RESEARCH ARTICLE

Impact damage and repair in shells of the limpet *Patella vulgata*

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ABSTRACT

Experiments and observations were carried out to investigate the response of the *Patella vulgata* limpet shell to impact. Dropped-weight impact tests created damage that usually took the form of a hole in the shell's apex. Similar damage was found to occur naturally, presumably as a result of stones propelled by the sea during storms. Apex holes were usually fatal, but small holes were sometimes repaired, and the repaired shell was as strong as the original, undamaged shell. The impact strength (energy to failure) of shells tested *in situ* was found to be 3.4-times higher than that of empty shells found on the beach. Surprisingly, strength was not affected by removing the shell from its home location, or by removing the limpet from the shell and allowing the shell to dry out. Sand abrasion, which removes material from the apex, was found to have a strong effect. Shells were also subjected to repeated impacts, which caused failure after 2–120 repetitions. *In situ* shells performed poorly in this test. It is proposed that the apex acts as a kind of sacrificial feature, which confers increased resistance but only for a small number of impacts. Microscopy showed that damage initiates internally as delamination cracks on low-energy interfaces, leading to loss of material by spalling. This mode of failure is a consequence of the layered structure of the shell, which makes it vulnerable to the tensile and shear stresses in the impact shock wave.

KEY WORDS: Limpet, *Patella vulgata*, Fatigue, Damage, Spalling, Delamination

INTRODUCTION

The term 'limpet' is used rather loosely to include any aquatic snail having a shell with a simple conical (patelliform) shape. The species studied in this work, *Patella vulgata*, is a member of the family Patellidae within the clade of marine gastropods Patellogastropoda. It is very common in intertidal zones in northern Europe and elsewhere. Limpets commonly live for more than 10 years and have been known to live for centuries. The shell protects the animal from the sun and serves to prevent dehydration during the periods when the limpet is out of the water. It also acts as protection from mechanical forces and it is this role which is of interest in the present work. The shells of limpets and other marine animals often become damaged. Typical damage takes the form of a hole in the apex of the shell, a crack somewhere in the shell body or loss of part of the shell rim where it meets the rock surface (Harper et al., 2012; Cadée, 1999; Shanks and Wright, 1986). In some cases, this damage is caused by predators such as gulls and crabs, but there is evidence to show that impact by seaborne objects such rocks, ice and driftwood

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can be a major cause of lethal damage. Shanks and Wright (1986) demonstrated the destructive power of wave-borne missiles by setting up targets to record impacts in a given area. They studied four limpet species, finding that they were much more likely to be lost in a location where there were many movable rocks and pebbles compared with a location consisting largely of solid rock mass. Examining the populations over a one year period, and making a number of assumptions about size distributions and growth rates, they estimated that 47% of shells were destroyed in the former location, compared with 7% in the latter (Shanks and Wright, 1986). Another study (Cadée, 1999) reported that impact damage by ice blocks and stones was the major cause of damage to the limpet *Nacella concinna*.

Major damage, such as extensive cracking of the shell or the creation of a large hole, is assumed to lead to death shortly after, for example by predation or dehydration. However, there have been no studies to investigate this assumption. Small amounts of damage can be repaired by further growth on the inside of the shell and much of our knowledge about damage has been obtained from observations that living limpets show evidence of having repaired their shells (e.g. Cadée, 1999; Harper et al., 2012). The prevalence of repaired damage found in shells of limpets and other marine animals collected from their normal habitats varies enormously, from 3.2 to 93% (Cadée, 1999). From these observations, it is clear that cracks and holes cannot be filled in, instead the repair takes the form of new material deposited on the inside of the shell. This is evidently a carefully orchestrated biological process, because this extra material is localised to the damaged area. Laboratory studies of biological responses to damage (e.g. Sleight et al., 2015; Fleury et al., 2008) have involved drilling small holes in shells: under these *in vitro* conditions the holes become occluded within 2–4 months by formation of new material on the inside, but the holes themselves remain visible. Others have presented evidence to suggest that shells in the wild are normally repaired within 3 months (Shanks and Wright, 1986). Blundon and Vermeij found that shells of the gastropod *Littorina irrorata* with repaired rim damage were just as strong in compression tests as those with no damage; so far, this is the only paper to specifically investigate the mechanical performance of repaired shells (Blundon and Vermeij, 1983).

The literature contains many reports of biomechanical studies conducted to measure the material properties of the shells of limpets and other molluscs (e.g. Currey and Taylor, 1974; Blundon and Vermeij, 1983; Cabral and Natal Jorge, 2007). Properties measured include strength, stiffness and toughness. Almost all of these tests involved the application of a gradually increasing force and deformation to the shell, or a sample cut from it. For example, Cabral and Natal Jorge tested *P. vulgata* and three other limpet species in this way. They placed the shell with its rim on a flat horizontal steel surface and applied a vertical downwards force at the apex until failure occurred (Cabral and Natal Jorge, 2007). Tests were carried out with shells in dry and wet conditions, and limpets were either left *in situ* attached to the rock surface or placed on a steel surface. The *in situ* limpets were found to be stronger and shells from

which the animal had been entirely removed were found to be weaker in some species (but not in all), leading these workers to propose that the animal itself had some role in resisting the applied force and delaying failure. This type of test is known as a 'quasistatic' test because it allows ample time for the applied stress to be distributed throughout the sample. By contrast, an impact test involves the rapid, localised application of force using a striker such as a metal weight; the resulting pattern of stress and damage may be very different from that in the quasistatic test. The only previous work involving impact testing of limpet shells was conducted by Shanks and Wright; they removed limpets from their home locations, placed them on a horizontal rock surface and dropped weights from different heights to measure the impact energy needed for failure, as a function of shell size and species (Shanks and Wright, 1986).

Limpets move around to feed by grazing, but each individual has a fixed 'home' location where it spends most of its time; its shell grows in such a way as to fit closely to the surface of the rock in that location. The shell consists almost entirely of calcium carbonate, with a small percentage of organic material and water. The microscopic structure is very complex and varies with species (Ortiz et al., 2015). Fig. 1 shows a simplified illustration of the layered structure of *P. vulgata*; a number of layers can be identified, including the M-layer (the myostracum, to which the adductor muscle attaches), and layers above and below the M-layer denoted M−1, M−2, M+1 etc. Each layer has a different structure – some layers are made from calcite and some from aragonite, and the orientation and arrangement varies from layer to layer including prismatic and lamellar arrangements of crystal units. The basic structure of M-layers is known as the first-order structure, with second and third orders being identified at finer scales (see for example Ortiz et al., 2015; Szabó and Koppel, 2015).

There is considerable interest in understanding the relationship between structure and mechanical properties in the shells of molluscs. These materials have been found to have remarkably high toughness – more than 10-times higher than calcium carbonate in mineral form – prompting much research to develop biomimetic materials (e.g. Barthelat et al., 2007; Zhang et al., 2016). Some engineering materials also have laminated structures and for these materials impact strength is also a matter of concern. Glass fibre composites, for example, have good impact resistance but if the impacts are repeated they gradually weaken and fail as a result of build-up of microscopic damage (Azouaoui et al., 2010; Schrauwen and Peijs, 2002). This type of failure, known as impact fatigue, has not previously been investigated for mollusc shells.

The present research aimed to address the following questions. Is impact failure a significant cause of death? What is the mechanism of impact damage and failure? What factors affect impact resistance? Does impact fatigue occur as a result of repeated impacts? Can impact damage be repaired; are the repaired shells as strong as undamaged ones?

MATERIALS AND METHODS

The test site (Fig. 2) was located on the South side of Dublin Bay in Ireland at the following coordinates (53°17′18″N; 6°6′42″W). It is an area consisting partly of a solid rock platform and partly of individual boulders of 1 m typical size, with very little sand or small pebbles. There is relatively little human footfall on the site because, although close to a residential area, the site is not attractive for recreational activities such as fishing, swimming or beach activities, which are catered for in other locations nearby. All tests were carried out during the period 22 May to 30 August 2016. Limpets (*Patella*
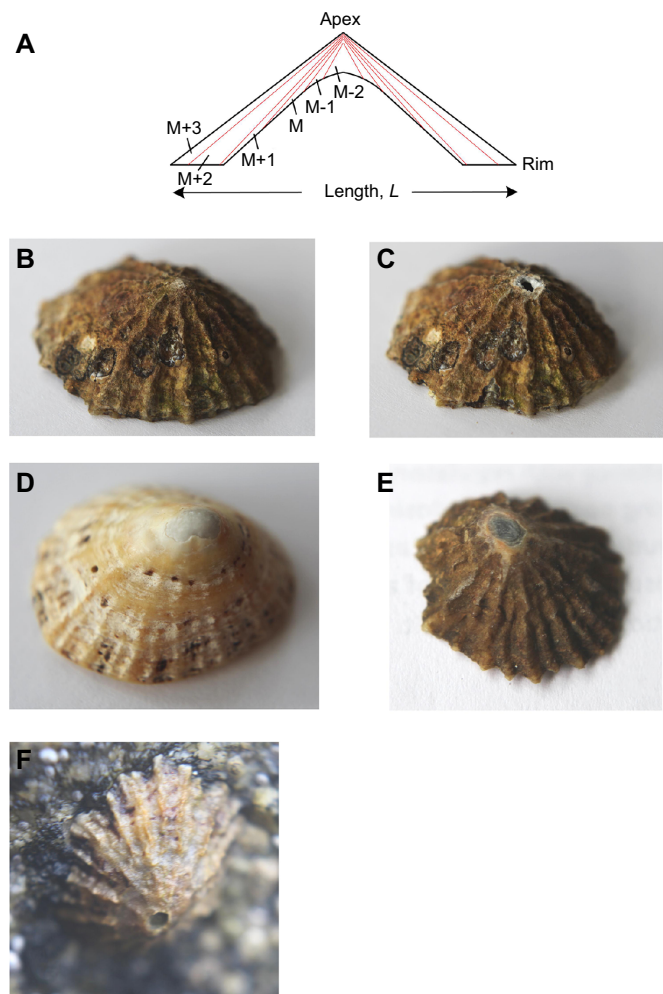

Fig. 1. Structure and appearance of the *Patella vulgata* shell. (A) A simplified representation of the layer structure of the limpet shell adapted from Ortiz et al. (2015). (B) A typical *in situ* specimen after removal from the site. (C) The same specimen after impact testing which has created an apex hole. (D) A typical beach specimen. (E) A specimen from the abraded group. (F) An example of a limpet at the site having a naturally occurring apex hole that has been repaired.

vulgata Linnaeus 1758) were abundant in the intertidal zone: the ones chosen for this study were located approximately at mid-tide, so they would have spent about half their time underwater. Limpets have a shape which is approximately a cone, but they are slightly elliptical and the cone apex is slightly off centre. The length (*L*) of each limpet was measured, defined as the maximum diameter at the rim.

Impact tests were carried out using a flat-ended steel cylinder of mass (*m*) 123 g placed in an aluminium tube of diameter 25 mm. The weight was allowed to fall vertically from different heights (*h*); the applied impact energy was calculated as *mgh* where *g* is the acceleration due to gravity. This applied energy could be varied from 0.03 J to 1 J. In total, 219 limpet shells were tested. Most of the tests were carried out on one of two groups, which are referred to as *in situ* and beach. *In situ* specimens were limpets tested on site, in place in their normal 'home' location. Rocks that were approximately horizontal (no more than 15 deg of inclination) were chosen. Any algae or other foreign material attached to the shell was removed as this might have absorbed some of the impact energy. Beach specimens were empty limpet shells taken from the

Fig. 2. The study site on the south side of Dublin Bay. The box on the inserted map of Ireland shows the general area.

nearby beach at Sandycove. Specimens were avoided if they were obviously damaged, for example having apex holes or areas missing from the rim.

To help understand differences between these two groups, a further three groups were tested, as follows:

Moved – these limpets were removed from their home location by carefully prising the shell off using a sharp knife. They were placed on a nearby flat rock, left for 15 min to allow the animal to adhere to the rock, and then impact tested. Empty – these limpets were prised from the rocks and the animal was removed with a sharp knife. They were left to dry under normal atmospheric conditions for 4 days before being impact tested on a flat rock. Abraded – these limpets were prised off the rocks, the animal was removed and the apex was abraded using a metal file, until these resembled the apices of the beach samples, which showed evidence of material removal in a circular region of diameter typically 20% of the rim diameter. Fig. 1 shows typical *in situ*, beach and abraded shells.

For each of the above five groups, impact strength was determined as follows. Shells were chosen to represent a range of sizes. Each shell was impacted once at a given energy level, and was recorded as having either failed or survived. Failure was defined as a significant amount of damage, sufficient to compromise the integrity of the shell and likely lead to death of the animal. Subsequent experiments (see below) confirmed the link between damage and fatality. In almost all cases, failure occurred by the formation of a hole at or near the apex of the shell (see Fig. 1). These data were analysed to obtain a critical shell size for failure and a critical failure energy, as described in detail below.

Shells in the *in situ* and beach groups that did not fail after the first impact were subjected to repeated impacts at the same energy level until failure occurred. This type of failure is known as 'impact fatigue', the general term fatigue applies to any type of failure that occurs as a result of repeated or cyclic loading. The number of impacts to failure in these tests varied from 2 to 120.

A small number of tests was also conducted in which beach shells were slowly crushed between parallel steel plates in an Instron testing machine, using the same method as Cabral and Natal Jorge (2007). The applied force and displacement were recorded throughout the test; the total applied energy to failure was calculated as the area under the force–displacement curve.

Two further experiments were carried out to investigate the relationship between damage and repair. Firstly, live limpets on site were closely examined to look for signs of naturally occurring damage. A total of 107 limpets were examined at seven locations

within the test site, chosen to include rocks inclined at different angles to the horizontal and facing in different directions with respect to the sea. Records were made of any visible shell damage and any signs that the damaged areas had been repaired. Secondly, limpets were deliberately damaged *in situ* so as to create apex holes. Damage was applied in two different ways: 23 specimens received impacts whilst a further 10 samples were given small (2–2.5 mm diameter) apex holes by gently tapping a nail into the apex. They were left in place and examined periodically to record whether they survived and whether repair occurred. If repair did occur then the specimen was re-impacted to gauge the success of the repair.

Selected samples were examined using a scanning electron microscope (Zeiss Ultra). Some shells were sectioned vertically through the apex and polished to a 1 μm finish using silicon carbide paper and diamond-impregnated cloth. Other shells were examined on fracture surfaces created during the above experiments. All samples were coated with a 10 nm layer of gold/palladium and viewed in secondary electron imaging mode.

Where relevant, Student's *t*-test was used to test for statistical significance between groups. The term significant difference implies a *P*-value of 0.05 or less.

RESULTS
Damage and repair *in vivo*
Of 107 live limpets examined *in situ*, a total of 7 (6.5%) were found to have apex holes which had been repaired. Fig. 1F shows an example: new material has been deposited to fill the gap, but the original hole is still visible. The diameters of these holes varied from 2 to 6 mm. A further 10 limpets (9.3%) showed some evidence of removal of material from the apex, which may have been abrasion (as was common on beach specimens – see Fig. 1D) or spalling due to impact (see below for more discussion of spalling).

To further study repair, apex holes were created in 33 limpets located on two different rocks. Hole diameters varied from 1.5 to 12 mm. After 10 days, 6 limpets (18%) remained. After 28 days, only 2 remained and these stayed in place for 78 days by which time there was evidence of repair material forming below the hole. These specimens were then retested by applying the same impact energy (0.3 J) which had been used to create the holes originally. Both specimens survived the impact, showing that they were at least as strong as they had been originally. In general, the specimens having larger holes tended to disappear soonest, and the two survivors had relatively small holes (1.5 mm and 2.5 mm). However, a further 17 specimens with hole diameters of 2–3 mm did not survive. Of 40 undamaged limpets under observation on the same rocks as the damaged ones, only 8 (20%) were lost, and these were all lost from the same location at the same time, perhaps as a result of a particular predation event.

Impact and quasistatic testing
During the impact tests (including also the impact fatigue tests described below), almost all failures (205/219; 94%) occurred by formation of an apex hole: Fig. 1C shows a typical example. The other 14 failures, which occurred only in the beach and abraded groups, took the form of cracks running either from the rim to the apex around the circumference, causing part of the rim to break away.

Fig. 3 shows a typical dataset obtained from the impact testing: *in situ* specimens tested with an impact energy of 0.5 J. Clearly, smaller shells tend to fail and larger ones tend to survive, but there is an overlap region, in this case from L=25.5 to 28.7 mm. A step function can be defined, as shown by the red dashed line, having a transition at some critical value of L, denoted L_{crit}. This can be considered as a fitting line, to which the individual points either fit
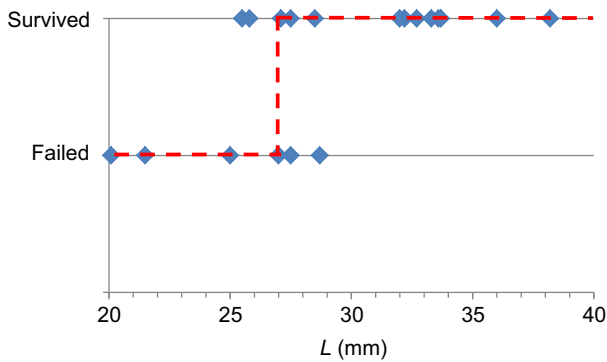
Fig. 3. A typical dataset from the impact tests for *in situ* specimens tested at an impact energy of 0.5 J. The outcome (failed or survived) is plotted as a function of shell length. The red dashed line indicates the step function that gives the best fit to the data. In this case, the critical length is 26.9 mm.

exactly, or have some error, *e*. Given a set of results with values L_i, where *i* is a number from 1 to *n*, the error e_i is defined as zero if the point falls on the fitting line. For points not on the line, i.e. shells having $L<L_{crit}$ that survived and shells having $L>L_{crit}$ that failed, the error is defined as:

$$e_i = L_i - L_{crit}. \qquad (1)$$

The correct value of L_{crit} is defined as the one for which the sum of all e_i is zero. The uncertainty on this result, created by scatter in the data, can be defined as the standard deviation (s.d.) of the dataset consisting of all e_i. A problem with defining the s.d. in this way is that it can be made artificially smaller by including many tests at very low *L* values (which all fail) and very high *L* values (which all survive). To avoid this problem, when s.d. was calculated, only those zero-error values from *L* within 10% of L_{crit} were included.

Table 1 shows the values of L_{crit} for the *in situ* specimens tested at three different impact levels: 0.3 J, 0.5 J and 1 J. The table also shows results for the other four specimen groups, all of which were tested at 0.5 J. For the tests at 0.5 J, the results are almost identical for three groups: *in situ*, moved and empty, and indeed there was no significant difference between them. Likewise the two groups beach and abraded showed no significant difference. However, there was a significant difference between the first three groups and the other two groups, implying that moving and emptying the shells does not reduce impact strength, but abrasion does, and the abraded shells have similar impact strength to the beach shells.

Fig. 4A shows this information graphically, plotting the applied energy *E* against *L*. Included on the graph are individual test results from the slow compression tests performed on beach samples. Also included are some other results from slow compression tests on dried *P. vulgata* shells, which were tested as part of the work reported in Cabral and Natal Jorge (2007). The impact energies for

Table 1. Impact test results

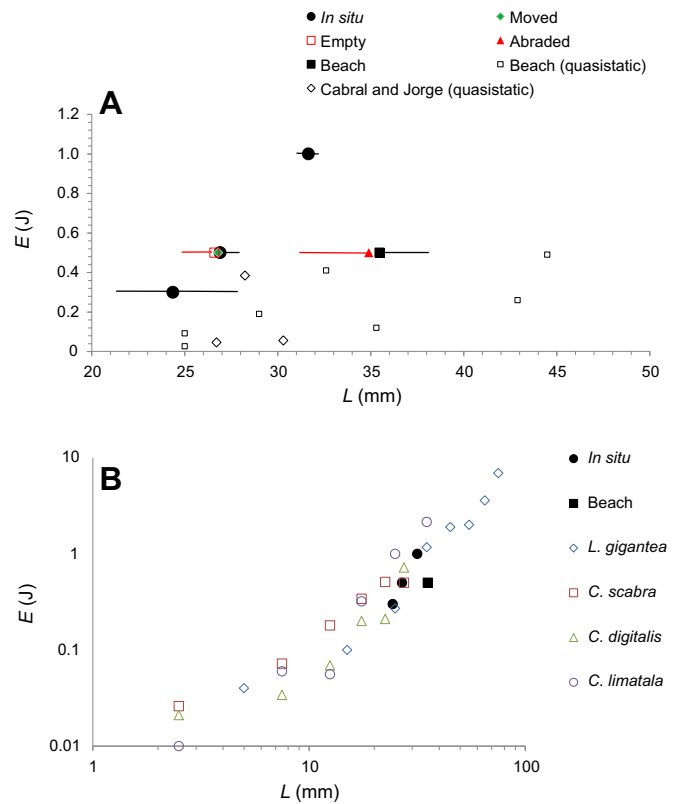| Group	Applied energy (J)	L_{crit} (mm)	E_n (MJ m$^{-4.6}$)
In situ	0.3	24.3±3.9	7.91
In situ	0.5	26.9±0.9	8.36
In situ	1.0	31.7±0.5	7.91
Moved	0.5	26.8±1.6	8.50
Empty	0.5	26.6±1.6	8.80
Abraded	0.5	34.9±3.8	2.52
Beach	0.5	35.5±2.6	2.34

L_{crit} measurements are mean±s.d.

Fig. 4. Impact strength test results plotting the critical length L_{crit} as a function of impact energy for the five study groups. (A) All groups were tested at an energy of 0.5 J and the *in situ* group was also tested at 0.3 J and 1.0 J. Error bars show s.d.: these have been simplified somewhat in the case of some data points that are almost coincident. See Table 1 for numerical data. Also shown are values of energy to failure for specimens tested in quasistatic compression, from the present study (beach group) and also from Cabral and Natal Jorge (2007). (B) Impact strength results as in A, for the *in situ* and beach groups, plotted on logarithmic scales, along with data on four different limpet species from Shanks and Wright (1986).

these shells were calculated from force–displacement data kindly supplied by Professor Cabral. It is clear from the impact data on the *in situ* specimens that larger shells are capable of resisting greater impact energy. This can be allowed for by defining a normalised energy E_n. One possible normalisation would be to divide the applied energy *E* by the volume of the shell. Since it has previously been shown that all linear dimensions, including shell length, width, height and thickness, tend to scale in simple proportionality (Cabral and Natal Jorge, 2007), then dividing by shell volume is equivalent to dividing by L^3. In fact, a better fit to these three data points is obtained by dividing by a somewhat higher power of *L* – the best fit occurs when:

$$E_n = E/L^{4.6}. \qquad (2)$$

As Table 1 shows, this gives values of E_n that are almost constant for all *in situ* tests. E_n values are also shown for the other groups, which have the same similarities and differences as found in the L_{crit} values. The advantage of using E_n is that it's now possible to define differences in energetic terms. The *in situ* specimens fail at an impact energy which is larger than the beach specimens by a factor of 3.4.

Fig. 4B shows the same impact energy data plotted along with data obtained from a paper by other workers who tested four

different limpet species (Shanks and Wright, 1986). Their approach to obtaining the impact energy was comparable to that used in the 'moved' group in the present work.

Impact fatigue

Specimens tested with repeated impacts also failed by formation of an apex hole in almost all cases. Fig. 5A shows the results of the fatigue tests carried out on *in situ* and beach specimens. The number of impacts to failure N_f is plotted as a function of the applied energy. The normalised energy E_n as defined in Eqn 2 has been used here again. Data points indicate the actual energy values used for the *in situ* specimens, showing that E_n does indeed provide a consistent description of the data. Smaller E_n causes failure after a larger number of impacts in both groups. There is considerable scatter, with values of N_f for the *in situ* group varying by about one order magnitude for a given E_n; however, this amount of scatter is not unusual in fatigue results from brittle ceramic materials, even when testing specimens of identical shape and size. The impact strengths (and their s.d. values) for the two groups are also shown on this
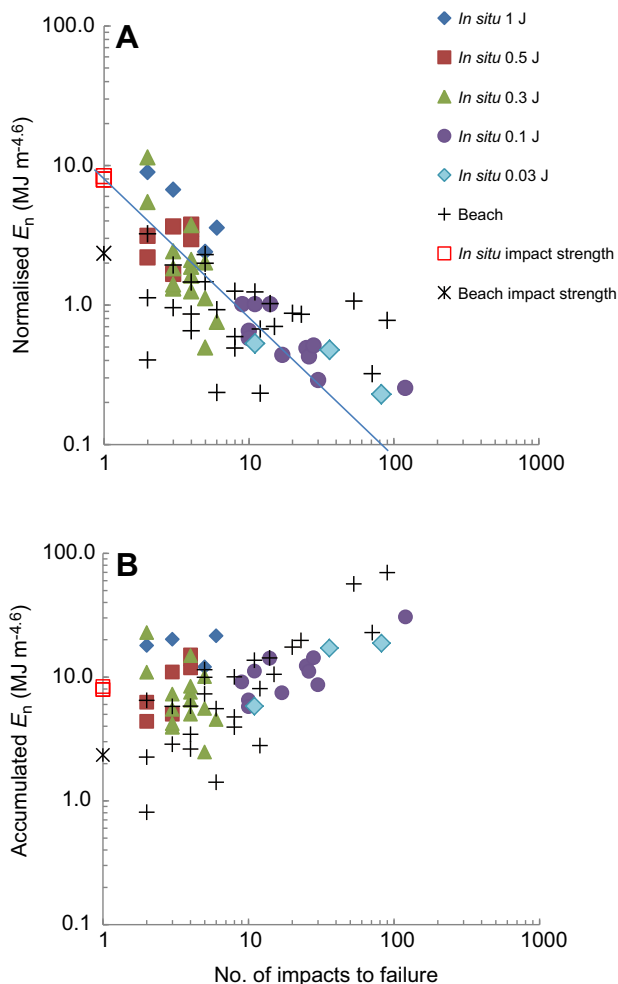

Fig. 5. Impact fatigue test results plotting the number of impacts to failure N_f as a function of the applied normalised energy E_n. (A) Data are shown for both the *in situ* and beach groups: for the *in situ* group the applied energy in Joules is also identified. The energies to failure in a single impact (i.e. the impact strength as shown in Table 1) are plotted here on the axis at $N_f=1$. The straight line represents a constant value of the total accumulated E_n, being equal to the single-impact value for *in situ* specimens. (B) The same data as in A, plotting the total accumulated E_n for each specimen.

graph, on the $N_f=1$ axis. Although there is a large difference in the impact strengths for single impact failure between these two groups, this difference is not apparent in the fatigue data. Taking all the results at impact energies less than $E_n=2$ MJ m$^{-4.6}$, the mean (±s.d.) value of N_f is 18.9±27.1 for the *in situ* specimens and 16.2±22.6 for the beach specimens – a non-significant difference. Another way to describe the fatigue data is by plotting the total accumulated energy, defined as E_n multiplied by N_f for each specimen (see Fig. 5B). For the *in situ* specimens the single-impact E_n is 8.06 MJ m$^{-4.6}$, whilst the accumulated energy in fatigue is just slightly larger at 10.58±6.2 MJ m$^{-4.6}$ (mean±s.d.). Linear regression analysis showed that the total accumulated energy in fatigue is given by 8.55+0.16N_f, indicating that it is almost constant but does increase slightly with the number of impacts. For the beach specimens the single-impact energy is 2.34 MJ m$^{-4.6}$ whilst the accumulated energy in fatigue is 12.3±16.1 MJ m$^{-4.6}$ (mean±s.d.), much larger than the single-impact energy but similar to the fatigue energy of *in situ* specimens. For beach specimens, the total accumulated energy is related to N_f as 2.38+0.65N_f.

Figs 6 and 7 show images of fracture and damage from some typical specimens. Fig. 6 shows a vertical section cut through the apex of a specimen which had been loaded slowly in a quasistatic test by compressing between steel plates, until failure occurred (in this case by rim cracking). Extensive internal cracking can be seen, especially in the region near the apex. Most of the cracks run parallel to the shell surface, and these cracks are very smooth, indicating an easy, low-energy path. These cracks will be referred to as delamination cracks because they appear to follow the boundaries between elements of the first order structure (between M-layers) or run parallel to laminations within M-layers (second-order structure). Occasionally, a crack will turn at right angles and run perpendicular to the main cracking direction: these will be referred to as perpendicular cracks – the crack surfaces in these regions are much rougher, indicating that more energy was needed for crack growth. For comparison, Fig. 6 includes an image for a limpet which was not loaded: no cracks were found, demonstrating that these cracks are indeed formed by mechanical loading. Some white lines were visible on the unloaded limpet, which are probably the traces of the M-layer boundaries: they coincide approximately with the main cracks on the tested specimen.

Fig. 7 shows typical damage in a limpet after one impact which was not sufficient to cause total failure. Flakes of material formed and detached from the outer surface (close to where contact occurred with the indenter) and also on the inside surface near the apex. This kind of failure, which is known as spalling, was very common during impact testing, occurring in almost all cases as a precursor to hole formation. This mechanism of failure is the same as that illustrated in Fig. 6: cracks form internally and grow on surfaces parallel to the outer and inner surfaces of the shell. Eventually, some perpendicular cracking also occurs, allowing flakes of material to detach. Fig. 7 shows the appearance of one of these smooth, low-energy fracture surfaces at high magnification. It consists of corrugated sheets of crystalline material, with occasional small steps between the sheets. The step height is approximately 100 nm. The same type of surface can also be seen in Fig. 6 for the delamination crack. In contrast, Fig. 7 also shows an example of one of the rare cases of an impact test in which failure occurred not at the apex, but by a crack in the side of the shell. The fracture surface in this case is seen to be much rougher, indicating a high-energy process. The crack was forced to deviate through large angles in order to pass through the various different M-layers, because of their different crystal structures and different orientations.
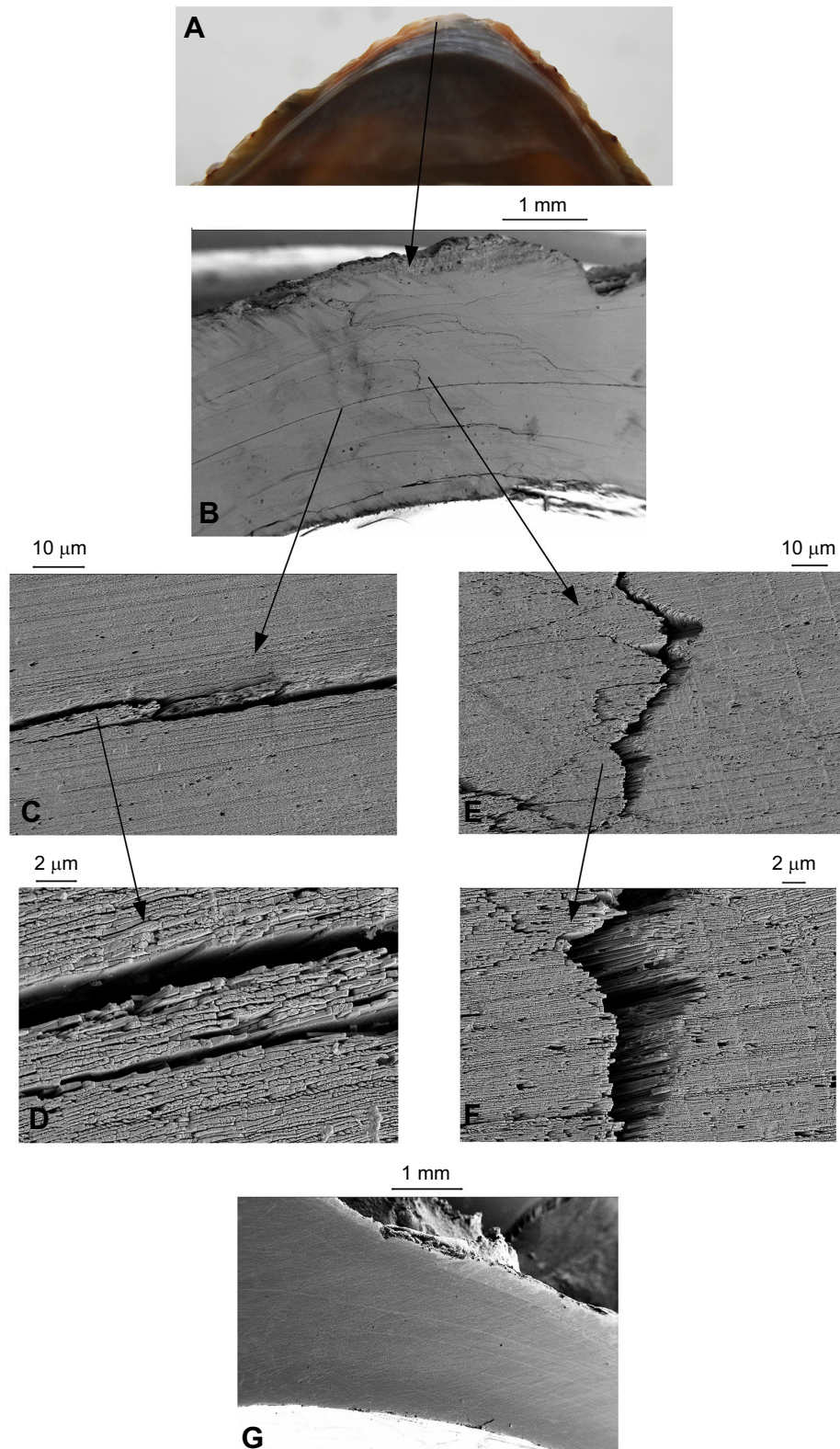
Fig. 6. Scanning electron microscopy of the *Patella vulgata* shell after testing. (A) A vertical section cut through a specimen after testing. (B) SEM image of part of the cut section, near the apex, showing extensive cracking. (C,D) Images at increasing magnification of part of a delamination crack from B. (E,F) Images at increasing magnification of part of a perpendicular crack from B. (G) A section from a shell that had not been impacted, showing no cracking.

DISCUSSION

Damage and repair *in vivo*

The failure modes observed during the present work were the same as those noted by previous workers (Shanks and Wright, 1986; Cadée, 1999; Harper et al., 2012). In the present case one particular mode – formation of a hole at or near the apex – predominated over all others. Shanks and Wright found that this was the predominant failure mode for one of their species: *Collisella scabra*, and that *Collisella limatula* also tended to form apex holes by failing around the muscle attachment. However, they found that other types of cracking dominated in their other species, suggesting species-related differences which may merit further investigation.
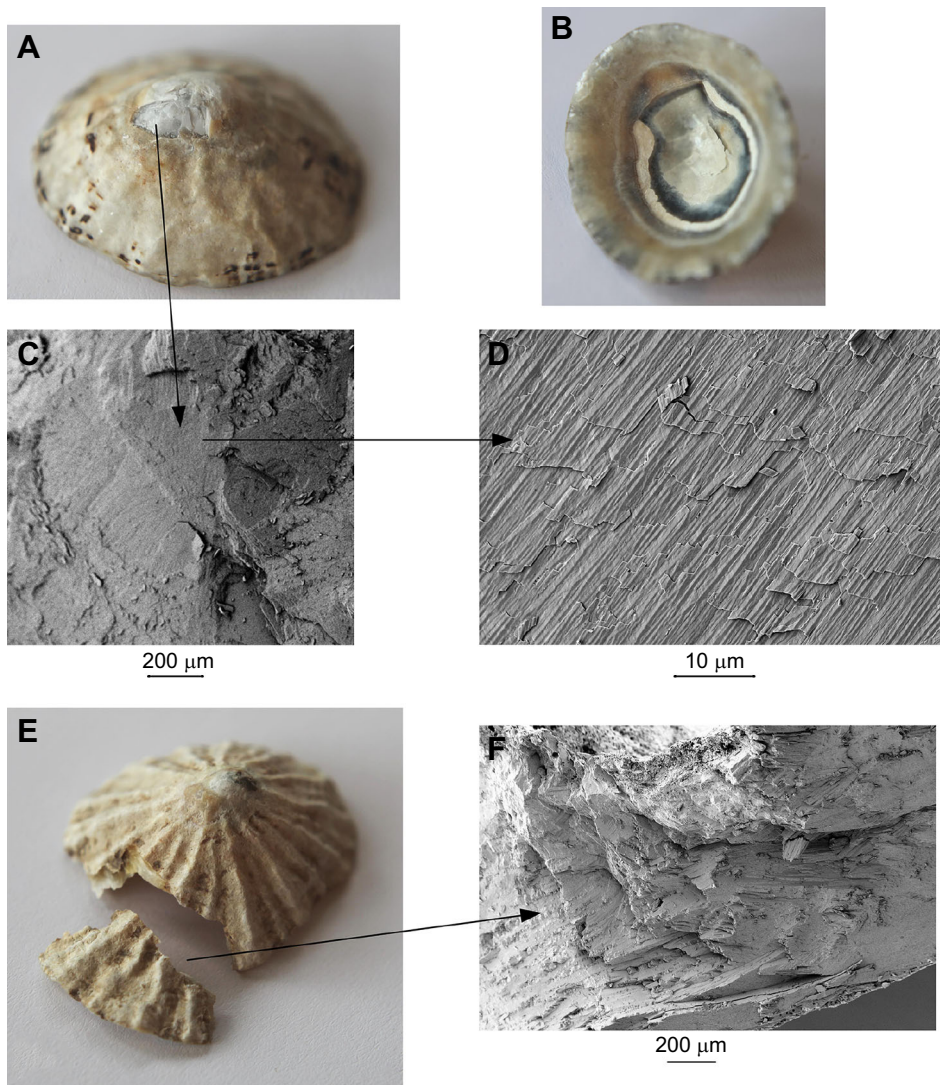
Fig. 7. Scanning electron microscopy of the *Patella vulgata* shell after subcritical impact testing. (A,B) A typical specimen after receiving a subcritical impact, showing spalling of material near the apex on both the outside (A) and inside (B). (C,D) SEM images at increasing magnification of part of the fracture surface seen in A. (E) A specimen which failed by cracking near the rim. (F) SEM image of part of the fracture surface of E.

Tests conducted on live limpets confirmed that those with badly damaged shells generally do not survive more than a few days. Even quite a small amount of damage, for example a 2-mm-diameter hole in a shell of length 40 mm, can be fatal. Possible reasons for death of damaged limpets are predation (for example, by gulls) or dehydration, when the limpet is exposed to the air. The number of test specimens here was relatively small and so not useful for statistical purposes, but this is the first systematic study to confirm the general assumption that shell damage is fatal. However, two limpets (6%) with relatively small holes did survive, and after 78 days had repaired the holes and made them at least as strong as they were before damage. Repaired holes of very similar appearance were also seen naturally occurring in 6.5% of limpets examined. This demonstrates that the damage/repair process generated in the experiments was also happening naturally. Although it is not possible to say for certain, one might speculate that impact damage could be responsible for a very large number of deaths. Any shells with relatively large holes would be lost immediately – within one or two days – and therefore would not be seen upon inspection of the site. Many empty shells found on the beach contained large holes, usually including the apex. It is possible that these holes formed after death, when these shells were moving in the sea, but this is unlikely. Shells are relatively light and so would have to be impacted against rocks at very high velocity to generate the necessary impact energy. Furthermore it was noted during testing that impacts usually caused spalling inside the apex, but almost no shells found on the beach contained these spalled areas, suggesting that the main type of damage experienced post mortem is sand abrasion, rather than impact damage.

Impact and quasistatic testing

The method devised for measuring impact strength and expressing this as a normalised energy allowed results from a range of shell sizes to be combined with relatively little scatter in the resulting data. The applied energy was simply calculated as the kinetic energy of the falling weight. Given that the limpet shell is much more flexible than either the weight or the substrate it can be assumed that all the applied energy passes into the shell, apart from some minor losses due to air resistance etc. This energy will cause elastic deformation in the shell, which will subsequently relax, causing partial rebound of the weight. If the applied energy is large enough, then the non-elastic part will largely be consumed in causing damage. Other possible forms of energy dissipation are plastic deformation and viscous flow, but given that the shell is almost pure ceramic material, these can be assumed to be negligible. Impact strength, in the present work and in previous work (Shanks and Wright, 1986), is defined as the total applied energy needed to cause failure.

As Fig. 4 shows, the present work conducted on *in situ* specimens yielded impact strength values which were very similar to those obtained by Shanks and Wright (1986). Within a certain scatter band, the effect of shell size on impact strength is quite consistent over a range of species. Beach specimens had significantly lower impact strengths: they required 3.4-times less energy for failure than *in situ* specimens.

The small number of quasistatic tests conducted in the present study, along with those obtained from a previous study, showed a very large amount of scatter: a few specimens failed with energies close to those recorded for the impact specimens, but most failed at much lower energies, up to 20-times lower. The likely reason for this is the irregular shape of the shell rim, which means that when placed on a flat surface it only makes contact at three points. When compressive force is applied, large stresses will build up at these points. If the shell is relatively flexible and the rim relatively flat, these high stresses may be smoothed out, but if the shell is relatively stiff or irregular then a crack may form near the rim and gradually propagate to cause failure at a low load. This type of failure was frequently observed both in the present study and by previous workers (Cabral and Natal Jorge, 2007). This may also explain why Cabral and Natal Jorge found higher failure forces when they tested shells which were still attached to rocks in their 'home' locations: these shells, having grown to conform to the local surface of the rock, would have been better able to distribute the applied forces around the rim.

However, this raises an apparent anomaly. In the present work, it was found that impact strength was not affected if the limpets were removed from their home locations and tested on flat surfaces. One might have expected that this would lead to a reduction in strength and an increase in scatter, mimicking the quasistatic tests. A possible explanation lies in the difference in stress distribution between these two types of test. When an impact occurs between two relatively stiff objects, a shock wave propagates out from the impact point. In this case, the shock wave will be highly concentrated near the apex, but will tend to dissipate as it moves down the cone towards the rim. Thus, the highest stresses will be experienced near the apex and any stress concentrations that might occur as a result of limited contact at the rim will be relatively insignificant. In order to investigate this mechanism, it would be necessary to carry out further experimental work to measure the elastic and damping properties of the shell material, and further analysis to determine the magnitude and extent of the shock wave. This would also explain the rather surprising result that the impact energies to failure are higher than the quasistatic energies (see Fig. 4). In a material sample of more regular shape one would normally expect impact failure to occur more easily than quasistatic failure, owing to the concentrating effect of the shock wave. This implies that the cone shape is a good way to prevent material failure at all locations except the apex of the cone. The behaviour of the apex in this case will be discussed further below. The ability of the limpet to grow its shell in close contact with the surrounding rock may have other benefits such as reducing dehydration and preventing certain kinds of predation; what this work has shown is that it does not improve impact resistance.

Further testing showed that impact strength was also not affected by removing the limpet from the shell and allowing the shells to dry out. It might have been expected that the soft tissues of the animal would have had some shock-absorbing effect but it seems this is not the case, probably because the shell itself is very stiff and the soft tissue is located on the far side of the impact point, not directly interposed between the shell and the impacting object. In retrospect perhaps this is not so surprising: after all it is the shell that is protecting the animal, not the other way around. Drying causes large changes in properties in other stiff biological tissues, such as bone and insect cuticle (Dirks and Taylor, 2012), but these tissues contain much more water (about 30–40%).

Shells taken from the beach showed much lower impact strengths. Given the above results it is clear that this difference is not attributable to the uneven shape of the rim, to the presence of the animal or to the state of hydration of the shell material. Another difference which was clear when observing the beach shells is that in almost all cases material had been removed from the apex as a result of the shells being scoured by sand particles. When this abrasion was reproduced artificially using a file, the impact strength dropped to be the same as that of the beach specimens. This provides further evidence for the statements above, to the effect that the material near the apex is crucial in absorbing energy from the impact shock wave. Material in this area is thicker than elsewhere, as can be seen in Fig. 6A. Measurements on a typical shell removed from the rocks (of length 39.5 mm, shown in Fig. 6G) showed that it had a thickness at the apex of 2.0 mm, whereas elsewhere the thickness varied from 1.0 to 1.5 mm. Abrasion will remove a very small volume of material (compared with the total volume of the shell) but crucially, it will reduce the thickness, raising the peak impact stresses. Further insight into the function of the apex in impact resistance was obtained by analysing the data on impact fatigue, as described in the following section.

Impact fatigue

The results presented in Fig. 5 reveal that *in situ* limpet shells perform poorly when it comes to resisting repeated impacts. For small numbers of impacts the total accumulated energy remains almost constant, similar to the energy for single-impact failure. So, for example, when the energy is reduced to one-quarter of the single-impact value, failure occurs after about four impacts. Most materials perform much better than this: for example a glass-fibre composite material failed after about 70 impacts when loaded at one-fourth of the impact strength (Schrauwen and Peijs, 2002). Bone samples loaded cyclically at half their compressive strength took, on average, 80,000 cycles to fail (O'Brien et al., 2003). Further work is required to understand this poor response to repeated loading, but it is probably related to the low-energy damage mechanism described above and shown in Figs 6 and 7, which involves delamination cracking. During these tests, it was noted that spalling occurred after only a few cycles, even in specimens that took many more cycles to develop a hole. This suggests that the threshold energy for delamination is much lower than that for complete failure. However, delamination was also found to be the predominant damage mode in a glass-fibre composite material and was found to occur at a threshold of less than one-tenth of the impact strength (Schrauwen and Peijs, 2002), so it would be worthwhile studying the similarities and differences between shell materials and engineering composites.

Much has been written about how the microscopic structure of shell materials (especially nacre) enhances toughness by increasing the energy needed for crack propagation (e.g. Currey et al., 2001; Barthelat et al., 2007). This may also be true for limpet shell material as regards the propagation of through-thickness cracks, which generate very rough fracture surfaces (see Fig. 7F). However, during impact, the shock wave creates stresses (both tensile and shear) on planes parallel to the layer structure, on which cracks can propagate much more easily. This demonstrates how considerations of material toughness must be related to the kinds of loading which these shells experience in their natural habitat.

A surprising finding of the present work is that the fatigue performance of beach shells was almost identical to that of *in situ* specimens, despite the very different impact strengths of the two groups. The beach specimens showed more variability, i.e. more scatter in the number of cycles to failure for a given impact energy, which could be attributed to greater specimen-to-specimen variability, especially in the amount of shell abrasion. Beach samples showed accumulated energies in fatigue which were, on average, 5.3-times higher than their single-impact energy. In a certain sense, then, they show better fatigue performance than normal, *in situ* shells. Further work is also needed to explain the mechanisms underlying these findings, but a possible explanation is related to the discussion above about the role of the apex. Beach specimens, it was argued, are weaker in single-impact situations because they have lost material from the tip of the apex by abrasion. In impact fatigue tests on *in situ* specimens, it was noted that they invariably lost material from the apex during the first few impacts. Apices became flattened and thinner as a result of spalling. This suggests that the apex may function as a sacrificial feature. It is effective in providing resistance to one impact, or a few impacts, but it soon becomes damaged and loses its effectiveness, making the shell susceptible to failure by a larger number of relatively small impact events.

We do not know how many impacts a limpet may experience during its lifetime, and no doubt this varies considerably depending on the local conditions. One study (Shanks and Wright, 1986) recorded large numbers of impacts on targets that they set up on intertidal boulders, although they did not attempt to correlate the energy of these impacts with that needed to cause shell damage.

This study had some limitations. Only one limpet species was considered, and all observations and tests were carried out on specimens from one specific location, during one 3 month period. Repeated impacts were applied in quick succession: this might also occur naturally, for example during a storm, but if impact events were more spaced out then this might allow time for repair. However, the time needed for repair is relatively long – in the order of weeks – and currently, it is not known whether limpets can detect and repair partial damage that does not penetrate the shell thickness.

Another limitation of the present study was that all the impacts occurred at or close to the apex of the shell because the impacting object had a flat bottom and a diameter similar to that of the shells themselves. This, however, seems to be a fair simulation of natural events: Shanks and Wright (1986), using their impact strength values (which are similar to the present ones), estimated the size of a rock that would be necessary to cause failure, assuming that impact occurred at a typical velocity of 3 m s^{-1}. They found that the rock would have a diameter similar to the length of the shell; unless such a rock is very irregular and jagged in shape, it will almost always strike the shell near the apex. They concluded, 'The ocean does not need to throw boulders to wreak havoc amongst intertidal organisms; it seemingly needs only throw pebbles'.

The work has provided evidence that impact damage is often fatal, but in some cases, damage can be repaired to completely restore the strength of the shell. For the species studied, apex hole formation emerges as the predominant type of impact damage during testing and was also observed to occur naturally. Shells were found to be highly susceptible to failure by repeated impact – a mechanism not previously studied. Some insights into the relatively high impact strength of shells *in situ*, and their relatively poor fatigue resistance, were obtained from microscopy. Damage starts as internal delaminations, taking advantage of a natural weakness in the layered structure, and proceeds via spalling to hole formation. Thick material at the apex may act as a sacrificial impact resistance feature. From this, and previous work, impact damage emerges as an important cause of mortality for limpets and other molluscs, at least under some circumstances. The relative importance of impact compared with other causes, such as dehydration, overheating and predation, is difficult to assess and no doubt depends strongly on local environmental factors.

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