

Seasonal disturbance to mussel beds: Field test of a mechanistic model predicting wave dislodgment

Emily Carrington,^{1,*} Gretchen M. Moeser,¹ James Dimond,² Joseph J. Mello,³ and Michael L. Boller⁴

Department of Biological Sciences, University of Rhode Island, Kingston, Rhode Island

Abstract

We report the first field confirmation of a mechanistic model predicting fine-scale temporal dynamics of wave dislodgment, an important disturbance process structuring many temperate rocky intertidal communities. A biomechanical approach is used to predict the frequency and severity of mussel dislodgment from wave-swept shores in Rhode Island over a 3-yr period. Using inputs of wave height and mussel attachment, the model correctly predicts strong dislodgment events during hurricane season (August to October, ~10% monthly loss), a period when large waves coincide with relatively weak mussel attachment. Such a mechanistic approach, incorporating temporal variation in both environmental challenges and physiological tolerances, is necessary to predict patterns of environmental stress; such predictions cannot be made from environmental forecasts alone. In addition to wave dislodgment, we report substantial mussel mortality due to temperature stress (up to 50% monthly loss). These two physical agents, which caused equivalent mussel mortality in our 3-yr study, are likely to be influenced by future global climate shifts.

The controlling influence of climate change on species distribution and community structure is evident worldwide (Hughes et al. 2003; Parmesan and Yohe 2003). Efforts to predict future effects of altered climates on species assemblages have been hindered, in part, by the lack of a mechanistic understanding of how the physical environment influences ecological processes (Helmuth et al. 2005; Pörtner and Knust 2007). Whereas several mechanistic approaches have emerged in recent years (Denny et al. 1985; Denny 1995; Helmuth 1998), detailed field tests of such theories are rare.

The marine intertidal zone is one habitat considered particularly sensitive to climate shifts (Helmuth et al. 2002; Harley et al. 2006). Attached plants and animals alternate between oceanic and terrestrial conditions with the rise and fall of each tide, and it is well known that physical factors can limit species distribution and abundance on wave-swept rocky shores worldwide (Lewis 1964). Furthermore, the dynamics of removal of space-dominating organisms, such as bivalves and macroalgae, has a controlling influence on community structure (Dayton 1971; Levin and Paine 1974; Bertocci et al. 2005).

One major determinant of the survival of a rocky shore organism is its ability to resist dislodgment by waves, and great progress has been made in recent decades using engineering theory to predict wave disturbance events

(Denny et al. 1985; Koehl 1999; Denny 2006). The general method, outlined in detail by Denny (1995), estimates the probability that a wave of a given height will generate a hydrodynamic force greater than an organism's attachment strength. Whereas this approach has been successful in predicting the consequences of wave disturbance to benthic communities (e.g., survival along an exposure gradient, maximum size of wave-swept algae, coral size and shape [Denny 1995; Madin and Connolly 2006; Wolcott 2007]), explicit field tests of the approach are lacking.

In this study, we focus on the rate of dislodgment of mussels by waves, a common source of mortality (Hunt and Scheibling 2001a; Zardi et al. 2006). These bivalve molluscs often dominate primary space on temperate rocky shores, excluding competitors and providing habitat for a rich associated community. Mussels tether themselves to hard substrates by means of a byssus, a collection of extracellular collagenous fibers (byssal threads) produced by the mussel's foot. In the blue mussel, *Mytilus edulis*, byssus strength varies twofold during the year, but this seasonal cycle does not align precisely with seasonal patterns in wave activity (Price 1980; Carrington 2002a). To evaluate the consequences of variable attachment strength, Carrington (2002a) developed a model to predict wave disturbance to *M. edulis* beds in Rhode Island. Importantly, this model incorporated annual variation in both environmental (waves) and biological factors (attachment strength) that determine dislodgment risk. The greatest dislodgment was predicted for periods when large storms coincide with weak mussel attachment strength, during late summer and early fall for mussels at this location.

The prediction of Carrington (2002a) is consistent with many field studies of mussel dislodgment conducted in the Northwest Atlantic. For example, dislodgment increases in fall compared with summer in Nova Scotia (Hunt and Scheibling 2001a) and large removal was reported in late

*Corresponding author: ecarring@u.washington.edu; formerly E.C. Bell.

Present addresses:

¹Department of Biology and Friday Harbor Laboratories, University of Washington, Friday Harbor, Washington.

²Marine Biological Laboratory, Woods Hole, Massachusetts.

³NOAA National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, Massachusetts.

⁴Biology Department, Saint John Fisher College, Rochester, New York

summer at some sites in Maine (Lubchenco and Menge 1978). To date, however, no study has quantified dislodgment with the temporal resolution necessary to adequately test the mechanistic model. The primary purpose of this study is, therefore, to compare model predictions of Carrington (2002a) to detailed, long-term observations of wave dislodgment rates in the field.

Mussels are not only subject to mortality by waves, but also to a broad range of biotic and abiotic stressors, such as predation and extreme temperatures (Paine 1974; Menge 1976; Helmuth 1998). Whereas several studies have noted how the relative importance of predation decreases along a gradient of increasing wave exposure (Menge 1976; Hunt and Scheibling 2001a), few have compared the rates of multiple abiotic stressors to intertidal organisms. Our detailed observations of wave mortality incidentally provided a unique opportunity to quantify the relative importance of another source of mortality to mussels, namely exposure to extreme aerial temperatures.

Methods

Field sites—Field measurements were conducted at two sites in Rhode Island Sound, Bass Rock (BR; 41.4°N, 71.5°W; Carrington 2002a), and Black Point (BP; approximately 1 km south of BR). The two sites sloped eastward, were exposed to moderate wave action, and provided habitat for dense aggregations of the blue mussel, *M. edulis*, in the middle intertidal zone (+0.5–1.0 m above mean lower low water). Multiple layers of mussels were rare at these sites; this study targeted monolayered mussels in beds attached to primary substrate.

Measuring temperature—At BR, a temperature logger (TidBit, Onset Computers) was mounted on an adjacent rock in the mussel zone. The sensor was shaded from direct sunlight by an opaque, neutral-colored plastic sheet and recorded in situ temperature every 5 min. Daily average and extremes were calculated. The logger was periodically exposed to air by the tides; these data reflect a hybrid of daily water and air temperatures. Although the logger does not mimic the thermal properties of a mussel (Helmuth 1998), it reports the thermal conditions of a shaded microhabitat, which crudely approximates a mussel bed.

Predicting dislodgment—The mechanistic approach of Denny (1995) was used to predict mussel dislodgment at the two field sites over 3 yr, 2001–2003, with several modifications described previously by Carrington (2002a). In general, nearshore wave height measurements were used to estimate maximal hydrodynamic forces on bed mussels, which were in turn compared with measured distributions of mussel attachment strength to determine the probability of dislodgment over given time intervals. A more detailed description of the model follows.

Mussel attachment strength, or tenacity, was measured quasimonthly (during extreme spring low tides) along a ~10-m transect established through a mussel bed at each site (BR and BP). Individuals ranged 25–45 mm in shell length and were surrounded by neighboring mussels, but

were otherwise selected haphazardly. Following Bell and Gosline (1997), a small hole was drilled in the mussel shell to accommodate a hook that was attached to a recording spring scale. A steady tensile force was applied to the mussel normal to the substrate until dislodgment occurred, within 1 s. Shell length, width, and thickness were measured to the nearest millimeter using a vernier caliper. The force to dislodge each mussel was divided by an index of mussel size (planform area, A_{pl} , in m^2) to yield tenacity, or Ten , in $N\ m^{-2}$. Because bed mussels typically orient their anterior–posterior axis perpendicular to the substrate, A_{pl} was calculated as the area of an ellipse with shell height and shell width as the major and minor axes, respectively (Bell and Gosline 1997). Sample size was 50 mussels during 2001 and was reduced to 40 thereafter. Force recordings were unavailable during Jan–Apr 2001; tenacity for each of these months was estimated as the mean of monthly data collected in the following 2 yr. The difference in mean monthly tenacity between sites was evaluated using a paired *t*-test.

Nearshore wave characteristics were quantified using a SBE26 Seagauge (Seabird Electronics) throughout the study period. The pressure logger was mounted at 7 m depth, approximately 200 m offshore from the intertidal site at BR. Bursts of 1024 pressure measurements were recorded at 2 Hz every 4 h. Seasoft software (Seabird Electronics) was used to calculate significant wave height (H_s) for each burst, and daily means $H_{s,daily,BR}$ were calculated. Monthly means, $H_{s,mean}$, and maxima, $H_{s,max}$, were determined from the daily mean values. Data were absent from the Seagauge on the following dates: 01 Jan–18 Jul 2001, 22 Feb–08 Jun 2002, 05–13 Aug 2002, and 01–06 June 2003. These gaps were filled with estimates on the basis of measurements reported by the nearest station maintained by the National Data Buoy Center (www.ndbc.noaa.gov), BUZM3, approximately 40 km to the east of BR (41.4°N, 71.0°W). These estimates were based on linear regression analyses of over 500 d of concurrent wave measurements from the two sensors. Because the sites are sheltered from western wave exposure, the data were separated with respect to daily vector-averaged wind direction, as reported by BUZM3: east wind (0–180°), $H_{s,daily,BR} = 0.693H_{s,daily,BUZM3} + 0.190$, $r^2 = 0.35$, $n = 151$; west wind (180–360°), $H_{s,daily,BR} = 0.318H_{s,daily,BUZM3} + 0.296$, $r^2 = 0.20$, $n = 380$.

It was assumed that bed mussels exposed to the bores of breaking waves experienced lift, acting perpendicular to the direction of flow (Denny 1987; Bell and Gosline 1997; Carrington 2002a): lift = $\frac{1}{2} \rho U^2 C_l A_{pl}$, where ρ is the density of seawater ($1024\ kg\ m^{-3}$), U is water velocity over the mussel bed ($m\ s^{-1}$), and C_l is the lift coefficient (0.88, Denny 1987). Dislodgment occurs when lift on a mussel exceeds its attachment force. Dividing lift by A_{pl} therefore defines a critical tenacity, or Ten' , that a mussel must exceed to remain attached to the substratum: $Ten' = \frac{1}{2} \rho U_{max}^2 C_l$, where U_{max} is the maximal water velocity ($m\ s^{-1}$) experienced by a mussel during a given time interval. In this study, the time interval was established by the biweekly censusing of mussel populations, described in the following section.

Tricker's wave bore theory was used to estimate U_{\max} from the celerity of a nearshore wave as water depth approaches zero (Tricker 1964): $U_{\max} = (kgH_{\max})^{0.5}$, where k is a wave constant, g is gravitational acceleration (9.81 m s^{-2}), and H_{\max} is the height of the largest wave between censuses (approximated as the maximal $H_{s,\text{daily,BR}}$ between censuses). U_{\max} was calculated for two values of k ; $k = 1$ applies to bores of very small amplitude, whereas $k = 2$ describes larger bores (Tricker 1964). In this manner, two estimates of Ten' were calculated ($k = 1$ or 2) using the maximal daily mean significant wave height recorded between censuses. It is important to note that there is considerable uncertainty inherent in modeling surf zone flows (Gaylord 1999; Denny et al. 2003) and these calculations therefore only crudely estimate maximal hydrodynamic forces on mussels.

Ten' was used to determine the probability of dislodgment between biweekly censuses at each site. Tenacity measurements for each sample date were ranked in increasing order, and the probability p of having a tenacity less than a mussel of rank j was estimated as $p = j/(n + 1)$, where n is mussel sample size. The probability of dislodgment was determined as the maximum p among mussels with tenacities less than or equal to Ten' . Roughly half of the biweekly Ten' estimates did not coincide with monthly tenacity measurements; in these instances, tenacity distributions from the nearest preceding tenacity sample date were used to predict mussel dislodgment probability. Percentage data were arcsine transformed and the difference in predicted dislodgment between sites for each value of wave constant, k , was evaluated using a paired t -test. A nonparametric Wilcoxon signed rank test was used when data were not normally distributed.

Monitoring mortality—Mussel mortality during 2001–2003 was quantified from biweekly photoquadrats along five permanent transects through mussel beds at BR and BP (two and three transects at each site, respectively). Each transect was 3–5 m in length, and was within 15 m of the tenacity transects described above. Eight permanent rectangular quadrats ($22.5 \text{ cm} \times 17.5 \text{ cm}$) spaced evenly along each transect were photographed biweekly during spring low tides using a digital camera. Each photoquadrat was analyzed visually using a 200 random dot procedure, where mussel percentage cover on census date t , M_t , was estimated as the percentage of dots overlaying live mussels. For each quadrat, the change in mussel cover, ΔM_t , on census date t was expressed as a percentage of mussel cover on the previous census date, $t - 1$:

$$\Delta M_t = (M_t - M_{t-1})/M_{t-1} \text{ 100\%}.$$

Photoquadrats with less than 40% mussel cover were omitted from the analyses for three reasons. First, the hydrodynamic mechanism for dislodgment, excessive lift forces, assumes that flow skims over densely aggregated mussels (~100% cover). In contrast, solitary mussels are likely to be subjected to drag (Bell and Gosline 1997). Whereas the mussel density at which lift dominates is not known precisely, 40% cover is considered a conservative

cutoff given the ability of small patches of mussels to ameliorate flow at the 5-cm scale (Carrington et al. 2008, O'Donnell 2008). Second, the measurement error for the random dot technique increases with decreasing percentage cover, as the detection of rare individuals becomes unreliable. In a preliminary comparison of 40 quadrats with 40–100% mussel cover, estimates using the random dot technique were on average within 3% of measurements of images traced and quantified with an image processor (SigmaScan, SPSS). Third, the calculation of ΔM_t amplifies the absolute change in mussel cover in quadrats with few mussels. For example, an absolute loss of 5% mussel cover converts to a change of 10% for a quadrat with 50% cover, and 25% for a quadrat with 20% cover. Thus whereas the choice of 40% mussel cover as a lower cutoff for analysis is arbitrary, it minimizes these three concerns. Over 66% of the quadrats met this criterion on each census (except following a major freeze event in winter 2003, *see* Results section).

The change in mussel cover in each quadrat between censuses reflects the net effects of mussel growth, recruitment (larval settlement and postlarval migration), and mortality (Petratis 1995). For comparison with the mechanistic model that predicts mortality by wave dislodgment alone, it was necessary to further process the photoquadrat data to reduce the influence of growth and recruitment. It was assumed that positive values for ΔM_t were the result of growth or recruitment (mortality equals zero), whereas negative values reflected mortality alone. In this manner, the mortality (%) between each census, m_t , was quantified as the absolute value of all negative ΔM_t , and was set to zero for all other values of ΔM_t . Note that this algorithm likely underestimates mortality because mussels may fill in, via growth and recruitment, gaps that form before the next census (Petratis 1995). Because the sample frequency is relatively high (2 wk), it was assumed that the magnitude of this underestimation was small.

For each mortality event, defined as a mean loss of at least 3% cover, the probable cause of death was determined. Most events were considered wave dislodgment, and were characterized by the appearance of bare rock, or a "gap," in an area inhabited by live mussels in the previous census (Fig. 1). Mortality due to exposure to an extreme air condition (temperature or desiccation stress, but hereafter discussed as the former) was evidenced by a dead mussel with gaping valves. The shell remained attached to the substratum for several censuses and internal tissues were often visible. These relatively infrequent events were further confirmed by coincidence with days when extreme in situ temperatures were recorded (*see* Results section). Mortality due to predation was assumed to be negligible. In visual surveys conducted during 2001–2002, predator activity during high tide was generally weak at these wave-exposed intertidal sites. Large mobile predators, such as crabs and sea stars, were not commonly observed and the predatory gastropod *Nucella lapillus* was present from summer to early winter, but in low abundance (<5 individuals m^{-2} ; Carrington unpubl.). Empty shells with drilled holes were rarely observed.

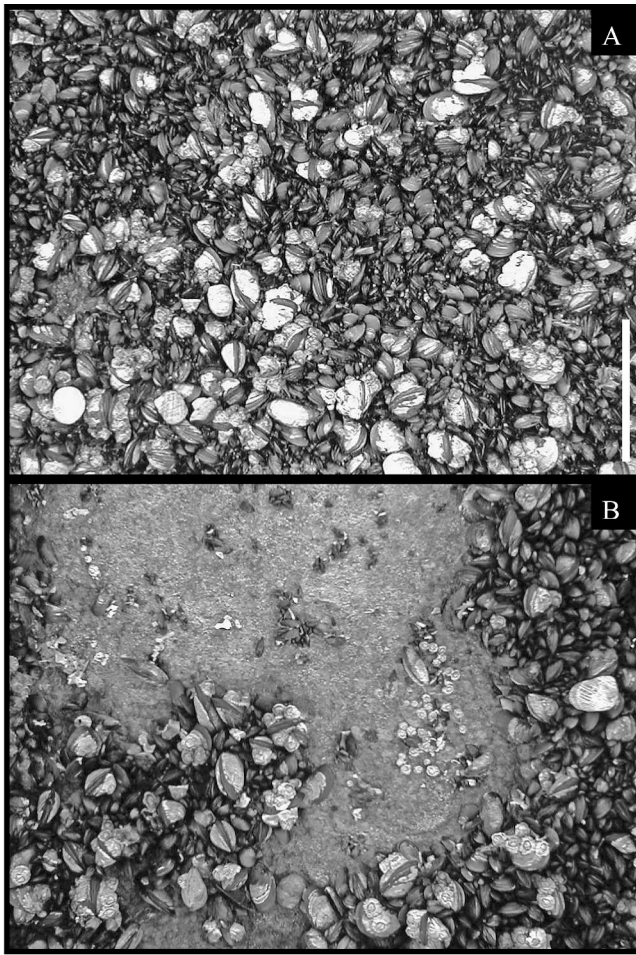


Fig. 1. Photographs of the same quadrat from Black Point, taken on (A) 03 October and (B) 21 October 2001. Mussels (*M. edulis*) were dislodged by waves between the two censuses, as evidenced by the large gap of bare rock in the latter image. Scale bar = 5 cm.

Missing values for mortality were common for any given quadrat, usually due to low mussel cover (*see above*). Wave dislodgment and temperature stress data were analyzed separately; transect means were calculated for each census date only when data from more than two quadrats were available. Percentage data were arcsine transformed and the effect of site and transect within site on mean mortality over time was evaluated using a repeated-measures design. A nonparametric Friedman's test was used when the data were not normally distributed. Monthly mortality was calculated as the sum of mean values of each month's censuses, and a two-way ANOVA evaluated the effects of month and year on monthly mortality. Linear regression analysis was used to evaluate the ability of the mechanistic model to predict the observed variation in wave dislodgment. All statistical tests were conducted using SigmaStat version 3.1 (Systat).

Results

The environmental conditions to which mussels were exposed varied seasonally during 2001–2003 (Fig. 2A,B).

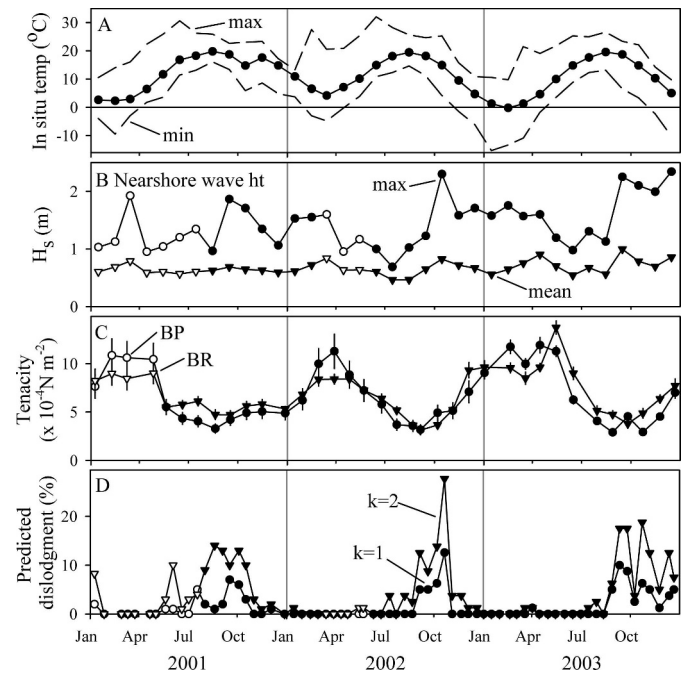


Fig. 2. Environmental conditions, tenacity, and predicted dislodgment for *M. edulis* in Rhode Island, 2001–2003. Vertical reference bars distinguish years. (A) Monthly summary of in situ temperature. Circles are means and dashed lines are monthly minima and maxima temperatures. (B) Monthly summary of significant wave heights recorded at a nearshore location at Bass Rock. Circles and triangles are the mean and maximum, respectively, of each month's daily mean. (C) Tenacity of *M. edulis* at Bass Rock (circles) and Black Point (triangles). Symbols are mean \pm SE of 40–50 samples. (D) Mussel dislodgment predicted from the mechanistic model following the biweekly field census schedule. Symbols indicate the method used to estimate U_{max} , either $k = 1$ (circles) or $k = 2$ (triangles). Open symbols in panels B–D represent estimates of missing data (>10 d, *see Methods* for details).

The monthly average intertidal temperature typically ranged from 0°C in winter to 20°C in summer. The most extreme temperatures coincided with periods of emersion during low tide. The winter of 2003 was the coldest of the 3 yr, with minimum temperatures below -10°C recorded from January through March. In situ temperatures exceeding 30°C were recorded in June of 2001 and 2002, but were not observed in 2003. Nearshore wave conditions measured at BR, $H_{s,mean}$, and $H_{s,max}$ were generally calmer in summer months. The seasonal pattern is less distinct in $H_{s,max}$, with considerable interannual variation in the timing of large storm events.

Mean tenacity also varied seasonally at BR and BP, increasing in late winter and early spring and decreasing in warmer summer months (Fig. 2C). Tenacity did not differ between sites (paired t -test, $t = -0.857$, $df = 35$, $p = 0.40$). Similarly, predicted dislodgment did not differ between BR and BP for either value of k (Wilcoxon signed rank test, $n = 70$; $k = 1$: $W = -63$, $p = 0.25$; $k = 2$: $W = 125$, $p = 0.40$). Predictions for the two sites were therefore pooled for subsequent analyses. For both values of k , dislodgment events were predicted to increase in frequency and severity

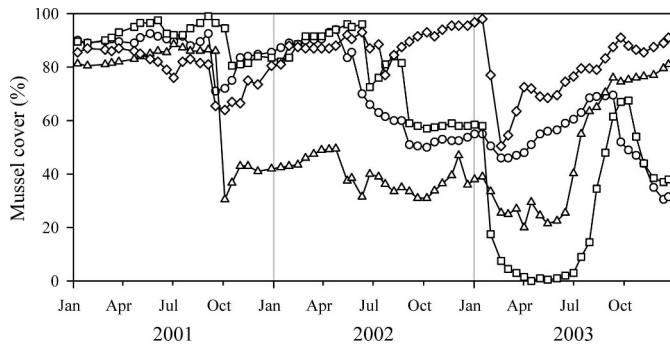


Fig. 3. Representative time series of *M. edulis* cover in four quadrats along one Black Point transect during 2001–2003. Vertical reference bars distinguish years. Each symbol corresponds to a different quadrat along the transect. A sharp decline in mussel cover at a given census represents a mortality event; the precise timing and severity of these events varied among quadrats. Mortalities due to temperature stress were observed in June 2002 (heat) and January 2003 (freeze). All other mortalities were categorized as wave dislodgment. Note that quadrats can increase in percentage cover over time, due to a combination of growth and recruitment (larval settlement and postlarval migration).

during the latter half of each year (Fig. 2D). Mussel dislodgment was predicted to be rare from January to July, despite the occurrence of extreme storms during this time (e.g., March 2001). When the more conservative method for estimating U_{\max} , $k = 1$, was used, predicted dislodgment was lower overall, never exceeding 15%.

Mortality was commonly observed in all photoquadrats from both sites during 2001–2003, and the precise timing and severity of these events varied among quadrats (Fig. 3). A severe freeze event in early 2003 reduced mussel cover in most quadrats to below 40%; thus mortality estimates were not available from 04 March to 12 April 2003. Wave dislodgment was the most frequent source of mortality, with the largest single loss of 65% observed in a BR quadrat on 09 October 2003. Within each site, wave mortality did not differ significantly among transects (BR: paired t -test, $t = 0.723$, $df = 21$, $p = 0.48$; BP: Friedman's test on ranks, $\chi^2 = 0.49$; $n = 66$, $p = 0.78$; data not shown). Data were therefore pooled within sites, revealing a general trend of increased wave dislodgment in the latter half of each year (Fig. 4A). The highest mean wave dislodgment for a site was 11.6%, observed at BR on 09 October 2003. Whereas wave dislodgment was significantly higher at BP than BR (paired t -test, $t = 2.58$, $df = 65$, $p < 0.05$), the magnitude of the difference between sites was small (3-yr means of 1.2% and 1.5% for BR and BP, respectively). Furthermore, data were often not available for one of the BR transects (<2 quadrats in approximately half of the censuses); thus transects from both sites were pooled for further analyses.

Wave dislodgment varied over time, with the largest mortality events occurring from late August to the end of October (Fig. 4B). In the 3 yr studied, no wave dislodgment events were observed from November to July of the following year. A similar pattern is evident for monthly mortality (Fig. 5A); wave mortality varied significantly with census month, but not year (Table 1; $p < 0.001$ and p

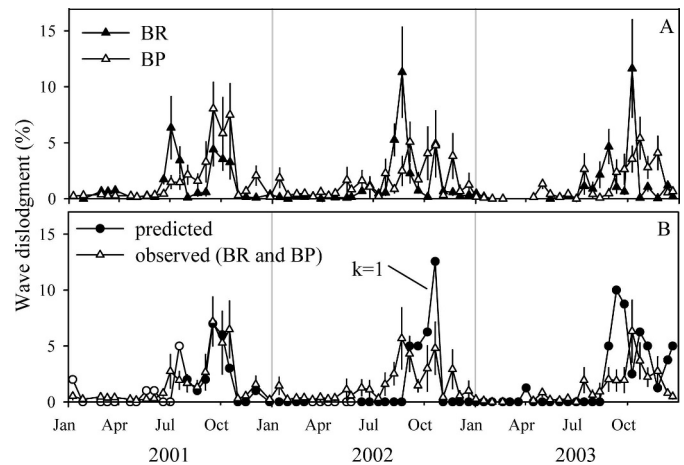


Fig. 4. Wave dislodgment of *M. edulis* in biweekly censuses of intertidal sites in Rhode Island. (A) Mean (\pm SE) observed dislodgment for BR (closed triangles) and BP (open triangles), pooled among quadrats on all transects. Sites with fewer than five quadrats satisfying the criterion for analyses were not included. (B) Observed mean dislodgment (\pm SE, triangles) pooled from BR and BP quadrats. Predictions using the lower wave constant ($k = 1$, circles) closely matched the range of observed values, although the precise timing and magnitude of peaks in dislodgment were not always in alignment. Open circles represent estimates of missing data (>10 d, see Methods for details). Predictions using the higher constant ($k = 2$; Fig. 2) greatly overestimated actual mortalities and thus were not evaluated further.

$= 0.08$, respectively). In pairwise multiple comparisons (Holm-Sidek method, $p < 0.05$), months with the highest wave mortality (August, September, and October) were statistically indistinguishable, as were the months with the lowest mortality (November to July). Overall, cumulative mortality from wave dislodgment was relatively consistent among years, ranging from 26% to 34% annually (Table 2).

Mortality events due to temperature stress were highly sporadic (Fig. 5B). Modest mortality (<5%) was observed in the summers of 2001 and 2002, coinciding with in situ temperatures over 30°C (Fig. 2). In contrast, massive mortality (35–50%) due to freezing was observed in January and February 2003 (Fig. 5). Compared with the first 2 yr of the study, the winter of 2003 was much colder and in situ temperatures below -10°C were observed over several months (Fig. 2). Overall, cumulative mortality from temperature stress was inconsistent among years, ranging from 4% to 84% annually (Table 2). When averaged over the 3-yr study period, mortalities due to wave dislodgment and temperature stress were similar (32% and 31%, respectively; Table 2).

Predicted wave dislodgment using the lower wave constant ($k = 1$) closely matched the range of observed values, although the precise timing and magnitude of peaks in dislodgment were not always in alignment (Fig. 4B). A linear regression of observed vs. predicted values was significant ($r^2 = 0.38$, $p < 0.001$, $n = 63$, observed = $0.077 + 0.378 \times$ predicted). Removing estimated predicted values did not alter this analysis substantially ($r^2 = 0.38$, $p < 0.001$, $n = 49$, observed = $0.083 + 0.378 \times$ predicted). Because of this small difference, predictions on the basis of

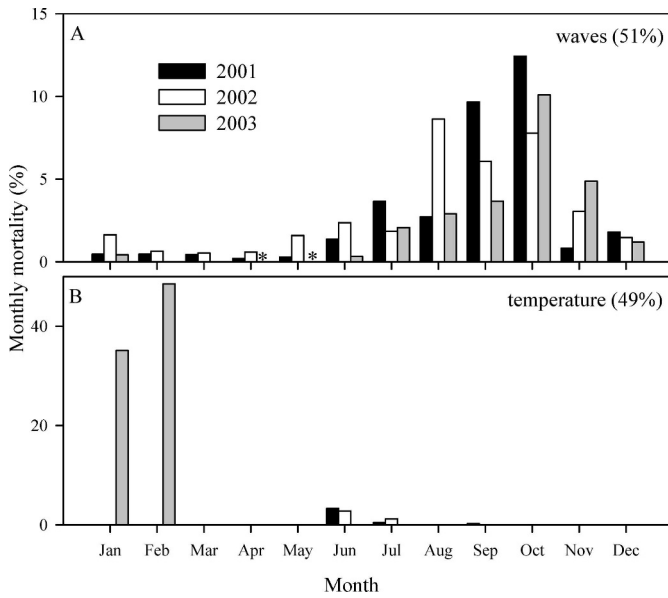


Fig. 5. Agents of mortality of intertidal *M. edulis*, 2001–2003. Bars represent the total mortality observed each month due to (A) wave dislodgment or (B) temperature stress. Shading represents year, as indicated by the legend. Asterisks denote months with missing data. When summed over the study period, the contributions of wave dislodgment and temperature stress to total mortality were similar (51% and 49%, respectively; Table 2).

estimated inputs were used in all subsequent analyses. Predictions using the higher constant ($k = 2$; Fig. 2) greatly overestimated actual mortalities and thus were not evaluated further.

When averaged over 3 yr, the predictions of the mechanistic model matched observed patterns, with min-

Table 1. Summary of two-way ANOVA of monthly wave dislodgment in mussel populations, with census month and year as factors. Data were arcsine transformed before analysis. Because data for some months were missing in 2003, interactions between the two factors were not evaluated. In pairwise multiple comparisons (Holm-Sidak method, $p < 0.05$), months with the highest wave mortality (August, September, and October) were statistically indistinguishable, as were the months with the lowest mortality (November to July). MS = mean square.

Source of variation	df	MS	F	P
Month	11	0.0218	10.543	<0.001
Year	2	0.0057	2.780	0.086
Residual	20	0.0021		
Total	33	0.0087		

Table 2. Summary of mortality observed in biweekly censuses of mussel populations in Rhode Island, 2001–2003. Values in parentheses are the relative contribution (%) of each physical agent to total mortality. SE = standard error.

	2001	2002	2003	Mean ± SE
Cumulative annual mortality (%)				
Wave dislodgment	34.3 (89)	36.2 (90)	25.6 (23)	32.0 ± 3.3 (51)
Temperature stress	4.2 (11)	4.0 (10)	83.7 (77)	30.6 ± 26.5 (49)
Total	38.5	40.2	109.3	62.7 ± 23.3

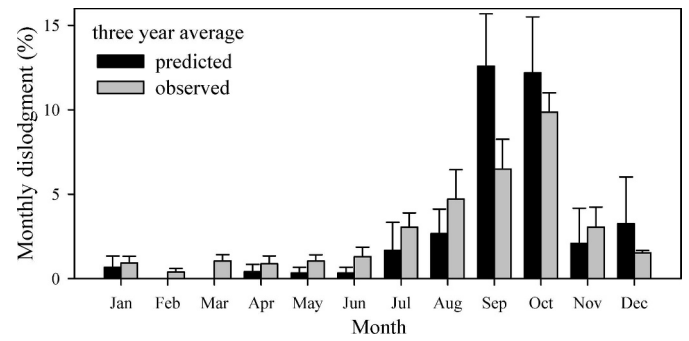


Fig. 6. Summary of mussel dislodgment in Rhode Island, 2001–2003. Bars are means (\pm SE) of monthly values of predicted (black) and observed (gray) mortality.

imal dislodgment from November to July and peak dislodgment in September and October (Fig. 6). Overall, the mechanistic model accounts for over 80% of the variation in mean monthly wave dislodgment during the study (linear regression, $r^2 = 0.85$, $p < 0.001$, $n = 12$, observed = $0.08 + 0.574 \times$ predicted).

Discussion

This study represents the first field validation of the mechanistic approach of Denny (1995) to predict fine-scale temporal patterns of wave dislodgment. The simple mechanistic model, which pits wave activity against attachment strength, accounted for 38% of the variation in bimonthly mussel dislodgment from 2001 to 2003. When the data were consolidated to emphasize seasonal trends, the model accounted for 85% of the variation in mean monthly mussel dislodgment. Importantly, wave activity alone was a poor predictor of wave disturbance; dislodgment was only observed when large storms coincided with periods of weak attachment. These results underscore the importance of evaluating environmental challenges in the context of physiological tolerances, both of which may vary spatially and temporally. In short, a mechanistic approach is necessary to predict environmental stress (Helmuth et al. 2005; Wang and Overgaard 2007).

Indeed, the strong seasonality in wave dislodgment observed in Rhode Island mussels is driven primarily by the annual cycle in attachment strength, a physiological process, rather than wave climate. This trait plasticity is a common feature of *M. edulis* (Price 1980; Hunt and Scheibling 2001b; Carrington 2002a) and other mussel species (Zardi et al. 2007), but its cause is not known. Several correlative studies suggested that the seasonal

variation in attachment strength reflects increased byssal thread production in response to increased wave action, thereby enhancing attachment strength during storm season (Price 1982; Carrington 2002a; Zardi et al. 2007). Through a combination of field and laboratory experiments, however, Moeser et al. (2006) found little support for this hypothesis. In *M. edulis* in Rhode Island, byssal thread production was greatest during calm summer months, not winter, perhaps due to increased metabolism with elevated water temperatures or energetic constraints during the spawning period (Carrington 2002a). Instead, the annual cycle in attachment strength was best explained by seasonal variation in thread material properties (strength, extensibility, and durability); mussels were weaker in summer and late fall because they produced mechanically inferior threads that decayed rapidly (Moeser and Carrington 2006). Given the economic and ecological importance of mussels in temperate waters worldwide, the proximal cause of this variation in material properties is an important area of future study.

The rate of wave dislodgment observed in *M. edulis*, approximately 30% per year, was considerably higher than that predicted for many other wave-swept organisms (<5%, Denny 2006). Kelps, limpets, barnacles, and sea urchins have extremely high safety factors (the ratio of attachment strength to applied stress, where values ≤ 1 imply dislodgment) and this “overdesign” renders individuals largely immune to hydrodynamic stresses unless first damaged by predation or epibionts (Denny 2006). *Mytilus edulis*, however, does not maintain a consistently high safety factor (Carrington 2002a). This relatively low investment in attachment strength may represent an evolutionary strategy to reallocate resources to growth and reproduction (Carrington 2002a,b; Zardi et al. 2007).

One powerful insight provided by the mechanistic approach is that it pinpoints what weather patterns may be most damaging to an organism. In the case of mussels in southern New England states of the United States, risk of wave dislodgment is greatest when attachment strength declines each August through October. Large waves in this region are produced by two types of cyclonic storms, tropical hurricanes and extratropical “Nor’easters” (so named for their northeasterly winds). Activity of the former peaks during August–September–October (Goldenberg et al. 2001), whereas the latter is most severe from September to April. Of these storm types, it is hurricane activity that poses the greatest threat to mussels because it is most frequent in months when attachment is weakest and has increased in frequency and severity in recent years, a trend that has been linked to accelerated increases in sea surface temperature (Goldenberg et al. 2001; Webster et al. 2005). The predicted consequence of this large-scale climatic perturbation to mussels in Rhode Island is more frequent and severe dislodgment events compared with those that occurred in previous decades.

Several caveats concerning the mechanistic model are worth noting. First, the model presented here was tailored to a specific site in Rhode Island, and may not apply to mussels in other locales. Several recent studies suggest that

mussels in Canadian Atlantic waters exhibit dislodgment dynamics similar those presented here (Hunt and Scheibling 2001b; Lachance et al. 2008). In the United Kingdom, however, weak attachment strength for *M. edulis* occurs in spring (Price 1980) and thus dislodgment is predicted to be greatest in spring rather than fall (Carrington 2002b). The difference in the timing of disturbance and the appearance of new patches for colonization may influence community dynamics at these sites on opposite sides of the Atlantic (Levin and Paine 1974).

Second, the fact that the model accounted for a significant proportion of the variation in dislodgment does not imply that each step is represented correctly. Numerous simplifying assumptions concerning hydrodynamic forces on mussels were made and warrant further scrutiny. For example, maximal significant wave height is a statistical term used to describe the distribution of wave heights and does not represent the largest wave during a time interval (Denny et al. 1985). Additionally, the value we used for wave constant ($k = 1$) was not tested empirically; water velocities produced by waves hitting rocky shores are notoriously variable, in part due to topographic complexities and tide effects (Gaylord 1999; Denny et al. 2003). Further, patch formation likely involves the local destabilization of mussels following the removal of an individual from the bed (Denny 1987; Guichard et al. 2003), a more complex process than is considered here. Indeed, these simplifying assumptions may be responsible for the model’s overall underestimation of observed dislodgment, evidenced by a regression slope less than one. Direct measurements of wave forces on mussels in the surf zone would clarify many of these issues.

Third, the dislodgment predictions relied on estimates to fill gaps in the primary data. We have confidence in these estimates for a number of reasons. Six years of tenacity measurements (Carrington 2002a, this study) reveal a surprisingly robust seasonal cycle, one that is consistent with the four monthly values estimated in this study. More extensive were the gaps in the wave data, but these occurred in the first half of the year, a period when mussels are not prone to dislodgment anyway because of their strong attachment (Carrington 2002a). Thus no substantial dislodgment predictions relied upon estimated data; the exclusion of these data does not alter the conclusions of this study.

Our 3-yr monitoring of mussel dislodgment by waves provided a unique opportunity to quantify another source of mortality, temperature stress. Modest mortality events (4%) were observed in the summers of 2001 and 2002, whereas a severe freezing event (84%) occurred during winter of the following year (Table 2). Overall, temperature stress accounted for 49% of the mortality observed during the study period, a proportion comparable with wave dislodgment. Thus temperature is clearly an important environmental factor influencing the ecology of intertidal mussels, and mechanistic models (Helmuth et al. 2002; Gilman et al. 2006) are powerful tools for predicting when and where extreme weather conditions coincide with tidal emergence. Interestingly, it was a freezing event that produced catastrophic mortality, despite the fact that the

study was conducted in the southern range of distribution of *M. edulis* in the Northwest Atlantic. This unexpected result suggests that freeze tolerance may be an important physiological driver of intertidal species distribution, a process that is often overlooked in previous studies that focused on the distribution and response of organisms in geographic “hot spots” (Helmuth et al. 2002; Tomanek and Helmuth 2002).

Of the two common agents of mortality in this study, wave dislodgment emerges as more consistent from year to year, ranging between 25% and 36%. This is at first surprising, given the uncertainty associated with measuring and predicting temporal and spatial patterns of wave forces on organisms, as discussed earlier. In the case of mussel dislodgment, however, much of this environmental variation is masked when attachment strength is strong (ensuring safety factor is high, Carrington 2002a). Large waves cause dislodgment only when attachment strength cycles through a weak state. In comparison, the relative importance of mortality by temperature stress varied considerably in the years studied, despite little variation in the annual cycle of mean temperature. This stochasticity is largely due to the requirement that two physical conditions, extreme temperature and tidal emergence in air, must co-occur to thermally stress intertidal organisms (Helmuth et al. 2002, 2006; Gilman et al. 2006).

This study demonstrates that mussels, which form the foundation of many coastal ecosystems, are subject to at least two environmental stressors that have been linked to large-scale climate change (waves and temperature). This is a likely scenario for organisms worldwide, and the future challenge for ecologists will be to unravel where and when such stressors exceed physiological thresholds, and the extent to which synergisms are involved. To this end, mechanistic models hold great promise to predict temporal and spatial patterns of physical forcing, patterns that cannot be predicted from environmental forecasts alone.

Acknowledgments

We thank Hillary Welsh Vargas for the analysis of wind and wave data, and Graham Ferrier, George Kamajian, Eric Zabel, and Shanna Brazee for assistance with field sampling. We are grateful to numerous undergraduate students for photoquadrat analysis, especially Mike Concodello, Ben Rutt, Jessica Ritchie, Vince Politano, and Amanda Chesler. Ken Sebens provided diving support and made helpful comments on the manuscript, as did Mark Denny, Robert Paine, Eric Tytell, Josef Ackerman, and two anonymous reviewers.

Funding was provided by National Science Foundation awards to E.C. (OCE-97118893, OCE-0082605, and OCE-0322892) as well as the Coastal Fellows Program of the University of Rhode Island.

References

- BELL, E. C., AND J. M. GOSLINE. 1997. Strategies for life in flow: Tenacity, morphometry, and probability of dislodgment of two *Mytilus* species. *Mar. Ecol. Prog. Ser.* **159**: 197–208.
- BERTOCCI, I., E. MAGGI, S. VASELLI, AND L. BENEDETTI-CECCHI. 2005. Contrasting effects of mean intensity and temporal variation of disturbance on a rocky seashore. *Ecology* **86**: 2061–2067.
- CARRINGTON, E. 2002a. Seasonal variation in the attachment strength of blue mussels: Causes and consequences. *Limnol. Oceanogr.* **47**: 1723–1733.
- . 2002b. The ecomechanics of mussel attachment: From molecules to ecosystems. *Integ. Comp. Biol.* **42**: 846–852.
- , G. M. MOESER, S. B. THOMPSON, L. C. COUTTS, AND C. A. CRAIG. 2008. Mussel attachment on rocky shores: The effect of flow on byssus production. *Integ. Comp. Biol.* **48**: 808–822.
- DAYTON, P. K. 1971. Competition, disturbance, and community organization—provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* **41**: 351–389.
- DENNY, M. W. 1987. Lift as a mechanism of patch initiation in mussel beds. *J. Exp. Mar. Biol. Ecol.* **113**: 231–245.
- . 1995. Predicting physical disturbance—mechanistic approaches to the study of survivorship on wave-swept shores. *Ecol. Monogr.* **65**: 371–418.
- . 2006. Ocean waves, nearshore ecology, and natural selection. *Aquat. Ecol.* **40**: 439–461.
- , T. L. DANIEL, AND M. A. R. KOEHL. 1985. Mechanical limits to size in wave-swept organisms. *Ecol. Monogr.* **55**: 69–102.
- , L. P. MILLER, M. D. STOKES, L. J. H. HUNT, AND B. S. T. HELMUTH. 2003. Extreme water velocities: Topographical amplification of wave-induced flow in the surf zone of rocky shores. *Limnol. Oceanogr.* **48**: 1–8.
- GAYLORD, B. 1999. Detailing agents of physical disturbance: Wave-induced velocities and accelerations on a rocky shore. *J. Exp. Mar. Biol. Ecol.* **239**: 85–124.
- GILMAN, S. E., D. S. WETHEY, AND B. HELMUTH. 2006. Variation in the sensitivity of organismal body temperature to climate change over local and geographic scales. *Proc. Natl. Acad. Sci. USA* **103**: 9560–9565.
- GOLDENBERG, S. B., C. W. LANDSEA, A. M. MESTAS-NUNEZ, AND W. M. GRAY. 2001. The recent increase in Atlantic hurricane activity: Causes and implications. *Science* **293**: 474–479.
- GUICHARD, F., P. M. HALPIN, G. W. ALLISON, J. LUBCHENCO, AND B. A. MENGE. 2003. Mussel disturbance dynamics: Signatures of oceanographic forcing from local interactions. *Am. Nat.* **161**: 889–904.
- HARLEY, C. D. G., AND OTHERS. 2006. The impacts of climate change in coastal marine systems. *Ecol. Lett.* **9**: 228–241.
- HELMUTH, B. S. T. 1998. Intertidal mussel microclimates: Predicting the body temperature of a sessile invertebrate. *Ecol. Monogr.* **68**: 51–74.
- , AND OTHERS. 2006. Mosaic patterns of thermal stress in the rocky intertidal zone: Implications for climate change. *Ecol. Monogr.* **76**: 461–479.
- , C. D. G. HARLEY, P. M. HALPIN, M. O'DONNELL, G. E. HOFMANN, AND C. A. BLANCHETTE. 2002. Climate change and latitudinal patterns of intertidal thermal stress. *Science* **298**: 1015–1017.
- HELMUTH, B., J. G. KINGSOLVER, AND E. CARRINGTON. 2005. Biophysics, physiological ecology, and climate change: Does mechanism matter? *Annu. Rev. Physiol.* **67**: 177–201.
- HUGHES, T. P., AND OTHERS. 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* **301**: 929–933.
- HUNT, H. L., AND R. E. SCHEIBLING. 2001a. Patch dynamics of mussels on rocky shores: Integrating process to understand pattern. *Ecology* **82**: 3213–3231.
- , AND ———. 2001b. Predicting wave dislodgment of mussels: Variation in attachment strength with body size, habitat, and season. *Mar. Ecol. Prog. Ser.* **213**: 157–164.

- KOEHL, M. A. R. 1999. Ecological biomechanics of benthic organisms: Life history mechanical design and temporal patterns of mechanical stress. *J. Exp. Biol.* **202**: 3469–3476.
- LACHANCE, A. A., B. MYRAND, R. TREMBLAY, V. KOUTITONSKY, AND E. CARRINGTON. 2008. Biotic and abiotic factors influencing attachment strength of blue mussels *Mytilus edulis* in suspended culture. *Aquat. Biol.* **2**: 119–129.
- LEVIN, S. A., AND R. T. PAINE. 1974. Disturbance, patch formation, and community structure. *Proc. Natl. Acad. Sci. USA* **71**: 2744–2747.
- LEWIS, J. R. 1964. The ecology of rocky shores. English Univ. Press.
- LUBCHENCO, J., AND B. A. MENGE. 1978. Community development and persistence in a low rocky intertidal zone. *Ecol. Monogr.* **48**: 67–94.
- MADIN, J. S., AND S. R. CONNOLLY. 2006. Ecological consequences of major hydrodynamic disturbances on coral reefs. *Nature* **444**: 477–480.
- MENGE, B. A. 1976. Organization of the New England rocky intertidal community: Role of predation, competition, and environmental heterogeneity. *Ecol. Monogr.* **46**: 355–393.
- MOESER, G. M., AND E. CARRINGTON. 2006. Seasonal variation in mussel byssal thread mechanics. *J. Exp. Biol.* **209**: 1996–2003.
- , H. LEBE, AND E. CARRINGTON. 2006. Seasonal influence of wave action on thread production in *Mytilus edulis*. *J. Exp. Biol.* **209**: 881–890.
- O'DONNELL, M. J. 2008. Reduction of wave forces within patches in mussel beds. *Mar. Ecol. Prog. Ser.* **362**: 157–167.
- PAINE, R. T. 1974. Intertidal community structure: Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* **15**: 93–120.
- PARMESAN, C., AND G. YOHE. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37–42.
- PETRAITIS, P. S. 1995. The role of growth in maintaining spatial dominance by mussels (*Mytilus edulis*). *Ecology* **76**: 1337–1346.
- PÖRTNER, H. O., AND R. KNUST. 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* **315**: 95–97.
- PRICE, H. A. 1980. Seasonal variation in the strength of byssal attachment of the common mussel *Mytilus edulis* L. *J. Mar. Biol. Assoc. UK* **60**: 1035–1037.
- . 1982. An analysis of factors determining seasonal variation in the byssal attachment strength of *Mytilus edulis*. *J. Mar. Biol. Assoc. UK* **62**: 147–155.
- TOMANEK, L., AND B. HELMUTH. 2002. Physiological ecology of rocky intertidal organisms: A synergy of concepts. *Integ. Comp. Biol.* **42**: 771–775.
- TRICKER, R. A. R. 1964. Bores, breakers, waves, and wakes: An introduction to the study of waves on water. American Elsevier.
- WANG, T., AND J. OVERGAARD. 2007. The heartbreak of adapting to global warming. *Science* **315**: 49–50.
- WEBSTER, P. J., G. J. HOLLAND, J. A. CURRY, AND H. R. CHANG. 2005. Changes in tropical cyclone number, duration, and intensity in a warming environment. *Science* **309**: 1844–1846.
- WOLCOTT, B. D. 2007. Mechanical size limitation and life-history strategy of an intertidal seaweed. *Mar. Ecol. Prog. Ser.* **338**: 1–10.
- ZARDI, G. I., C. D. MCQUAID, AND K. R. NICASTRO. 2007. Balancing survival and reproduction: Seasonality of wave action, attachment strength and reproductive output in indigenous *Perna perna* and invasive *Mytilus galloprovincialis* mussels. *Mar. Ecol. Prog. Ser.* **334**: 155–163.
- , K. R. NICASTRO, C. D. MCQUAID, M. RIUS, AND F. PORRI. 2006. Hydrodynamic stress and habitat partitioning between indigenous (*Perna perna*) and invasive (*Mytilus galloprovincialis*) mussels: Constraints of an evolutionary strategy. *Mar. Biol.* **150**: 79–88.

Associate editor: Josef D. Ackerman

Received: 23 October 2007
 Accepted: 03 November 2008
 Amended: 24 December 2008