

THE IMPORTANCE OF A CREVICE ENVIRONMENT TO THE LIMPET *HELICION PECTUNCULUS* (PATELLIDAE)

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ABSTRACT

Helcion pectunculus has an organized distribution within rock crevices with smaller, younger limpets towards the back of the crevice and larger, older limpets towards the crevice mouth. The crevice refuge provides *H. pectunculus* with a stable and buffered environment with higher relative humidities and lower rock surface temperatures than adjacent exposed rock surfaces. Limpet body temperatures were significantly lower in crevice refuges compared with limpets on adjacent exposed rock surfaces. Body temperatures never exceeded the rock surface temperatures. It is suggested that this is a result of morphological adaptations such as short spines on the shell and allometric growth (shell increasing in height faster than length). Compared with other South African patellids, less force is required to detach *H. pectunculus* from the substratum and individuals deprived of a crevice refuge experienced extremely high mortalities, 45% of limpets being lost during the first high tide period.

INTRODUCTION

A number of physical factors influence the ecology of intertidal organisms (Moore, 1972; Wolcott, 1973; Branch, 1981; McMahon, 1990). The upper limits of their distribution, especially for sessile species such as barnacles (Connell, 1961) and algae (Schonbeck & Norton, 1978), are thought to be controlled by extremes of temperature and desiccation. Limpets are often the dominant mobile herbivores on temperate and tropical shores (Branch, 1981) and the upper limits of their distribution have also been shown to be set by physical extremes (Wolcott, 1973; Newell, 1976, 1979 for reviews; Williams & Morritt, 1995). High-shore species, in particular, experience high temperatures with associated thermal and desiccation stresses (Moore, 1972). Such species usually have increased physiological tolerances (Newell, 1976, 1979), as well as morphological and behavioural adaptations to reduce physiological stress. Morphological adaptations include shell ornamentation (Branch & Branch, 1981), alteration of shell shape (Vermeij, 1973) and allometric growth whereby the shell increases in height more rapidly than in length (Branch, 1981).

Some limpets adapt their behavioural patterns by retreating to refuges, i.e. cracks and crevices (Williams & Morritt, 1995), sealing their shells with mucus (Garrity, 1984) and positioning their shells to minimize exposure to insolation and maximize evaporative cooling (Garrity, 1984; Williams & Morritt, 1995). Limpets that use refugia can desiccate and die if prevented from returning to home sites after foraging (Garrity, 1984; Williams & Morritt, 1995). Limpets also exhibit a wide range of behavioural rhythms, some species foraging while submerged or immersed during the day or night and returning to a fixed scar, while other species select suitable non-permanent resting sites (Branch, 1981; Little, 1989; Hodgson, 1999). It has been hypothesized that wave activity may limit limpet distribution on the shore and that many of the behavioural traits exhibited by limpet species also ensure that the limpets are safe from dislodgement by strong wave activity (Branch & Marsh, 1978).

Numerous workers have investigated the physiological tolerances of limpets by measuring limpet body temperature, corresponding water loss and ionic concentrations of the

haemolymph or extravisceral water (Segal & Dehnel, 1962; Davies, 1970; Wolcott, 1973; Verderber, Cook & Cook, 1983; Lowell, 1984; Branch & Cherry, 1985; Williams & Morritt, 1995). Limpets have been shown to be remarkably resilient to such extremes (Wolcott, 1973) and their physiological limits measured in the laboratory are rarely exceeded under field conditions.

Helcion pectunculus (Gmelin, 1791) is one of the most abundant limpet grazers in the upper intertidal of many South African rocky shores. During high tides and diurnal low tides this limpet retreats to crevices (Gray & Hodgson, 1998, 1999). This study aimed to test the hypothesis that the crevice environment not only acts as a buffer to the physical extremes (temperature and wave activity) of the upper intertidal, but is also necessary for the survival of *H. pectunculus*.

MATERIAL AND METHODS

Size distribution of Helcion pectunculus within crevices

During diurnal low tides, *H. pectunculus* resides on a home scar within a crevice. To determine how limpets are arranged within crevices, 25 horizontal, west-facing crevices, all of which had an approximate depth of 100 mm and width of about 0.25 m, were chosen for study at Port Elizabeth (33°58' S, 25°38' E) in the Eastern Cape of South Africa. All limpets were removed from each crevice starting at the outer lip and moving towards the back of the crevice. Different 'rows' of limpets were recognized and the shell length of limpets within these rows was measured (to the nearest millimetre) using vernier calipers.

Physical factors within and outside the crevice

To determine whether the crevice provided *H. pectunculus* with a stable and buffered environment, horizontal (<45°) rock surface temperatures were taken at hourly intervals during daytime periods of emersion on a spring-full moon tide, a neap-quarter moon tide and a spring-new moon tide in each of spring, summer, autumn and winter using a hand held thermometer (±0.1°C; Hanna instruments HI 9040 microcomputer thermometer) both inside and outside of a representative crevice (depth ~100 mm) containing limpets. Relative humidity was

also recorded at hourly intervals from both inside and outside of the crevice using a Hygrocheck relative humidity probe ($\pm 2\%$). Rock temperatures were measured by placing the tip of the temperature probe in direct contact with the rock surface. The probe was insulated from the surrounding air using thick (50 mm) polystyrene. Humidity measurements were taken by placing the humidity probe into the crevice until it was between 20 and 40 mm from the back, air humidity readings were taken between 20 and 40 mm above the rock surface.

Data were analysed using a repeated measures two-factor analysis of variance (using Statgraphics version 5). All assumptions for the use of ANOVA (equality of variance and normality) were met.

Limpet body temperatures

Body temperatures of limpets were measured using thermocouples. Each thermocouple was inserted onto the foot by pushing between the shell and the rock surface (Wolcott, 1973; Williams & Morritt, 1995). There was no evidence (100% recapture of marked individuals) that inserting a probe under the shell of limpets had any negative effect on them. The daytime body temperatures of marked limpets were measured hourly during emersion on a particularly hot spring-tide day in summer (maximum air temperature = 32°C). Twenty limpets were measured while 'at home' in their crevice, while another 20 were measured having had their crevice destroyed, i.e. the limpets were experimentally exposed to sunlight during emersion. As individual specimens were monitored at hourly intervals during the day, statistical analysis of diurnal changes is inappropriate because readings from individuals are not independent.

The effect of crevice removal on the survival and behaviour of limpets

Work was carried out at Cannon Rocks ($33^\circ 44' \text{S}$, $26^\circ 35' \text{E}$) in the eastern Cape of South Africa where previous activity studies had been undertaken (Gray & Hodgson, 1998). To determine whether *H. pectunculus* was able to survive high on the shore when deprived of its crevice refuge, individual limpets ($n = 97$ from a total of five crevices) were marked with non-toxic paint. As soon as all the limpets had left the crevices to forage, the crevices were filled with 'Styrafoam'. The foam, once hard ($\sim 1 \text{ h}$), was filed down and smoothed to follow the contours of the rock to prevent the limpets from finding any form of refuge upon their return from foraging. At the next low tide, the position of the marked limpets was recorded as (1) missing, (2) adjacent to their home crevice, (3) in a new crevice within 1 m from their old crevice, (4) in a new crevice $> 1 \text{ m}$ but $< 2 \text{ m}$ away from their old crevice, and (5) in a new crevice $> 2 \text{ m}$ away. The limpets were observed at every low tide for 1 week and then at monthly intervals for a period of 6 months. Control limpets (i.e. limpets allowed to return to a crevice) were not used as results from an overlapping study on growth rate (Gray & Hodgson, 2003) at the same site revealed that crevice fidelity was high and long-term mortality negligible.

*Force required to detach *H. pectunculus* from rock*

The force required to detach limpets ($n = 30$), in their natural habitat, was measured using two loops of fishing line slipped under the anterior and posterior edges of the limpet shell and spaced in such a way that force would be equally distributed to the two loops. The fishing line was then attached to a 25 kg Salter spring balance modified to give a permanent record of the maximum force, normal to the substratum, required to detach each limpet. As duration of force affects measurements, force was exerted for $\sim 5 \text{ s}$ in all cases. As the correlation between

force of dislodgement and surface area of foot results in a high r^2 value (see Results), it is unlikely that any variation in force required, resulting from differing initial pull strengths, is important.

Forces required to detach limpets from the substratum were measured while the 30 animals were on their home scars. No attempt was made to record the force required to detach limpets while they were mobile because, as the initial pull is made, the limpet clamps down onto the rock and thus a measurement of 'mobile tenacity' is not gained. Once detached from the substratum, each limpet was allowed to re-attach to a sheet of transparent acetate. The foot area was drawn around with a water-proof marker pen. In the laboratory, the area of the foot was acquired by superimposing the acetate sheet onto graph paper and counting the number of squares within the area of the foot.

RESULTS

*Size distribution of *Helcion pectunculus* within crevices*

The smallest individuals (mean shell length $\pm \text{SE}$: $10.4 \pm 0.28 \text{ mm}$) were found at the rear of the crevice (row 1, Fig. 1). Limpets progressively increased in size towards the front of the crevice with the largest animals (mean shell length $\pm \text{SE}$: $27.4 \pm 0.5 \text{ mm}$; Fig. 1] in the outer row (row 4).

Physical factors within and outside the crevice

During all daytime low tide periods in all seasons, the relative humidity within the crevice refuge [$74.3 \pm 1.3\%$ (mean $\pm \text{SE}$)] was significantly higher (Table 1) than the relative humidity outside of the crevice [$64.7 \pm 1.5\%$ (mean $\pm \text{SE}$)]. Furthermore, the humidity within the crevice never dropped below 50% (lowest recorded at 1400 h during an autumn spring tide), whereas outside the crevice the humidity was only 38%. Relative daytime humidity, however, varied significantly with season (Table 1) with the highest mean values in spring [inside crevice,

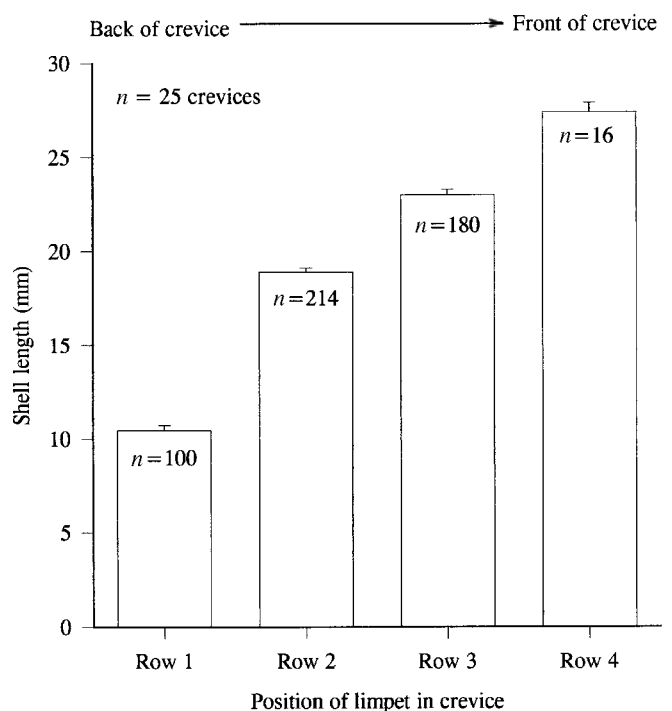


Figure 1. The size-frequency distribution (mean shell length $\pm \text{SE}$) of *Helcion pectunculus* in crevices ($n = 25$) on a South African rocky shore.

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81.9 ± 1.3% (mean ± SE); outside crevice, 72.8 ± 2.8% and lowest in autumn [inside crevice, 68.2 ± 4.1% (mean ± SE); outside crevice, 58.9 ± 2.9%].

Rock surface temperature during all low tide periods in all seasons was also always found to be significantly lower within crevices [20.7 ± 0.2°C (mean ± SE)] compared with exposed rock surfaces (23.0 ± 0.4°C) (Table 2). Rock surface temperatures within the crevice refuge were never recorded above 26°C (maximum = 25.7°C during a summer spring tide) while outside the crevice, rock surface temperatures in summer of up to 33.4°C were measured. Rock surface temperature also differed significantly with season (Table 2). As would be expected, higher temperatures were obtained in spring [outside crevice, 24.0 ± 0.7°C (mean ± SE); inside crevice, 21.4 ± 0.2°C] and summer [inside crevice, 25.6 ± 1.0% (mean ± SE); outside crevice, 21.4 ± 0.5°C] when compared with those of autumn [outside crevice, 21.1 ± 0.8°C (mean ± SE); inside crevice, 17.9 ± 0.6°C] and winter [outside crevice, 21.3 ± 0.5°C (mean ± SE); inside crevice, 18.7 ± 0.3°C].

Table 1. Results of a two-factor analysis of variance to determine the effect of microenvironment (inside *vs* outside crevice) and season on relative humidity.

Source of variation	SS	d.f.	MS	F	P
Main effects					
Inside vs. outside	2136.08	1	2136.08	26.13	<0.0001
Season	9701.75	3	3233.92	39.56	<0.0001
Residual	11118.16	136	81.75		
Total (corrected)	23191.85	143			

The interaction between microenvironment and season was not significant ($P > 0.05$).

Table 2. Results of a two-factor analysis of variance to determine the effect of microenvironment (inside *vs* outside crevice) and season on rock surface temperature.

Source of variation	SS	d.f.	MS	F	P
Main effects					
Inside vs. outside	335.74	1	335.74	43.50	<0.0001
Season	609.88	3	203.29	26.35	<0.0001
Residual	1049.24	136	7.72		
Total (corrected)	1998.77	143			

The interaction between microenvironment and season was not significant ($P > 0.05$).

Limpet body temperatures

Rock temperatures and limpet body temperatures were cooler by up to 12°C in crevice habitats compared with exposed habitats (Fig. 2). Exposed limpet body temperatures were found to be ~2°C lower than the substratum on which they were situated, dependent on the time of day. Body temperatures of limpets located in crevices were found to follow the temperature of the substratum much more closely (Fig. 2).

Removal of the crevice habitat

On returning to their crevice filled with 'styrofoam', limpets actively sought out a new crevice refuge. Of 97 limpets labelled, 33 settled immediately adjacent to their old crevice (but never on the styrofoam) (Table 3), while 20 found new crevices close by (<1 m). Forty-four limpets were lost during the first high tide period after the crevices were filled. After 1 month, 83 limpets had been lost and after 6 months, 94 of the original 97 limpets

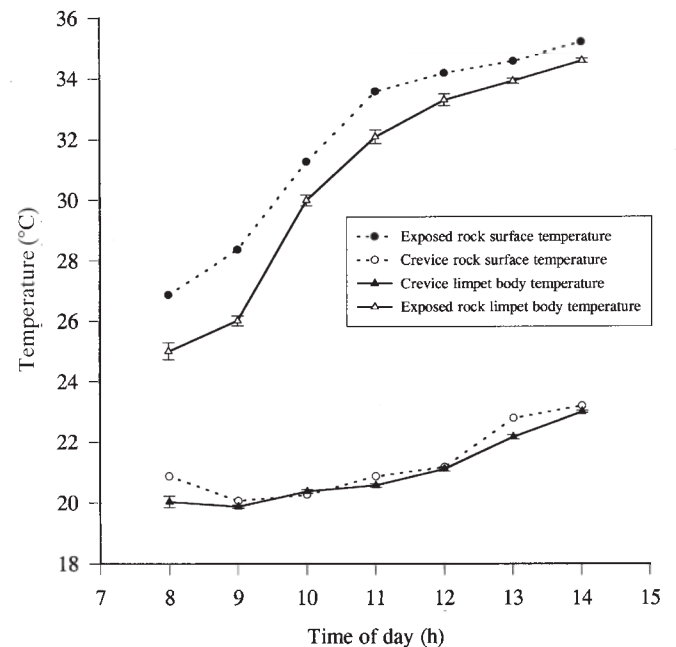


Figure 2. A comparison between rock surface temperatures and limpet body temperatures (mean ± SE) both inside a crevice refuge ($n = 20$) and while exposed to direct sunlight ($n = 20$) over a diurnal period of emersion on a spring tide day in mid-summer.

Table 3. Numbers and location of marked limpets recorded at regular intervals after having removed their crevice refuges while they were actively foraging.

Time	No. in crevices	No. immediately adjacent	New crevice <1 m	New crevice <2 m	New crevice >2 m	Gone
0 h	97	0	0	0	0	0
12 h	0	33	20	0	0	44
24 h	0	17	18	1	0	61
48 h	0	11	23	1	0	62
72 h	0	11	9	1	1	75
96 h	0	11	6	1	1	78
120 h	0	11	3	1	2	80
1 month	0	11	0	1	2	83
3 months	0	4	0	0	2	91
6 months	0	2	0	0	1	94

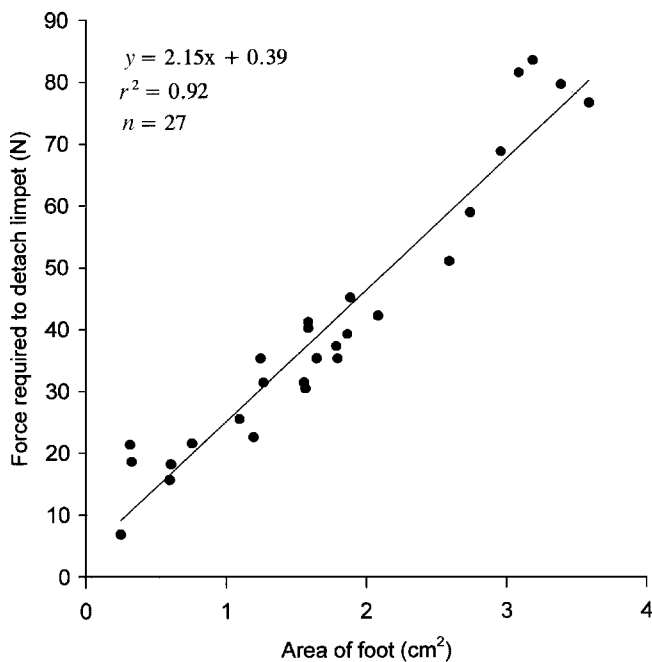


Figure 3. Relationship between surface area of the foot and force required to dislodge *Helcion pectunculus* from rock.

were no longer present, two limpets still maintained their position adjacent to their old crevice, while one limpet had managed to find a new crevice refuge >2 m from its original 'home' crevice.

Force required to detach limpets

A linear relationship was found between the force required to detach limpets and foot area (cm²) using linear regression ($r^2 = 0.92$; Fig. 3). The mean (\pm SD) tenacity value of *H. pectunculus* was 26.95 ± 1.27 N cm⁻².

DISCUSSION

Crevice refuges are known to reduce desiccation, and juveniles of many limpet species are restricted to the low shore or damp crevices (Branch, 1976). During high tides and diurnal low tides *Helcion pectunculus* resides in crevices and under boulders in the upper balanoid zone of the intertidal rocky shore (Gray & Hodgson, 1998). The size gradient of *H. pectunculus* within crevices is to be expected as only small individuals will be able to fit at the back of crevices. However, the fact that small individuals are always at the rear of a crevice suggests that this is a site of juvenile settlement. This distribution of limpets within a crevice means that small limpets not only begin foraging once the larger limpets have left the crevice, but that they return to the crevice first (D. R. Gray, unpublished data).

Using the growth equation from Gray (1996) for southeast coast *H. pectunculus*, the ages of limpets within crevices can be calculated. The smallest limpets found within crevices had a mean shell length of 10.4 mm, and therefore an average age of ~7 months, while the smallest limpet found had a shell length of 6.1 mm and would be 3.8 months old. The largest individuals in the crevices had a mean shell length of 27 mm which corresponds to an age of 3 years. Thus, as limpets grow, they must migrate towards the mouth of the crevice due to the spatial constraint imposed by the shape of the crevice.

Within 1 year of settlement *H. pectunculus* will grow to be ~15–20 mm in shell length. These individuals will have moved from the back of the crevice into the 'second row', leaving space for the next recruits to settle at the back of the crevice. Clearly, the number of rows present in a crevice will depend on the depth of the crevice. All crevices used during this study had a depth of about 100 mm which allowed a maximum of four rows of limpets. It is not known whether *H. pectunculus* larvae settle selectively and actively search out the rear of crevices. However, many larvae respond in a gregarious fashion to chemical cues (for a review, see Chia, 1989) and in the high-shore limpet *Lottia digitalis*, larvae recruit to the adult habitat (Kay, 2002). It is possible therefore that larvae of *H. pectunculus* respond in the same way.

The measurements of rock surface temperature and relative humidity show that limpets within crevice refuges experience a stable and buffered environment compared with that outside the crevice. During diurnal low tides, crevices are significantly more humid and have lower rock surface temperatures than adjacent exposed rock surfaces. Other species of limpet, e.g. *Cellana grata* on Hong Kong shores, actively search out damp or shaded habitats or refuges on hot summer days (Williams & Morritt, 1995). However, rock surface temperature is also dependent on the aspect of the rock surface and the inclination to the sun (Davies, 1969; Wolcott, 1973). Williams (1994) suggested that duration of emersion and rock aspect are probably the most important factors affecting individual survival in *C. grata*. These factors also appear to play a major part in the life of *H. pectunculus*.

The body temperatures of *H. pectunculus* were never found to exceed the rock surface temperatures unlike the results for *C. grata* (Williams & Morritt, 1995), *Fissurella* species (Lewis, 1963) and *Siphonaria* species (Vermeij, 1971). Williams & Morritt (1995) suggested that the higher limpet body temperature may be due to the rock surface being cooled evaporatively by wind, while the sole of the limpet foot prevents this. The limpet may, therefore, heat up via radiation from the sun and conduction from the rock (Davies, 1970) while not experiencing the same degree of convective heat loss as the open rock surfaces. *Helcion pectunculus* has a highly prickled shell surface (Kilburn & Rippey, 1982) that may well increase the amount of re-radiation of heat back into the air (Branch, 1981). *Helcion pectunculus* also exhibits strong allometry with its shell increasing in height faster than length, i.e. during growth the shell becomes taller and hence volume increases more than the foot surface area from which water loss occurs and over which conduction from the rock surface takes place. These morphological adaptations could be one reason why the body temperature of *H. pectunculus* seldom rises above that of the rock surface on which it is attached.

Limpet body temperatures within crevices are significantly lower than of those attached to rock surfaces that are fully exposed to the insolation. The maximum body temperature of crevice-inhabiting *H. pectunculus* was 23°C compared with 34°C for limpets not in a crevice. Crevice refuges high up on the shore therefore reduce thermal stress on these limpets and may be why they are able to survive on the high shore. In a study examining the thermal tolerance of another high-shore limpet, Williams & Morritt (1995) found that during diurnal low tides *C. grata* occupied areas of the shore that were significantly cooler than adjacent habitats. They found that vertical rock surfaces shaded from direct sunlight were cooler compared with horizontal surfaces, and that surfaces facing west heated up greatly during the latter part of the day. *Cellana grata* was also found to exhibit clustering behaviour at rock pool interfaces, a behaviour also found in *Patella granularis* (Branch, 1975). Branch (1975) suggested that *P. granularis* uses the pool interfaces as means of evaporative cooling.

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Helcion pectunculus therefore resides in environments, in the form of crevices, which remain humid during diurnal low tides, keeping limpet body temperatures relatively low. *Helcion pectunculus* also homes to a fixed scar, a behaviour which has been shown to reduce desiccation in both siphonariid (Verderber *et al.*, 1983; Branch & Cherry, 1985; Hodgson, 1999) and patellid limpets (for a review, see Branch, 1981). A further adaptation of *H. pectunculus* to reduce thermal stress is being active during nocturnal low tides and diurnal low tides while in the shade (Gray & Hodgson, 1998). This behaviour is also found in many other limpets (Branch, 1981; Hodgson, 1999).

Field determinations of the force required to detach *H. pectunculus* revealed that it is one of the least tenacious limpets occurring along the South African coast (for data on six species of patellid see Branch & Marsh, 1978), and that there is a linear relationship between force of attachment and foot area. Branch & Marsh (1978) found that limpets that grow allometrically (e.g. *P. argenvillei* and *P. granatina*) exhibit a curvilinear relationship between tenacity and foot area. This, they suggest, is because as size increases, force per unit area of foot also increases. Shell growth in *H. pectunculus* is strongly allometric and a curvilinear relationship would be expected, but this is not the case. A possible reason for this is that *H. pectunculus* is a small limpet compared with other South African limpets with its largest recorded size being approximately 35 mm in length (Gray, 1996).

Branch & Marsh (1978) suggested that there was a relationship between tenacity and wave action experienced in the six patellids they studied. For example *P. cochlear* has a high tenacity of $50.76 \pm 1.96 \text{ N cm}^{-2}$ (mean \pm SE) and experiences high wave activity, while *P. oculus* has a low tenacity of $19.11 \pm 1.18 \text{ N cm}^{-2}$, experiences lower wave activity but has a very large foot surface area. It is suggested that the same does not hold true for *H. pectunculus*. Individuals of *H. pectunculus*, although occurring high up on the shore, experience very strong wave activity especially during the stormy season mainly due to the geomorphology of the shores they inhabit. They have a very low tenacity and a small foot surface area and removal of the crevice refuge is catastrophic to them. A large proportion of limpets (45%) deprived of their refuge were lost during the first high tide, and after the first week without a crevice 82% of the limpets were lost. While it is possible that some of this loss is due to predation (e.g. by the specialist limpet-feeding fish *Chorisochismus dentax* (Stobbs, 1980; Lechanteur & Prochazka, 2001), most limpets were probably lost to wave action.

In summary, the hypothesis that the crevice environment acts as a buffer to the physical extremes of the upper intertidal, and is necessary for the survival of *H. pectunculus*, is supported. Crevices provide more equitable rock surface temperatures and humidities, reduce thermal stress and desiccation and result in lower limpet body temperatures. The crevice also acts as an essential refuge from wave activity, reducing the chance of the limpets being washed away by the incoming tide.

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