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The Effect of Depth on the Attachment Force of Limpets

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A wide variety of marine animals, including animals as different as cephalopods, echinoderms and fish, use suction adhesion for temporary or long-term attachments (1). One aspect of suction adhesion that has been discussed, but never tested experimentally, is its dependence on depth. The change in hydrostatic pressure with depth may exert a marked effect on the force of attachment produced by suction (2–6). This study was designed to confirm this effect experimentally, using limpets as a test case. Limpets rely on suction to resist dislodgment by predators and crashing waves (7, 8). We measured the suction tenacity of four species of limpets at sea level and at increased ambient pressure in a hyperbaric chamber. Tenacity is defined as the force of attachment divided by the area of the foot contacting the substratum. Change in ambient pressure had a small but significant effect on limpet tenacity. These results show that depth can affect attachment up to a point, but the mechanics of limpet feet appear incapable of producing dramatically larger tenacities.

Increasing hydrostatic pressure raises the upper limit on the force of attachment that a sucker can create (5). This can be explained as follows. A sucker forms an attachment by decreasing the pressure of the water it encloses. This results in a differential between the pressure of the water outside the sucker and the pressure inside. This differential pulls the sucker against the substratum. The pressure outside the sucker is the ambient pressure, which increases by 100 kPa (1 atm) with each 10-m depth increase. The minimum pressure inside the sucker is limited by water's tensile strength. The sucker can reduce the pressure until the tension in the water reaches a critical value, at which point the water cavitates; it undergoes cohesive failure and gas bubbles expand suddenly. The minimum pressure is known as the cavitation threshold. Thus, the greatest possible pressure differential equals the difference between ambient pressure and the cavitation threshold. Because the cavitation threshold is relatively independent of depth, and ambient pressure increases with depth, the maximum possible pressure differential, and thus the force of attachment, increases with depth.

If animals using suction can take advantage of this increased potential, then depth may have a profound impact on the effectiveness of their attachment. The musculature of the sucker and its ability to maintain a seal will determine the extent to which the animal can take advantage of this potential. Each sucker has an intrinsic limit to the pressure differential that it can produce. Once it reaches this limit, it will be unable to generate greater pressure differentials, no matter how much the depth increases (see Fig. 1). This potential limit on the effect of depth on suction adhesion has not been emphasized previously.

We tested the effect of depth on four species of limpets: *Lottia pelta* (Rathke), *Lottia gigantea* Sowerby, *Lottia limatula* (Carpenter), and *Macclintockia scabra* (Gould) (formerly *Collisella scabra*). Chuck Winkler Enterprises (San Pedro, California) supplied limpets for these experiments. The limpets were kept in an artificial seawater aquarium at 21°C.

Tenacity measurements were made with a strain gauge force transducer described in detail previously (7). The transducer was tied in series with monofilament fishing line such that pulling on the line deformed the transducer by three point loading. The force transducer could be attached to the limpet by a Lucite harness glued to the shell. The limpets were allowed 5–15 h to attach to a clear Lucite sheet in the aquarium. The area of the limpet's foot was estimated with calipers as described previously (7). For each force measurement, the force was increased quickly

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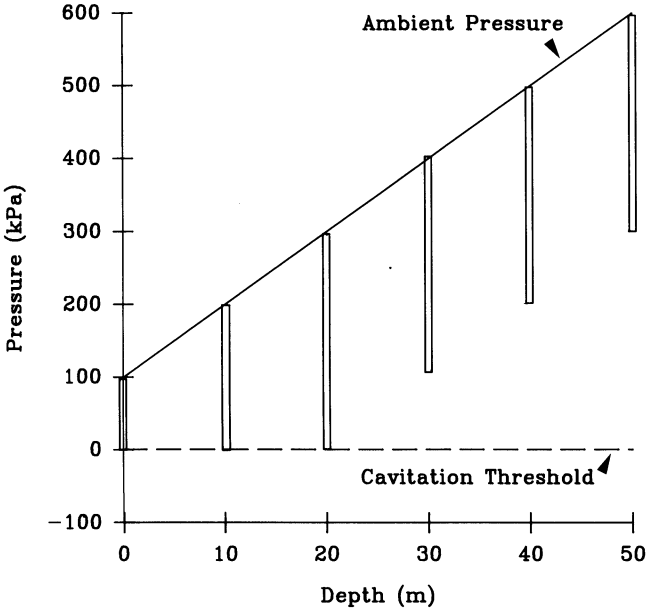

Figure 1. Graph demonstrating the effect of depth on a hypothetical sucker. The maximum possible pressure differential is the difference between ambient pressure and the cavitation threshold. For simplicity, the cavitation threshold is taken to be 0 kPa. The pressure differential created by the sucker is represented by a vertical bar descending from ambient pressure. If the sucker musculature can generate a pressure differential of 300 kPa, then from 0 to 20 m, cavitation limits the sucker and the force of attachment increases with depth. At depths greater than 20 m, the sucker will reach the limit of its musculature before cavitation occurs and the attachment force remains constant despite depth changes.

but steadily until the limpet's attachment failed. The peak force was recorded. Most measurements lasted roughly one second.

Immediately before a tenacity measurement, the limpet was moved by sliding it a few millimeters across the surface to ensure that it was using suction and not a glue-like adhesive (7). Because limpets can use either of these two attachment mechanisms, which have different tenacities, measurements are meaningless unless one knows the attachment mechanism in use (7, 8). We chose to investigate the effects of increased ambient pressure on suction adhesion rather than glue-like adhesion, because increased ambient pressure is not expected to affect glues.

Tenacity measurements at sea level were made in Chapel Hill, North Carolina. Tenacity measurements at increased ambient pressure were made in the hyperbaric chamber operated by the National Oceanographic and Atmospheric Administration National Undersea Research Center (NURC) at the University of North Carolina, Wilmington, North Carolina. Four dives to a pressure of 200 kPa (corresponding to 10 m of water) were made in the chamber. Each dive was approximately one hour in length. In addition, one dive was made to 340 kPa (24 m of water) for approximately 40 min. Two researchers were in the chamber, one to measure foot area and attachment force, the other to videotape the soles of the limpet feet as they were being detached. The limpets were in a 60 × 30 × 30 cm aquarium in the chamber. The force transducer was wired to an amplifier and chart recorder as described previously (7); the amplifier and recorder were both outside the chamber. A VHS video camera in an underwater housing was used with underwater floodlights. The videos were analyzed frame-by-frame after the experiments to determine the mode of failure of the limpet's attachment.

Increased ambient pressure had a small but significant effect on limpet attachment. At sea level, the mean suction tenacity of all four limpet species combined was 50 ± 31 kPa (mean ± S.D., n = 162 trials) (100 kPa = 1 atm). In the hyperbaric chamber, the mean suction tenacity for all four species combined was 59 ± 33 kPa (n = 138). The difference between these means was statistically significant (*t*-test, $P = 0.0094$). Increasing ambient pressure increased the suction tenacity of each of the four species, but this increase was significant only for *L. pelta* (Table I). Further increase of the pressure from 200 kPa to 340 kPa did not affect the limpets' attachment. The mean suction tenacity of all limpets at 200 kPa ambient pressure was 59 ± 34 kPa (n = 115), and the mean suction tenacity of those at 340 kPa was 60 ± 31 kPa (n = 23). There was no significant difference between these means (*t*-test, $P = 0.43$). The tenacity of limpets was consistent among dives. There was no significant variation among the mean tenacities found on the 5 dives (ANOVA, $P > 0.75$). Similarly, there was no significant variation among the mean tenacities measured for each day at sea level (ANOVA, $P > 0.1$). Although not measured quantitatively, the tenacity of limpets using glue-like adhesion did not seem to change with depth. Their shear tenacity, as observed when forcing them to slide slightly to break any glue-like bonds, was not noticeably different at increased pressure relative to their shear tenacity at sea level.

To understand these results, it is helpful to analyze the effect of depth more thoroughly. Cavitation in seawater

Table I

Effect of ambient pressure on suction tenacity, by species

Species	Mean tenacity (kPa) Sea level	Mean tenacity (kPa) Hyperbaric	*P*-value
Lottia gigantea	44 ± 16 (n = 24)	48 ± 36 (n = 28)	0.29
L. limatula	50 ± 29 (n = 73)	54 ± 29 (n = 34)	0.24
L. pelta	46 ± 18 (n = 29)	59 ± 28 (n = 46)	0.012
Macclintockia scabra	59 ± 46 (n = 36)	74 ± 39 (n = 30)	0.084

t-tests were used for comparison of means. Hyperbaric includes ambient pressures of 200 and 340 kPa. Values are mean ± standard deviation.

will not occur until the absolute pressure drops below approximately 20 kPa (9). Thus, at sea level (ambient pressure = 100 kPa) limpets can generate a pressure differential of up to 80 kPa without being limited by cavitation. Greater pressure differentials can occur because seawater can sustain negative pressures, but cavitation becomes possible at pressure differentials greater than 80 kPa.

If the pressure differential acts over the entire area of the foot, then a pressure differential of 80 kPa creates a tenacity of 80 kPa. This probably does not occur, however, because limpets must press the perimeter of their feet down to form a seal. The area that must be in direct contact with the substratum to form a seal reduces the available area over which the pressure differential acts. Thus, a given pressure differential creates lower attachment forces and consequently lower tenacities. Since the area that the pressure acts over can be as small as one half the actual pedal area (7), a pressure differential of 80 kPa might create a tenacity of only 40 kPa. Given these considerations, the tenacity at which cavitation may be limiting ranges from 40 to 80 kPa, depending on the area over which the pressure acts. For this reason we chose 60 kPa as a rough cutoff point; at higher tenacities cavitation may be limiting at sea level.

In 73% of the trials at sea level, the tenacity of limpets on Lucite was less than 60 kPa. Increased depth would probably not have affected these limpets. On the other hand, increased depth may have allowed higher tenacities for the other 27%. This would have led to the increase in the mean for the entire population when tested at depth. Increasing ambient pressure to 200 kPa increased the pressure differential that was possible without cavitation to 180 kPa. Thus, at a depth of 10 m, cavitation would not have been limiting until the tenacity was between 90 to 180 kPa, depending on the area over which the pressure acted. On the videotape of the trials at 200 kPa ambient pressure, cavitation was seen in two cases, at tenacities of 117 and 130 kPa. These two limpets might have been able to take advantage of an even greater increase in ambient pressure.

The extent that limpet tenacity increases with depth depends on the ability of the pedal musculature to produce a larger differential. Because the overall change in tenacity was small and further increase in pressure to 340 kPa did not lead to a further increase in tenacity, it appears that the mechanics of the foot largely determine the tenacity of limpets. Specifically, limpets seem limited in their ability to maintain a seal at the margin of their feet. Analysis of the videotapes of limpets being detached in the hyperbaric chamber showed that most of the attachments failed by the formation of a leak at the foot's margin.

Depth may affect limpets in the field to a larger extent than seen in this study. The suction tenacity of limpets in the field is estimated to be roughly 90 kPa (80 kPa for the species used in this study) (8) as compared to 50 kPa on Lucite at sea level. Because Lucite is smooth, limpets may have greater difficulty preventing the edge of their foot from sliding in towards the center, and thus breaking the seal at the margin. The roughness of many natural substrates may facilitate this seal and allow more limpets to achieve tenacities that are cavitation-limited. Previous data for *Patella vulgata* show that the tenacity on rough slate is 23% higher than on smooth slate and 38% higher than on Lucite (10), although it is uncertain which mechanism these limpets were using. Also, undisturbed mucus at the margin of the foot may help to maintain the seal of limpets that have not been moved prior to the tenacity measurement. Thus, increases in depth may have a larger effect in the field than seen in this experiment.

Another reason for lower tenacity on Lucite is that the Lucite surface affects the limpets' behavior. Limpets are more likely to remain active on Lucite than on natural substrates. Active limpets often do not attach firmly; therefore many of the limpets had low tenacities (below 30 kPa). This clearly diminished the overall effect produced by increased ambient pressure. Differences in activity within the population also probably account for the large standard deviations in the measurements. It is interesting to note that many of the limpets that were firmly attached and not active had tenacities similar to limpets in the field. This demonstrates that it is possible for limpets to achieve high suction tenacities on Lucite, regardless of its smoothness.

Because of surface roughness and a lower level of activity, depth should have a greater effect in the field than in this study. Most likely, a larger percentage of limpets would be cavitation limited and thus affected by depth. This would lead to a greater average increase in tenacity. The data suggest, however, that the pedal musculature is still not capable of large increases in suction tenacity (more than 50%, for example).

A limited effect of depth on suction tenacity is not surprising for intertidal animals that are typically subject to small increases in depth. The limpets used in this study are commonly found in the upper to the middle or lower intertidal (11). There may not be an advantage to increasing the complexity or strength (maximum tensile stress) of their pedal musculature to produce pressure differentials beyond the range that is typically possible for them. Depth changes in the range they experience, however, will have an effect. An animal in the middle to lower intertidal experiences significant depth changes during the day. An increase of 2 m could increase limpet tenacity by 20 kPa (a 25% increase if the tenacity at sea level is 80 kPa).

One of the species used in this study, *L. pelta,* has a broader depth distribution, having a depth range from the intertidal to the subtidal, as low as 50 m (11). This species also experienced the clearest change in tenacity with depth, although the change was still small. It would be interesting to compare the effect of depth on other subtidal limpets with the results found here for limpets collected from the intertidal. Limpets from the subtidal may have adapted to conditions where the upper limit on tenacity is higher, and they may have the musculature to take advantage of it.

In summary, we have provided experimental confirmation of the effect of depth on suction attachment. We have also demonstrated that intertidal limpets are capable of taking advantage of this effect to a small extent. This study highlights the fact that sucker musculature may limit an animal's ability to take advantage of the effect of depth; this has been overlooked in previous work.

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