



Compressive strength of *Mytilus californianus* shell is time-dependent and can influence the potential foraging strategies of predators

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Abstract

The calcareous exoskeletons of bivalve molluscs protect the organisms from environmental stressors, including physical loads like impacts (e.g., from wave-borne rocks) and compressions (e.g., from predators). The magnitude and time scales of physical loads can occur over a wide range of values, and little is known about how the strength of bivalve shells are affected by the speed of impact or compression. We used the intertidal mussel *Mytilus californianus* to test how the rate of compression affects the strength of the mussel's shell. Shell strength was time-dependent, and shells withstood 11.5% larger loads if those loads were applied quickly than if they were applied slowly. We then tested whether the shell's time-dependent strength could influence the strategy of predators trying to compress and fracture the shells. Between strategies with the same compression rate, using more force reduced the time and mechanical work to fracture shells. However, between strategies with the same force, compressing shells slowly reduced the time required to fracture large shells, while the opposite was true for small shells. These results indicate that shell strength is not a static property. Time-dependent strength can influence the interactions between mussels and the physical loads they experience in nature, including their interactions with predators. Studies investigating the influence of climate change on the architecture and strength of mollusc shells should incorporate a range of ecologically relevant compression rates in their measurements to better understand how climate change will affect these organisms.

Introduction

Benthic organisms in marine habitats are frequently exposed to forces (i.e., physical loads) from their external environment that can negatively affect the organisms. On wave-swept shores, hydrodynamic forces from waves and currents can impose loads on benthic organisms, dislodging the organisms if the loads exceed the organisms' attachment

strengths (Miller et al. 2007; Wolcott 2007; O'Donnell et al. 2013), and move large objects (e.g., boulders, logs) that can strike and damage the benthic organisms (Sousa 1979; Shanks and Wright 1986). Additionally, predators can impose loads on their prey through biting, crushing, suction and drilling (Elnor 1978; Westneat 1994; Sanford 2002; Van Wassenbergh et al. 2013). Many marine invertebrates have exoskeletons that provide a physical barrier that protect the animals against the loads they are likely to encounter in their habitat, from both abiotic and biotic sources (Vincent 2012). Understanding the mechanisms by which marine organisms withstand the physical loads in their environment is a crucial component of predicting how changes in those loads or changes to the structures of the organisms will impact marine ecosystems (O'Donnell et al. 2013; Cai et al. 2014).

Bivalve molluscs are suspension-feeders that are common on many coastlines around the world, often forming dense aggregations of individuals (Bayne 1976). Because of their large numbers and suspension-feeding, bivalves play an important role in marine and aquatic ecosystems by recycling nutrients in the water column (Newell 2004). Furthermore, some species are the dominant occupiers of

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space on the benthic substrata in their respective habitats (Paine and Levin 1981) and also create habitats (i.e., the interstitial space between individuals) for other organisms (Bertness et al. 2006). Bivalve molluscs are characterized by a soft body contained within a bilateral shell (valves), and the valves are composed of calcium carbonate that occurs in two polymorphs, aragonite and calcite. In the intertidal mussel *Mytilus californianus*, the outer- and innermost layers of each valve are made of calcite in a prismatic, columnar arrangement, while the middle layer of each valve is nacreous aragonite. The aragonite in nacre is arranged as overlapping plates, or tablets, separated by an organic protein matrix (Taylor et al. 1969). The particular crystalline arrangement of calcite and aragonite (i.e., the microstructure) varies among species (Taylor et al. 1969), and the ratio of calcite to aragonite can change depending on environmental parameters such as temperature, salinity, and acidity of the water (Dodd 1963, 1965; Mackenzie et al. 2014; Li et al. 2015).

Nacreous aragonite is a notable material, because it is found in the shells of many molluscan taxa, and its structure (i.e., the overlapping arrangement of aragonite plates in an organic matrix) can limit the propagation of cracks through the shell, including cracks that originate in the outer prismatic calcite (Currey 1977; Jackson et al. 1988). When subjected to an external load, such as bending or tension, nacre can deform as the aragonite plates slide relative to one another within the organic matrix. When the load is removed, the nacre can slowly recover from its deformation over time, indicating that nacre is a viscoelastic material (Currey 1977). The deformation of viscoelastic materials is dependent on the rate, or time course, of loading (Vincent 2012), and while the properties of isolated nacreous material have been extensively studied (Currey 1977; Jackson et al. 1988; Barthelat et al. 2007), little is known about the effect of dynamic loading (i.e., different time courses) on the mechanical properties of a whole bivalve valve. Furthermore, in nature, the orientation of loading relative to the nacre can vary with the bivalve species and the source of the loading. In laboratory studies, isolated nacreous material can withstand large forces before deforming or failing in compression, it can deform more easily in tension than in compression (Hamza et al. 2013), and it can slow crack propagation in bending (Currey 1977). However, when the entire valve experiences an external load, there is compression, tension, and bending occurring simultaneously at different parts of the valve. Therefore, the findings of laboratory studies on the mechanical properties of isolated shell material cannot be extrapolated to the entire valve.

Bivalve molluscs on wave-swept rocky shores can experience physical loads from a wide range of biotic and abiotic sources, and those loads can occur over a wide range of time scales. Within an aggregation of bivalves, a growing individual can slowly exert a load on its neighbors' valves

as the individual grows in size (Seed 1968). Crustacean predators can slowly and repeatedly squeeze the valves to crack them and gain access to the bivalve's soft tissue inside (Elner 1978; Boulding and LaBarbera 1986). In contrast, impacts to bivalves from wave-borne boulders can impose large forces over short time scales (Sousa 1979; Shanks and Wright 1986). Similarly, avian predators of bivalves can rapidly impose large forces on bivalves by flying with a bivalve into the air and dropping it on to a hard substratum, often repeating the process numerous times until the valves crack and the birds gain access to the bivalve's soft tissues (Davenport et al. 2014). The structural integrity of bivalve molluscs allows them to persist in physically stressful environments and strongly influences their interactions with predators and other members of the biological community, and while many biological structures are viscoelastic and have strengths that are dependent on the rate of loading (Vincent 2012), little is known of how bivalve shell integrity is impacted by physical loads on different time scales (Currey 1977).

Here, we used the mytilid bivalve, *Mytilus californianus*, as a model organism to determine how the time scale of compression of the valve (i.e., compression rate) affects the load, time, and work required to fracture the valve. We chose *M. californianus* because it is one of the dominant space-occupying organisms in the rocky intertidal zone along the west coast of North America, and it can experience many physical and biological stressors in its habitat that apply loads to its valves over a wide range of time scales (e.g., Sousa 1979; Shanks and Wright 1986; Robles et al. 1990; Davenport et al. 2014). Our specific questions were: (1) how does the strength of a *M. californianus* valve change with compression rate? (2) How does compression rate affect the susceptibility of the valve to fracture by predators?

Methods

Compression rate and valve strength

To test whether the rate of compression of a *Mytilus californianus* valve influenced the strength of the valve, we collected mussels from two rocky intertidal boulder fields in northern California, USA in January and February, 2017: McClures Beach (38°11'3"N, 122°58'2"W) in the Point Reyes National Seashore and Miwok Beach (38°21'25"N, 123°4'2"W) near Bodega, CA. In each month and at each site, mussels were collected along a transect that ran parallel to the shoreline. We randomly selected no more than three mussels from each boulder encountered along the transect until a total of 40 mussels were collected from that site and month. Mussels were brought back to the laboratory where they were sacrificed and all soft tissue was removed. We separated the valves to be consistent with previous studies

of valve strength (Mackenzie et al. 2014; Li et al. 2015) and to use the organism's natural symmetry to compare an individual's strength under different loading conditions. The height and thickness of each mussel's two valves (Fig. 1a) were measured to the nearest 0.1 mm using digital calipers, while the projected planform area, length, and width of each valve (Fig. 1a) were measured using a digital photograph of the valve in ImageJ (NIH, version 1.50). Valve planform area was measured to the nearest 0.01 cm² and valve length and width were each measured to the nearest 0.01 cm. The values of each morphological feature were averaged across the two valves of each mussel.

An Instron material-testing machine (Model 5544, Norwood, MA) was used to measure the load, time, and mechanical work required to fracture the valves. Each valve was placed between the horizontal jaws of the Instron, which made contact with the margin of the valve (i.e., where the valves make contact with each other) and the umbo (i.e., the valve's apex). The jaws of the Instron were polished stainless steel and we assumed no friction between the margin of the valve and the face of the Instron jaw. The valves were compressed by the Instron at a specified rate, and the resulting compression and load on the valve were recorded (similar to Mackenzie et al. 2014; Li et al. 2015) (Fig. 1b). The compression and load at which the valve fractured were recorded by a computer. The area beneath the curve in the graph of the compression and load on the valve gave the mechanical work required to fracture the shell (Fig. 1c). To prevent drying of the shells, each pair of valves was kept in air in a separate, sealed 100 mL container until the time of measurement, and all strength measurements were made within 3 h of the mussels being sacrificed.

Mussels were randomly assigned to one of five experimental groups, in which one of each mussel's valves was compressed at a rate of 2, 4, 6, 8, or 10 mm min⁻¹. These rates are in the range of rates used by predatory crabs that crush molluscs (Boulding and LaBarbera 1986) and the rates used by previous research studies to measure shell strength (Mackenzie et al. 2014; Li et al. 2015). Because each mussel has two valves, we were able to do pairwise comparisons of valve strength between a baseline compression rate and an experimental compression rate. For each mussel, the valve to be compressed at the experimental rate was randomly chosen, and the remaining valve was compressed at a rate of 2 mm min⁻¹ as a baseline measurement. The order in which each group was measured was determined using a random number generator. The Instron had a maximum load of 400 N, thus all mussels were fractured with a single compression and a load no greater than 400 N. Mussels whose valves did not fracture with a single compression were discarded. The load, mechanical work to fracture, total compressibility of the valve (i.e., how far it was compressed before fracturing), and the stiffness of the valve (i.e., the

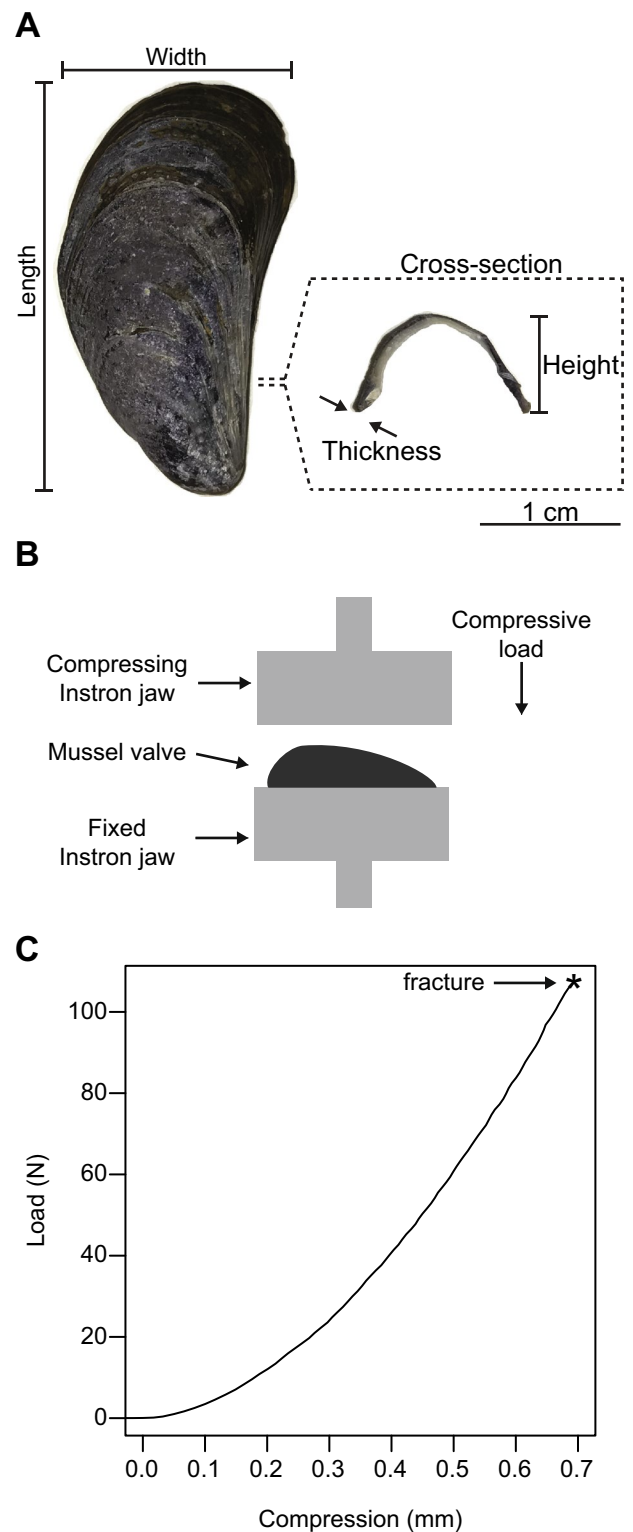


Fig. 1 **a** Morphological features measured for each mussel valve. **b** Strength of mussel valves was measured in an Instron material-testing machine that compressed each valve between two horizontal jaws and measured the resulting load on the valve. **c** A representative compression-load curve a *M. californianus* valve being compressed by the Instron to the point of fracture

mean slope of the load-compression graph, such as Fig. 1c, which describes how easily a valve was compressed; hereafter “valve stiffness”) were calculated from the Instron data. We compared these data between the baseline compression rate (i.e., 2 mm min⁻¹) and the experimental compression rate (i.e., 2, 4, 6, 8, or 10 mm min⁻¹) using paired *t* tests (paired by individual mussel).

Predator strategy and valve strength

We tested whether the foraging strategy of a predator, such as a crab that fractures the valves of *M. californianus* via repeated slow compressions (Boulding and LaBarbera 1986), influenced how easily and quickly the valves fractured. We used the Instron to simulate two pairs of foraging strategies: one pair with different maximum loads and the same compression rate, and another pair with the same maximum load but different compression rates. Mussels were randomly assigned to one of the pairs of strategies, and each of their valves experienced a different strategy, allowing for pairwise comparisons. Mussels were collected from Miwok Beach in March and September, 2017 using the same collection protocol described above. Mussels were returned to the laboratory, sacrificed, and the valve morphology was measured as described above. Mussels were randomly assigned to be fractured by either the first pair of foraging strategies (i.e., same compression rate, different maximum loads) or the second pair of foraging strategies (i.e., different compression rates, same maximum load).

With the first pair of foraging strategies (i.e., Experiment 1), one valve of each mussel was compressed at a rate of 2 mm min⁻¹ up to a maximum load of 100 N, and the remaining valve was compressed at a rate of 2 mm min⁻¹ up to a maximum load of 150 N. The maximum loads of each strategy were within the range of compressive loads that can be produced by predatory crabs and lobsters that feed on bivalve molluscs (Elner 1978; Elner and Campbell 1981; Taylor et al. 2009). With the second pair of foraging strategies (i.e., Experiment 2), one valve of each mussel was compressed at a rate of 2 mm min⁻¹ up to a maximum load of 100 N, and the remaining valve was compressed at a rate of 4 mm min⁻¹ up to a maximum load of 100 N. For both pairs of predators, if the valve did not fracture on the initial compression, the applied load was cycled between the maximum load of the respective predator and a minimum load of 10 N until the valve fractured. This was done by cycling the Instron jaws up and down at the respective strategy’s compression rate, with the jaws always in contact with the valve. If the valves did not fracture within 10 min, the mussel was discarded. The time and mechanical work to fracture each valve were calculated from the Instron data. Within each experiment, the time and mechanical work to fracture the

valves were compared between the foraging strategies using paired *t* tests (paired by individual mussel).

All statistical analyses were done using R Statistical Software (v. 3.3.2; R Core Team 2016).

Results

Compression rate and valve strength

We tested whether compression rate affected the strength of *Mytilus californianus* valves. Mussels used in this experiment ranged in length from 1.54 to 3.73 cm (median = 2.46, *n* = 151). Other measures of valve morphology are given in Table S1. There were no differences in valve morphology among the five experimental compression rates (Kruskal–Wallis test, *p* > 0.05, *df* = 4, *n* = 29–32 mussels in each treatment group). Each of the morphological features correlated with all other morphological features (linear regressions, *p* < 0.05, *n* = 151) (Table S2). The breaking load, mechanical work to fracture, and compressibility of the mussel valves under the baseline compression rate (2 mm min⁻¹) each correlated with every morphological feature (linear regressions, *p* < 0.05, *n* = 126 to 151) (Table S3). The valve stiffness, however, was only correlated to the valve height and valve thickness (linear regressions, *p* < 0.05, *n* = 139). The compressive loads required to fracture mussel valves did not change with compression rates between 2 and 8 mm min⁻¹ (paired *t* tests, *p* > 0.05, *df* = 28–30). However, loads required to fracture valves under a compression rate of 10 mm min⁻¹ were 11.5% (median) larger than loads required to fracture valves from the same mussels under a compression rate of 2 mm min⁻¹ (paired *t* test, *p* = 0.01, *df* = 31) (Fig. 2a). We then tested whether the valves fractured under a compression rate of 10 mm min⁻¹ (1) required more mechanical work to fracture, (2) compressed more before fracturing, or (3) were stiffer than the valves fractured under a compression rate of 2 mm min⁻¹. There were no consistent differences in work, compressibility, or valve stiffness between the two compression rates (paired *t* tests, *p* > 0.05, *df* = 23–31), suggesting that the larger breaking loads of mussels compressed at 10 mm min⁻¹ were not due to a single mechanism for all valves. Next, we compared the ratio of valve stiffness under each compression rate (10 mm min⁻¹:2 mm min⁻¹) to the ratio of compressibility under each compression rate, and found that the valves were able to resist larger forces in the fast strain rate in one of two ways: being stiffer or compressing more before fracturing (Fig. 2b; Kendall’s ranked correlation test, *p* < 0.05 *n* = 24). There were no morphological correlates for whether a valve was strong by being stiff or by being compressible (Kendall’s ranked correlation tests, *p* < 0.05).

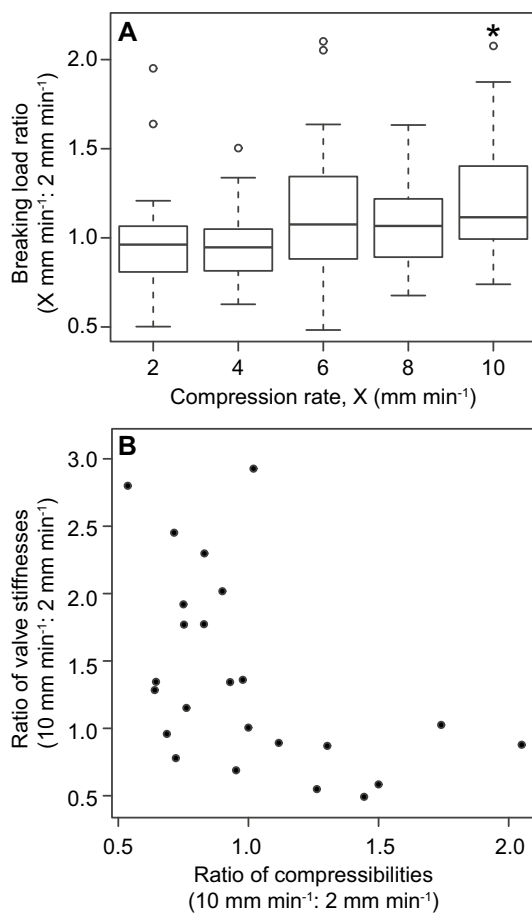


Fig. 2 **a** The ratios between the load required to fracture a valve at an experimental compression rate (2, 4, 6, 8, or 10 mm min⁻¹) and the load required to fracture a valve of the same mussel at a compression rate of 2 mm min⁻¹. Boxes indicate the first quartiles around the median, error bars show the most extreme data point that is no more than 1.5 times the interquartile range from the box, and circles indicate values beyond 1.5 times the interquartile range from the box. The asterisk shows which compression rates made the mussel valves break at a significantly different load from the control compression rate of 2 mm min⁻¹ (paired *t* test, $p < 0.05$, $df = 31$). **b** The ratios of valve stiffness (i.e., the slope of the load-compression curve) and compressibility (i.e., how far the valve compressed before fracturing) between compression rates of 10 and 2 mm min⁻¹. There was a negative correlation between the change in stiffness and the change in compressibility (Kendall's ranked correlation test, $p < 0.05$)

Predator strategy and valve strength

We tested whether foraging strategy affected how quickly and easily *M. californianus* valves fractured. Mussels used in this experiment ranged in length from 1.26 to 3.32 cm (median = 2.15, $n = 82$). Other measures of valve morphology are given in Table S4. There were no differences in the individual values of valve morphology between the two experiments (Mann–Whitney *U* tests, $p > 0.05$, $n = 39$ mussels in Experiment 1, 43 mussels in Experiment 2). In Experiment 1, valves were compressed by either a

compression rate of 2 mm min⁻¹ with a maximum load of 100 N (Strategy A) or a compression rate of 2 mm min⁻¹ with a maximum load of 150 N (Strategy B). Following the behavior of crabs that compress mussel valves (e.g., Boulding and LaBarbera 1986), the compression rate of each valve's respective treatment was used to cycle between the maximum load of the treatment and a minimum load of 10 N until the valve fractured (Fig. 3a). Valves compressed by Strategy A took longer and more work to fracture than valves from the same mussels that were compressed by Strategy B (paired *t* tests, $p < 0.05$, $df = 26$) (Fig. 3b, c). In Experiment 2, valves were compressed by either a compression rate of 2 mm min⁻¹ with a maximum load of 100 N (Strategy C) or a compression rate of 4 mm min⁻¹ with a maximum load of 100 N (Strategy D). There were no differences in the mechanical work required to fracture valves by either predator (paired *t* test, $p > 0.05$, $df = 27$), but there was a difference in the time each predator took to fracture the valves: Strategy C (i.e., compression rate = 2 mm min⁻¹) was able to fracture large mussels (median length = 2.22 cm, range = 1.26–2.69 cm, $n = 12$) more quickly than Strategy D (i.e., compression rate = 4 mm min⁻¹), whereas Strategy D was able to fracture small mussels (median length = 1.83 cm, range = 1.38–2.14 cm, $n = 16$) more quickly than Strategy C (Mann–Whitney *U* test for valve morphology, $p < 0.005$, $n = 12$ mussels fractured more quickly by Strategy C, 16 mussels fractured more quickly by Strategy D) (Fig. 4a, b).

Discussion

Bivalve molluscs are the dominant space-occupying organisms on many rocky shorelines, and their valves protect these sessile organisms against physical loads (e.g., impact forces) that could damage their soft, inner tissues (predation, wave-borne boulders) (Sousa 1979; Shanks and Wright 1986). Here, we show that the resistance of mollusc valves to breaking under a compressive load was influenced by how quickly the load was applied, and that a valve's time-dependent strength can influence the foraging strategies of predators trying to fracture those valves. The time-dependent strength of *M. californianus* valves arises from the organic matrix that allows the aragonite plates in the middle layer of the valve to deform under the external load by sliding relative to each other (Currey 1977; Barthelat et al. 2007; Vincent 2012). The viscoelasticity of the organic matrix, and consequently the whole structure, suggests that the valves deform more easily under a slowly applied load than they do under a rapidly applied load (Currey 1977; Vincent 2012). Repeated, slowly applied loads can deform the valve more and more on each subsequent compression, because the viscoelastic matrix and aragonite do not recover immediately after each

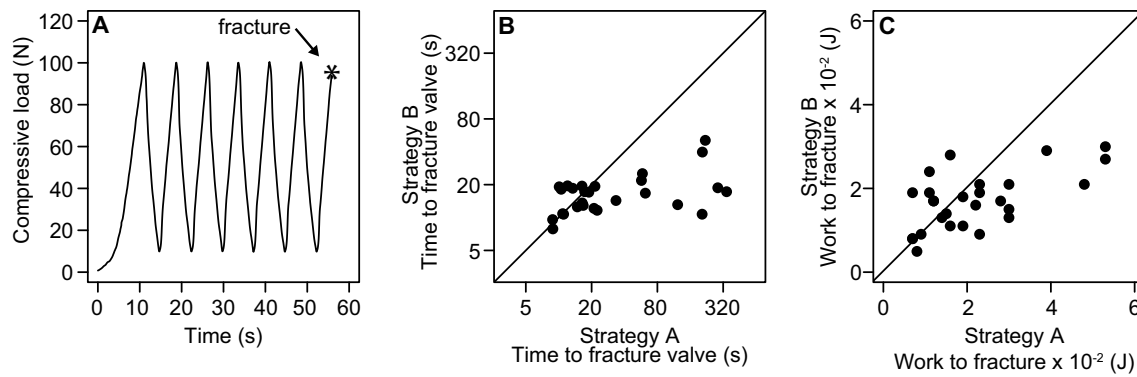


Fig. 3 **a** To simulate different predation strategies, compressive loads on mussel valves were cycled between the maximum load of the respective predator simulation (i.e., 100 or 150 N) and a minimum load of 10 N until the valve fractured (see arrow). The temporal load pattern was achieved by moving the Instron jaws up and down at the prescribed compression rate (i.e., 2 or 4 mm min⁻¹). The time **b** and

work **c** required for Strategy A (i.e., maximum load = 100 N, compression rate = 2 mm min⁻¹) to fracture mussel valves was greater than the time and work required for Strategy B (i.e., maximum load = 150 N, compression rate = 2 mm min⁻¹) to fracture valves of the same mussels (paired *t* test, *p* < 0.05). The lines in **B** and **C** are 1:1 lines for reference

previous loading cycle. During these repeated loads, small cracks can travel throughout the matrix between the aragonite plates (Currey 1977; Jackson et al. 1988; Vincent 2012), which may be why we observed that *M. californianus* withstood a larger load that was applied quickly than one that was applied slowly. Understanding the basic principles of the mussel's time-dependent strength can help predict how populations of *M. californianus* and their associated biological communities will be affected by future changes in the temporal regime and magnitude of physical loads experienced in marine ecosystems, and how predators may need to adjust their foraging strategy to compensate for future changes in the strength or mechanical behavior of mussel valves (e.g., weakened valves due to ocean acidification, warming ocean temperatures, and increased storm activity) (Melzner et al. 2011; Gazeau et al. 2013; Cai et al. 2014; Mackenzie et al. 2014). However, future climate change may also impact the ability of predators to forage on mussels by altering the predators' behaviors and even their strength (e.g., hardness and strength of crab chelae), which could nullify or exacerbate the ecological consequences of any changes in the strength or mechanical behavior of mussel valves (Landes and Zimmer 2012; Dodd et al. 2015; Coffey et al. 2017).

Physical loads in the intertidal zone

The physical loads that *M. californianus* can experience in the rocky intertidal zone occur over a range of time scales and magnitudes. Slowly applied loads, such as being squeezed between two neighboring mussels or boulders, occur over long time scales (i.e., > 1 s) and can be common in the lifespan of a mussel (Seed 1968; Sousa 1979; McGuinness 1987), such that the mussel does not have adequate time to repair any cracks between consecutive

loadings (Beedham 1965). Thus, for a population of mussels to survive in this habitat, most of the individuals will need to have valves that are strong enough to withstand regimes of common compressive loads (Alexander 1981). Rapidly applied loads, such as the impact of wave-borne projectiles or attempted predation via valve fracturing (e.g., being dropped by a bird on to a hard substratum, struck by the heel of a stomatopod), occur over short time scales (i.e., < 1 s) and are likely rare in the lifespan of a mussel (Dayton 1971; Shanks and Wright 1986; Patek et al. 2004; Davenport et al. 2014). Individuals within a population of bivalves are likely able to resist fracturing by the most common physical loads but not the statistically rare physical loads that are relatively large in magnitude (Alexander 1981). This is because valves represent a significant metabolic investment (Palmer 1992; Melzner et al. 2011), so mussels whose valves are strong enough to resist both the relatively low-magnitude common loads and the relatively high-magnitude rare loads, are overly protected for an event that may never occur. The time-dependent strength of *M. californianus* valves that we describe here suggests that mussels can grow valves that are sufficiently strong to resist fracturing under the relatively low magnitude, slowly applied loads that are common in their habitat, but that those valves can also resist larger, more rare loads, provided those loads are applied quickly (Fig. 2). The time-dependent strength, and its ecological implications, are likely present in other closely-related bivalve molluscs, such as *Mytilus edulis*. This congener has a similar calcite and aragonite microstructure to *M. californianus* (Taylor et al. 1969), breaking loads that scale with morphology in a similar way as *M. californianus* (Elnor 1978; Li et al. 2015), and can compress to the same

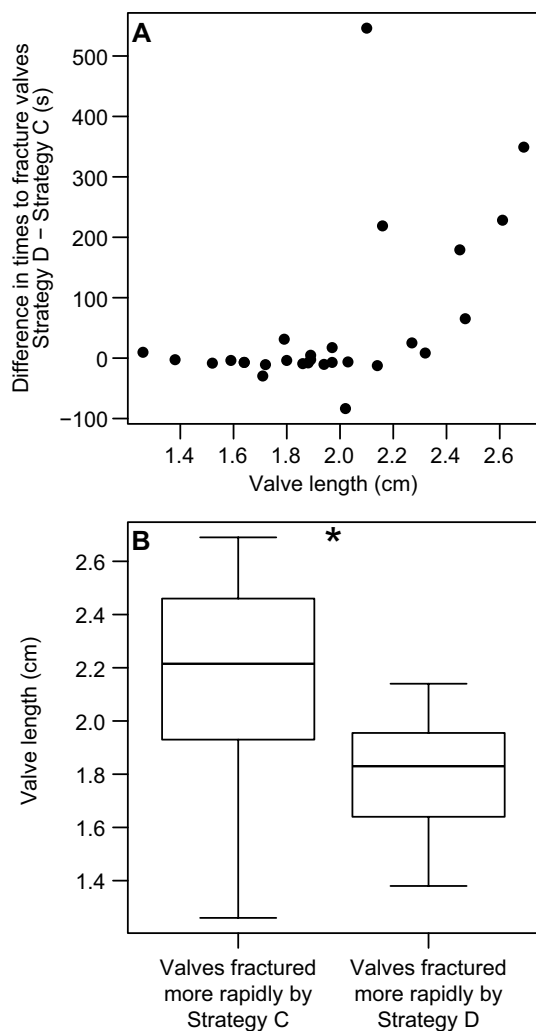


Fig. 4 **a** Simulated predation strategies with different compression rates but the same maximum load took different amounts of time to fracture valves over a range of mussel sizes. Values are the difference between the time Strategy D took to fracture the valves and the time Strategy C took to fracture the valves. **b** Strategy C (i.e., maximum load = 100 N, compression rate = 2 mm min⁻¹) was able to fracture large mussels more quickly than was Strategy D (i.e., maximum load = 100 N, compression rate = 4 mm min⁻¹). Strategy D, on the other hand, was able to fracture small mussels more quickly than was Strategy C. Boxes indicate the first quartiles around the median, error bars show the most extreme data point that is no more than 1.5 times the interquartile range from the box, and circles indicate values beyond 1.5 times the interquartile range from the box. The two size classes of mussels were significantly different (Mann–Whitney *U* test, $p < 0.005$)

degree as *M. californianus* before fracturing (Mackenzie et al. 2014). Of course, loads that are excessively large will fracture the valves regardless of the time scale over which they occur, but if those excessively large loads were common, *M. californianus* and other bivalve molluscs would

likely not be present in that particular locality (Dayton 1971; Paine and Levin 1981).

Foraging strategies of predators

Repeated, slow compressions is a strategy used by many predatory crabs to fracture the valves of their bivalve prey (Elner 1978; Boulding and LaBarbera 1986), and our results further suggest that small variations in the strength or speed of the predators' compressions can lead to large differences in the work and time needed to fracture bivalve shells, as well as the size of bivalve that the predator can access (Figs. 3, 4). Repeated slow compressions can allow small cracks to spread through the organic matrix of the nacreous aragonite in the valve with each compression, eventually leading to failure at a smaller compressive load than expected for a similarly-sized valve that is subjected to a single compressive load (i.e., a load that increases in magnitude until the valve fractures) (Currey 1977; Jackson et al. 1988). In our study, when using the same compression rate, a foraging strategy with a large maximum load (150 N) could quickly crack mussel valves in a single compression, whereas a foraging strategy with a weak maximum load (100 N) required multiple compressions to fracture the other valves of the same mussels. When foraging strategies had the same maximum load (100 N) but different compression rates, the strategy with fast compressions (rate = 4 mm min⁻¹) fractured the valves of small mussels faster than did the strategy with slow compressions (rate = 2 mm min⁻¹). However, the strategy with slow compressions was able to fracture the valves of large mussels (i.e., mussels that required multiple compressions to fracture) faster than did the strategy with fast compressions (Fig. 4). The size difference between the large and small mussels was only about 4 mm in length (based on medians), but could represent a much larger difference in soft tissue mass to be consumed by the predator (nearly 100% increase in soft tissue mass between the two size classes of mussel; McKinney et al. 2004). These unintuitive results indicate that predators can have a reduced handling time for large prey by compressing them slowly, rather than quickly, which will give those predators more time to consume their prey or to find other prey afterward (Yamada and Boulding 1998). Interestingly, predators may try different predation strategies on the same prey, such as compressing the valves in different places until they find a weak area that will fracture (Yamada and Boulding 1998). Future climate change may drive changes in the foraging strategy of predators feeding on bivalve molluscs. For example, increases in ocean acidification may weaken the chelae of predatory crabs (Coffey et al. 2017) such that they use less force and a slow compression rate to fracture valves, whereas increases in temperature may increase chelae strength (Landes and Zimmer 2012), such that crabs can use more force and a fast

compression rate to fracture bivalves. Overall, using slow compressions is likely a suitable, general strategy for predators, because it would save the predator time on the prey that provided a lot of soft tissue (i.e., large mussels), and it would only cost a short amount of time [7.6 s (median) in the present study] to use on the prey that provided less soft tissue (i.e., small mussels).

Future changes in bivalve strength and compressive loads

The structure and composition of mollusc shells can vary with local environmental conditions such as water chemistry and temperature, with recent studies showing that decreases in ocean pH and increases in water temperature can each reduce the strength of bivalve shells (Melzner et al. 2011; Mackenzie et al. 2014; Li et al. 2015). Moreover, changes in the biological community can also impact the strength of shelled organisms, such as the introduction of a boring polychaete that weakens shells or the removal of a predator that then allows prey to survive with weak shells or exoskeletons (Buschbaum et al. 2007; Pascoal et al. 2012; Spyksma et al. 2017). Studies that have examined the mechanical properties of bivalves frequently omit the compression rate used to make their measurements, although recent studies by Welladsen et al. (2010) and Mackenzie et al. (2014) have begun reporting those values (4 and 5 mm min⁻¹, respectively) in their measurements of breaking loads and compressibility. Not surprisingly, the effect of future climate change on the time-dependent mechanical properties of mollusc shells has largely been overlooked. The time-dependent strength of mollusc shells could be a valuable response variable for experiments that manipulate water chemistry and other factors, while simply controlling for time-dependent strength, especially when the organisms span a wide range in body sizes, could benefit other studies. In total, considering time-dependent strength in molluscan research can improve our predictions of how molluscs will fare with future changes in ocean water chemistry (Li et al. 2015), storm activity (Cai et al. 2014), and community assemblages (Buschbaum et al. 2007; Spyksma et al. 2017). Future work should also examine the strength of mussel valves and other mollusc shells under compressions on extremely long time scales (i.e., on the order of days or weeks), such as those encountered during growth (Seed 1968), under compressions on extremely short time scales ($\ll 1$ s), such as those encountered during rapid impact (Davenport et al. 2014), and how time-dependent strength changes over the ontogeny of molluscs.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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