exposure gradient, the size of wave-swept algae, and the percentage of mussels dislodged from beds during winter storms (Gaylord et al. 1994;

Denny 1995; Blanchette 1997). Modifications to this mechanistic approach have been suggested recently (Bell 1999; Denny 1999; Gaylord 1999, 2000), and more stringent tests of the approach are currently underway (M. Denny pers. comm.).

The mechanistic approach allows for the prediction of disturbance in populations exposed to a wave climate that may vary seasonally, annually, or over even longer time periods. Indeed, long-term variation has been observed for the waviness of the sea offshore, and the trend is generally toward increasing wave height. For example, the mean wave height in the North Sea has increased since 1950 at a rate of about 2% per year (Bacon and Carter 1991; Hoozemans and Wiersma 1992) and may be correlated with regional atmospheric pressure gradients (Bacon and Carter 1993). On the west coast of North America, years when large wave heights were recorded coincide with strong El Niño–Southern Oscillation (ENSO) events (Seymour et al. 1984; Seymour 1996). The frequency and severity of ENSO events have increased dramatically in recent times (Trenberth 1993; Wellington and Dunbar 1995), which suggests a concomitant increase in the severity of the wave climate. In the North Atlantic, the level of hurricane activity during 1995–2000 was the highest on record and is likely due to a climatic shift that will persist for another 10–40 yr (Goldenberg et al. 2001). If, as these studies suggest, future wave climates will be more severe, the rate of disturbance on rocky shores will likely increase as well.

While implementing the mechanistic approach to predict future rates of disturbance on rocky shores is enticing, there is one major limitation that must be addressed. A simplifying assumption is that the morphology and mechanics of a species will remain constant even if the wave climate changes. However, numerous studies indicate that organisms respond to their flow environment by modifying their size or shape

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(altering their hydrodynamic loading) and/or by modifying their structural strength. For example, mussels vary their attachment seasonally (Price 1980, 1982; Hunt and Scheibling 2001); snails on exposed shores produce a larger pedal surface area and are more resistant to dislodgment than conspecifics on sheltered shores (Etter 1988; Wahl 1997); gastropod shell and sea urchin test morphology varies with flow environment (Struhsaker 1968; Denny and Gaylord 1996); and sponges produce stiffer tissues in response to increased water motion (Palumbi 1986). Furthermore, macroalgae passively prune themselves when transplanted to exposed shores (Blanchette 1997) and are streamlined in high flow environments (Koehl and Alberte 1988; Johnson and Koehl 1994; Shaughnessy et al. 1996), probably in response to increased tensile forces placed on the blades (Gerard 1987).

Such plastic responses to flow can greatly affect an organism's susceptibility to dislodgment by wave action and must be incorporated into the prediction of the consequences of a shift in wave climate. For example, if an organism responds to increased waviness by becoming stronger or more streamlined, then predictions of disturbance based on current estimates of strength and morphology could be gross overestimates. Furthermore, the plastic response may come at the expense of some other aspect of the organism's ecology, such as reproductive effort or competitive ability, potentially altering overall community structure.

The purpose of this study is to examine the ability of the competitively dominant mussel, *Mytilus edulis*, to adjust its attachment strength in response to changes in the hydrodynamic environment. This study provides insight into the mechanics that contribute to the dominance of this species on rocky shores (thereby increasing our general understanding of intertidal ecology) and develops quantitative predictions of how these animals are affected by variations in the wave climate. Thus, this study furthers our understanding of the pivotal role of mussels in current and future intertidal communities.

Materials and Methods

Introducing the mussel—Mussels of the genus *Mytilus* are distributed throughout cool waters worldwide and often dominate exposed or moderately exposed rocky shore communities (Paine 1966, 1974; Lubchenco and Menge 1978; Dayton 1971; Seed and Suchanek 1992). This study focuses on the species common to the Atlantic coast of North America, *Mytilus edulis*, which ranges from the Canadian Maritimes to North Carolina. Morphologically similar species (e.g., *M. trossulus* and hybrids) have only been reported well to the north of Cape Cod (Hilbish et al. 2000). At levels on the shore above the physiological limits of their major predators and in the absence of physical disturbance, mussels can form a virtual monoculture. The ability of mussels to dominate primary space is largely due to their gregarious settlement behavior, which results in tightly packed beds of adult mussels adhered both to the rock and to each other. As a dominant competitor for space, *M. edulis* has the potential to reduce the diversity of primary space-occupying species on the shore. Consequently, the rate at which mussels are

disturbed by waves has a controlling influence on species richness of the midintertidal community (Levin and Paine 1974; Lubchenco and Menge 1978; Paine and Levin 1981; Suchanek 1981, 1985).

Mussels attach to the substratum by means of a byssus, an extracellular, collagenous structure secreted by the foot. The byssus is composed of three distinct parts: (1) the *root*, which is embedded basally into the foot and connects the byssus to the byssus retractor muscles; (2) the *stem*, which is an outward extension of the root and supports each byssal thread; and (3) the *byssal threads*, which radiate from the stem and ultimately attach to the substratum via an adhesive plaque. Laboratory experiments provide preliminary evidence that increased wave action triggers thread production (Young 1985; Lee et al. 1990; Dolmer and Svane 1994). Mussels are typically tethered to the substratum by 20–70 threads, and this thread number is the primary determinant of attachment strength (Bell and Gosline 1997). If numerous byssal threads are produced (i.e., >100), the upper limit of attachment strength is set by the strength of the root/byssus gland junction. This upper limit is met infrequently (~10% of mussels in the field, Bell and Gosline 1997). To maintain a constant attachment strength, decaying byssal threads must be replenished; the lifetime of an individual thread in the field is not known precisely, but is likely 4–6 weeks (Carrington unpubl. data).

Tenacity and reproductive condition—All *Mytilus edulis* samples for this study were taken from a moderately wave-exposed rocky shore adjacent to Bass Rock in Rhode Island Sound (41.4°N, 71.5°W). The population inhabits the middle intertidal zone (+0.5–1.0 m above MLLW) and spans approximately 10 m along the granitic shore. Samples were collected on a quasimonthly basis (during spring low tides) from January 1998 to December 2000. Samples included only bed mussels (those surrounded by neighbors on all sides) ranging 30–50 mm in shell length, but were otherwise selected haphazardly from the population. Multiple layers of mussels were not observed at this site.

The attachment strength, or tenacity, of an individual mussel in a bed was measured following the methods of Denny (1987) and Bell and Gosline (1997), where a small hole was drilled through the mussel shell, a hook inserted that was attached to a recording spring scale, and the mussel was pulled normal to the substratum until dislodgment occurred. Shell length, width, and thickness were measured to the nearest mm using a vernier caliper. The number of byssal threads present was estimated to the nearest ten threads (through September 1999 only). Attachment force, F_{attach} , was normalized to mussel size (planform area, A_{pl}) to yield tenacity, or Ten, in N m^{-2} :

$$\text{Ten} = F_{\text{attach}}/A_{\text{pl}} \quad (1)$$

where A_{pl} is the silhouette view of a mussel from above. Bed mussels typically orient with their anterior–posterior axis perpendicular to the substratum (Bell and Gosline 1997); thus A_{pl} was approximated as the area of an ellipse, with shell height and shell width as the major and minor axes, respectively. Note that tenacity is a scaled force, and does not represent the material strength of a mussel's byssal at-

tachment. A total of 50 individuals were measured each sample date.

Additionally, 25 mussels were collected each sample date and assessed for reproductive condition, employing two commonly used indices. The first index, gonad index 1, or GI1, is simply the proportion of mussel biomass composed of mantle tissue (the site of gametogenesis in *M. edulis*). For each animal, the wet mantle was dissected from the wet body and dried at 60°C to a constant weight. Both samples were weighed to the nearest 0.001 g and GI1 was then calculated as the dry mantle weight divided by the whole body (the sum of the dry weights of the mantle and remaining body).

In some cases, GI1 may not provide an accurate estimate of reproductive condition because it includes nongameto-genic tissue (Kreeger 1993). Thus, a second method for assessing reproductive condition was used at the beginning of the study that measures the proportion of mussel biomass composed of gametes, or body gamete weight. The second method (gonad index 2, or GI2) was used from January 1998 to February 1999. For GI2, the methods described above for GI1 were modified as follows, according to the protocol of Kreeger (1993). The dissected wet mantle tissue was weighed, then one of the dissected wet mantle lobes was subsampled (by cutting a ~0.1 g transverse section) and fixed. The remaining mantle tissue was reweighed and dried to a constant weight, and the dry weights of the whole mantle and whole body determined. The fixed mantle lobe section was embedded in paraffin, thin sectioned (6 µm), and stained with hematoxylin/eosin. Three thin sections per sample, separated by a minimum of 60 µm in the paraffin block, were selected for image analysis. SigmaScan Pro (SPSS) was used to determine the fractional area occupied by developing or ripe eggs and sperm of each thin section (mantle gamete area, MGA). MGA was then multiplied by total mantle dry weight to estimate total gamete dry weight, which was then divided by whole body dry weight to yield body gamete weight, or GI2.

Oceanographic data—Weekly water column data for the period 1998–2000 were obtained from two long-term monitoring studies conducted by researchers at the University of Rhode Island Graduate School of Oceanography (GSO). In situ sea surface temperature adjacent to Fox Island (~19 km NNE of Bass Rock) was provided by the Narragansett Bay Weekly Fish Trawl (J. Collie pers. comm.). Sea surface Chl *a* and salinity measurements at the GSO pier (~11 km NNE of Bass Rock) were provided by C. Oviatt (pers. comm.).

The sea surface temperature data were used to determine the onset of seasons during the study period, following the method of D. Kester (pers. comm.), where a histogram analysis of in situ sea surface temperature at the GSO pier from 1995 to 1999 suggested that winter was distinguished by water temperatures less than 6°C, and that summer was distinguished by water temperatures exceeding 18°C. Weekly Fox Island sea surface temperatures from 1998 to 2000 were smoothed with a five-point running average. A linear interpolation between the smoothed data points was used to determine the dates corresponding to transitions below and above 6°C (winter start and end, respectively) and above and below 18°C (summer start and end, respectively).

Significant wave heights (H_s) during the study period were obtained from the nearest station maintained by the National Data Buoy Center (www.ndbc.noaa.gov), BUZM3, located approximately 40 km to the east of Bass Rock (41.40°N, 71.03°W). Daily mean values were calculated from these hourly values, and monthly means ($H_{s,mean}$) and maxima ($H_{s,max}$) were determined from the daily mean values. Thus $H_{s,mean}$ is the mean daily mean significant wave height and $H_{s,max}$ is the largest daily mean significant wave height of a given month. The BUZM3 wave record was not continuous, with gaps in January 1998, November 1998 to February 1999, September to October 1999, and July 2000. These gaps were filled with estimates based on measurements from the closest station in operation, 44008, located approximately 200 km to the SE of Bass Rock, using the following linear expressions obtained from regression analysis of 26 months of concurrent data: $H_{s,mean,BUZM3} = 0.435H_{s,mean,44008} + 0.128$ and $H_{s,max,BUZM3} = 0.474H_{s,max,44008} + 0.289$ ($r^2 = 0.67$ and 0.59 , respectively). Data for January 1998 were not available for either buoy.

To provide a long-term perspective of seasonal trends in wave conditions near Bass Rock, significant wave height data were obtained for Sta. 44008 from the NDBC for the period September 1982 to December 2000 (a long-term record for BUZM3 was not available). Monthly mean ($H_{s,mean}$) and maxima ($H_{s,max}$) were determined as described above, and the 18 yr of historical data were summarized by month. Only months with >90% of days reported were included in this analysis.

Statistical analyses—Cross-correlation analyses were performed on the data using Systat software (DOS v. 5, SPSS). To perform these time series analyses, it was necessary to assign tenacity and reproductive condition measurements to evenly spaced monthly intervals. Samples were generally assigned to the month in which they were collected, but were occasionally shifted to the previous month when sample dates fell at the beginning of the month. For example, when two spring tides occurred in August 2000, the first sample on 01 August was assigned to July, while the sample on 28 August was assigned to August. The assigned month never strayed more than 1 week from the sample date. Missing values (two and seven dates for tenacity and GI1, respectively) were interpolated using local quadratic smoothing.

Predicting dislodgment and safety factors—The percentage of mussels dislodged each month at Bass Rock was predicted following the general method of Denny (1995), with modifications suggested by Gaylord (1999, 2000) and Denny (1999). Specifically, it was assumed that the primary hydrodynamic load for bed mussels is lift, acting perpendicular to the direction of flow (Denny 1987, Bell and Gosline 1997):

$$\text{Lift} = \frac{1}{2} \rho U^2 C_l A_{pl}, \quad (2)$$

where ρ is the density of seawater (1,024 kg m⁻³), U is water velocity over the mussel bed, C_l is the coefficient of lift (0.88 for bed mussels, Denny 1987), and A_{pl} is mussel planform area, as described above. A mussel will become dislodged

if the maximum load applied by a given wave exceeds its attachment force, F_{attach} :

$$\text{Lift}_{\text{max}} > F_{\text{attach}} \quad (3)$$

Substituting Eq. 2 for lift and dividing by both sides by A_{pl} yields a new criterion for dislodgment:

$$\frac{1}{2} \rho U_{\text{max}}^2 C_1 > \text{Ten}, \quad (4)$$

where U_{max} is the maximal water velocity that effects maximum lift. The left-hand side of Eq. 4 thus defines a critical tenacity, or Ten' , that a mussel must exceed to remain attached during the passing of a wave of a given water velocity. Substituting constants,

$$\text{Ten}' = 450.6 U_{\text{max}}^2 \quad (5)$$

Long-term maximal water velocity measurements for Bass Rock during the study period were not available; thus two methods were used to approximate U_{max} from the celerity of a nearshore wave height, H , as water depth approaches zero (Tricker 1964). The first, more conservative, method applies only to bores of small amplitude: $U_{\text{max}} = (gH)^{0.5}$. The second method applies to larger bores: $U_{\text{max}} = (2gH)^{0.5}$, where g is gravitational acceleration, 9.81 m s^{-2} . While neither of these theoretical approximations were intended for surf-zone flows, Gaylord (1999) has shown that the first method nonetheless accurately describes the maximum velocities generated by newly breaking waves. The second method is very similar to the empirical relationship derived by Gaylord (1999) for fully breaking waves on a specific shore: $U_{\text{max}} = 3.76H^{0.57}$. Nearshore wave height, H , was approximated as the maximum significant wave height at BUZM3. In this manner, Ten' was calculated on a monthly basis using the maximum daily mean significant wave height recorded at BUZM3 each month. While more detail on the general nature and prediction of surf-zone flows is provided by Gaylord (1999), it is important to note that individual waves can greatly exceed maximum significant wave height and that these calculations only roughly approximate velocities experienced by intertidal mussels.

The probability of dislodgment was determined for each sample date as follows. Tenacity measurements for each month were ranked in increasing order, and the probability p of having a tenacity less than a mussel of rank j was estimated using the equation $p = j/(n + 1)$, where n is the number of mussels sampled. The probability of dislodgment was determined as the maximum p among mussels with tenacities less than or equal to the month's Ten' .

Safety factor, SF, is a useful engineering concept for describing the "reserve" strength of a structure relative to the loading it encounters (Wainwright et al. 1976). An SF of one implies a structural design that precisely matches the applied load; man-made structures are typically engineered with safety factors of three to eight, or even greater (Gordon 1978). The mean safety factor for mussel attachment was calculated for each sample date by dividing the mean tenacity by Ten' .

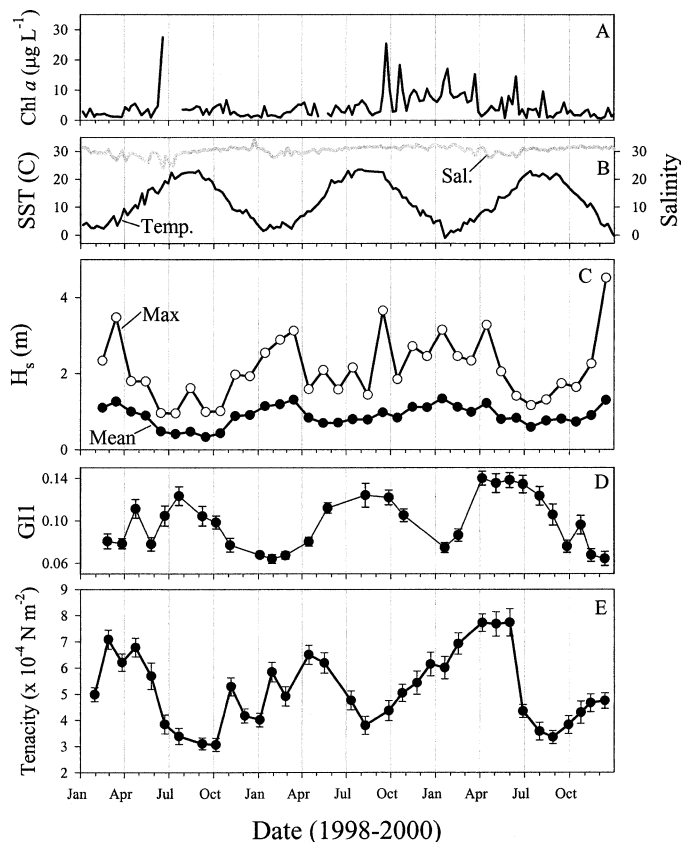


Fig. 1. Physiological and environmental characteristics of *M. edulis* in Rhode Island, 1998–2000. Vertical reference lines approximately demarcate seasons. (A) Weekly chlorophyll *a* estimates at GSO pier. (B) Weekly sea surface temperature (SST) and salinity at Fox Island. (C) Monthly summary of significant wave heights recorded at Sta. BUZM3. Closed circles are mean of daily mean significant wave height, and open circles are maximum daily mean significant wave height. Symbols are arbitrarily plotted on the 15th day of each month. (D) Reproductive condition, GI, of *M. edulis* at Bass Rock. Circles are mean $\pm$ SE of 25 samples. (E) Tenacity of *M. edulis* at Bass Rock. Circles are mean $\pm$ SE of 50 samples.

Results

Tenacity and reproductive condition—Mean tenacity of *M. edulis* at Bass Rock was not constant during the study period, but rather displayed a strong seasonal cycle with a twofold increase in late winter/early spring relative to summer (Fig. 1). The precise timing, amplitude, and duration of cycle peaks and troughs varied from year to year. For example, the decrease in tenacity in summer 1999 was not as severe or prolonged in comparison to other years. Mean tenacity was significantly correlated with the mean number of byssal threads present (Fig. 2, $P < 0.01$).

Mean mussel shell length varied between sample dates, ranging from 36 to 47 mm (data not shown). While both tenacity and byssal thread number significantly covaried with shell length (decreasing and increasing with size, respectively; $P < 0.001$), the effect of the covariate was not consistent over time. Adjustments to monthly mean values for shell length were typically $<10\%$ and did not alter the

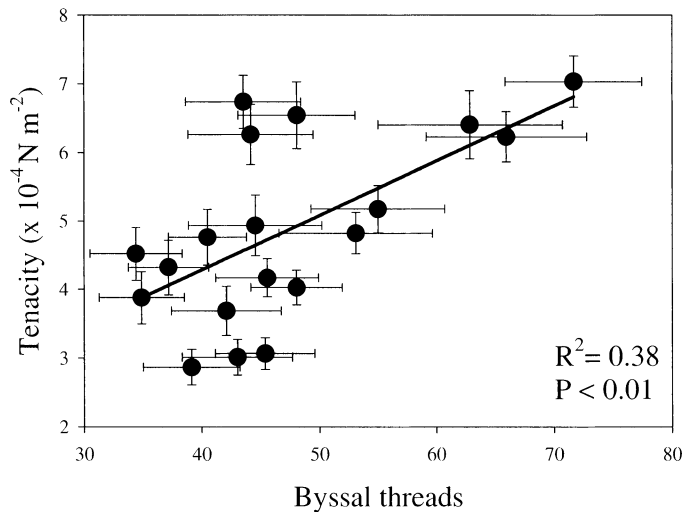


Fig. 2. Mussel tenacity depends on the number of byssal threads produced. Symbols are mean values ($\pm$ SE, $n = 50$) of quasimonthly samples from Bass Rock, 1998–1999.

general temporal patterns in the data. Thus subsequent analyses were conducted on the original (unadjusted) data.

Reproductive condition also displayed seasonal cycles: GI1 was low in late fall/winter, rose as gonads developed during spring and summer, then plummeted again after spawning in late summer (Fig. 1). A comparison of GI1 and GI2 during the first year of the study indicated that the two methods for assessing reproductive condition were highly correlated (Fig. 3, $P < 0.001$). Because the GI2 method was costly (histology) and very time consuming (image analysis of multiple thin sections), the simpler GI1 was the only index of reproductive condition used after February 1999.

Oceanographic data—Seasonal cycles were observed in all oceanographic data, with the exception of Chlorophyll *a* (Fig. 1). Both $H_{s,mean}$ and $H_{s,max}$ decreased each summer and increased in winter. This trend was less distinct in $H_{s,max}$ due to the sporadic nature of storm events. For example, a major tropical storm (Floyd) increased southern New England wave heights in September 1999, but not in the other two years. Sea surface temperature ranged from ~ 3 to 25°C from winter to summer, and salinity decreased slightly during each spring rainy season. Chlorophyll *a* was temporally variable, but did not follow any clear seasonal cycle.

Statistical analyses—Cross-correlation analysis of tenacity with reproductive condition, GI1, revealed a strong correlation between the two variables, especially when tenacity preceded GI1 by 3 or 4 months (Fig. 4). Note that other lag times also yielded significant (but lower) correlations, falling well outside the approximate 95% confidence limits. When tenacity was cross correlated with $H_{s,mean}$, a peak in correlation occurred when tenacity lagged behind 1 month (Fig. 4). Similar trends were observed with tenacity versus $H_{s,max}$ cross correlations, but the correlation coefficients were reduced overall in comparison to $H_{s,mean}$. Tenacity was significantly correlated with other oceanographic features as well. Most striking was the strong negative correlation with sea

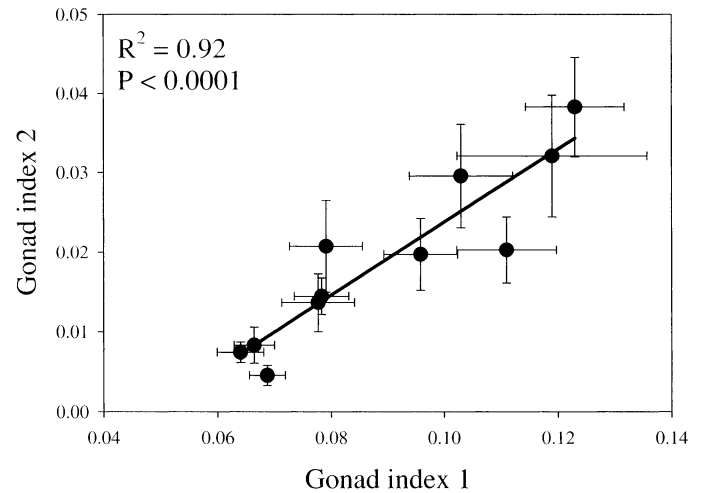


Fig. 3. Two commonly used indices for estimating mussel reproductive condition are highly correlated ($P < 0.001$). Symbols are mean values ($\pm$ SE, $n = 25$) from quasimonthly samples collected at Bass Rock from April 1998 to March 1999.

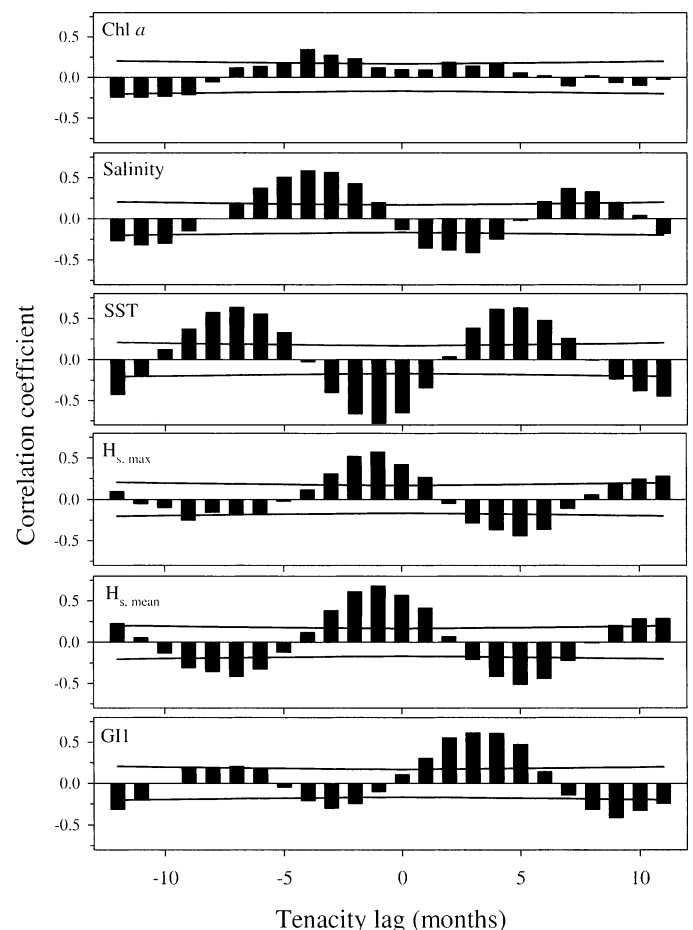


Fig. 4. Cross-correlation analyses of mean monthly tenacity with each of six other time series presented in Fig. 1. Bars are correlation coefficients; curved lines are approximate 95% confidence levels for the significance of each correlation.

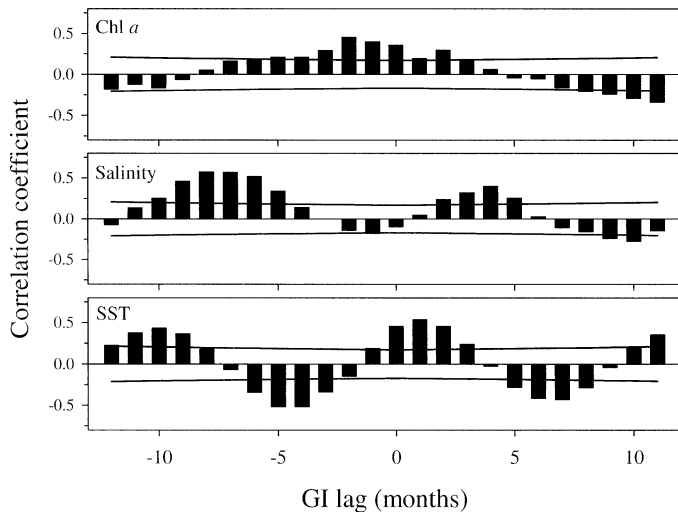


Fig. 5. Cross-correlation analyses of mean monthly GI1 with each of three other factors presented in Fig. 1. Bars are correlation coefficients; curved lines are approximate 95% confidence levels for the significance of each correlation.

surface temperature when tenacity lagged behind 1 month. When tenacity lagged behind 4 months, a strong correlation with salinity and a relatively weak correlation with Chl *a* was observed (Fig. 4).

Like tenacity, GI1 was significantly correlated to several oceanographic features (Fig. 5). A strong negative correlation with sea surface temperature was observed, peaking when GI1 lagged behind 4 or 5 months. GI1 was most positively correlated with salinity when it lagged behind 7–8 months. The correlation of GI1 with Chl *a* was modest in comparison, but was maximal when GI1 lagged behind 2 months.

The cross-correlation relationship between tenacity and GI1 is evident when the two physiological parameters are plotted against each other (Fig. 6). When each sample date is assigned to a season (see Table 1), summer emerges as a period of high reproductive condition and low tenacity, while winter is a period of low reproductive condition and increasing tenacity. Spring and fall are transitional periods between these two physiological states.

Predicting dislodgment and safety factors—The seasonal cycle in tenacity can also be observed in the whole population in the cumulative probability plots of Fig. 7, where each month's curve describes the probability that a mussel chosen at random will be weaker than a given tenacity. The curves shift up and down in time, with ridges of high tenacity each spring, followed by valleys of low tenacity in summer. Note this trend is apparent across the tenacity distribution; even the strongest individuals modify their tenacity.

Predicted dislodgment rates for the first method for estimating $U_{\max}$ ($gH)^{0.5}$, were modest throughout the study period, never exceeding 12% of the population (Figs. 7, 8). Dislodgment rates for the second method ($U_{\max} = (2gH)^{0.5}$) were higher overall, with a major dislodgment event predicted for September 1999 (40%) and more modest events

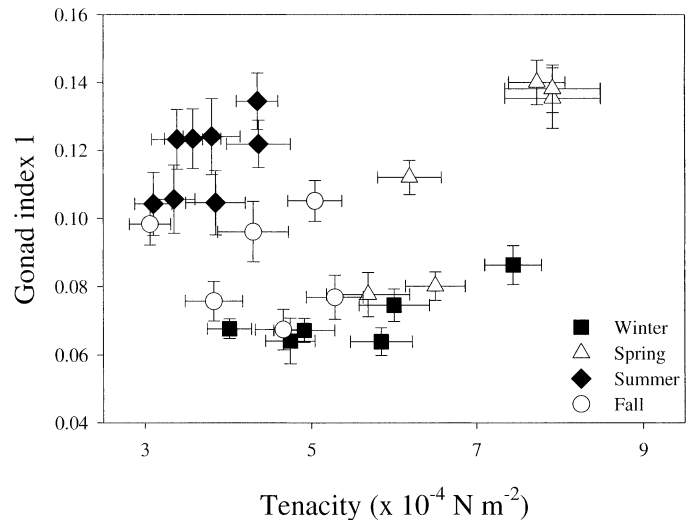


Fig. 6. Mussel reproductive condition, GI1, versus tenacity, 1998–2000. Symbols are mean monthly values $\pm$ SE, and were coded for season by referencing each sample date to Table 1.

in February 1999 (22%) and the fall of 2000 (24–28%). Note that maximal wave height alone is not a good indicator of mussel dislodgment. For example, equally large wave heights were observed in March 1998 and September 1999, but only the latter storm event challenged the tenacity of a substantial proportion of the population.

Safety factor for mussel tenacity was not constant in time, regardless of the method used for estimating $U_{\max}$. Calculations using $U_{\max} = (gH)^{0.5}$ produced the largest SF, with mean tenacity ranging up to nine times the predicted critical tenacity. Safety factors using $U_{\max} = (2gH)^{0.5}$ for fully breaking waves were lower, approaching the critical value of one on two occasions.

The seasonal cycle in mussel tenacity is also apparent when monthly samples are averaged across the 3 yr of this study (Fig. 9). Historical records of wave climate in southern New England (1982–2000) indicate a strong seasonality in both monthly mean and maximal wave heights (Fig. 9). On average, the waviest periods occur from October to April, but the largest storms of the 18-yr period occur during hurricane season (September and October), a time when mussel tenacity is not maximal.

Table 1. Timing of seasons during the study period, as determined by the in situ temperature threshold method of D. Kester (pers. comm.). See text for details.

Season	Begin date	End date
Winter 1997–1998	30 Nov 1997	16 Mar 1998
Winter 1998–1999	19 Dec 1998	26 Mar 1999
Winter 1999–2000	24 Dec 1999	21 Mar 2000
Winter 2000–2001	1 Dec 2000	4 Apr 2001
Summer 1998	20 Jun 1998	30 Sep 1998
Summer 1999	3 Jun 1999	3 Oct 1999
Summer 2000	15 Jun 2000	24 Sep 2000

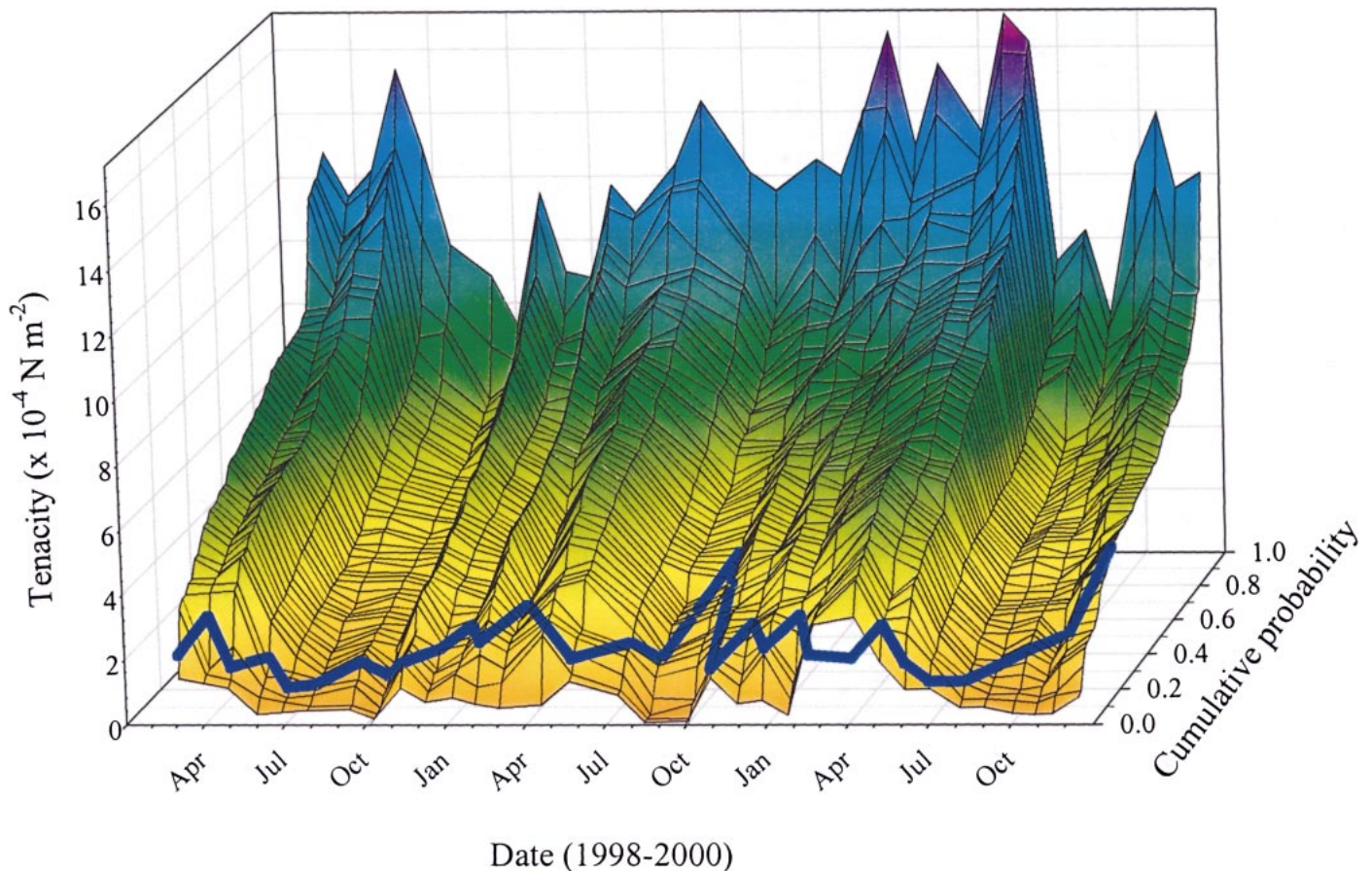


Fig. 7. Cumulative probability distribution of tenacity at Bass Rock, 1998–2000. For each quasimonthly sample date, a cumulative probability curve is plotted, indicating the probability that a mussel chosen at random will be weaker than a given tenacity ($n = 50$ for each date). Coloring represents level of tenacity, ranging from weak (yellow) to strong (purple). The curves are connected to illustrate the shifts in the tenacity distribution through time. The solid blue line defines the intersection of critical tenacity, Ten' , with the cumulative probability curve for each sample date, thereby describing the probability of dislodgment. U_{max} was estimated at $(2gH)^{0.5}$; see Fig. 8 for predictions for $U_{max} = (gH)^{0.5}$.

Discussion

Seasonal variation in tenacity: causes—The major experimental finding of this study is that mussel tenacity is not constant, but instead follows a distinct seasonal cycle, increasing twofold in late winter/early spring relative to summer (Fig. 1). Based on the three annual cycles documented here, the precise timing and duration of cycle peaks and troughs vary from year to year. The entire cumulative probability distribution shifts up and down, which suggests that the change in mean tenacity is due in part to changes at the individual level, rather than the addition or removal of individuals to the population. Tenacity is significantly correlated with the number of byssal threads tethering a mussel to the substratum (Fig. 2), which is consistent with the observations of Bell and Gosline (1997) that the primary determinant of mussel tenacity is thread number. While other factors likely influence the tenacity of an individual mussel (e.g., thread strength, extensibility; Bell and Gosline 1996) the seasonal cycle of mussel tenacity can be viewed to a first approximation as the result of net thread production during fall/winter, and net thread decay during spring.

The specific cue for increased thread production by a mussel is not known. Although a number of exogenous factors are correlated with tenacity, many lines of evidence suggest that the most likely candidate is some aspect of wave action. First, numerous laboratory studies have demonstrated that mussel byssal thread production increases with increased water motion, thereby creating a stronger attachment (Young 1985; Lee et al. 1990; Dolmer and Svane 1994). Second, this study provides field evidence consistent with those observations; the seasonal cycle of mussel tenacity generally mirrors the seasonal cycle of waviness of the sea offshore. Similar observations have been made for *M. edulis* in the UK (Price 1982) and *Mytilus* spp. in Nova Scotia (Hunt and Scheibling 2001), leading Price (1980) to surmise that the twofold increase in attachment strength in fall/winter is in response to (or anticipation of) increased hydrodynamic loading associated with fall/winter storms, thereby increasing survivorship during this physically stressful time. Third, thread production and attachment strength increase with an assumed increase in hydrodynamic forces within a site (fringe > bed, Witman and Suchanek 1984; solitary > bed, Bell and Gosline 1997). Fourth, attachment strength increas-

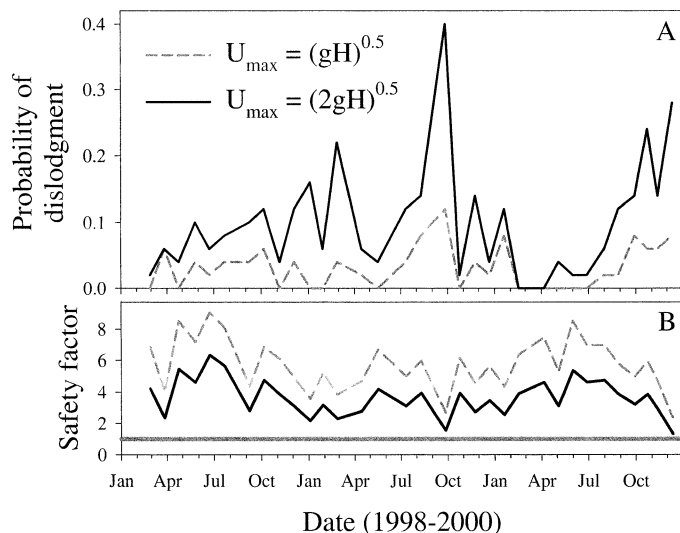


Fig. 8. (A) Predicted probability of dislodgment of mussels at Bass Rock, using two methods to estimate U_{max} . See text for details. (B) Safety factor, calculated for each of the two U_{max} methods. Horizontal shaded line represents the critical safety factor of one.

es with increased wave exposure between sites (Witman and Suchanek 1984). Finally, when experimentally dislodged mussels are replaced on the substratum and covered with a mesh, those held firmly in place do not produce byssal threads, while those loose under the mesh produce many threads (Seed and Suchanek 1992). Such observations led Seed and Suchanek (1992) to suggest that “*Mytilus* detects and responds to movement by wave energy [...] by the production of increased numbers of byssal threads.”

Note that the response of mussels to modify tenacity is neither rapid nor precise. Mussels in the laboratory have been observed to produce a new byssal thread approximately every 5 min (pers. obs.), so a doubling of tenacity could presumably be accomplished within a day or two. Instead, tenacity lagged behind $H_{s,mean}$ and $H_{s,max}$ by approximately 1 month, and safety factor was not constant, regardless of the calculation method used. The lag of 1 month for tenacity, however, should be interpreted with caution because sample dates were shifted to evenly spaced intervals to allow for time series analyses (Fig. 4) and the wave data were arbitrarily plotted on the midpoint of each month (Fig. 1). Given these limitations, it is not possible to resolve the lag between the tenacity and wave height with any precision below 1 month. While a shorter lag is likely, mussels do not appear to be perfectly tuned to their flow environment; it is clear from Fig. 1 that there are periods of high wave activity that do not coincide with high tenacity, most notably in September 1999.

Thus, as intuitive as the scenario of mussels modifying their attachment strength in response to their flow environment may seem, there are alternative hypotheses that warrant attention. For example, seasonal variation in tenacity may represent a response to seasonal predator activity (e.g., Dolmer 1998; Leonard et al. 1999) or may represent temperature effects on thread strength (such as increased decay in summer). Yet another hypothesis, strongly suggested by the re-

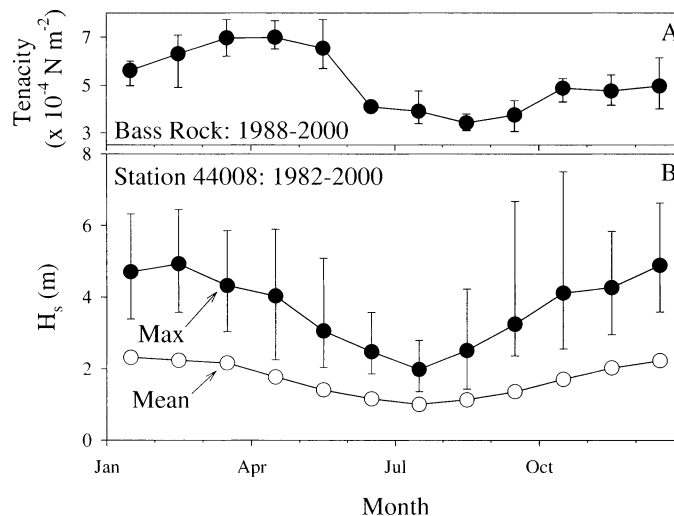


Fig. 9. Summary of long-term trends in mussel tenacity and wave climate by month. (A) Mean tenacity at Bass Rock, 1998–2000. Bars represent the range of monthly tenacity measured during the present study. (B) Historical records of significant wave height (H_s) at Sta. 44008, 1982–2000. Open circles are interannual mean of mean monthly H_s (only months with >90% of days reported were included). Closed circles are interannual means of monthly maximum H_s , with bars representing the range of monthly maximum H_s reported during the 18-yr interval.

sults of this study, is byssal thread production may be linked to seasonal shifts in energetic resource allocation.

Seasonal variation in tenacity: driven by hydrodynamics or energetics?—Tenacity is not the only aspect of a mussel’s physiology that exhibits a seasonal cycle. Reproductive condition, measured as GI1, also varies throughout the year, peaking in spring and summer, then declining after spawning in late summer (Fig. 1). This reproductive cycle closely follows trends in sea surface temperature (Figs. 1, 5), as has been previously documented for other *M. edulis* populations (Nelson 1987; Seed and Suchanek 1992). Salinity was also strongly correlated with GI1, but it is not likely that this relationship is causal, due to the small magnitude of the salinity fluctuation.

While both tenacity and reproductive condition follow expected environmental parameters (wave height and sea surface temperature, respectively), it is interesting to note that these two physiological parameters are negatively correlated, with peaks in GI1 lagging behind tenacity by 3 to 4 months (Figs. 1, 4). Thus it appears that *M. edulis* cycles between two alternate physiological states: high reproduction/low tenacity in summer and high tenacity/low reproduction in winter, with spring and fall as transitional periods (Fig. 6). Large mussels can allocate as much as 90% of their total production to gamete synthesis (Seed and Suchanek 1992). In comparison, the metabolic cost of byssal thread production is greatly reduced, but nonetheless substantial, forming up to 8% of a mussel’s monthly energy expenditure (Hawkins and Bayne 1985). Thus an alternative explanation of seasonal variation in tenacity has clearly emerged: byssal thread production may occur only when energetic resources are avail-

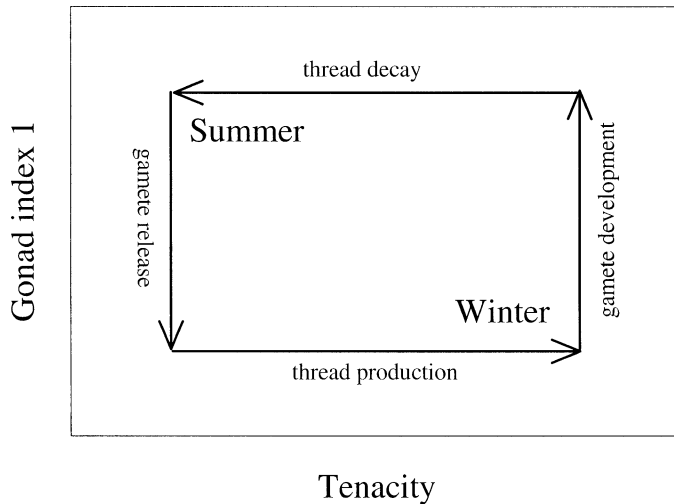


Fig. 10. Proposed scheme for energetic tradeoff between tenacity and reproduction. See text for details. Note that this model is presented as a box to emphasize the processes involved. In reality, the trajectories may be curved (i.e., gamete development and thread decay occur concurrently) and paths may vary from year to year.

able (i.e., not allocated to reproduction) regardless of the prevailing wave conditions. This model of an energetic tradeoff between tenacity and reproduction is diagramed in Fig. 10 and results in an annual cycle with time moving counterclockwise. Following gamete release in late summer, energy is available for byssal thread production and tenacity increases. With the onset of gamete development in early spring, thread production halts and tenacity decreases as threads decay. In this manner, the observed seasonal cycle in attachment strength may be interpreted to represent a seasonal decrease in byssal thread production due to an internal shift in the allocation of energy resources to gamete production, rather than a plastic response to an environmental cue.

Laboratory tests of this hypothesis are currently underway, but, if confirmed, tenacity may be more closely linked to changes in seawater temperature or food supply than previously thought. Indeed, other studies linking attachment strength to flow (e.g., Witman and Suchanek 1984; Okamura 1986; Newell 1990) are confounded by the possibility that thread production may depend primarily on food supply. Furthermore, it is interesting to note that in this study, coincident peaks in tenacity and reproductive condition occurred only in spring 2000, which followed a period of unusually high phytoplankton abundance (Fig. 1).

Seasonal variation in tenacity: consequences—Regardless of what contributes to the variation in mussel tenacity (hydrodynamics, energetics, predation, temperature, or some combination), one can ask whether a mussel's tenacity in any given month is sufficient to withstand the hydrodynamic loading it encounters. That is, are there months where mussels are at risk for dislodgment by waves? While rates of dislodgment were not measured for the Bass Rock population presented in Fig. 1, some general observations may provide some insight into this issue. At Sta. BUZM3 during

1998–2000, mean monthly significant wave height was fairly consistent from year to year, with calm periods in summer followed by stormier periods in fall and winter (Fig. 1). Maximum significant wave height (the month's most damaging waves) also varied seasonally but was less consistent between years; some years were stormier (had larger waves) than others. For example, the annual peak in $H_{s,max}$ was substantially higher in 2000 compared to the other two years. Furthermore, the timing of storm events varied interannually, with the year's most extreme storms falling either in March, September, or December. In considering long-term trends in wave climate in southern New England (1982–2000), the waviest periods on average occur from October to May, but extremes in wave height can be observed during hurricane season in September and October (Fig. 9).

Comparing these trends in wave height to mussel tenacity (Figs. 1, 9), it is clear that September and October are particularly risky months for mussels because extreme waves arrive at a time when tenacity is moderate. Storms later in the season, even if they are more severe, pose less of a dislodgment threat because tenacity has increased accordingly. The only major dislodgment event observed at Bass Rock during the study period was due to tropical storm Floyd in mid-September 1999. The mussel bed was visibly depleted, and shorelines all over Narragansett Bay were littered with loose mussels (pers. obs.). This event was in qualitative agreement with the mechanistic model predictions using $(2gH)^{0.5}$ to estimate U_{max} . More moderate ($\sim 25\%$) dislodgment events were also predicted for other months, but none was readily apparent at Bass Rock (pers. obs.). Clearly, a detailed, quantitative monitoring of dislodgment rate is needed in order to resolve this discrepancy and to provide a more rigorous test of the mechanistic approach in general. The first method for estimating U_{max} led to only modest predictions of dislodgment and failed to predict a strong dislodgment event in September 1999. Thus this method is probably not appropriate for predicting mussel dislodgment because it does not apply to those waves that generate the largest flows (Gaylord 1999).

The time required to produce a strong byssus can affect the survival of mussels in the wave-swept environment. While there is no indication that mussels can respond rapidly to the onset of an early season (September–October) storm to reduce their risk of dislodgment, by nonetheless responding, those mussels that do survive and maintain a strong byssus have a greater chance of surviving ensuing storm waves. For example, the increase in tenacity comes earlier in fall 1999 than 1998 (Figs. 1, 7). This likely reflects the strengthening of the entire population (by increased thread production) following tropical storm Floyd. Alternatively, the increase in mean tenacity could be due to the removal of weaker individuals by Floyd, or some combination of the two mechanisms. The dislodgment rates predicted for the months following, October 1999 to February 2000, are lower than rates predicted for similar periods in other years with no major hurricane activity. Similarly, the predicted dislodgment for the largest storm of the study period (December 2000) is surprisingly moderate, perhaps due to individual or population level response to a dislodgment event two months prior.

While this study provides the most detailed temporal analysis of mussel attachment to date, it is limited to only one site. A number of lines of evidence, however, suggest these findings are nonetheless robust. Monitoring of a second site a few kilometers to the south of Bass Rock was initiated in October 2000, and preliminary data indicate that trends in tenacity and reproductive condition are similar between the two sites. Furthermore, the predictions for dislodgment are consistent with those of Hunt and Scheibling (2001) for *M. edulis* and *M. trossulus* in Nova Scotia, where mortality occurs primarily from mid-August to mid-September (Mallet and Carver 1995). Lubchenco and Menge (1978) also report heavy *M. edulis* mortalities in late summer at some sites in Maine. Attachment strength of cultured mussels in the Canadian maritimes typically weakens in summer, to a point where substantial losses (falloff due to excessive weight) occur during fall harvesting (B. Myrand pers. comm.). Similarly, Dare (1976) reports highest mortality by storms in September and October for *M. edulis* in Morecambe Bay, England.

While the cause of weak tenacity in Bass Rock mussels during late summer/early fall remains unknown, the consequence is quite clear—they are simply ill-prepared to withstand large storm waves from August to October. Historically, large storms occur sporadically in southern New England in September and October and are typically of tropical origin. Note that while peak hurricane season is August to October, those formed in August generally track to the Gulf of Mexico; thus large tropical storms do not occur in August in New England. Tropical storms are not necessarily the largest storm event each year; extratropical storms occur from October to May (J. Boothroyd pers. comm.) and can often exceed tropical storms in intensity. However, extratropical storms occurring later in the season pose less of a threat, since it is not only the magnitude of a storm that determines when disturbance events will occur, but its timing relative to the tenacity cycle as well. Thus, mussels seem especially sensitive to the recent shift to increased hurricane activity in the North Atlantic reported by Goldenberg et al. (2001). The predicted consequence of such a climatic shift to mussels is more frequent and more severe disturbances compared to those that occurred just a few years ago, during 1971–1994. It will be interesting to follow what effect, if any, increased disturbance will have on mussels, and on the many organisms that are intimately linked to their persistence.

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