Vol. 362: 157–167, 2008
doi: 10.3354/meps07435

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published June 30

OPEN ACCESS

Reduction of wave forces within bare patches in mussel beds

Michael J. O'Donnell[1,2,*]

[1]Hopkins Marine Station, Stanford University, Pacific Grove, California 93950, USA

[2]*Present address:* Marine Science Institute, University of California Santa Barbara, Santa Barbara, California 93106-9150, USA

ABSTRACT: Wave forces on rocky shores can be an important agent structuring the ecology of intertidal communities. Proximity to nearby structures, such as those formed by mussel beds, may buffer organisms from the full danger of wave forces. This experiment measured the reduction of wave forces experienced by an object due to a surrounding artificial mussel bed. By being situated within a small (5 cm in radius) bare patch in this bed, a test object 1 cm in diameter experienced 30 to 62% reduction in wave forces compared to an unsheltered object. The effect drops off as bare patch size increases and is not noticeable in patches with radii of 15 cm or larger. This level of force reduction is relevant for a number of species living on rocky shores since measured, unmitigated wave forces exceed published tenacity values of many organisms. Thus, providing protection from wave forces offers a physical mechanism by which mussel beds help structure intertidal communities.

KEY WORDS: Intertidal · Wave mechanics · Mussel bed · Hydrodynamic force

INTRODUCTION

The intertidal regions of wave-swept shores are subjected to rapid water movements that, along with the resulting hydrodynamic forces, contribute to the intense levels of physical disturbance characteristic of this habitat (e.g. Dayton 1971, Menge 1976, Paine & Levin 1981, Bell & Gosline 1997). Organisms reduce these dangers through a variety of means. Some utilize streamlined shapes and tenacious attachments (Koehl 1984, Gaylord & Denny 1997). Others actively choose locations within their habitat where they presumably find shelter from hydrodynamic forces, either at settlement for sessile organisms (e.g. Wethey 1986) or as mobile adults (e.g. Emson & Faller-Fritsch 1976, Raffaelli & Hughes 1978, Underwood & Chapman 1989, Addy & Johnson 2001). Previous investigations have generally inferred that topographic complexity, by providing shelter from flow, leads to reduction in hydrodynamic forces; however, this assumption has not been directly tested under natural conditions in the surf zone. Understanding variation in wave-induced forces around topographic structures is necessary for understanding the influence of hydrodynamic stresses on the distribution of organisms.

Organisms themselves are often an important source of topographic complexity on wave-swept shores. On many temperate wave-swept shores, the community of intertidal organisms is dominated by space-occupying species, which add to the shore's topographic structure (e.g. musssels and barnacles, Dayton 1971, Paine & Levin 1981). Because of the structure they create, these species should have a noticeable effect on the flow of water around them.

Where they occur, mytilid mussels are often the competitive dominant for space, forming dense monocultures that occupy the majority of the primary substratum. The ecological interactions that lead to mussel dominance have been well studied (e.g. Dayton 1971, Paine 1974), as have the mechanical mechanisms by which mussels thrive in highly wave-exposed environments (Waite 1986, Bell & Gosline 1997, Hunt & Scheibling 2001).

Despite their propensity for excluding other organisms from primary space on intertidal rocks, mussel beds host diverse infaunal communities (Hewatt 1935,

*Email: odonnell@msi.ucsb.edu

Dittmann 1990, Hammond & Griffiths 2004). There are a number of factors that account for the richness of communities living within mussel beds. For example, mussels provide protection from predators (Thiel & Ullrich 2002), trap passive larvae (Gutierrez et al. 2003), and form a buffer from high temperatures at low tide (Stephens & Bertness 1991). It is also possible that mussel beds provide shelter from wave forces. Lists of infaunal species found within mussel beds (e.g. Hewatt 1935, Suchanek 1979) contain organisms commonly associated with such low-flow habitats as mudflats and sand (e.g. peanut worms, amphipods), which lack the means to robustly attach to the substratum. Removing beds of mussels, even on highly wave-exposed shores, reveals pockets of loose sediment that have accumulated beneath the shells. These observations suggest that mussel beds greatly reduce hydrodynamic forces within their matrix. There have been a few attempts to make such connections directly. For instance, Hammond & Griffiths (2004) showed that the diversity of infauna varied with the level of wave exposure, reaching maxima at high and low levels of wave exposure, presumably due to interactions with the flow environment, but they did not delve into the mechanisms underlying their observations. Mussel beds are also known to provide hydrodynamic protection for their own members (Denny 1987).

These effects may extend beyond the bed itself. Patches of bare space within mussel beds are important areas for colonization of intertidal shores, and the dynamics of bare patches in mussel beds on wave-swept shores are an important component of the population structure of this region (Levin & Paine 1974, Paine & Levin 1981). Investigators have hypothesized that reducing wave forces is a potential mechanism by which bare patches in mussel beds help to shape the communities living within them. Suchanek (1979) showed that on rocks surrounding beds of mussels, mobile grazers foraged to a distance of about 30 cm away from the edge of the bed, leaving distinct grazing halos around the beds. These ecological effects were hypothesized to result, in part, from protection from wave impacts.

Despite speculated connections, direct measurements have not been made on the effect of mussel beds on flow and associated hydrodynamic forces in the area outside, but adjacent to, the beds themselves. To fill this gap, this study quantifies the reduction of hydrodynamic forces within a bare patch in an artificial mussel bed and explores the relationship between patch size and force reduction. By comparison with previous estimates of bare patch size within mussel beds and tenacity of intertidal organisms, it seeks to explore the potential ecological significance of reduction in wave force.

MATERIALS AND METHODS

Study locations. Forces experienced by small spheres were measured while connected to electronic force transducers. While not a specific model of any particular organism, spheres are excellent measurement tools because they are non-directional and provide reproducible measures of hydrodynamic forces. A sphere can serve as a useful first approximation of the hydrodynamic behavior of some intertidal organisms, such as snails (e.g. Wahl 1996). Around one of the measurement spheres, an artificial mussel bed was manipulated to see how proximity of the bed modifies the forces experienced nearby.

These experiments were conducted in the intertidal zone at the Stanford University Hopkins Marine Station, Pacific Grove, California. The experimental apparatus (Fig. 1) consisted of an aluminum plate, $60 \times 60 \times 1.2$ cm, secured to a vertical rock face low in the surf zone and situated in a depression chiseled such that the plate edges were flush with the rock. The drag measurement sphere at the center of the plate was located ~0.5 m above mean lower low water (MLLW). The location was selected, by observation, to balance a high level of wave exposure with accessibility at low tide. Vertical surfaces are a common feature of the substratum at this site, and support large populations of

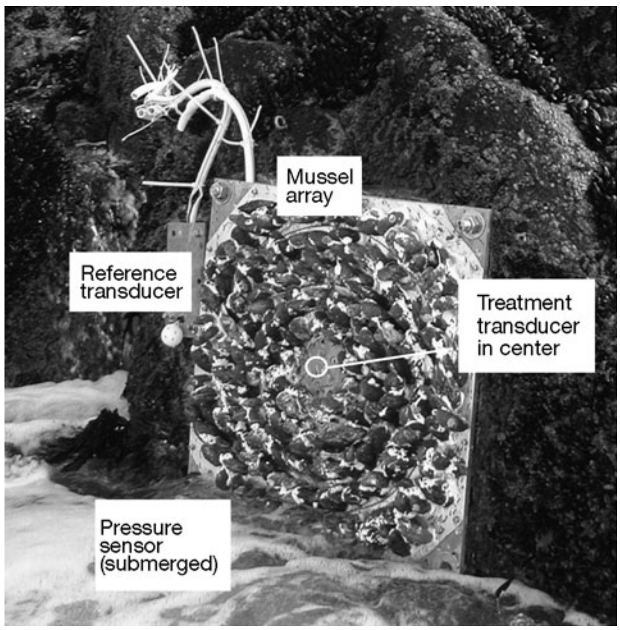

Fig. 1. Measurement apparatus mounted in the field. The plate is 60×60 cm. The drag measurement sphere connected to the treatment transducer is 0.95 cm in diameter and in the center of the clearing in the rings of mussels. The rings of mussels surrounding the ball are in the '5 cm' configuration, denoting the radius of the bare patch in the center

mussels, although they are not necessarily characteristic of intertidal mussel beds at other sites. Placing the plate on a vertical surface increased the exposure to waves that had not dissipated most of their energy in breaking over a horizontal bench (Denny et al. 2003). Thus, these experiments examine a relatively extreme flow situation where protection from wave force is likely to have the greatest biological impact. It is important to note that these measurements were conducted at only a single measurement location along the shore. Thus, extrapolation of these results to other locations requires great care, as waves breaking in different locations will experience different interactions with shoreline topography.

Roughness arrays. The drag measurement sphere was located in a gap in an artificial mussel bed, and the size of this gap was varied at each low tide. The bed consisted of epoxy casts of mussels *Mytilus californianus* attached to a nested series of concentric rings of aluminum plate. Casts were made by taking unoccupied shells from the environment and casting them in Silastic Rubber S (Dow Corning); these molds were then filled with polyester resin to make replica mussels. Casts came from 5 different mussels (lengths: 77, 65, 60, 60, and 51 mm), each used with approximately equal frequency. Mussels were selected haphazardly and attached to the aluminum rings using Z-Spar (Splash Zone Compound A-788, Kop-Coat). Supplementing these cast mussels were smaller mussel shells filled with resin and interspersed in the array. Mussels were arranged on the plate to mimic the appearance of actual mussel beds, although they were slightly less densely packed to allow removal of individual rings. Though the largest mussels were 77 mm long, they were placed at an angle to the plate, resulting in a bed with a thickness of ~50 mm. Due to their low density (~600 ind. m^{-2}), the artificial bed allowed water to flow more freely through the bed structure than would natural mussel beds, likely resulting in higher hydrodynamic forces than would be expected if the beds were packed naturally. Thus, although this sparse packing was not desirable, it should result in a conservative estimate of the potential protection due to natural mussel beds. Fig. 1 shows the plate, with roughness arrays, installed in the field.

The total array consisted of 6 rings of mussels of various inner diameters (1, 5, 10, 15 cm). The outer diameters of the rings were 5 cm larger than the inner diameter (the plate material was 0.16 cm thick). The outermost ring was shaped to reach the outer edge of the square plate. The innermost ring had mussel casts within 1 cm of the drag sphere on the treatment transducer. Subsequent treatments, in which rings were removed from the inside, had mussels within 5, 10, or 15 cm of the treatment transducer, equivalent to the radius of a bare patch within a mussel bed. The final treatment was with all rings removed from them plate, leaving a surface free of mussel-sized structures for at least 40 cm from the force transducer. Data sets are identified by the distance from the transducer to the edge of the mussel bed.

The force measurements were conducted with 2 force transducers mounted beneath the aluminum plates affixed to the rock surface. The 'treatment' transducer (mounted under the plate described above) had a 0.95 cm sphere attached to it via fishing line (nylon sphere, ~0.5 g, McMaster-Carr; line was low-stretch Spectra® PowerPro 80 lb test, Innovative Textiles) passing through a nylon sleeve in the plate (Fig. 2). The transducer was a cantilever beam design with a resonant frequency in water of ~1950 Hz. The 0.95 cm diameter ball was about 20% of the height of the surrounding artificial mussel bed. Many organisms that live close to mussel beds in the field (such as whelks, chitons, and barnacles) have a body length of ~1 cm, making this a relevant size choice.

Because wave forces are highly variable at a location through time, a reference force is needed that would allow the analysis of any potential effects of structure on a wave-by-wave basis. Accordingly, a second force transducer (referred to as the 'reference' transducer) was installed on a smaller plate flush with the rock surface ~10 cm from the edge of the large plate and at similar tidal height and angle to the incoming waves. This transducer had as a drag sphere a 4.1 cm diameter 'wiffle' golf ball. The string was Dacron (130 lb test Izorline, Paramount), and the force transducer had a resonant frequency of ~1400 Hz in water. Both transducers were cabled back to shore using 4-conductor, shielded cable connected to an instrumentation amplifier, the output of which was routed to a 12 bit data acquisition system collecting at 1000 Hz. This setup enabled simultaneous observation of the forces experienced by 2 spheres subjected to the identical waves, and isolation of the effect of topography around the treatment transducer from variation in the incoming waves.

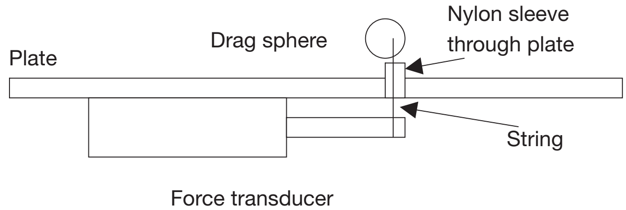

Fig. 2. Force transducer, mounted on the underside of the aluminum plate and connected to the drag sphere via string. The string and sleeve arrangement transfers forces on the ball in any direction into bending of the beam. Thus, force is recorded as magnitude with no directional information

The 4.1 cm diameter ball on the reference transducer was chosen to be larger than the topographic roughness of the surrounding rock so as to prevent the ball being sheltered in low-flow environments downstream of roughness elements (see Denny 1988). The 10 cm spacing between the reference transducer and the edge of the treatment plate was a compromise dictated by space limitations on the rock and by the desire to have the 2 drag spheres as close together as possible (<0.5 m in this case) so that they would be subjected to each wave at roughly the same time. It had the disadvantage that it placed the reference sphere within 10 cm of the edge of the artificial mussel bed, potentially confounding the results from this control if the mussel bed reduced the force experienced by the reference transducer in the cases where there were mussels versus no mussels. However, if the reference sphere were indeed partially protected, its use as a standard for comparison would lead to an underestimate of the degree of force protection afforded the treatment sphere by the mussels around the treatment transducer. Hence, the conservative assumption is that the presence of nearby mussels did not affect the reference transducer.

Force transducers were calibrated while installed in their respective plates and calibration forces were applied parallel to the plate, the direction wave forces were expected to act in the field. The transducers were calibrated in air, but the string and sleeve were wetted to mimic the reduced friction of field conditions. The transducers were calibrated by tying a string from the ball to a calibrated electronic load cell that was pulled against the string, and the force output by the experimental transducer was plotted against the known force output by the load cell. The ratio of force to voltage from 5 pulls was recorded and averaged for each transducer.

Wave heights. A pressure transducer (PX176, Omega Engineering) was mounted in a PVC housing in a small tidepool at the base of the rock below the force plate. This data signal was connected to a third channel of the data acquisition system and sampled at 1000 Hz. These pressure data provided a record, independent of the recorded force, of when waves impacted the plate.

To get an estimate of the sea state during this experiment, offshore significant wave height (H_S) was measured using a Seabird SBE26 wave height meter (SeaBird Electronics). Significant wave height, a common index of sea state, was defined as the average height of the highest one-third of waves. It is calculated as 4 times the SD of surface elevation. The meter was mounted in approximately 10 m of water, in a kelp bed approximately 125 m from the intertidal sites. The meter measured surface elevation at 4 Hz for 8.53 min every 6 h, resulting in 2048 measurements of sea-surface elevation from which the meter computed significant wave height (see Helmuth & Denny 2003). These parameters provided 4 to 6 measurements of H_S during collection of data for each treatment, providing an estimate of the sea state during these experiments.

Data extraction. The data were conditioned and individual waves extracted using an automated routine written in Labview (National Instruments); data were manually inspected during automatic extraction as a check on the routine. The program considered 60 s of data at a time. The data from the pressure transducer were low-pass filtered using a FIR filter routine built into Labview to minimize electrical noise in the signal that confused the peak detection algorithm (Filter parameters: Equi-ripple FIR; 30-taps, lower pass band 20 Hz, lower stop band 30 Hz).

Individual wave events were identified by looking for changes in water elevation over the pressure transducer. To determine the timing of each wave, the mean of a 60 s moving window was subtracted; hence, only elevation differences that occurred over less than this time were used. A peak detection algorithm built into Labview was used to seek 'valleys' in the pressure data (Fig. 3). To do so, the underlying algorithm of the peak detector fit a quadratic equation to sequential groups of data points, and then looked for slope transitions. The threshold and minimum width of the valleys were set such that the water level needed to remain below the 60 s mean for 2.5 s before an inflection point could be considered a trough between waves. These parameters were chosen by inspection of the water height data. Each valley represented the end of one wave event and the start of the next.

The start and stop time of each wave as determined from the pressure data was used to set the timing of each wave event in the force records. Within each wave, the intention was to measure the maximum force on each transducer. To avoid the contribution of transducer noise to the maximum, the 10th highest force point measured during a wave was recorded as the maximum force. This arbitrary choice is analogous to choosing the 99th percentile force of a 1 s wave

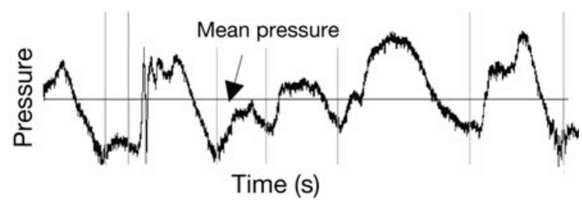

Fig. 3. Sample of a 60 s wave pressure trace. Pressure is in arbitrary units and proportional to the height of the water above the plate. Each vertical line marks the end of one wave event and the beginning of the next

event; unlike percentiles, however, this measure is insensitive to the length of time between the end of one wave and the beginning of the next.

In total, more than 25 000 waves were extracted from the data record. A very small number (n = 37) had a reference force so close to zero (arbitrarily chosen as <0.01 N), that they skewed the data when plotted on log-log axes, a requirement for the analyses (see 'Results'). These points were removed, but the overall trend was not affected.

In these experiments, measured force is a function of both treatment (distance to the mussel bed) and incident wave height (as indexed by the force measured by the reference transducer). Traditionally, the effects of wave height would be taken into account through an ANCOVA. In essence, this analysis plots force measured by the treatment transducers as a function of force measured by the reference transducer. For each treatment, the effect of wave height determines the slope of this relationship and the effect of the treatment its intercept. If the slopes of all these relationships are the same, the effect of treatment can then be assessed. Unfortunately, due to the large number of data in these experiments, it is almost inevitable that slopes of different treatments are significantly different, even if they are very similar, thereby invalidating the ANCOVA approach (see Johnson 1999 for discussion of significance testing). Instead of relying on measures of statistical significance, the measured results are reported and biological examples are used to suggest whether the effects of the treatment are ecologically relevant.

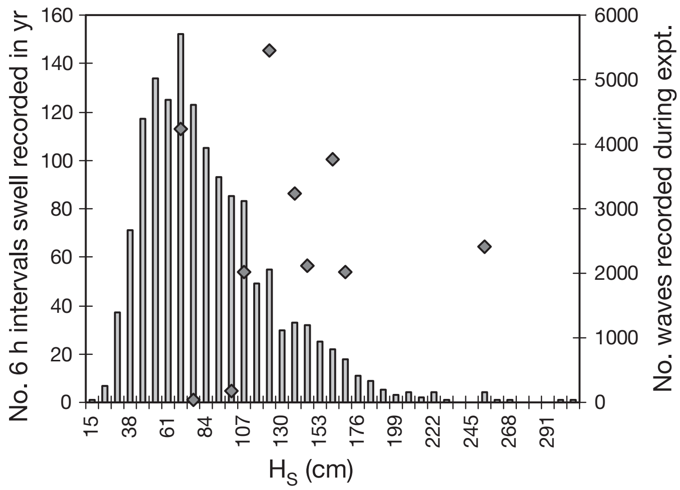

Fig. 4. Significant wave heights H_S recorded every 6 h at Hopkins Marine Station from April 2004 to March 2005 (left-hand *y*-axis, bar). Number of waves included in the current dataset that were collected when waves were at the given H_S (right-hand *y*-axis, grey diamond). Waves were time-stamped when collected, and associated with the nearest H_S measurement from the wave meter

RESULTS

Offshore waves during the experiment

Significant wave heights in the year prior to the experiment, as well as the wave heights during this experiment, are shown in Fig. 4. During the course of the experiment, waves were collected near 10 separate measures of H_S. These ranged from 63 to 246 cm, most within the middle of this range. These correspond to moderate to severe wave conditions at this site.

Reduction in wave force

Due to the stochastic nature of individual waves and the varying wave conditions during the days of the experiment, the appropriate way to visualize these data is by comparing the relationship between forces recorded on the reference transducer with forces recorded on the treatment transducer. Shifts in this relationship indicate effects of the proximity to the artificial mussel bed. These relationships are plotted as linear regressions of the maximum force (as described in the methods) recorded on each transducer for each individual wave. An example of the raw force data is shown in Fig. 5a, while the regression lines for the other treatments (without the underlying data points) are shown in Fig. 5b. The equations of the regressions for all treatments are presented in Table 1. These regressions illustrate that for wave forces of a given magnitude on the reference transducer, the treatment transducer sees a different force depending on the proximity of the artificial mussel bed. For the flat plate case and that with the mussel rings 15 cm away, the lines are essentially identical, indicating that the relationship between forces on the 2 transducers is unchanged by this treatment. In the case of the other 3 treatments, on a wave-by-wave basis, the treatment transducer experiences lower forces for a given force on the reference transducer than expected in the absence of the artificial mussel bed.

It is worth a moment to explain the distinct banding pattern observed in the data in Fig. 5a. These data were collected with a 12 bit analog to digital (A/D) converter which could resolve differences in forces on the reference transducer to 0.17 N. At the lowest forces (which accounted for a large number of the waves recorded), these binary steps (the difference between a single bit in the A/D system) become apparent, especially when plotted on logarithmic axis as in Fig. 5a. Essentially, this is a rounding error, as analog voltages

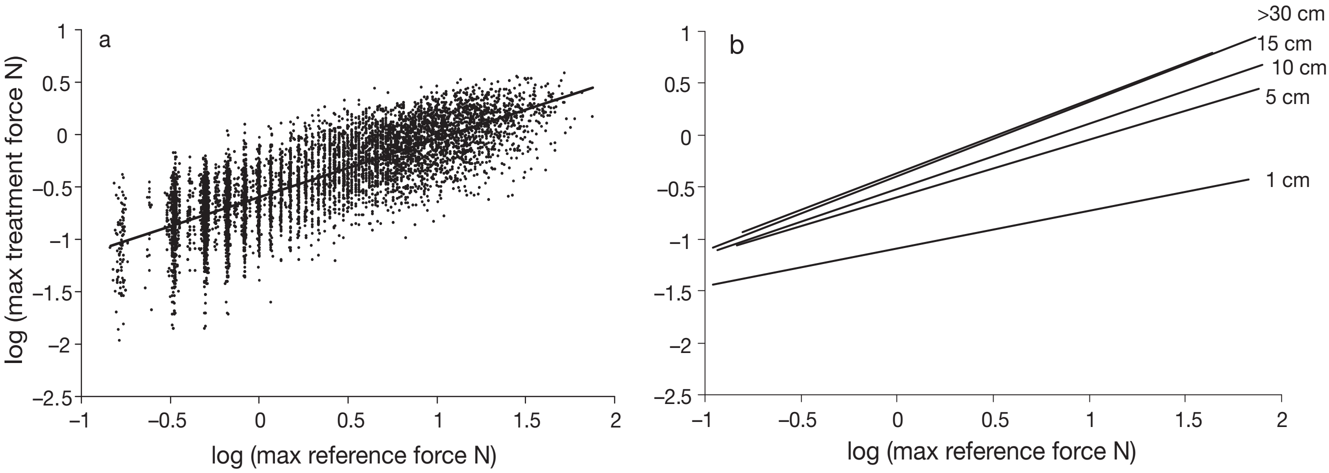

Fig. 5. (a) A sample of the raw wave data and linear regression for the 5 cm case. Each point is an individual wave seen simultaneously by both transducers, with the abscissa showing the force experienced by the reference transducer and the ordinate showing the force experienced by the treatment transducer for each wave. The distinct banding pattern noticeable at low forces is an artifact of the analog to digital conversion that could only resolve differences in forces on the reference transducer of 0.17 N and accentuated by the log-log scale as explained in the text. (b) Linear regressions of all 5 patch sizes with individual points removed for clarity. Axes are the same as for (a). Equations are given in Table 1

Table 1. Equations of linear regressions of log (Max force, treatment) by log (Max force, reference) for each treatment. Treatment is the distance from the measurement probe to the edge of the artificial mussel bed. n: no. of individual waves incorporated into regression. The underlying data for the 5 cm treatment are shown in Fig. 5a; lines are plotted in Fig. 5b

Treatment (cm)	Equation	r^2	n
30	Log (Max force, treatment) = 0.707 × log (Max force, reference) – 0.3672	0.72	623
15	Log (Max force, treatment) = 0.7174 × log (Max force, reference) – 0.4001	0.78	6704
10	Log (Max force, treatment) = 0.6308 × log (Max force, reference) – 0.5176	0.78	6896
5	Log (Max force, treatment) = 0.5552 × log (Max force, reference) – 0.5956	0.63	7444
1	Log (Max force, treatment) = 0.3647 × log (Max force, reference) – 1.0968	0.44	4376

Table 2. Predicted forces (Treatment force; TF, N) at treatment ball for given force on reference ball (Reference force; RF, N). Treatment is the distance from the measurement probe to the edge of the artificial mussel bed. Percent reduction (% red.) is relative to the flat plate condition. Forces on the 1 cm treatment ball are calculated using linear regression equations from Table 1

Treatment	RF = 0.32		RF = 1		RF = 10		RF = 17.78	
(cm)	TF	% red.	TF	% red.	TF	% red.	TF	% red.
30	0.19	–	0.43	–	2.19	–	3.29	–
15	0.17	8	0.40	7	2.08	5	3.14	4
10	0.15	23	0.30	29	1.30	41	1.87	43
5	0.13	30	0.25	41	0.91	58	1.25	62
1	0.05	72	0.08	81	0.19	92	0.23	93

are coerced to the nearest 0.17 N bin by the digital system (with some variability due to zero drift through the course of the experiment). Although puzzling to see on a graph, when averaged over a large number of measurements, these cumulative digitization errors should have no effect on the regressions calculated from these data.

Having calculated the relationships between reference and treatment forces for the various mussel beds, it is possible to make predictions about the level of protection from wave forces that proximity to mussel beds might provide. To illustrate the potential force reduction, the regression slopes from Table 1 were used to make predictions about the reduction in force that 1 cm objects might obtain by being located near mussel beds as compared to being on flat rock (Table 2, Fig. 6). For these calculations, a force on the reference ball was used to predict the force on the treatment ball

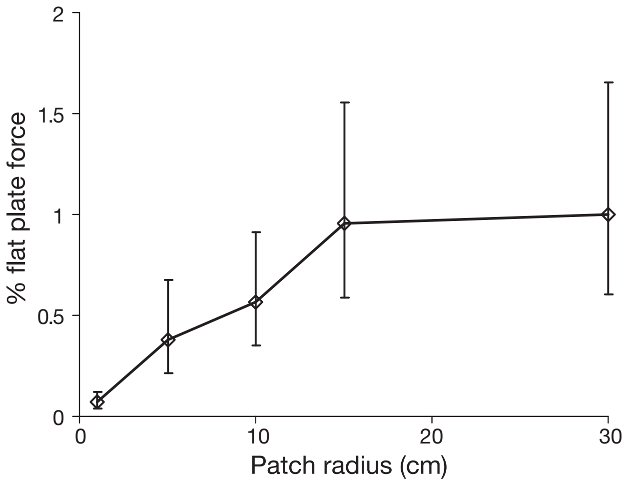

Fig. 6. Relative reduction in wave impact force for a 1 cm object located within mussel-bed bare patches of various radii when subjected to a wave that produced a reference force of 17.8 N. The maximum treatment force in this case would be 3.3 N, close to the maximum force measured during this experiment. Reduced forces were calculated from the regression equations in Table 1. The scaled forces are normalized by the maximum force expected over a flat plate. Error bars are ±1 SD of the predicted force also normalized by the force over the flat plate

for each condition and reference forces were chosen that spanned the range of forces experienced during this experiment. A 1 cm object experiences some level of protection from waves for every wave exposure when located in a patch in a mussel bed no larger than 15 cm. Within a patch 5 cm in radius, the reduction in wave force is between 30 and 62%.

DISCUSSION

By modifying environmental conditions around them, mussels act as habitat engineers (Gutierrez et al. 2003), facilitating many other components of the intertidal community of wave-swept shores (Bertness & Leonard 1997, Stachowicz 2001). The results of this experiment demonstrate that proximity to mussel beds can provide substantial reduction in hydrodynamic forces on objects 1 cm in diameter. The degree of protection depends on distance away from the bed and extends at least 10 cm from the edge of the mussel bed. By a distance of 15 cm from the edge of the structure, forces are indistinguishable from those occurring on a flat plate.

The sort of reductions of hydrodynamic forces measured here are likely to be a frequent component of the intertidal environment, even at locations without mussels. On the shoreline at Hopkins Marine Station where these experiments were conducted, the mussel beds do not form dense monocultures. Generally, aggregations of mussels are less than 1 m in diameter and are interspersed with bare rock. Much of the bare rock area within the mussel zone is within 15 cm of either mussel shells or other topographic features of similar size. On other shores, such as those examined by Levin & Paine (1974), bare patches are a common feature of mussel beds; thus, protection of their surroundings from wave forces is another mechanism by which mussels influence their communities. Furthermore, real beds are often more tightly packed as well as several layers thick (e.g. Suchanek 1979). Within bare patches in such beds the degree of protection, and the distance over which protection extends, are likely to be larger. Although the focus of this study has been on mussels, which provided an ecologically relevant agent of topography, these results would likely have been obtained by structure created by any similar sized biological or abiotic feature.

Causes of force reduction

There are several possible causes for the observed reduction in force, and the precise mechanism depends on the nature of the forces experienced. Most obviously, the wake region downstream from a structure such as a mussel shell is an area of reduced water velocity and hydrodynamic forces will be lower in this region as a result (Denny 1988). Almost certainly this well-studied phenomenon is an important component of the force reduction measured here. In addition to this direct effect of reduced water velocities, however, there are other mechanisms that might explain the observed reduction in forces. One such mechanism, water retention, deserves discussion here since it is not widely appreciated but could influence the generality of these results.

The most severe hydrodynamic load imposed by breaking waves occurs as objects in air are suddenly inundated with moving water (Denny 1951, Wiegel 1964, Schmidt et al. 1993). A small covering of water is known to provide an important cushion from 'shock pressure' beneath breaking waves (Carstens 1968). Although this phenomenon was not specifically tested during these experiments, visual observation of waves breaking on the plate during data collection suggests that the highest forces were recorded at times when the measurement probes were completely out of the water as the next wave impinged on them. If water retention is a source of the reduction in force, then structures need not be as rigid as mussels to resist the flow and provide hydrodynamic protection for their neighbors; it is conceivable that flexible algae, which survive on wave-swept shores by 'going with the flow'

(Koehl 1986), might reduce impingement forces on their neighbors by inhibiting the draining of water between waves. This bears further consideration and testing. As these experiments were conducted on vertical surfaces, water drained rapidly away from this site; on the horizontal benches common at many intertidal locations, water will drain away more slowly and mussel beds could, conceivably, provide greater protection in bare patches even larger than those measured here. Future research should investigate the interactions between retained water and wave forces in intertidal habitats.

Implications for dislodgement

The force reduction measured here could have important implications for many organisms. Many small (~1 cm) mobile grazers in the intertidal zone have measured tenacity values (i.e. the force required to dislodge the organism from the substratum) lower than the forces measured in this experiment (see Table 3). These data predict that, on bare rock, individuals of these species would be removed from the substratum by breaking waves. The data in Table 3 were selected and scaled to a body size of 1 cm according to the subsequent rules. Where investigators presented dislodgement force data (Gubbay 1983, Denny 1985, Etter 1988, Bell & Gosline 1997, Trussell 1997), the table presents a force value that corresponds to an organism with a major body dimension of 1 cm. In other cases, where authors presented tenacity data as the force per unit area of attachment surface (e.g. Miller 1974), conversion to force on a 1 cm snail required an estimate of the relationship between attachment surface area and shell diameter. A value of 18 mm^2 for a 10 mm shell size was chosen based on Atkinson & Newbury's (1984) measurements on *Littorina rudis*. The foot sizes of other species may be different from that of *L. rudis*, but these numbers are sufficiently precise to provide a first approximation of the forces required to dislodge these organisms. Where different tenacity values were available for stationary or moving organisms, the table presents the highest value.

The tenacity values given in Table 3 indicate that the levels of protection measured in the artificial mussel bed at this location are relevant to all of these organisms under certain conditions. For instance, consider the case of a wave that produces a force on the reference transducer of 10 N. Table 2 presents predicted forces on the 1 cm treatment probe for given forces on the reference probe; without protection, the 1 cm diameter treatment probe would experience a mean force of 2.19 N, in excess of the dislodgement force for 60% of the species presented. Moving within 10 cm of the edge of a mussel bed, however, reduces the predicted force to 1.30 N, which is close to the dislodgement force of *Nucella emarginata* and *Littorina scutulata*. Moving another 5 cm closer to the mussel bed drops the expected force to 0.91 N, which is well below the dislodgement force for *N. emarginata* and *L. scutulata*. Finally, moving to within 1 cm of the structure of the mussel bed provides a 90% reduction in force. This brings the predicted force down to 0.19 N, a force low enough that none of the listed species are predicted to be dislodged.

If mussels provide the same level of protection from even more extreme forces than those measured in this study, the benefits of living near mussel beds could be even more impressive. Helmuth & Denny (2003) measured wave forces along the stretch of shoreline where these experiments were conducted, allowing the prediction of the maximum forces that the reference ball might experience at different locations. For an offshore wave height of 200 cm, the highest force measured by

Table 3. Tenacities and attachment strengths of various intertidal organisms

Taxon	Size (cm)	Direction of applied force	Tenacity (N cm^{-2})	Foot size (cm^2)	Scaled force (1 cm) (N)	Source
Littorina obtusata	–	Shear	–	0.22	0.2	Trussell (1997)
Nucella emarginata	–	Shear	2.16	0.18[a]	0.4	Miller (1974)
Nucella lapillus	–	Shear	–	–	0.5	Etter (1988)
Tegula funebralis	–	Normal	3.14	0.18[a]	0.6	Miller (1974)
Nucella emarginata	–	Normal	7.16	0.18[a]	1.3	Miller (1974)
Littorina scutulata	–	Normal	10.50	0.18[a]	1.6	Miller (1974)
Mytilus trossulus	2 × 1	Normal (solitary)	–	–	5	Bell & Gosline (1997)
Mytilus californianus	2 × 1	Normal (solitary)	–	–	11	Bell & Gosline (1997)
Balanus sp.	1 × 1 × 1	Tension	–	–	30	Gubbay (1983)
Lottia pelta	1	Normal	–	–	27–92	Denny (1985)

[a]0.18 cm^2 foot size calculated from Atkinson & Newbury (1984)

the reference probe on this shore would be approximately 194 N (M. W. Denny pers. comm.), more than twice as high as the maximum forces measured on the reference transducer (79.5 N) during this experiment. Based on the regression equations from Table 1, a 194 N reference force corresponds to a 17.8 N force on the treatment transducer on a flat rock, a force greater than the attachment strength of 80% of the organisms listed in Table 3. The predicted force on the treatment probe within 5 cm of the bed would be 4.7 N; thus, a solitary *Mytilus trossulus* (with predicted attachment strength of 5 N) far from a bed would likely not survive such a wave, while one close to a bed would have a much better chance. Within 1 cm of the mussel structures, the predicted force drops to 0.55 N, a force sufficiently low that even *Nucella emarginata* would be at little risk. These values are extrapolations and should be treated with caution, yet they do provide an illustration of the important function topographic structures might provide to intertidal organisms

The direction of maximum forces beneath breaking waves is often not predictable (Denny 1983, Gaylord 2000), so the specific level of protection measured here may be limited to the special case of objects within a circular patch in a mussel bed, that is, with structures close by in all directions. However, on wave-swept shores dominated by *Mytilus* mussels, bare patches within mussel beds similar to the size tested here are quite common. Paine & Levin (1981) examined the patch dynamics of mussel beds in Washington for several years. At one of their sites on Tatoosh Island, Washington (Strawberry), over a 4 yr period, they observed that, on average, 38% of the primary substratum in mussel beds occurred as bare patches rather than mussels. The average initial size of these bare patches was 1900 cm^2. Assuming that these bare patches were circular, this corresponds to a radius of ~25 cm. Forty percent of the area within such a patch would be within 10 cm of its edge and might expect a level of protection similar to that measured here. As Paine & Levin (1981) demonstrated, such bare patches are an important part of the landscape of the intertidal zone by opening up primary space to permit competitively inferior species to persist on wave-swept shores. The sizes of many of the bare patches that Paine & Levin (1981) measured are small enough that mussels likely facilitate survival of other organisms that settle within them.

Implications for grazing

By offering protection from hydrodynamic forces, the physical structures of mussel beds can influence the ecology of other species in the intertidal zone. Many species live in the interstitial spaces of mussel beds and depend on the habitat provided by the mussel matrix (Thiel & Ullrich 2002). Given this protection, grazers and predators can take advantage of food resources both within mussel beds and short distances away. Suchanek (1979) and Seed & Suchanek (1992) showed that various species such as limpets and chitons living within mussel beds graze a halo surrounding the beds approximately 25 cm wide. They also showed that in bare patches smaller than ~25–30 cm in radius, the entire substratum within the patch is heavily grazed. The results of this study provide support for Suchanek's (1979) suggestion that the dimensions of these halos might be governed by a need for protection from hydrodynamic forces. As noted above, on natural shores, mussel beds are likely to be denser than this artificial array, which could enhance the protective effect. Suchanek did not report the thickness of the beds around which he measured grazing halos, but the average of the other beds he reported was 12.6 cm thick (Suchanek 1979). This is more than twice as thick as the 5.6 cm artificial mussel bed used in these experiments, suggesting that his beds may have provided a greater level of protection from waves than described here.

It is important to note that mussel bed communities respond to a number of biotic and abiotic conditions. For instance, Wootton (1992) details the indirect effects of mussels in protecting interstitial neighbors from bird predation. Obviously, such biological interactions are highly important components of rocky shore ecology, and the relative importance of biological versus abiotic factors will vary depending on the particular system. The results presented here do not diminish the importance of ecological interactions, but provide data with which to assess the relative importance of wave disturbance. Additionally, it is worth reiterating that these data were collected at a single shore location without spatial replication. Obviously, the physics of wave breaking will be the same from place to place, but unique factors such as the aspect of this site to incoming swell direction may limit the degree to which these results can be directly applied at other sites. These results should be seen as a guide to potential reduction in hydrodynamic force rather than an absolute measure of the effect of mussel beds. Acknowledging this caveat however, this study shows that mussel beds can reduce the hydrodynamic forces experienced by objects in close proximity to the mussel structures. Given the importance of wave disturbance on rocky shores, such protection could be an important mechanism by which mussel beds create habitable space for other, less tenacious, organisms. The influence of mussels extends beyond the actual physical limits of the beds they create, extending their ecological influence to adjacent areas.

Acknowledgements. The author thanks the staff and students of Hopkins Marine Station, especially J. Lee for assistance with instrumentation. T. Finkler provided programming help. L. Miller, L. Hunt, P. Martone, K. Mach, K. Heiman, and S. Cowden assisted with field installations. B. Broitman, S. Monismith, E. Thornton, and J. Watanabe helped with data analysis. H. Stewart, C. Blanchette, E. Carrington, and 3 anonymous reviewers made useful suggestions for improving the manuscript. C. Harley and M. Denny contributed at every stage of this project. This research was supported by NSF grant OCE-9985946 to M. Denny. This is contribution no. 287 from PISCO (Partnership for Interdisciplinary Studies of Coastal Oceans), funded primarily by the Gordon and Betty Moore Foundation and the David and Lucile Packard Foundation.

LITERATURE CITED

Addy TC, Johnson LE (2001) Littorine foraging behavior and population structure on a wave-exposed shore: non-linear responses across a physical gradient. J Shellfish Res 20: 385–391

Atkinson WD, Newbury SF (1984) The adaptations of the rough winkle *Littorina rudis* to desiccation and to dislodgement by wind and waves. J Anim Ecol 53:93–106

Bell EC, Gosline JM (1997) Strategies for life in flow: tenacity, morphometry, and probability of dislodgment of two *Mytilus* species. Mar Ecol Prog Ser 159:197–208

Bertness MD, Leonard GH (1997) The role of positive interactions in communities: lessons from intertidal habitats. Ecology 78:1976–1989

Carstens T (1968) Wave forces on boundaries and submerged bodies. Sarsia 34:37–60

Dayton PK (1971) Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol Monogr 41: 351–389

Denny DF (1951) Further experiments on wave pressures. J Inst Civil Eng 35:330–345

Denny MW (1983) A simple device for recording the maximum force exerted on intertidal organisms. Limnol Oceanogr 28:1269–1274

Denny MW (1985) Wave forces on intertidal organisms: a case study. Limnol Oceanogr 30:1171–1187

Denny MW (1987) Lift as a mechanism of patch initiation in mussel beds. J Exp Mar Biol Ecol 113:231–245

Denny MW (1988) Biology and the mechanics of the wave-swept environment. Princeton University Press, Princeton, NJ

Denny MW, Miller L, Stokes M, Hunt L, Helmuth B (2003) Extreme water velocities: topographical amplification of wave-induced flow in the surf zone of rocky shores. Limnol Oceanogr 48:1–8

Dittmann S (1990) Mussel beds: amensalism or amelioration for intertidal fauna? Helgol Meeresunters 44:335–352

Emson RH, Faller-Fritsch RJ (1976) An experimental investigation into the effect of crevice availability on abundance and size-structure in a population of *Littorina rudis* (Maton): Gastropoda: Prosobranchia. J Exp Mar Biol Ecol 23:285–297

Etter RJ (1988) Asymmetrical developmental plasticity in an intertidal snail. Evolution 42:322–334

Gaylord B (2000) Biological implications of surf-zone flow complexity. Limnol Oceanogr 45:174–188

Gaylord B, Denny MW (1997) Flow and flexibility. I. Effects of size, shape and stiffness in determining wave forces on the stipitate kelps *Eisenia arborea* and *Pterygophora californica*. J Exp Biol 200:3141–3164

Gubbay S (1983) Compressive and adhesive strengths of a variety of British barnacles. J Mar Biol Assoc UK 63: 541–556

Gutierrez JL, Jones CG, Strayer DL, Iribarne OO (2003) Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos 101:79–90

Hammond W, Griffiths CL (2004) Influence of wave exposure on South African mussel beds and their associated infaunal communities. Mar Biol 144:547–552

Helmuth B, Denny MW (2003) Predicting wave exposure in the rocky intertidal zone: Do bigger waves always lead to larger forces? Limnol Oceanogr 48:1338–1345

Hewatt WG (1935) Ecological succession in the *Mytilus californianus* habitat as observed in Monterey Bay, California. Ecology 16:244–251

Hunt HL, Scheibling RE (2001) Predicting wave dislodgment of mussels: variation in attachment strength with body size, habitat, and season. Mar Ecol Prog Ser 213:157–164

Johnson DH (1999) The insignificance of statistical significance testing. J Wildl Manage 63:763–772

Koehl MAR (1984) How do benthic organisms withstand moving water? Am Zool 24:57–70

Koehl MAR (1986) Seaweeds in moving water: form and mechanical function. In: Givnish TJ (ed) On the economy of plant form and function. Cambridge University Press, Cambridge, p 603–634

Levin SA, Paine RT (1974) Disturbance, patch formation, and community structure. Proc Natl Acad Sci USA 71: 2744–2747

Menge BA (1976) Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecol Monogr 46:355–393

Miller SL (1974) Adaptive design of locomotion and foot form in prosobranch gastropods. J Exp Mar Biol Ecol 14:99–156

Paine RT (1974) Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15:93–120

Paine RT, Levin SA (1981) Intertidal landscapes: disturbance and the dynamics of pattern. Ecol Monogr 51:145–178

Raffaelli DG, Hughes RN (1978) The effects of crevice size and availability on populations of *Littorina rudis* and *Littorina neritoides*. J Anim Ecol 47:71–84

Schmidt R, Oumeraci H, Partenscky HW (1993) Impact loads induced by plunging breakers on vertical structures. In: Edge BL (ed) Coastal engineering 1992, Vol 2. Proc 23rd Intl Conf Coast Eng, Venice, Italy, 4–9 October 1992, American Society of Civil Engineers, New York, p 1545–1558

Seed R, Suchanek TH (1992) Population and community ecology of *Mytilus*. In: Gosling E (ed) The mussel *Mytilus*: ecology, physiology, genetics and culture. Elsevier Academic, Amsterdam, p 87–170

Stachowicz JJ (2001) Mutualism, facilitation, and the structure of ecological communities. Bioscience 51:235–246

Stephens EG, Bertness MD (1991) Mussel facilitation of barnacle survival in a sheltered bay habitat. J Exp Mar Biol Ecol 145:33–48

Suchanek TH (1979) The *Mytilus californianus* community: studies on the composition, structure, organization, and dynamics of a mussel bed. PhD thesis, University of Washington, Seattle, WA

Thiel M, Ullrich N (2002) Hard rock versus soft bottom: the fauna associated with intertidal mussel beds on hard bottoms along the coast of Chile, and considerations on the functional role of mussel beds. Helgol Mar Res 56:21–30

Trussell GC (1997) Phenotypic plasticity in the foot size of an intertidal snail. Ecology 78:1033–1048

Underwood AJ, Chapman MG (1989) Experimental analyses of the influences of topography of the substratum on movements and density of an intertidal snail, *Littorina unifasciata*. J Exp Mar Biol Ecol 134:175–196

Wahl M (1996) Fouled snails in flow: potential of epibionts on *Littorina littorea* to increase drag and reduce snail growth rates. Mar Ecol Prog Ser 138:157–168

Waite JH (1986) Mussel glue from *Mytilus californianus* (Conrad): a comparative study. J Comp Physiol B 156:491–496

Wethey DS (1986) Ranking of settlement cues by barnacle larvae: influence of surface contour. Bull Mar Sci 39:393–400

Wiegel RL (1964) Oceanographical engineering. Prentice Hall, Englewood Cliffs, NJ

Wootton JT (1992) Indirect effects, prey susceptibility, and habitat selection: impacts of birds on limpets and algae. Ecology 73:981–991

Editorial responsibility: Otto Kinne, Oldendorf/Luhe, Germany

Submitted: September 3, 2007; Accepted: January 30, 2008
Proofs received from author(s): June 17, 2008