CEPHALOPOD SUCKER DESIGN AND THE PHYSICAL LIMITS TO NEGATIVE PRESSURE

ANDREW M. SMITH*

Laboratoire Arago, 66650 Banyuls-sur-Mer, France

Summary

Two factors determine the strength of pressure-based adhesive mechanisms such as suction: the magnitude of the pressure differential that their musculature and mechanics can produce and the pressure differential that water can sustain. This paper compares the adhesive strength of the primary cephalopod sucker types: the stalked suckers of decapods (cuttlefish and squid) and the unstalked suckers of octopods. These results are compared with the physical limits imposed by cavitation, the failure of water under negative pressure.

The maximum pressure differentials that suckers can produce were measured using a wettable pressure transducer or by measuring their force of attachment on a wettable surface and dividing by the area exposed to reduced pressure. The maximum pressure differentials that water can sustain on a typical marine surface were measured in a Z-tube. Fifteen cephalopod species representing three orders were studied. At sea level, cavitation limits all suckers to the same range of pressure differentials (100–200 kPa), regardless of their morphology. As ambient pressure increases with depth, cavitation ceases to be limiting. In this case, stalked decapod suckers produce greater pressure differentials than unstalked octopod suckers. In addition, small suckers produce greater pressure differentials than large suckers. Suckers larger than 7.5 mm^2, both decapod and octopod, typically achieve pressure differentials of 100 kPa. As their size decreases below 7.5 mm^2, octopod suckers get slightly stronger, sometimes producing pressure differentials of 250–300 kPa, while decapod suckers get exponentially stronger, sometimes producing pressure differentials near 800 kPa. There were no differences in sucker strength among the four octopod species, but seven of the ten decapod species differed from the overall decapod regression curve. The strongest suckers belonged to the fast-swimming, open-water species in the decapod sub-order Oegopsida.

Key words: pressure, cavitation, suction, adhesion, cephalopods, decapods, octopods.

Introduction

Many biological attachment mechanisms produce an area of reduced pressure between their adhesive surface and the substratum. They may decrease the pressure actively, as in suction adhesion (Kier and Smith, 1990) or the pressure may drop as a consequence of the adhesive interaction, as in Stefan adhesion (Banks and Mill, 1953) and capillary adhesion (O'Brien and Fan, 1975). In either case, the ability of water to sustain reduced pressure may limit the adhesion. This paper focuses on suction adhesion, because it produces large pressure differentials and has been well studied in octopuses (Smith, 1991a) and limpets (Smith, 1991b, 1992). The adhesive organs of these animals generate negative pressures, absolute pressures below 0 kPa in water (Smith, 1991a,b).

Strength of attachment is usually described by the term tenacity, the force per unit area of attachment. The tenacity of pressure-based adhesive mechanisms depends on the differential between ambient pressure and the pressure of the water enclosed by the adhesive surface. The lowest pressure the enclosed water can sustain is the cavitation threshold. Cavitation is the formation of gas bubbles in a fluid under reduced pressure. These gas bubbles cause failure of pressure-based adhesive mechanisms. Smith (1991a) has shown that cavitation limits the tenacity of octopus suckers at sea level.

While cavitation determines the lowest pressure an attachment mechanism can produce, the difference between this and ambient pressure determines the maximum pressure differential possible. Since ambient pressure increases with depth, suckers may be capable of much greater tenacities in the field than have been measured at sea level in the laboratory. In order to take advantage of this, suckers must be strong enough

*Present address: Department of Biological Sciences, Butler University, Indianapolis, IN 46208, USA.

to reach the cavitation threshold from the increased ambient pressure. If they are not, their musculature and mechanics, rather than cavitation, would be limiting (Smith *et al.* 1993). Thus, morphological variation of suckers may have a large effect on tenacity in deep water when cavitation is not limiting, which is masked at sea level when cavitation is limiting.

This question is particularly relevant to cephalopods, where there are two markedly different sucker types. Most coleoid cephalopods can be categorized either as decapods (cuttlefish and squid, orders Sepioidea and Teuthoidea) or octopods (order Octopoda). Decapods have stalked suckers (or sometimes just hooks), while octopods have unstalked, sessile suckers (Nixon and Dilly, 1977). Stalked suckers consist of a rigid cylinder, a muscular piston that fits into this cylinder, and a thin, tough stalk that connects the piston to the arm or tentacle club. Pulling on the stalk pulls the piston back against the resistance of the enclosed water. This reduces the pressure of the water. The harder the stalk is pulled, the greater the pressure differential, and the harder the sucker holds on (Naef, 1921–1923). This can continue until the stalk tears. Sessile suckers, in contrast, are flexible, muscular cups. The musculature of the wall of the cup generates an expansive force that decreases the pressure of the enclosed water (Kier and Smith, 1990). They are connected to the arm by a wide, fleshy base. The muscles attaching the cup to the arm insert near the rim rather than the base of the cup. Therefore, pulling the sucker away from the arm will not augment the pressure differential (Kier and Smith, 1990). Only the musculature of the cup contributes to the pressure differential. These differences in sucker anatomy suggest that stalked suckers may be capable of producing larger pressure differentials than sessile suckers.

In order for such a functional difference to be meaningful, however, one must know the physical limits that cavitation imposes on adhesion. The research described in this paper determines these limits under conditions relevant to marine animals. The pressure differentials of which decapod and octopod suckers are capable when cavitation is not limiting are then measured. With these data as a framework, one can compare the adhesive strength of different sucker types.

Materials and methods

The range of pressures possible in the marine environment

The cavitation threshold of water was measured using the Z-tube apparatus described by Smith (1991*a*). Briefly, a thin (3 mm internal diameter), Z-shaped glass tube, open at both ends, is filled with a sample of water and attached to a rotor. Spinning the tube subjects the water to centrifugal force, which pulls the water towards the ends of the tube. This results in a tension, or decreased pressure, at the center. Cavitation is observed using a stroboscopic light synchronized with the rotation rate. The pressure at which the water cavitates is calculated from the length of the water column and the rotational velocity at cavitation.

The cavitation threshold of artificial sea water from a filtered aquarium system was measured in two clean glass tubes (wettable) and two silicone-grease-lined tubes (non-wettable). Artificial sea water was used because its composition is consistent and it has the same cavitation threshold as sea water (Smith, 1991*a*). Typically, 15–20 samples were tested in each unlined tube because the cavitation threshold varies considerably among samples (Smith, 1991*a*). With the silicone-lined tubes, however, cavitation always occurred at numerous sites throughout the tube as soon as the pressure neared 0 kPa, so a large number of trials was considered unnecessary.

These tests were repeated after soaking the same tubes in sea water to coat their surfaces with a fouling layer typical of marine environments. The tubes were glued to a 40 cm×60 cm wooden board, which was then placed upside down in a large outdoor holding tank (9.1 m×18.2 m×0.75 m deep) so that the tubes were filled and continuously submerged. The tank was continually supplied with unfiltered sea water (30–34 ‰) pumped directly from Bogue Sound, North Carolina, USA. After 10 days of little to no rainfall, the tubes were removed and rinsed gently with artificial sea water. They were then attached individually to the rotor, and the cavitation threshold of artificial sea water was measured as before.

Maximum pressure differential achievable by sucker design: decapod

Attachment force measurements on a wettable surface

The pressure differential produced by a sucker can be determined by dividing its attachment force by the area exposed to reduced pressure. Force measurements were made on a wettable glass surface. On a less wettable epoxy surface, cavitation occurred under the suckers regularly at pressures of 0 to −100 kPa. Using a wettable surface should allow suckers to reach their maximum pressure differential, because the cavitation threshold becomes more negative as surface wettability increases (Smith, 1991*a*). The variability in the cavitation threshold complicates this approach. Nevertheless, on carefully selected clean glass surfaces, the cavitation threshold is between −200 and −1000 kPa (Smith, 1991*a*). This range should be sufficient to allow most suckers to reach their maximum pressure differential, but it is possible that cavitation could still occur and limit suckers that attached very strongly.

Most of the measurements (112 out of 129) were made with *Sepia officinalis* or *Loligo vulgaris* suckers because of the availability of live specimens and because they attached well to glass. Arms or tentacles were removed with a quick razor cut from animals anaesthetized in 2 % ethanol in sea water. They were then transferred to a basin filled with fresh sea water. The suckers were kept under water as much as possible. Suckers were then detached and used in these experiments. Even isolated from the arm, stalked suckers appear to function normally for an hour or more because of reflexes and the mechanical action of the piston; the force exerted by detached

suckers was not noticeably different from the force exerted by suckers still attached to the arm.

Force measurements were made using the transducer described by Smith (1991*b*). This was a thin, 4 cm^2 metal sheet with a strain gauge bonded to its surface. It was tied between two pieces of monofilament fishing line such that pulling on the free ends of the monofilament deformed the metal sheet in three-point loading. This transducer had an average error of 4.5 %, except for forces less than 0.3 N, where the error increased to 17.3 %. This was based on a comparison of known forces with the predictions of the calibration equation. The only suckers that produced forces less than 0.3 N were both small and relatively weak. For example, a sucker with a 2.5 mm^2 opening producing a pressure differential of 120 kPa exerts a force of 0.3 N. Because most suckers were either larger or produced greater pressure differentials, the higher error associated with forces less than 0.3 N probably had little effect on the analyses.

To measure the attachment force, the stalk of a sucker was gripped with forceps and allowed to adhere to a clean glass microscope slide. The microscope slide was held in a metal clip connected to the force transducer so that the sucker and slide could be pulled away from each other and the force measured at the moment of detachment. Each day, the glass slide was replaced, as its wettability decreased with exposure to air and sea water; slides were only used if water spread out rapidly over the entire dry surface, forming a thin film. After the force measurements, the diameter of the sucker opening between the inside walls of the rigid cylinder was measured using a dissecting microscope with an ocular micrometer. To take into account deviations from a circular outline, the diameter was measured in two mutually perpendicular directions and the average of these two values was used to calculate the area.

The reliability of the measurements was checked by comparison with a known pressure differential. In many trials, the water enclosed by the sucker did not sustain a negative pressure and cavitation occurred as the pressure neared 0 kPa. This provided a convenient, known pressure, hereafter referred to as the 'reference pressure'. At this pressure, clearly visible gas bubbles arose gradually. Thus, it could be distinguished easily from the sudden cavitation that occurred at negative pressures. The exact value of the reference pressure should be slightly higher than 0 kPa. Smith (1991*a*) found that the pressure after the gradual formation and expansion of a bubble was 8±6 kPa (mean ± S.D.). In their pressure probe, Zimmermann *et al.* (1993) found that the pressure after cavitation was equal to the saturation vapour pressure of water, 23 kPa at 20 °C. The lower pressure found by Smith (1991*a*) probably resulted from the greater expansion of the bubble and the lack of time to equilibrate. On the basis of these values, trials where a bubble formed gradually should produce pressure differentials from ambient, at sea level (100 kPa), of between 77 kPa and 92 kPa. The exact magnitude depends on the expansion of the bubble and whether or not it has time to equilibrate with water vapour.

The use of the reference pressure to check reliability is conservative. This is because, with small suckers, this pressure is likely to produce forces smaller than 0.3 N, where the force transducer is less accurate. Most tenacity measurements are at much greater pressure differentials, so they are likely to be more accurate than those at the reference pressure.

Typically, 4–8 force measurements were made for each sucker. Two data points per sucker were used in the analyses and in the comparison with octopod suckers: the attachment force at the first time the sucker produced a negative pressure, and the average attachment force at the reference pressure. These were then converted to pressure differentials. The first negative pressure was used because there was little variation among the negative pressures produced by each sucker. Thus, further measurements did not greatly increase the accuracy of the estimate of that sucker's strength and they complicated the statistical analyses.

The force required to break the sucker stalk

To compare adhesive strength among decapod suckers, a different method must be used to estimate the maximum pressure differential. Many squid are difficult to capture without seriously injuring them; by the time they arrive at the laboratory, their suckers no longer work well. In addition, some have rigid projections on their sucker rims that preclude attachment to a smooth surface. In these cases, the force that tears a sucker off the arm or tentacle was used to estimate the maximum possible pressure differential. Although this may seem to give an extreme estimate, it appears relevant. On isolated tentacles, suckers often stuck to nearby walls so firmly that they tore off. Thus, it appears that the pressure differentials they can actually produce are close to the values that would tear the stalk.

The pressure differential that would tear the stalk sets an upper limit to the sucker's adhesive strength. The maximum adhesive strength of any sucker must be at least as great as the pressure differential actually measured on a wettable surface, and it can be no higher than that which would break the stalk.

The forces required to break sucker stalks were measured on isolated arms or tentacles. The force transducer was connected to suckers with a loop of monofilament. This loop was slipped over the sucker like a noose. For smaller suckers, a small wire hook was used instead of monofilament. The stalk usually ripped at its connection with the arm or tentacle, rather than near the monofilament or hook. Thus, the connection to the transducer did not cause premature failure by damaging the stalk.

Force measurements on one individual each of *S. officinalis* and *Illex coindetii* were made with an elastic band whose extension had been calibrated for force. This was accurate for the high forces measured in these trials (error 2–4 %).

Eleven species from different habitats were studied. These represented six families in at least two orders (the status of the sepiolids is still undetermined; Boletzky, 1995) (Table 1). Animals were captured by trawls off the Mediterranean coast of France near Banyuls-sur-Mer, typically at 80 m, except for

Table 1. *Species used in this study, with their most common depth range*

Order Sepioidea
  Sepiidae
    Sepia officinalis L. (0–100 m)
    Sepia orbignyana Férrusac (80–150 m)
  Sepiolids
    Sepiolidae
      Rossia macrosoma (Delle Chiaje) (100–500 m)
Order Teuthoidea
  Myopsida
    Loliginidae
      Loligo vulgaris Lamarck (20–250 m)
      Alloteuthis media (Lamarck) (<200 m)
  Oegopsida
    Histioteuthidae
      Histioteuthis bonnellii (Férrusac) (0–600 m)
      Histioteuthis reversa (Verril) (0–1000 m)
    Ommastrephidae
      Illex coindetii (Verany) (0–600 m)
      Todaropsis eblanae (Ball) (250–450 m)
      Todarodes sagittatus (Lamarck) (0–800 m)
    Onychoteuthidae
      Ancistroteuthis lichtensteini (Orbigny) (0–250 m)
Order Octopoda
  Incirrata
    Octopodidae
      Eledone cirrhosa (Lamarck) (60–150 m)
      Eledone moschata (Lamarck) (15–90 m)
      Octopus vulgaris Cuvier (<100 m)
      Scaeurgus unicirrhus (Orbigny) (100–350 m)

Depth ranges are taken from Mangold and Boletzky (1987).

most of the oegopsid squids, which were captured off the Catalan coast near Blanes, Spain (*Todarodes sagittatus* at 240–260 m, *Histioteuthis bonnellii*, *H. reversa*, *Ancistroteuthis lichtensteini* and the sepiolid *Rossia macrosoma* at 320–450 m). At the time of the measurements, the two *Histioteuthis* species were not recognized as separate, and their measurements were pooled.

For both methods of measuring the maximum pressure differential, measurements were made on arm and tentacle suckers. The term 'arm' refers to the eight similar appendages of decapods or octopods. The term 'tentacle' refers to the two modified, prehensile appendages of decapods. The tentacles function primarily in high-speed strikes to capture prey.

Maximum pressure differential achievable by sucker design: octopod

Tenacity measurements on a wettable surface

The maximum pressure differential possible for octopod suckers was also calculated from the attachment force divided by the area of individual suckers on a wettable surface. Unlike decapods, however, it was not clear how much of the area under the sucker was exposed to reduced pressure. Octopod suckers have a broad, flat rim, the outer part of which presses against the surface to form a seal. The inner part of the rim is slightly raised, increasing the area exposed to reduced pressure.

It was possible to calculate the area exposed to reduced pressure by measuring the attachment force of a sucker producing a known pressure, such as when cavitation occurred gradually near 0 kPa. When this occurred, the force was divided by the known pressure differential to give the area exposed to reduced pressure. The pressure differential used in this calculation was the mean pressure differential at the reference pressure calculated from the tenacity measurements with decapod suckers. This ensured that the octopod and decapod measurements were comparable. The area exposed to reduced pressure was expressed as a fraction of the total area of contact. For each species, all the values of this fraction were averaged. The average was then used to convert all area measurements for that species from total contact area to area exposed to reduced pressure. This area was then used as the sucker size in all the figures and statistical comparisons.

Attachment forces were measured on glass as described previously. Isolated arms were used because suckers adhered strongly by reflex for up to an hour after the arm's removal. For each measurement, the arm was held against a glass slide until only one sucker attached, then the force required to detach that sucker was measured. For the area calculation, the diameter between the outer edges of the flattened rim was measured to the nearest 0.5 mm using a plastic ruler. Using a dissecting microscope did not improve the accuracy of this measurement.

Four different octopod species were tested, from different habitats (Table 1). Animals were collected by trawl from the Mediterranean near Banyuls-sur-Mer, France, typically at depths near 80 m. All the octopods were kept in an open, filtered seawater system in which they survived for many months.

Direct pressure measurements

Another experiment was performed allowing direct pressure measurements under suckers attaching to a wettable surface. Pressure measurements were made with the pressure probe described in detail by Smith (1991*a*). This was a 1.5 mm diameter pressure transducer (model 060s, Precision Measurement Co., Ann Arbor, MI, USA) mounted near the end of a 30 cm×3 cm×3 cm Lucite rod so that its sensing face was flush with the surface. The estimated error of pressure measurements using this transducer was 5 %.

Glow discharge polymerization was used to create a wettable surface over the pressure transducer. Glow discharge with nitrogen creates a cloud of ionized gas molecules, which polymerize on the exposed surfaces. The resulting polymer consists of a mixture of nitrogen-based groups, predominantly amines (Yasuda, 1985). The critical surface tension of wetting after such a treatment is typically $51×10^{-3}$ N m^{-1} (Inagaki *et al.* 1990). For comparison, glass is considered wettable ($45×10^{-3}$ N m^{-1}; Baier, 1970) and silicone is non-wettable ($22×10^{-3}$ N m^{-1}; Shafrin, 1975). The advantage of glow

discharge is that it changes the wettability without altering the sensitivity of the transducer.

The glow discharge apparatus was similar to the one described by Yasuda and Lamaze (1971). The following procedure was employed. The pressure probe was placed in a sealed reaction chamber. The chamber was evacuated to 0.5 Pa, then nitrogen gas was introduced at 3 Pa and ionized with a 30 W, 13.56 MHz radio frequency discharge for 40 min.

The glow discharge treatment produced a highly wettable surface over the pressure transducer. After dipping the transducer in water, a thin film of water clung to the treated surface. The surface maintained these characteristics for 3 days, whereupon it reverted to a lower wettability. The change in wettability was obvious and apparently abrupt; on removing the probe from the water after one of the measurements, water beaded up and ran off the surface rather than adhering in a thin film. Briggs *et al.* (1980) noted a similar, though less abrupt, loss of wettability.

Pressure measurements were made using one individual of *Octopus vulgaris*. The animal was trained to grab the transducer, which was pulled away when a sucker was observed to attach over the transducer (see Smith, 1991*a*). Measurements were taken for 3 days while the surface was wettable and for another 3 days after the surface had reverted to a lesser wettability. Only maximal pulls were considered in the analysis; data obtained when the animal lightly gripped or explored the transducer were discarded. This was done by excluding pressure differentials lower than 80 kPa. Cavitation does not occur at lesser differentials and thus cannot be limiting, and the animals are clearly capable of greater differentials.

All measurements are presented as means ± S.D.

Results

The range of pressures possible in the marine environment

After seawater-immersion, Z-tubes that were initially wettable converged on a moderate wettability. Before soaking in the ocean, the two glass tubes sustained mean pressures of -229 ± 340 kPa ($N=15$) and -10 ± 44 kPa ($N=18$) respectively. This variability within and among tubes is typical of cavitation threshold measurements (Smith, 1991*a*). The results from the first tube are typical of a high-wettability surface, while those of the second are more typical of a moderately wettable surface (see Smith, 1991*a*). After immersion in sea water, the mean pressures sustained by these tubes were -40 ± 73 kPa ($N=20$) and 1 ± 3 kPa ($N=15$). The change in cavitation threshold after immersion was significant for the first tube (Wilcoxon two-sample test, $P=0.01$), but not for the second ($P>0.1$). Another glass tube sustained pressures of -3 ± 9 kPa ($N=10$) after immersion, but there were no pre-immersion data as it was a replacement for a broken tube.

Immersion did not affect the non-wettable tubes. Before immersion, cavitation occurred in the two non-wettable tubes at numerous sites as soon as the pressure approached 0 kPa. The tubes sustained mean pressures of 8 ± 6 kPa ($N=5$) and 14 ± 4 kPa ($N=5$) respectively. After immersion, cavitation still occurred at numerous sites as the pressure approached 0 kPa, and the tubes sustained mean pressures of 10 ± 5 kPa ($N=4$) and 7 ± 18 kPa ($N=2$) respectively. These values were not significantly different from the results before immersion (Wilcoxon two-sample test, $P=0.65$, $P=0.43$, respectively).

Maximum pressure differential achievable by sucker design: decapod

Tenacity measurements on a wettable surface

Fig. 1A shows the pressure differentials produced by decapod suckers on a wettable surface. Regression was performed on log-transformed data to determine the relationship between pressure differential and sucker size (area exposed to reduced pressure). Small suckers were significantly stronger than large suckers ($P<0.001$). Suckers larger than 7.5 mm^2 produced pressure differentials near 100 kPa. Smaller suckers produced pressure differentials as large as 830 kPa (with one outlier at 1168 kPa). The regression equation for the pressure differential generated by a decapod sucker was:
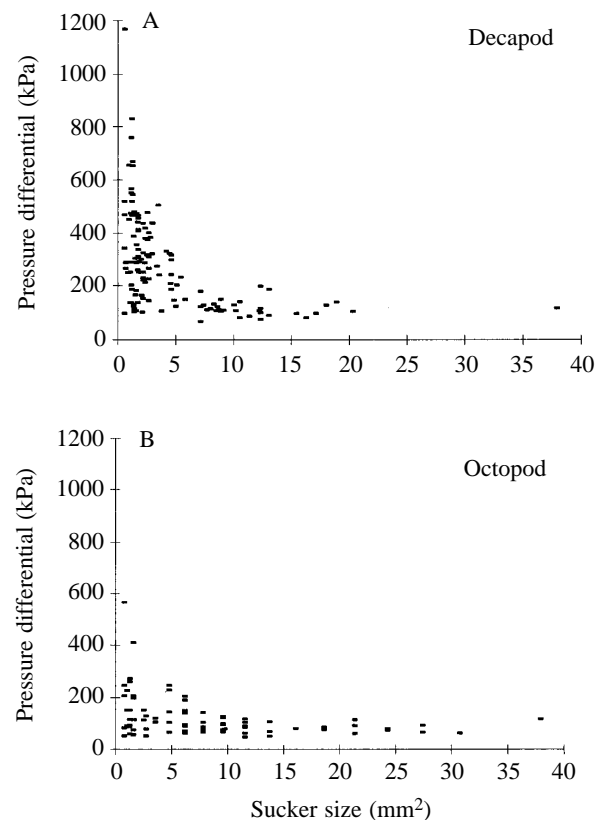
$$P_d = 340a_s^{-0.40}, \qquad (1)$$

Fig. 1. The relationship between the pressure differentials produced by suckers and their size. Size was taken to be the area exposed to reduced pressure. Pressure differentials were estimated from the tenacity of individual suckers on glass. Each data point represents the first negative pressure recorded for each sucker, or the first pressure differential that did not correspond to gradual cavitation near 0 kPa. (A) Decapod data, $N=129$, primarily from *Sepia officinalis* and *Loligo vulgaris*. (B) Octopod data, $N=85$.
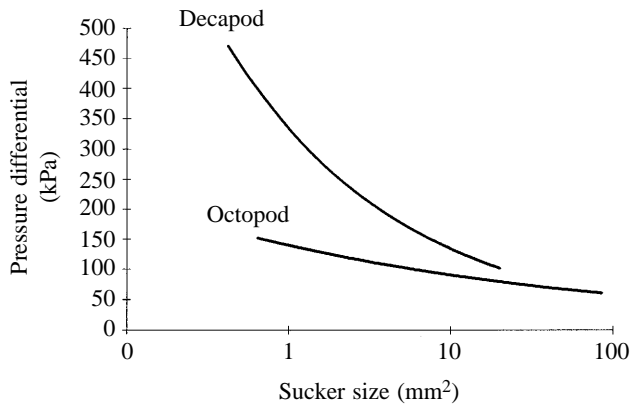
Fig. 2. The regression curves showing the pressure differential *versus* sucker size (area exposed to reduced pressure), plotted semilogarithmically. These data are based on the tenacity measurements on glass given in Fig. 1.

with pressure differential (P_d) in kPa and area (a_s) in mm^2 (N=129) (Fig. 2). There were no significant differences between the intercepts (P=0.61) or the slopes (P=0.76) of the lines for arm and tentacle (not shown). Thus, the arm and tentacle data were pooled for comparison with the octopod data.

The mean pressure differential at the reference pressure was 83±29 kPa (N=148 suckers). This was consistent among all but one of the 19 individuals where a measurement at the reference pressure was available. Measurements from this animal may have been systematically biased owing to the irregular shape of its sucker apertures. The mean pressure differential at the reference pressure for this individual was 142 kPa. To correct for this difference, the pressure differentials produced by this individual were multiplied by 83/142. Without this individual, the average pressure differential at the reference pressure was 79±23 kPa (N=138). This average value was used in the calculation of area exposed to reduced pressure under octopod suckers.

The force required to break the sucker stalk

The force required to break a sucker stalk was typically not much greater than the force of attachment on a wettable surface. When both values were available for a sucker, the attachment force was, on average, 69±44 % (N=96) of the force required to tear the stalk. This relationship showed no significant change with sucker size (regression, P=0.44).

Multiple regression analysis was used to determine the relationship between the predicted maximum pressure differential and the following independent variables: species, sucker size and location (arm or tentacle club). Pressure differential and size were log-transformed. Seven of the ten species had maximum pressure differentials that differed significantly from the others. Specifically, the intercepts of their regression lines were significantly different from the intercept of an overall regression line (Fig. 3; Table 2) (N=349; 220 tentacle suckers, 129 arm suckers). Smaller suckers had greater maximum pressure differentials than larger

Table 2. *Full model of the regression predicting the pressure differentials required to break the stalks of decapod suckers*

	Coefficient	P
Intercept	2.542	<0.001
log(area)	−0.283	<0.001
Arm	0.231	<0.001
T. eblanae	0.116	0.023
A. media	−0.811	<0.001
S. orbignyana	−0.149	0.001
S. officinalis	0.090	0.001
A. lichtensteini	0.177	0.001
T. sagittatus	0.337	<0.001
R. macrosoma	−0.139	0.009
A. media × arm	0.201	0.005

The regression line for all species and measurements is $\log P_d = -0.283 \log a_s + 2.542$, where P_d is pressure difference (in kPa) a_s is area (in mm^2).

If the sucker is on the arm or from any of the species listed, add the coefficient to the intercept (2.542) to determine the predicted pressure differential. For example, for a *T. eblanae* arm sucker, add 0.116 and 0.231 to the intercept.

All species that were not significantly different from the overall equation had P>0.5 (not listed).

suckers (P<0.001). The effect of size on sucker strength was the same for all species; none of the interactions between species and size was significant. Unlike the pressure
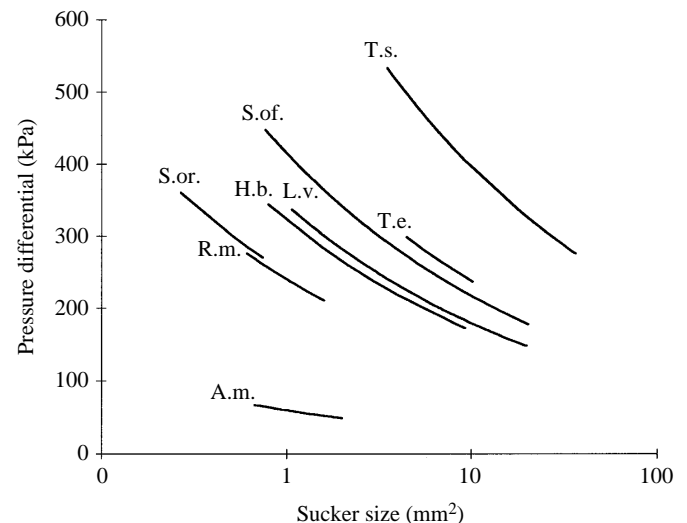

Fig. 3. Semilogarithmic plot of the regression curves showing the pressure differential *versus* size (area exposed to reduced pressure) for the tentacle suckers of different decapod species. Pressure differentials were estimated from the force required to break the stalk of each sucker. On a log/log plot, these curves would be straight lines with the same slope. To determine the predicted value for an arm sucker, multiply the value for a tentacle sucker by 1.7 (2.7 times for *A.m.*). A.m., *A. media*; H.b., *H. bonnellii* and *H. reversa*; L.v., *L. vulgaris*; R.m., *R. macrosoma*; S.or., *S. orbignyana*; S.of., *S. officinalis*; T.e., *T. eblanae*; T.s., *T. sagittatus*.

differentials measured in the previous section, suckers on the arm were 1.7 times stronger than suckers of the same size on the tentacle (*P*<0.001). None of the interactions of location and species was significant except for *A. media* (*P*<0.001). This means that the difference in strength between arm and tentacle suckers was generally the same across species.

Maximum pressure differential achievable by sucker design: octopod

Tenacity measurements on a wettable surface

The fraction of the total area of contact exposed to reduced pressure was 49±16% (*N*=21) for *Eledone cirrhosa*, 36±10% (*N*=6) for *E. moschata*, 51±16% (*N*=29) for *O. vulgaris* and 39±7% (*N*=3) for *Scaeurgus unicirrhus*. These values are similar to previous results for limpets (36–59%) (Smith, 1991*b*).

Fig. 1B shows the pressure differentials produced by octopod suckers on a wettable surface. Multiple regression analysis was used to determine the relationship between pressure differential and the following independent variables: species and sucker size (area exposed to reduced pressure). Both pressure differential and size were log-transformed. There were no significant differences among octopod species. Specifically, there were no significant differences among the intercepts of their regression lines (*P*>0.4 in all cases) or the slopes (*P*>0.1 in all cases) (*N*=85; 18 *E. cirrhosa*, 29 *E. moschata*, 31 *O. vulgaris*, 7 *S. unicirrhus*). The overall equation for the pressure differential produced by an octopod sucker was:

$$P_{d} = 141a_{s}^{-0.19}, \qquad (2)$$

with pressure differential (P_{d}) in kPa and area (a_{s}) in mm^2 (Fig. 2). Smaller suckers were stronger than larger suckers (*P*<0.001). Suckers larger than about 7.5 mm^2 produced pressure differentials close to 100 kPa, as was the case with decapod suckers. Smaller suckers produced pressure differentials as large as 271 kPa (excluding two outliers) (Fig. 1B).

The pressure differentials produced by octopod suckers were significantly weaker than those produced by decapod suckers of the same size. The intercepts of the octopod and decapod regression lines were not significantly different (*P*=0.68, intercept at 1 cm^2 due to log scale), but the slopes were significantly different (*P*<0.001) (Fig. 2). Whereas the pressure differentials produced by octopod suckers increased slightly with decreasing size, those produced by decapod suckers increased markedly with decreasing size.

Direct pressure measurements

On the highly wettable glow-discharge-treated surface, the maximum pressure differential that the octopus produced was 165 kPa, and the mean was 121±21 kPa (*N*=16). The results were significantly different after the wettability had reverted to a moderate level (Kolmogorov–Smirnov test for goodness of fit, *P*<0.01) (Fig. 4). When the surface was wettable, nearly all the maximal pulls generated a negative pressure. After the wettability had decreased, approximately half of the pulls
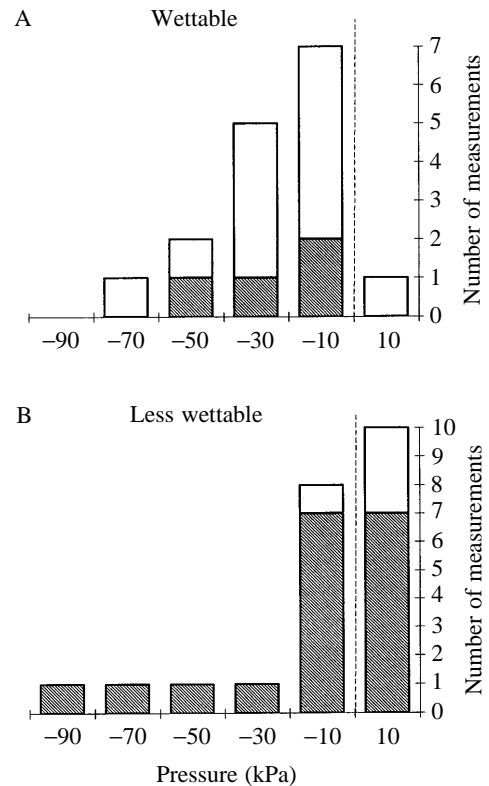

Fig. 4. (A) The distribution of pressures measured under octopus suckers attached to a highly wettable, glow-discharge-treated surface (*N*=16). (B) The distribution of pressures measured under octopus suckers attached to the same surface after the wettability had decreased (*N*=22). The dotted line demarcates the boundary between negative and positive pressures. Hatched regions represent instances where cavitation appeared to cause attachment failure. Unshaded regions of the bars indicate that cavitation did not appear to cause failure. This was determined from observations of the pressure recordings. Both graphs exclude pressures greater than 20 kPa.

generated negative pressure and the distribution of pressures resembled the distribution of cavitation thresholds on a moderately wettable surface reported by Smith (1991*a*).

The pressure recordings suggest that cavitation was not limiting on the wettable surface, but it was limiting after the surface had reverted to a lesser wettability. In 12 of the 16 trials on the wettable surface, the pressure continued to rise and fall after reaching a minimum value (Fig. 5A), rather than failing suddenly as would be the case with cavitation. This implies that cavitation did not occur and that the mechanics and musculature of the sucker, as well as the animal's behaviour, determined the pressure instead. After the wettability had decreased, 18 of 22 pulls released suddenly upon reaching a minimum pressure, presumably because of cavitation (Fig. 5B).

Discussion
The physical limits to negative pressure

The physical characteristics of water limit the magnitude of
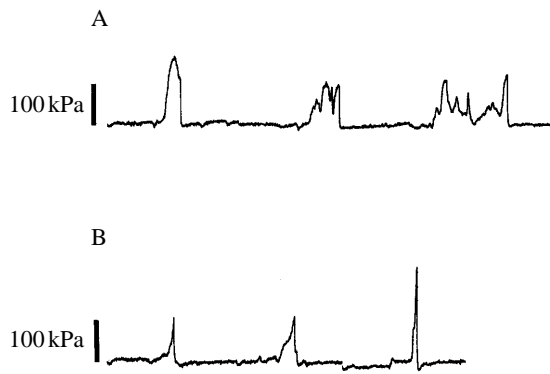
A

100 kPa |

B

100 kPa |

Fig. 5. (A) A pressure trace showing three consecutive measurements from different octopus suckers on the highly wettable, glow-discharge-treated surface. A pressure decrease is indicated by a rise in the trace; the baseline is ambient pressure. In all three, failure did not occur suddenly at a minimum pressure. (B) A pressure trace showing three consecutive measurements from different suckers on the same surface, after the wettability had decreased. Failure was sudden upon reaching a minimum pressure.

the pressure differential that a sucker can produce. Observations of cavitation combined with pressure measurements after the wettable, glow-discharge-created surface had washed off support Smith's (1991a) conclusions that cavitation can limit the pressures produced by suckers. Thus, the maximum pressure differential that is possible for a sucker equals the difference between the starting pressure (ambient) and the cavitation threshold. The cavitation threshold depends on the purity of the water and the wettability of the surfaces involved (Smith, 1991a). Although water purity affects the cavitation threshold, this effect is small unless the water is markedly turbid or carefully purified. Smith (1991a) found that the cavitation threshold of turbid sea water taken from a jetty was not significantly different from that of carefully maintained artificial sea water.

Wettability has a large effect on the cavitation threshold (Smith, 1991a), and long-term seawater immersion changes surface wettability. After soaking in the ocean, wettable glass tubes sustain pressures approximately in the range from 0 to −100 kPa, while non-wettable tubes sustain pressures near 0 kPa. Thus, cavitation will probably occur on most marine surfaces at pressures between 0 and −100 kPa. This means that, at sea level (ambient pressure 100 kPa), cavitation typically limits suckers to a pressure differential of 100–200 kPa. The ambient pressure, and thus the maximum possible pressure differential, increases by 100 kPa with each 10 m increase in depth. Thus, at 10 m depth, the limits will be 200–300 kPa, and at 50 m they will be 600–700 kPa.

Depth may also affect the cavitation threshold. Hayward (1971) showed that pressurization shrinks small bubbles that could nucleate cavitation, thus making the cavitation threshold more negative. This effect is only noticeable at high pressures such as 10 000 kPa. At depths great enough to produce this effect (1000 m), cavitation will not be limiting. Nevertheless,

many cephalopods undergo large vertical migrations. One side effect of this may be that the time spent at greater depth shrinks bubble nuclei on their sucker surfaces. This could slightly improve adhesion when hunting near the surface.

Functional differences between octopod and decapod suckers

This study provides quantitative evidence of a large functional difference between octopod and decapod suckers. At small sizes, decapod suckers can be several times stronger than octopod suckers. Nevertheless, this functional difference will only matter in deeper water when cavitation is not limiting. At sea level on most surfaces, the difference between octopod and decapod suckers is masked by cavitation, which limits all suckers to the same range of pressures. As depth increases, the difference will become more apparent.

Octopod suckers are limited by cavitation at sea level, but can only produce slightly greater pressure differentials as depth increases. Octopods typically generate pressure differentials near 100 kPa. The greatest pressure differential measured by Smith (1991a) for *O. vulgaris* was 268 kPa. In this study, the greatest pressure differential was 165 kPa on the glow-discharge-treated surface and 271 kPa on glass (excluding two outliers). At depths greater than 10 m, octopod suckers would have to produce pressure differentials of 300 kPa or more to cavitate water, but they do not appear to be capable of this. Thus, below 10 m they would not be able to cavitate water; their mechanics and musculature would limit them.

It is not likely that there are octopod species with significantly stronger suckers because there is no variation in strength among the octopod suckers tested. Also, the octopods in this study are active coastal species that are likely to have strong suckers. Many deep-sea species, particularly in the sub-order Cirrata, are much less active, less muscular and often gelatinous. These octopods may have weaker suckers.

Increasing depth will allow decapod suckers to take advantage of their greater strength. The greatest pressure differential measured under a decapod sucker (excluding one outlier) was 830 kPa. Some suckers can withstand pressure differentials of over 1000 kPa before the stalk breaks. Thus, cavitation will limit them to 100–200 kPa at sea level, but as depth increases, they will be able to produce greater pressure differentials. This may continue until the sucker reaches the limit of its musculature and/or stalk. Depending on the sucker, this can occur anywhere from 10 to 100 m.

It appears that, in general, cavitation will only be a factor at depths less than 100 m. This is only the top of the typical depth range of most cephalopods (Table 1). Nevertheless, this may be the crucial part of their range as many cephalopods hunt near the surface, particularly at night.

Unlike the octopods studied, decapods show considerable interspecific variation in sucker strength, which would become apparent as depth increases. There is no obvious pattern to this variation, except that three of the four species that had stronger than average suckers relative to their size were fast-swimming squid belonging to the family Oegopsida. Members of this family typically live in open water rather than coastal regions.

There does not, however, appear to be a clear correlation between sucker strength and a species' depth range. It is more likely that sucker strength is correlated to prey type.

The greater strength of decapod suckers may be particularly important for their mode of prey capture. During prey capture, the tentacles extend and strike the prey within 15–35 ms (Kier, 1982). Despite the speed of the strike, the success rate for capturing a prawn is 80–90 % on the first strike and 63 % even if the animals have only one tentacle (Messenger, 1968). The mechanical action of stalked suckers may be necessary to adhere during the brief impact. In addition, it seems likely that relatively few suckers will successfully adhere on impact; those that do should be as strong as possible.

The cost of this increased adhesive strength may be reduced flexibility as a result of the rigid cylinder. Flexibility may not be as important for decapods, which have a stereotyped attack (Messenger, 1968; Kier, 1982). Octopods, in contrast, have diverse methods of foraging and prey capture (see Norman, 1992). Octopod suckers are also used extensively in activities other than prey capture, such as locomotion. Correspondingly, they are more dexterous, capable of grasping a wide variety of irregular objects.

The morphological difference between octopod and decapod suckers probably arose in the mid-Mesozoic era, when the two groups presumably split independently from an ancestral stock. It is unknown which group split off first (Boletzky, 1992). Naef (1921–1923) suggests that octopod suckers are primitive on the basis of their simple structure. This implies that the stronger, stalked design is an evolutionarily derived feature.

The effect of sucker size

From the results presented here, one might predict that suckers smaller than those studied here would produce even greater pressure differentials. This could be a significant factor for juveniles. Nevertheless, extrapolation beyond the size range studied must be regarded critically. It is likely that the effect of size levels off; a continued exponential increase in strength is probably beyond the capacity of the tissues.

The reason for the greater strength of small suckers is unknown. It is possible that sucker size affects the ability to maintain a seal at the rim. Similar to Laplace's law for pressurized containers (Wainwright *et al.* 1976), the stress in the wall of a container holding a reduced pressure may be proportional to the container's radius. Thus, at a given pressure differential, a smaller sucker may experience lower stresses that might cause the seal at the rim to fail.

The optimum sucker size for a species probably depends on a variety of factors. Although smaller suckers create greater pressure differentials, the smaller area means that they produce less force. Also, the difference in strength will only matter in deeper water. The size of the prey will be an important factor. Finally, a low probability of successful attachment may favour a larger number of smaller, stronger suckers to ensure that at least one sucker sticks to the prey.

References

BAIER, R. E. (1970). Surface properties influencing biological adhesion. In *Adhesion in Biological Systems* (ed. R. S. Manly), pp. 15–48. New York: Academic Press.

BANKS, W. H. AND MILL, C. C. (1953). Tacky adhesion – a preliminary study. *J. Colloid Sci.* **8**, 137–147.

BOLETZKY, S. V. (1992). Evolutionary aspects of development, life style and reproductive mode in incirrate octopods (Mollusca, Cephalopoda). *Revue suisse Zool.* **99**, 755–770.

BOLETZKY, S. V. (1995). The systematic position of the Sepiolidae (Mollusca: Cephalopoda). *Bull. Inst. Océanogr. Monaco* special issue **16**, 99–104.

BRIGGS, D., RANCE, D. G., KENDALL, C. R. AND BLYTHE, A. R. (1980). Surface modification of poly(ethylene terephthalate) by electrical discharge treatment. *Polymer* **21**, 895–900.

HAYWARD, A. T. J. (1971). Negative pressure in liquids: can it be harnessed to serve man? *Am. Sci.* **59**, 434–443.

INAGAKI, N., TASAKA, S., OHKUBO, J. AND KAWAI, H. (1990). Hydrophilic surface modification of polyethylene by plasma of nitrogen oxides. *J. appl. Polymer Sci.: appl. Polymer Symp.* **46**, 399–413.

KIER, W. M. (1982). The functional morphology of the musculature of squid (Loliginidae) arms and tentacles. *J. Morph.* **172**, 179–192.

KIER, W. M. AND SMITH, A. M. (1990). The morphology and mechanics of octopus suckers. *Biol. Bull. mar. biol. Lab., Woods Hole* **178**, 126–136.

MANGOLD, K. AND BOLETZKY, S. V. (1987). Cephalopodes. In *Fiches FAO d'Identification des Espèces pour les Besoins de la Pêche. (Révision 1). Méditerranée et Mer Noire. Zone de Pêche 37*, vol. I, *Vegetaux et Invertebres* (ed. W. Fischer, M.-L. Bauchot and M. Schneider), pp. 633–714. Rome: FAO.

MESSENGER, J. B. (1968). The visual attack of the cuttlefish, *Sepia officinalis. Anim. Behav.* **16**, 342–357.

NAEF, A. (1921–1923). Cephalopoda. In *Fauna and Flora of the Bay of Naples*, no. 35, pp. 1–917, Jerusalem: Israel Program for Scientific Translation.

NIXON, M. AND DILLY, P. N. (1977). Sucker surfaces and prey capture. *Symp. zool. Soc., Lond.* **38**, 447–511.

NORMAN, M. D. (1992). Systematics and biogeography of the shallow-water octopuses (Cephalopoda: Octopodinae) of the Great Barrier Reef, Australia. PhD dissertation, University of Melbourne, Australia.

O'BRIEN, W. J. AND FAN, P. L. (1975). Capillary adhesion. In *Adhesion Science and Technology*, *Polymer Science and Technology*, vol. 9B (ed. L. H. Lee), pp. 621–633. New York: Plenum Press.

SHAFRIN, E. G. (1975). Critical surface tensions of polymers. In

Polymer Handbook, 2nd edn, vol. III (ed. J. Brandrup and E. H. Immergut), pp. 221–228. New York: John Wiley and Sons.

SMITH, A. M. (1991*a*). Negative pressure generated by octopus suckers: a study of the tensile strength of water in nature. *J. exp. Biol.* **157**, 257–271.

SMITH, A. M. (1991*b*). The role of suction in the adhesion of limpets. *J. exp. Biol.* **161**, 151–169.

SMITH, A. M. (1992). Alternation between attachment mechanisms by limpets in the field. *J. exp. mar. Biol. Ecol.* **160**, 205–220.

SMITH, A. M., KIER, W. M. AND JOHNSEN, S. (1993). The effect of depth on the attachment force of limpets. *Biol. Bull. mar. biol. Lab., Woods Hole* **184**, 338–341.

WAINWRIGHT, S. A., BIGGS, W. D., CURREY, J. D. AND GOSLINE, J. M. (1976). *Mechanical Design in Organisms*. New York: John Wiley and Sons.

YASUDA, H. (1985). *Plasma Polymerization*. Orlando: Academic Press.

YASUDA, H. AND LAMAZE, C. E. (1971). Polymerization of styrene in an electrodeless glow discharge. *J. appl. Polymer Sci.* **15**, 2277–2292.

ZIMMERMANN, U., HAASE, A., LANGBEIN, D. AND MEINZER, F. (1993). Mechanisms of long-distance water transport in plants: a re-examination of some paradigms in the light of new evidence. *Phil. Trans. R. Soc. Lond. B* **341**, 19–31.