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Impact resistance of limpet shells: a study of local adaptations

Niamh Harford[1] · Nessa O'Connor[1] · David Taylor[2]

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Abstract
Limpets are molluscs which have a conical shell that is well adapted to resist fracture by impact from projectiles such as rocks during storms. We hypothesised that the impact strength of the shell varies depending where the animal is located, reflecting the relative risk of high-energy impact. We quantified shell impact strength for the species *Patella vulgata* using a normalised energy. Limpets located in exposed places on open rock surfaces were found to be more than twice as strong as those living constantly underwater (7.34 MJ/$m^{4.6}$ v 3.48 MJ/$m^{4.6}$). This difference was discussed using a theoretical model based on the physics of projectiles moving through fluids. Limpets located in rocky crevices had an intermediate impact strength (5.43 MJ/$m^{4.6}$), attributed to the reduced probability of impact in these locations. Differences in impact strength were found to be linked to two geometric parameters: apex thickness and the ratio of apex height to rim diameter. Combining the present results with data from previous work, we developed a theoretical model which was able to predict impact strength accurately as a function of rim diameter, apex height and apex thickness. These results demonstrate the considerable plasticity of form, which this species is capable of, helping to explain why it is so abundant. The findings may be valuable in the biomimetic development of lightweight impact resistant structures.

Keywords Limpet · Habitat · Impact strength · Fracture · Shell

1 Introduction

Molluscs such as the common limpet, *Patella vulgata* Linnaeus, 1758 protect themselves with a hard, rigid shell of calcium carbonate, which guards against predation, reduces water loss when the animal is exposed at low tide, and crucially provides mechanical resistance to physical impact. Impacts can occur during storms as a result of stones and other debris such as driftwood and ice which are thrown up by waves [1, 2]. For the limpet, the creation, growth and maintenance of the shell presumably involves considerable energetic cost. The problem is similar to that of designing an engineering structure to provide protection against impact which is also required to be relatively light in weight. Under these circumstances, information about the threat level—the size, velocity and probability of projectiles—is crucial in determining the optimal solution.

The general ecology of limpets and related species has been extensively studied. Many, including *Patella vulgata,* are intertidal gastropods. They are known to be an important element of the ecosystems of many parts of the world [3, 4] [5–7], systems which are affected by local physical conditions at the scale of the whole shore (e.g., exposure to wave action) [8–11]. But far less is understood about how limpets respond to differences in physical conditions within a shore, such as the network of patches of different local habitats like rock pools, crevices and exposed rocks in a given area [12–16]. Limpets may occupy some habitats preferentially because they provide protection from impact damage during storms. However there will be other relevant factors such as grazing pressures and competition from other species [17, 18] which may lead to limpets occupying habitats where there is greater risk of storm damage.

Several researchers have demonstrated that fracture of the shell by impact is a significant factor in limpet survival. For example, occupancy was found to be lower in areas subject to frequent heavy storms [19] and a greater rate of annual loss of limpets was recorded in areas where there were

✉ David Taylor
dtaylor@tcd.ie

1 Department of Zoology, Trinity College Dublin, Dublin, Ireland

2 Department of Mechanical & Manufacturing Engineering, Trinity Centre for Biomedical Engineering, Trinity College Dublin, Dublin 2, Ireland

many loose rocks and pebbles, compared to areas consisting largely of solid rock [1]. Other kinds of projectile material have been found to cause shell damage, e.g., ice blocks [2].

In previous work, we addressed the impact strength of the limpet shell and the response of limpets to shell damage. We developed an experiment to characterise shell impact strength in terms of the energy of the impact, showing how this varied with shell size and other factors [20]. We found that damage in the form of a hole or crack occurred naturally and that it had a significant effect on the animal's survival. But we also found that limpets were able to repair damage, restoring impact strength to its original value within about 2 months, by targeted deposition of new material [21]. This repair happened even in cases of minor damage which did not cause through-thickness holes. This implies that the limpet possesses subtle mechanisms for monitoring its physical environment and the impact strength of its shell, and responding accordingly.

The above work was conducted using limpets found on areas of open, exposed rock surfaces. However, we observed limpets residing in other habitats in the same general areas. Considerable numbers were found in crevices in the rocks, and at low tide we observed some limpets still underwater, in rock pools. Because they live in a tidal zone, most limpets spend some time underwater and some time out of the water. But those found in rock pools at low tide are effectively living underwater all the time. Figure 1 shows examples of these various different states. It is well known that most limpet species tend to live in a fixed "home" location, only moving whilst feeding [22], so one can hypothesise that a given limpet will adjust the impact strength of its shell to reflect the conditions at this location.

We also found that some limpets tended to become covered with abundant growths of algae (Clorophyta), whilst others remained bare. This occurred in all three habitats. We hypothesised that this covering might protect the shell by absorbing impact energy, allowing the limpet to reduce the impact strength of the shell itself.

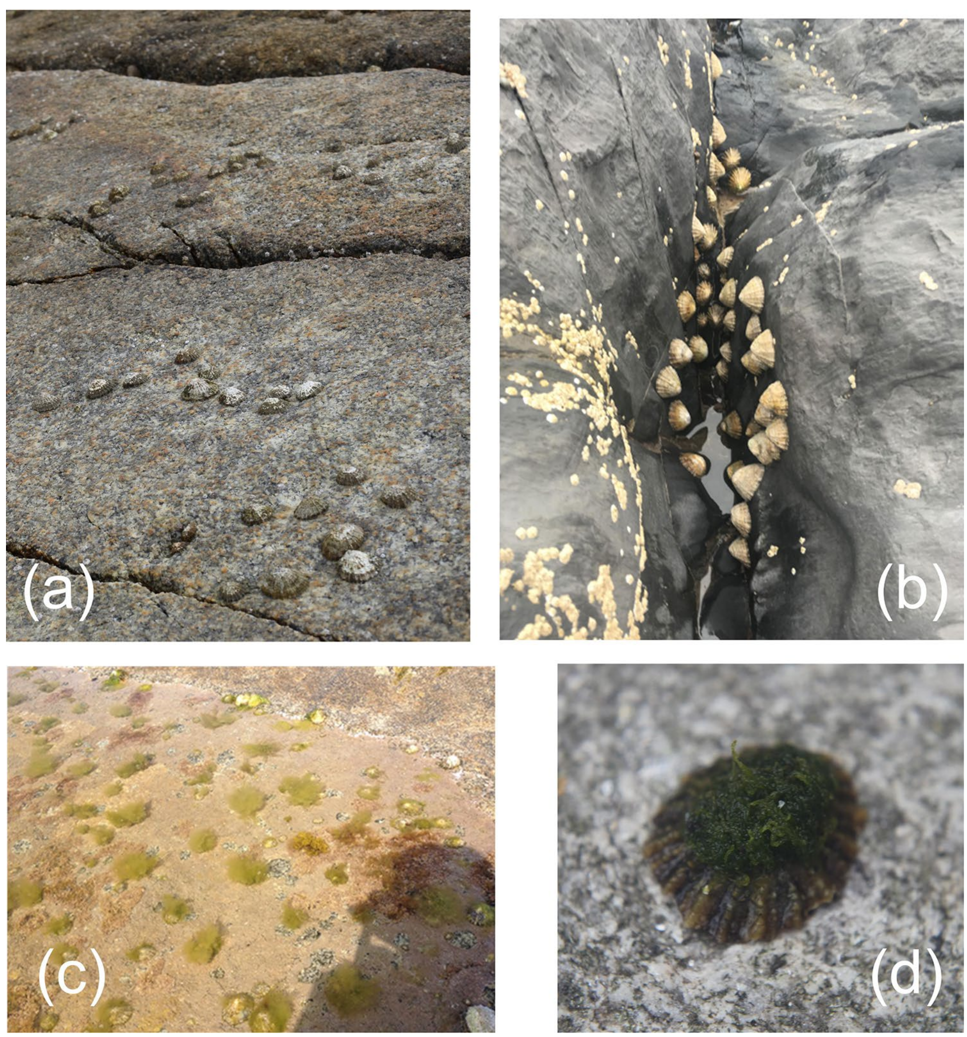

Fig. 1 Examples of the habitats studied: **a** open rocks; **b** crevices; **c** rock pools (note limpets within the pool and near to its edge); **d** algae covering the shell apex

The present paper describes experimental studies and theoretical modelling which was conducted with the aim of answering the following questions:

1. Is the impact strength of the limpet shell different in limpets found in different locations, comparing those on open rocks, those in crevices and those located permanently underwater?
2. Is impact strength different for those shells covered in algae?
3. Can these differences be predicted theoretically?
4. How are these differences related to the size and shape of the shell?
5. Can the impact strength of a given shell be predicted based on measurable parameters of its size and shape?

2 Methods

The limpet species used in this study was *Patella vulgata*, which can be found in abundance on rocky shores near Dublin. Samples were collected from two sites: Sandycove (coordinates 53°17′18″ N; 6° 6′ 42″ W) which was used in previously-published work [20, 21] and Rush (coordinates 53°31′2″N, 6° 5′ 2″W). Both sites consisted primarily of solid rock, with abundant limpet populations and relatively little human footfall.

The following six groups were defined:

1. *Open Rock*. Limpets located on exposed, approximately horizontal rock surfaces (Fig. 1a).
2. *Crevices*. Limpets located in crevices in the rocks (Fig. 1b).
3. *Rock Pools*. Limpets found within rock pools at low tide (Fig. 1c).
4. *Near Rock Pools*. Limpets found within a distance of 100 mm from the edges of rock pools at low tide (Fig. 1c).
5. *Limpets with epibiotic algae attached*. Samples having algae on the apex were chosen from Open Rock areas (Fig. 1d).
6. *Limpets with epibiotic algae removed*. Samples from group 5 which had their covering of algae removed before testing.

Shells were removed from the rock using a sharp knife inserted at the rim, taking care not to damage the shell in the process. The living organism was removed before testing: previous work has shown that its presence does not affect the results [20]. All tests were carried out within 24 h of removal. Three shell dimensions were measured (Fig. 2a). The rim of the shell is slightly elliptical, so we defined shell length *L* as the largest diameter at the rim and width *W* as the smallest diameter. We defined height *H* as the distance from the base to the apex. Measurements were made using digital calipers: the estimated measurement accuracy is ± 0.5 mm. We calculated two shape parameters as the ratios *H/L* and *W/L*.

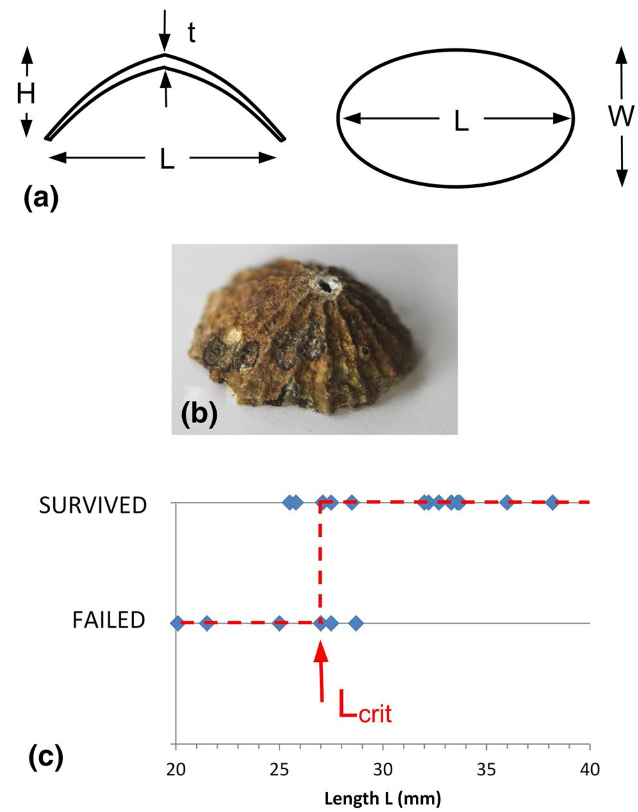

Fig. 2 (a) Definition of the measured dimensions *L, H, W* and *t*. (b) Impact damage typically took the form of a hole at the apex. (c) A typical data set: each data point is an individual shell, tested with an impact energy of 0.5 J, which either failed or survived. The data can be fitted to a step function (dashed line) with a critical length L_{crit}, chosen to minimise the errors, i.e., the distances between the points and the line

Impact testing was carried out with the same protocol as used in previous work [20, 21]. Briefly, a given impact energy *E* was applied using a weight (a flat-ended steel cylinder of mass 123 g) falling inside an aluminium tube (diameter 25 mm), striking the apex of the shell. The shell was defined as broken if a hole formed at the apex, or if a major crack formed elsewhere, though in practice hole formation was by far the most common mode of failure (see Fig. 2b for an example). In the present work, shells were selected having lengths *L* in the range 25–35 mm. A constant impact energy of 0.5 Joules was applied to each shell. Since small shells will tend to break and large shells tend to remain intact, it is possible to define a critical length L_{crit} which expresses the impact strength of limpets from a given group. A small value of L_{crit} indicates that limpets within that group are relatively strong. Figure 2c shows a typical set of results. There will be some scatter in the data, such that some relatively small shells may survive whilst some relatively large ones may break. The value of L_{crit} can be found by defining a step function with a line as shown on the figure, defining the error as (L-L_{crit}) for any point not on the line, and adjusting L_{crit} so as to minimise the sum of all errors. These errors can also be used to create a dataset which allows us to calculate a standard deviation for the result and to conduct analysis for statistical significance, using ANOVA to check for significant trends among groups and t tests to compare pairs of groups, with a critical p value of 0.05.

Previously we found that the critical impact energy to cause shell failure is related to shell size L raised to the power 4.6 [20]. We used this to define a normalized impact energy, which is given by:

$$E_n = \frac{E}{\left(L_{crit}\right)^{4.6}} \tag{1}$$

This allows one to compare the impact strength of shells from different groups in terms of the energy of the impact, in units of J/m$^{4.6}$.

Further samples were taken for dimensional measurements to assist in the analysis of the impact results. A group of 35 Open Rock shells having a larger range of sizes (20–50 mm) was measured in order to investigate whether the aspect ratio H/L changes with size L. Samples from selected groups (Open Rock, Crevices and Rock Pools: 10 shells per group) were sectioned vertically and polished to measure shell thickness (t) at the apex (see Fig. 2a), allowing us to define another shape factor t/L. These measurements were performed using an optical microscope with a graded eyepiece.

3 Results

Comparison of results from two groups (Open Rocks and Near Rock Pools) which were duplicated at the two sites showed no statistically significant effect of site, so the results for the two sites were combined. Table 1 shows the data obtained for the impact parameters L_{crit} and E_n and values of shape factors H/L and t/L. Figure 3 summarises the impact energy results. We found large differences between the groups of shells taken from different habitats. The Open Rock group was the strongest, having an impact energy of 7.34 J/m$^{4.6}$. This was 1.4 times stronger than the Crevices group, 1.5 times stronger than the Near Rock Pools group and 2.1 times stronger than the Rock Pools group. These four groups were all statistically different from each other ($p < 0.05$), the sole exception being that the Near Rock Pools group was not significantly different from the Crevices group ($p = 0.24$).

The group of shells covered with algae had an average impact strength of 8.15 J/m$^{4.6}$ which was slightly higher than shells taken from open rocks having no algae, but this difference was not significant. Removing the algae from algae-covered shells had no significant effect on their impact strength.

Table 1 (a) Summary of all Results (mean values with standard deviation in brackets). The number of samples in each case is given by n for all measurements except t/L, for which a different set of ten samples was used for each result. (b) Summary of p values for group-to-group comparisons of L_{crit}

(a)

Habitat	Number of samples	Impact strength E_n (MJ/m$^{4.6}$)	L_{crit} (mm)	H/L	W/L	t/L
Open rocks	26	7.34 (0.21)	27.67 (0.80)	0.42 (0.06)	0.83 (0.04)	0.09 (0.02)
Crevices	41	5.34 (0.31)	29.54 (1.70)	0.45 (0.08)	0.82 (0.06)	0.055 (0.01)
Near rock Pools	41	5.07 (0.21)	29.99 (1.25)	0.36 (0.06)	0.84 (0.04)	–
Rock pools	22	3.48 (0.12)	32.55 (1.08)	0.30 (0.04)	–	0.052 (0.01)
Algae covered	15	8.15 (0.51)	27.05 (1.68)	–	–	–
Algae Removed	11	8.10 (0.36)	27.08 (1.21)	–	–	–

(b)

	Open rocks	Crevices	Near rock pools	Rock pools	Algae covered	Algae removed
Open rocks		< 0.001	< 0.001	< 0.001	0.16	0.18
Crevices			0.24	< 0.001	< 0.001	< 0.001
Near rock pools				< 0.001	< 0.001	< 0.001
Rock pools					< 0.001	< 0.001
Algae covered						0.92

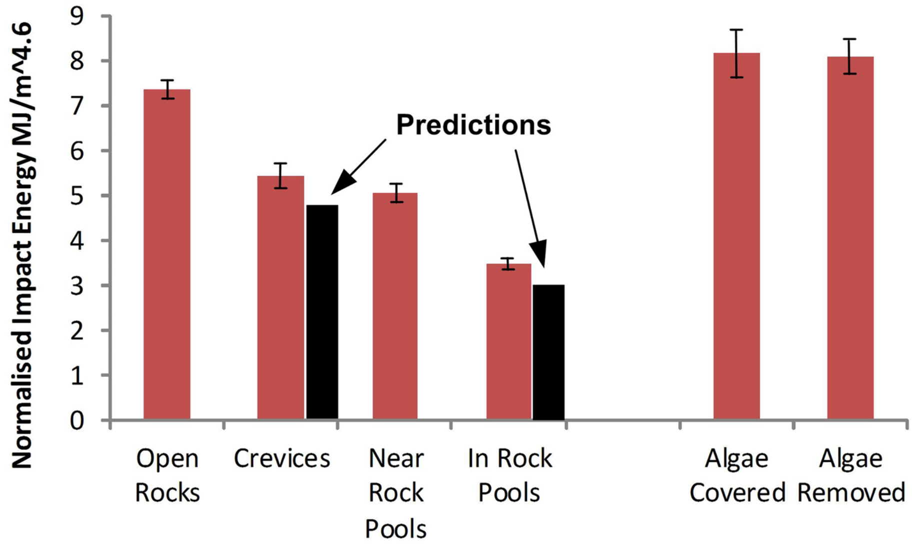

Fig. 3 Results of the impact tests, showing the normalised impact energy E_n for each habitat. Also showing theoretical predictions for two habitats: Crevices and Rock Pools. Error bars indicate standard deviation. The "Algae Covered" and "Algae Removed" groups were located on open rocks. There was no significant difference between the three groups Open Rocks, Algae Covered and Algae Removed, nor was there a significant difference between Crevices and Near Rock Pools. All other differences were statistically significant

The shape factor *W/L*, which records the extent to which the rim is elliptical rather than circular, did not change significantly between groups, having an average value of 0.83. On the other hand, there were significant differences in the factor *H/L* which records the aspect ratio of the shell, as shown in Table 1 and Fig. 4. The Open Rock and Crevices groups had high *H/L* values, with the Crevices result being slightly higher with a difference which just missed significance ($p=0.051$). The Near Rock Pools and Rock Pools groups had successively smaller *H/L* ratios, which were significantly different from each other and from the Open Rock and Crevice groups.

Shells from the Rock Pools and Crevices groups were found to be much thinner, with lower t/L values at the apex than those from the Open Rocks group. Those from Open Rocks had $t/L=0.090$ whilst those from Rock Pools and Crevices had $t/L=0.052$ and 0.055, respectively (see Fig. 4) both being significantly different from the Open Rocks group but not from each other. These shape measurements demonstrate a general trend in which increased impact strength is associated with increased apex thickness and with a more pointed shape (greater *H/L*).

Figure 5 shows the effect of shell size L on aspect ratio *H/L*. There is a quite a lot of scatter, but a clear trend in which *H/L* increases from 0.35 to 0.54 as *L* increases from 20 to 50 mm. *W/L* for these samples did not change significantly with *L*. Previous workers [23] have found this increase in *H/L* with *L* in some species (*P.vulgata* and *P. intermedia*) but not in others (*P.ulyssiponensis, P.rustica*).

3.1 Theoretical modelling

This section considers the prediction of the above results using theoretical models based on the physics of impact

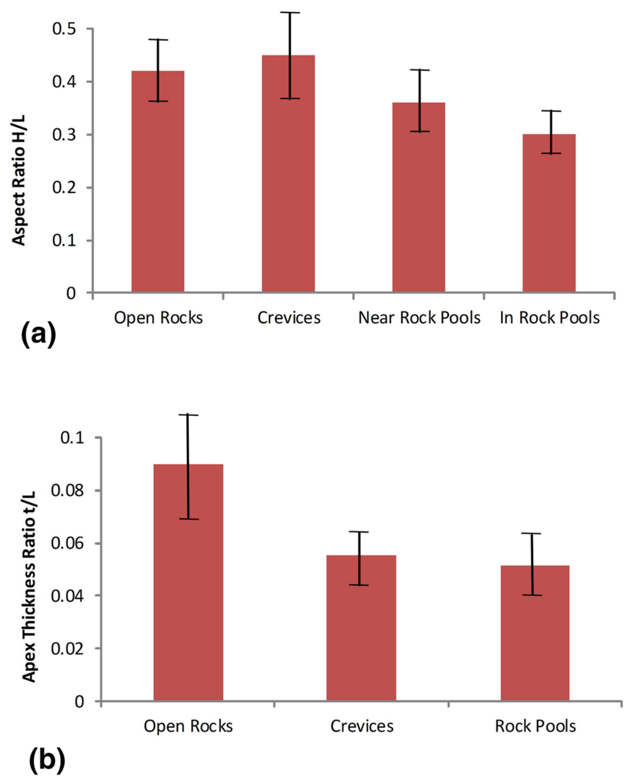

Fig. 4 Measured values of: **a** *H/L* and **b** *t/L* for shells from different habitats. Error bars indicate standard deviation. All groups are significantly different from each other except for t/L between Crevices and Rock Pools

and failure, and then extends these predictions to develop a general model of the effect of limpet morphology on impact strength.

Our hypothesis that a covering of algae would have a protective effect was disproved: algae-covered shells had the

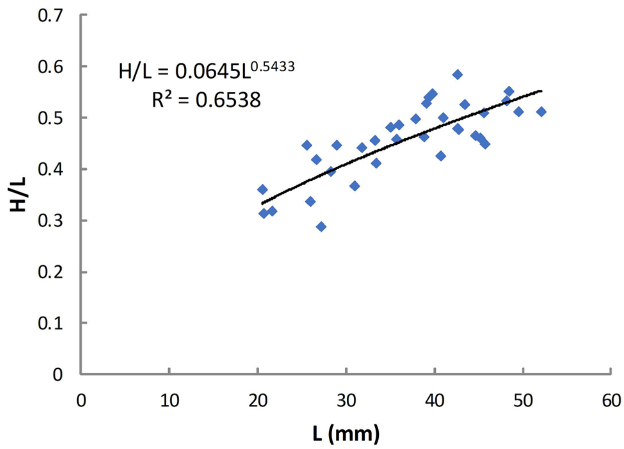

Fig. 5 Values of *H/L* for individual shells, all taken from the Open Rocks habitat, with best-fit power law dependence

same impact strength as bare shells from the same location. The reason for this was made clear by testing these shells with and without their algae; the fact that this had no effect on E_n clearly shows that the algal covering does not absorb any of the impact energy.

On the other hand, there were significant differences in impact strength and in morphology for limpets found in different habitats. Those taken from exposed areas on open rocks were more than twice as strong as those located in rock pools at low tide. They had shells which were 74% thicker at the apex and which had an aspect ratio H/L that was 40% greater. Limpets found in crevices, and those found near the edges of rock pools at low tide, also had distinctly different impact strengths and shape parameters.

It can be hypothesised that the advantage to being in a crevice is the reduced probably of receiving an impact. If a stone or other projectile does succeed in striking the shell, then its effect will be the same as for a more exposed limpet. However, the chance of this happening will be reduced by two effects: (i) the smaller area presented (the projectile must enter the opening of the crevice) and; (ii) the steep angle of entry (the projectile must be falling almost vertically). Even if these effects could be quantified, it would be difficult to predict how much of a reduction in shell impact strength would be appropriate to account for them.

3.2 Predictions for rock pools

In the case of rock pools, however, it is possible to carry out a more rigorous, quantitative analysis. The mechanical effect here is that of water in reducing the energy of the falling stone or other projectile before it reaches the target. The relevant equation is that describing fluid drag, which is the force F acting on a solid object moving through a fluid:

$$F = \rho A \frac{k}{2} v^2. \tag{2}$$

Here ρ is the density of the fluid, A is the area of the cross section of the projectile perpendicular to its line of movement, and v is its velocity. The parameter k is a constant which depends on the shape of the projectile, varying from 1.0 for a cube to less than 0.1 for some very streamlined shapes. Assuming that the projectile is a stone which is approximately spherical but with some sharp edges, a reasonable value for k is 0.6.

We assume that the stone is falling freely under gravity, having been thrown up into the air by wave action. For comparison with the impact energy used in our tests, we assume that the stone has a kinetic energy of 0.5 J when it reaches the surface of the water in the rock pool. Such a projectile would have just enough energy to break a shell from the Open Rocks group, of size $L = 27.7$ mm. As it enters the water, the fluid drag force acts upwards, tending to reduce its velocity by imparting a negative acceleration proportional to F/m, m being the mass of the stone. However it is falling under gravity which continues to impose a positive acceleration g so the stone's velocity may either increase or decrease at it travels through the water. As the velocity changes, the drag force changes accordingly.

In practice the size, mass and velocity of the projectile will vary considerably depending on the magnitude of the storm and other factors. Shanks and Wright [1] suggested a typical projectile velocity of 3 m/s. Assuming the rock is limestone, having a density of 2650 kg/m^3, then to have an initial kinetic energy of 0.5 J as we assumed, the stone will have a mass of 0.11 kg and thus a diameter of 43 mm. We found many stones of approximately this size at our study sites.

The above theory was applied, solving the equations numerically using Microsoft Excel. We found that the energy of the stone reduced by half, from 0.5 to 0.25 J, after penetrating a depth of 146 mm into the water. This would be similar to the depth at which many of our limpets were located, which concurs well with our finding that these shells have about half the impact strength of those located on open rocks. This analysis suggests that, for limpet shells in the size range we studied (25–35 mm), a reduction in impact strength of about one half will be appropriate, since it mirrors the reduction in the severity of the impacts that are likely to be experienced during storms.

Figure 6 shows the result of a more comprehensive analysis, in which we varied the initial velocity of the projectile, but also varied its size so as to keep the initial energy constant at 0.5 J. One can see that the results vary considerably. For a low velocity of 1 m/s, the projectile's kinetic energy continues to increase even after entering the water, because the drag force is low. For all other velocities the

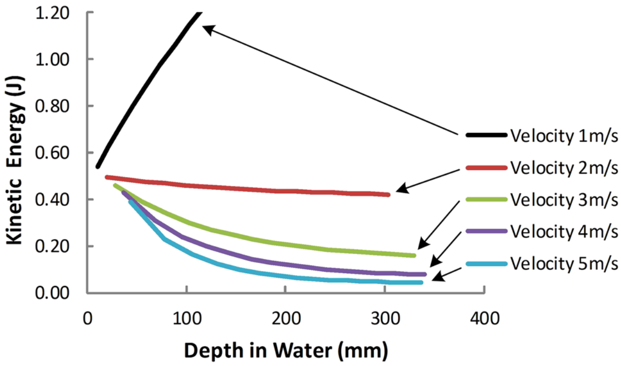

Fig. 6 Theoretical predictions of the change in kinetic energy of a projectile falling through water. The lines show results for different initial velocities: in each the initial energy is set to 0.5 J. Energy declines more rapidly at high velocities owing to the greater drag force

energy does decrease but at different rates. Interestingly, this shows that large, slow-moving rocks are more dangerous than smaller, fast-moving pebbles. The overall conclusion is that an impact from a falling stone will be less severe for a limpet located in a rock pool, for most likely cases. This analysis could be used in conjunction with information about the size and velocity of projectiles during storms to make more detailed predictions of shell failure and survival.

This analysis has several assumptions. We assumed, along with Shanks and Wright, that the impact occurred from a stone which had been lifted into the air by wave action, rather than one which is moving underwater or within a wave. Their figure of 3 m/s came from earlier work on the velocity of water during storms, rather than projectiles. Our prediction at 3 m/s requires quite a large stone being lifted out of the water: more common events probably involve smaller stones at higher velocities which, as Fig. 6 shows, are attenuated more effectively by the water.

3.3 Predictions of shape and size effects

A further question which can be addressed with a mechanics analysis is: how is impact strength affected by the size and shape of the shell? In previous work [20], we established through experimental testing that the energy required for impact failure is proportional to the shell's major diameter L, raised to the power 4.6. The samples used in that work were taken from exposed locations, and so would fall within what we here call the Open Rocks habitat. At the time we could offer no explanation for this exponent of 4.6, but by analysing our previous results along with the new results in this paper, an explanation emerges. In what follows we will show that the impact energy can be explained as depending on two factors: the volume of the shell and the thickness of its apex.

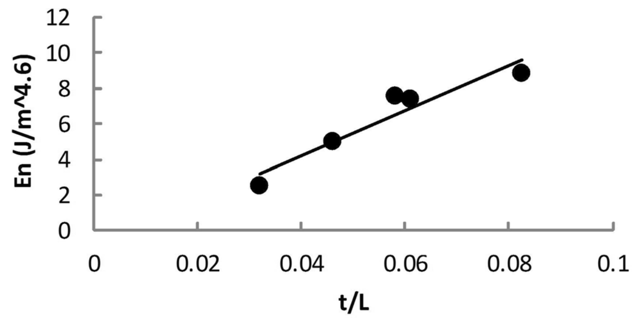

Fig. 7 Data from a previous study (O'Neill et al. 2018) showing a linear relationship between normalised shell thickness t/L and measured impact strength E_n for shells from the Open Rocks habitat

The energy of the projectile passes entirely into the shell, being distributed in some way throughout its volume. So a reasonable starting point would be to expect that the energy needed to break it will be proportional to the volume V of shell material. If there is no change in shape, i.e., if as the shell grows the dimensions L, W, H and t all increase in linear proportion, this is known as geometric similarity. In that case V will be proportional to L^3, and so we might expect that the failure energy E will also be proportional to L^3. However, we found in the present work that geometric similarity does not apply: H/L increases with L. As Fig. 5 shows, the data can be fitted to the following equation:

$$\frac{H}{L} = 0.0645L^{0.5433} \tag{3}$$

Volume will increase linearly with H/L (other factors remaining constant) so as the shell grows, its volume will rise not by L^3 but by $L^{3.54}$. And thus we can expect its impact strength to rise by a similar exponent.

Turning now to the effect of apex thickness, in previous work [21] we showed that in shells of the same size, impact strength E_n is directly proportional to apex thickness. We did this by abrading the apices of shells to reduce their thickness, typically from 3 to 1 mm. Some shells were tested immediately whilst others were left for various periods of time during which deposition occurred, increasing their thickness, and thus their impact strength, back to the original values. This allowed us to measure E_n in shells of the same size having different values of t/L. Figure 7 shows a summary of the results: it is clear that the relationship is close to a linear one. Other things being equal, impact strength is proportional to shell thickness. It is not surprising that the thickness of the apex will have a strong effect, since this is the part of the shell which will fail during the impact, though it is not obvious why the dependence on t/L should be linear.

This thickness effect adds an extra 1.0 to the exponent linking impact energy to size, giving us a final prediction of $L^{4.54}$ which is very close to the experimental value of $L^{4.6}$.

We can use the above approach to predict the results of the present work, by proposing an equation which links shell impact strength with the parameters describing shell size and shape. In the analysis above we showed that E depends linearly (and independently) on two factors: shell volume V and apex thickness t/L, therefore:

$$E = BV\left(\frac{t}{L}\right) \tag{4}$$

Here B is a constant. As noted above, V is proportional to L^3 under conditions of geometric similarity, but in the present case H/L changes with size and between groups (though W/L does not) so V will be proportional to $L^3(H/L)$. The constant of proportionality will have units of energy per unit volume, J/m^3. So we can rewrite Eq. 4 as:

$$E = CL^3\left(\frac{H}{L}\right)\left(\frac{t}{L}\right) \tag{5}$$

Here C is a constant. Written in this form the equation expresses the separate effects of size (L) and shape (H/L and t/L), but it is worth noting that it can also be written in a simpler form, as follows:

$$E = CLHt \tag{6}$$

Thus the impact strength of a given shell is seen to depend simply on three dimensions: L, H and t. We can check the accuracy of these equations using them to predict the experimental results in the present work. Starting with our result for the Open Rocks case ($E_n = 7.34$ J/m$^{4.6}$, $H/L = 0.42$, $t/L = 0.09$) we find the constant C to be 630,386 J/m^3. Using this constant in Eq. 5 we can predict values for E_n for the Rock Pools and Crevices groups to be 3.01 J/m$^{4.6}$ and 4.87 J/m$^{4.6}$ respectively. These predictions are very close to the experimental values, being lower by 13% and 10%, respectively (see Fig. 3).

Equation 6 can be interpreted as follows: the term LHt has units of length cubed and thus is related to volume. L and H determine the overall shape and size of the shell, whilst t is specific to the apex region. So LHt can be seen as relating to the volume of material in the region close to the apex, which receives the full force of the impact. A stress wave will pass through this region immediately after impact, causing failure if the energy density in that region is high enough. The physical interpretation of the constant C is that it is related to the material's critical strain energy density, which is the area under the stress/strain curve of a sample of material loaded until failure.

4 Discussion

This study has revealed remarkable differences in the morphology and impact strength of limpets found in different habitats located only a few metres from each other. This information, when combined with data from previous studies, has allowed us to formulate a general model linking impact strength to shell size, shape and thickness.

We found that two strategies are available to limpets which allow them to adjust the impact strength of their shells. They can alter the aspect ratio *H/L,* making the shell taller or flatter in form, and they can independently alter the thickness of the shell near the apex. Limpets located in crevices, and thus less likely to experience impacts, have a thinner shell, reducing the ratio t/L. Limpets in rock pools also have thinner shells, but in addition they adopt a flatter shape (lower *H/L*), creating a weaker shell which reflects the reduced energy of projectiles falling through water. The lower *H/L* ratio means that the volume inside the shell will be smaller for a given amount of shell material, raising the question of why this shape would be adopted. A possible answer is it provides the limpet with more stability, making it harder to detach from the rock surface when experiencing sideways forces due to water movement or interactions with other limpets. Another question which arises is: why would limpets choose to live in more exposed locations, on open rock surfaces, given that this requires them to create shells which are more than twice as strong, presumably involving considerable expenditure of energy in the process of biomineralisation? The answer probably lies in the interaction between species in the ecosystem, competing for grazing resources, etc., as mentioned above and discussed by previous researchers [17, 18].

This work has some limitations. We considered only one species of limpet, in a limited range of shell sizes: impact strength was determined from shells with L = 25–35 mm and the general size/shape analysis covered data from the range L = 20–50 mm. Previous workers [1] studied four different species over a wider range of shell sizes and found varying effects of size on impact energy. We used a test involving a vertically falling weight striking the apex: in practice flying debris may approach from other angles and strike elsewhere, though given the likely size of dangerous projectiles, the shape of the shell ensures that almost all impacts will occur near the apex. Our analysis of shell impact strength assumed that the shell's primary purpose is to resist mechanical impact, though this is only one requirement among several: protection from predators, water retention, etc. For example, Cabral noted that H/L changes with position in the intertidal zone, suggesting that it may affect resistance to dessication [23].

We assumed that the shell material did not change from one habitat to another. This may have occurred, but the fact that we were able to predict all results based solely on geometric changes suggests that it does not. One issue which was not addressed in this study is the underlying biological mechanism by which the limpet is able to assess the risk and magnitude of likely impacts in a given habitat, and adjust its shell accordingly. Previously we found that, in response to non-critical impacts (i.e., an impact energy sufficient to cause internal damage to the shell but not sufficient to break it), the limpet was able to deposit new material on the inside of the shell which was targeted to the damaged apex [21]. These responses imply a system at the cellular level which is capable of detecting damage and/or mechanical strain in the shell, and orchestrating the biomineralisation process accordingly.

This work has demonstrated how a living organism has developed an impact-resistant ceramic structure which can achieve strength/weight efficiency by subtle adjustments to its shape. Better understanding of this system may help in the biomimetic design of engineering structures.

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References

1. A.L. Shanks, W.G. Wright, Adding teeth to wave action: the destructive effects of wave-borne rocks on intertidal organisms. Oecologia **69**(3), 420–428 (1986)
2. G.C. Cadee, Shell damage and shell repair in the Antarctic limpet Nacella concinna from King George Island. J. Sea Res. **41**(1–2), 149–161 (1999)
3. T. Fenger, D. Surge, B. Schne, N. Milner, Sclerochronology and geochemical variation in limpet shells (Patella vulgata): A new archive to reconstruct coastal sea surface temperature. Geochem. Geophys. Geosyst. **8**(1), 1–17 (2007)
4. G. Schaal, J. Grall, Microscale aspects in the diet of the limpet *Patella vulgata* L. Journal of the Marine Biological Association of the United Kingdom. **95**(6), 1155–1162 (2015)
5. S.R. Jenkins, R.A. Coleman, P. Della Santina, S.J. Hawkins, M.T. Burrows, R.G. Hartnoll, Regional scale differences in the determinism of grazing effects in the rocky intertidal. Mar. Ecol. Prog. Ser. **287**, 77–86 (2005)
6. N.E. O'Connor, T.P. Crowe, Biodiversity loss and ecosystem functioning: distinguishing between number and identity of species. Ecology **86**(7), 1783–1796 (2005)
7. P. Moore, R.C. Thompson, S.J. Hawkins, Effects of grazer identity on the probability of escapes by a canopy-forming macroalga. J. Exp. Mar. Biol. Ecol. **344**(2), 170–180 (2007)
8. B.A. Menge, J.P. Sutherland, Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Am. Nat. **130**(5), 730–757 (1987)
9. B.A. Menge, A.M. Olson, Role of scale and environmental factors in regulation of community structure. Trends Ecol. Evol. **5**(2), 52–57 (1990)
10. N.E. O'Connor, I. Donohue, T.P. Crowe, M.C. Emmerson, Importance of consumers on exposed and sheltered rocky shores. Mar. Ecol. Prog. Ser. **443**, 65–75 (2011)
11. R.J. Mrowicki, C.A. Maggs, N.E. O'Connor, Does wave exposure determine the interactive effects of losing key grazers and ecosystem engineers? J. Exp. Mar. Biol. Ecol. **461**, 416–424 (2014)
12. M.T. Burrows, S.J. Hawkins, Modelling patch dynamics on rocky shores using deterministic cellular automata. Mar. Ecol. Prog. Ser. **167**, 1–13 (1998)
13. L. Benedetti-Cecchi, F. Bulleri, S. Acunto, F. Cinelli, Scales of variation in the effects of limpets on rocky shores in the northwest mediterranean. Mar. Ecol. Prog. Ser. **209**, 131–141 (2001)
14. R.J. Mrowicki, C.A. Maggs, N.E. O'Connor, Consistent effects of consumer species loss across different habitats. Oikos **124**(12), 1555–1563 (2015)
15. L.B. Firth, R.C. Thompson, F.J. White, M. Schofield, M.W. Skov, S.P.G. Hoggart et al., The importance of water-retaining features for biodiversity on artificial intertidal coastal defence structures. Divers. Distrib. **19**(10), 1275–1283 (2013)
16. L.B. Firth, T.P. Crowe, Competition and habitat suitability: small-scale segregation underpins large-scale coexistence of key species on temperate rocky shores. Oecologia **162**(1), 163–174 (2010)
17. L.M.L.J. Noël, S.J. Hawkins, S.R. Jenkins, R.C. Thompson, Grazing dynamics in intertidal rockpools: connectivity of microhabitats. J. Exp. Mar. Biol. Ecol. **370**(1–2), 9–17 (2009)
18. A. Metaxas, R.E. Scheibling, Community structure and organization of tidepools. Mar. Ecol. Prog. Ser. **98**(1–2), 187–198 (1993)
19. D.T. Blackmore, Studies of *Patella vulgata* L.I. Growth, reproduction and zonal distribution. J. Exp. Mar. Biol. Ecol. **3**(2), 200–213 (1969)
20. D. Taylor, Impact damage and repair in shells of the limpet *Patella vulgata*. J. Exp. Biol. **219**, 3927–3935 (2016)
21. M. O'Neill, R. Mala, D. Cafiso, C. Bignardi, D. Taylor, Repair and remodelling in the shells of the limpet *Patella vulgata*. J. R. Soc. Interface **15**(145), 20180299 (2018)
22. A. Cook, O.S. Bamford, J.D.B. Freeman, D.J. Teideman, A study of the homing habit of the limpet. Anim. Behav. **17**(PART 2), 330–339 (1969)
23. J.P. Cabral, Shape and growth in European Atlantic Patella limpets (Gastropoda, Mollusca). Ecological implications for survival. Web Ecol. **7**, 11–21 (2007)