

The Structure and Adhesive Mechanism of Octopus Suckers¹

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SYNOPSIS. Octopus suckers consist of a tightly packed three-dimensional array of muscle with three major muscle fiber orientations: 1) radial muscles that traverse the wall; 2) circular muscles arranged circumferentially around the sucker; and 3) meridional muscles oriented perpendicular to the circular and radial muscles. The sucker also includes inner and outer fibrous connective tissue layers and an array of crossed connective tissue fibers embedded in the musculature. Adhesion results from reducing the pressure inside the sucker cavity. This can be achieved by the three-dimensional array of muscle functioning as a muscular-hydrostat. Contraction of the radial muscles thins the wall, thereby increasing the enclosed volume of the sucker. If the sucker is sealed to a surface the cohesiveness of water resists this expansion. Thus, the pressure of the enclosed water decreases instead. The meridional and circular muscles antagonize the radial muscles. The crossed connective tissue fibers may store elastic energy, providing an economical mechanism for maintaining attachment for extended periods. Measurements using miniature flush-mounted pressure transducers show that suckers can generate hydrostatic pressures below 0 kPa on wettable surfaces but cannot do so on non-wettable surfaces. Thus, cavitation, the failure of water in tension, may limit the attachment force of suckers. As depth increases, however, cavitation will cease to be limiting because ambient pressure increases with depth while the cavitation threshold is unchanged. Structural differences between suckers will then determine the attachment force.

INTRODUCTION

Octopuses use suckers for a remarkable variety of tasks including anchoring the body to the substratum, holding prey, locomotion, cleaning maneuvers, chemotactile recognition, behavioral displays, and manipulating, sampling and collecting objects (Packard, 1988). The suckers are capable of attaching to a wide diversity of objects. Strong attachment can be achieved not only on large flat surfaces, but also on irregular surfaces and on objects smaller than a single sucker. In addition to adhesion based on suction, the rim of the sucker can be bent on each side to enclose and grip thin filaments and sheets.

In this review, we will first describe the morphology of the suckers with particular focus on the general form of the sucker and the arrangement of the musculature and connective tissues. We will analyze this morphology from the standpoint of biomechanics in order to explain how suckers maintain a seal on an object or the substratum and how they generate the sub-ambient pressures required for attachment. We will then consider how the physical properties of water affect and potentially limit this adhesion mechanism. Such an analysis of the suckers of octopus helps to elucidate principles of design that are relevant for the potential development of human engineered suction adhesion devices.

SUCKER STRUCTURE

Gross morphology

The following summary of sucker structure is based on observations of *Octopus joubini*, *Octopus maya*,

Octopus bimaculoides/bimaculatus (See Pickford and McConaughey [1949] for systematic details), and *Eledone cirrosa*. The morphology and function of the suckers was found to be similar in the species examined (see Kier and Smith, 1990).

The exposed disc-like portion of the sucker is termed the infundibulum (Girod, 1884) (Fig. 1). When the sucker is active the infundibulum is flattened against the surface of the object to which the sucker is attached. The surface of the infundibulum bears a series of radial ridges and grooves (Fig. 2). It is covered by a chitinous cuticle or sucker lining that is shed periodically and continuously renewed (Girod, 1884; Naef, 1923; Nixon and Dilly, 1977; Packard, 1988). A rim of loose and folded dermis and epithelium encircles the infundibulum and is separated from it by a circumferential groove. The rim of loose epithelium is in turn surrounded by a zone of epithelium that includes cells with inclusions that have the staining characteristics of acid polysaccharides typical of molluscan mucus (Kier and Smith, 1990).

At the center of the infundibulum is an orifice that opens into an approximately spherical cavity called the acetabulum (Girod, 1884) (Figs. 2, 3). The chitinous cuticle that covers the infundibulum extends into and covers the inner surface of the acetabulum. The cuticle is shed from the infundibulum and the acetabulum simultaneously as a single unit.

The suckers are attached to the arm by a short muscular base. The base is capable of rotating the entire sucker in any direction and elongating up to twice its resting length. In addition to the role that the muscular bases play in orienting suckers for adhesion to an object, octopuses frequently use the suckers to “walk” an individual arm along the substratum or to pass food

¹ From the Symposium *Biomechanics of Adhesion* presented at the Annual Meeting of the Society for Integrative and Comparative Biology, 2–6 January 2002, at Anaheim, California.

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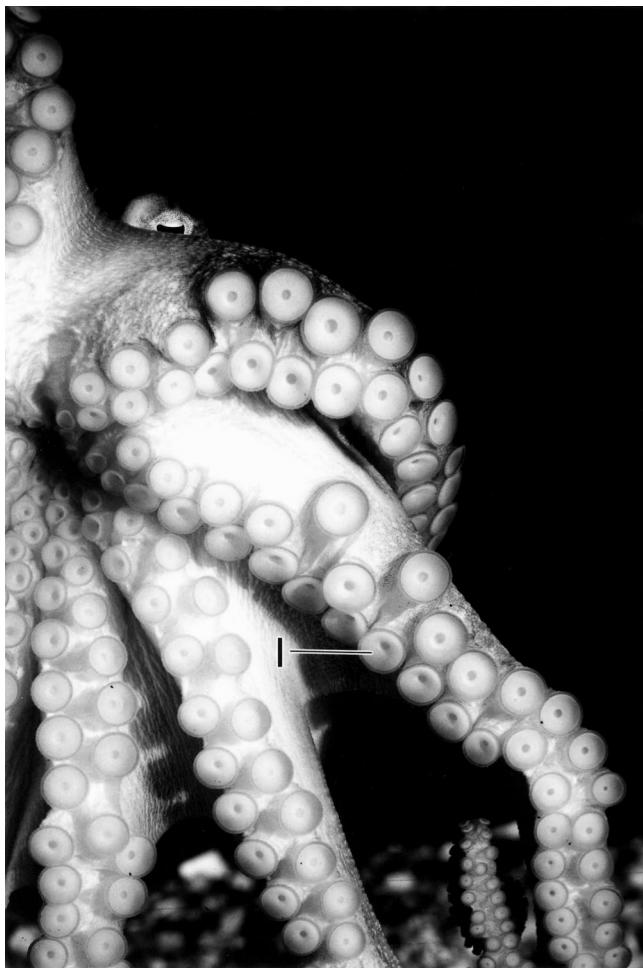


FIG. 1. Photograph of *Octopus* attached to wall of aquarium showing arrangement and general form of the suckers. I, infundibulum.

or other objects down the arm. In this behavior, an individual sucker extends forward, attaches to the object or substratum, rotates backward by bending the muscular base, and then detaches to repeat the cycle.

Sucker musculature

The musculature of the wall of the acetabulum and infundibulum, termed the intrinsic sucker musculature, consists of a tightly packed, robust, three-dimensional array of muscle (Girod, 1884; Guérin, 1908; Kier and Smith, 1990; Nachtigall, 1974; Niemiec, 1885; Tittel, 1961, 1964). No skeletal elements or fluid-filled spaces are present in the sucker wall. The roof of the acetabulum consists primarily of radial muscle fibers (Fig. 3). The radial muscle fibers extend through the thickness of the acetabular roof, perpendicular to the inner and outer surface. The radial muscle fibers have their origin and insertion on connective tissue capsules that cover the inner and outer surfaces of the wall of the acetabulum. In addition to the radial muscle fibers, the roof of the acetabulum includes meridional muscle fiber bundles that are adjacent to the outer surface of the acetabular roof and extend between the radial mus-

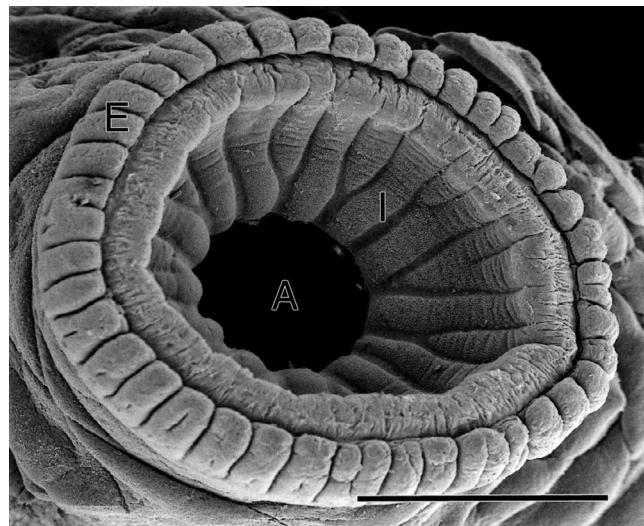


FIG. 2. Scanning electron micrograph of sucker of *Octopus bimaculoides/bimaculatus*. The radial grooves and ridges are visible on the infundibulum (I) and the orifice that opens into the acetabulum (A) is visible. The infundibulum is encircled by a rim of loose epithelium (E) that is separated from the infundibulum by a narrow groove. The scale bar equals 1.0 mm.

cle fibers (Fig. 3). The meridional fibers radiate out from a point at the apex of the roof of the acetabulum similar to lines of longitude, encircling the radial musculature and extending down to a connective tissue layer present at the border between the acetabulum and the infundibulum.

The musculature of the wall of the acetabulum has similar radial fibers and meridional bundles. In addition, a series of circumferential muscle bundles are present in the acetabular wall (Fig. 3). These circumferential muscle bundles are oriented parallel to the surface of the infundibulum. A particularly robust bundle of circumferential muscle fibers is observed adjacent to the inner surface and forms a large sphincter muscle at the level of the narrow orifice that connects the acetabulum and the infundibulum. A smaller, secondary sphincter is observed at the same level but near the outer wall.

The musculature of the wall of the infundibulum is similar to that of the acetabulum. A robust array of radial muscle is the predominant feature. The radial muscle fibers extend between a series of circumferential muscle bundles that are located adjacent to the inner surface of the infundibular wall. Meridional muscle bundles are also present in the infundibulum and extend from their origin on a connective tissue layer between the infundibulum and acetabulum to radiate out to the rim of the infundibulum.

The suckers are attached to the arms by a series of extrinsic muscle bundles. These muscles originate on a connective tissue layer that surrounds the arm musculature and extend down to converge on the sucker and insert on the outer connective tissue capsule of the acetabulum at the level of the sphincter muscle. A layer of circumferentially arranged muscle encircles the

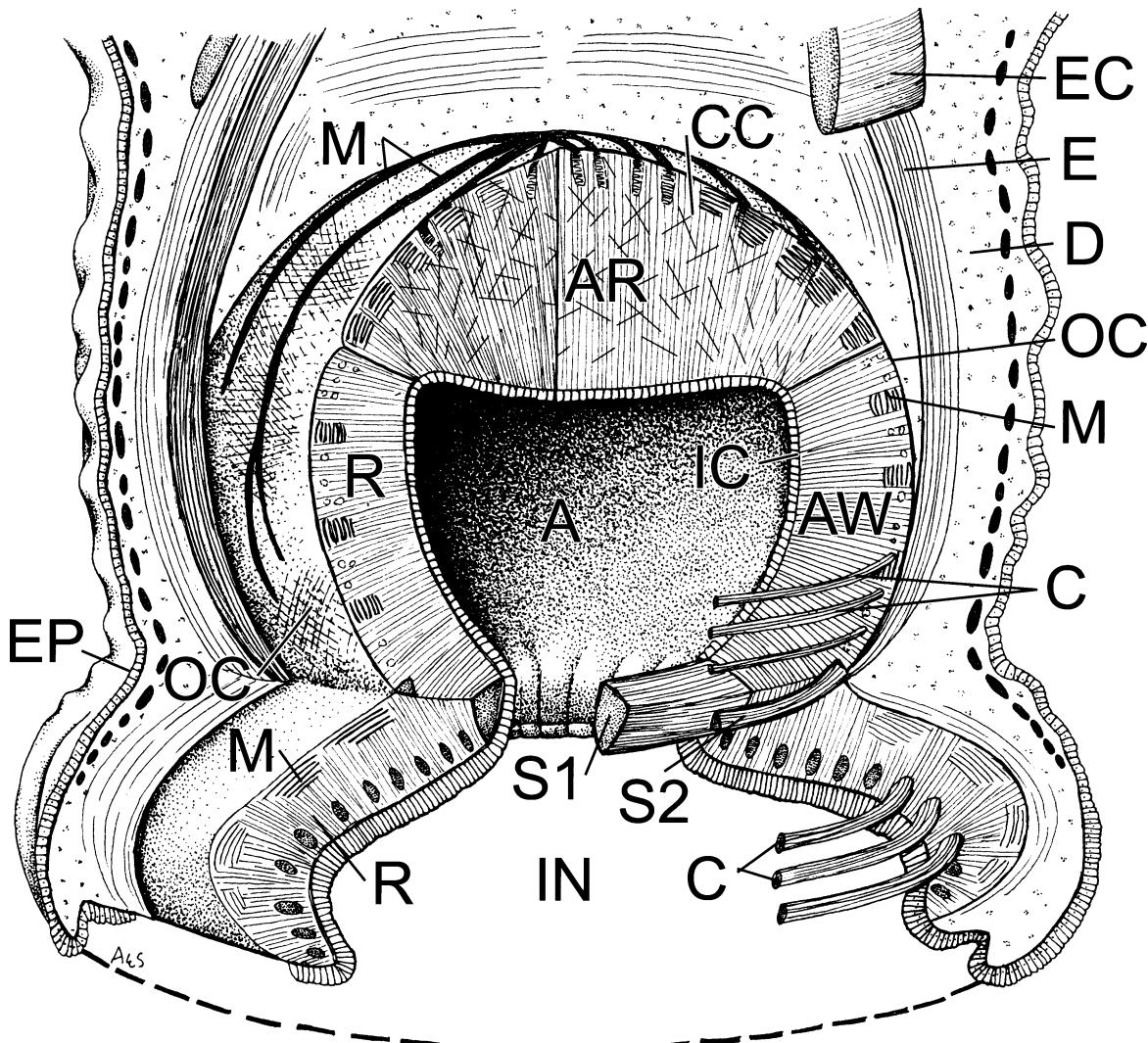


FIG. 3. Schematic cutaway diagram of an octopus sucker. A, acetabulum; AR, acetabular roof; AW, acetabular wall; C, circular muscle; CC, crossed connective tissue fibers; D, dermis; E, extrinsic muscle; EC, extrinsic circular muscle; EP, epithelium; IN, infundibulum; IC, inner connective tissue layer; M, meridional muscle; OC, outer connective tissue layer; R, radial muscle; S1, primary sphincter muscle; S2, secondary sphincter muscle.

extrinsic muscle bundles, forming a sphincter (see Kier and Smith, 1990). It is likely that the extrinsic muscle bundles bend the base and orient the sucker by selective contraction of a bundle or group of bundles on one side. The base can be elongated by contraction of the circumferential muscle layer, and shortened by simultaneous contraction of the extrinsic muscle bundles.

Sucker connective tissues

The sucker musculature is enclosed on its inner and outer surface by sheets of connective tissue fibers forming an inner and outer connective tissue capsule. The fibers of the capsules are highly birefringent and show staining characteristics typical of collagen. Histological sections that graze the connective tissue layer show that it consists of fibers arranged in a crossed-fiber array (see Kier and Smith, 1990). The outer con-

nective tissue capsule extends down and penetrates into the sucker wall at the level of the sphincter muscles. The extension of the outer connective tissue capsule that encloses the infundibulum is thinner than the portion covering the acetabulum.

The musculature of the roof of the acetabulum includes intramuscular crossed connective tissue fibers that are arranged obliquely to the radial muscle fibers and extend from the inner to the outer connective tissue capsules. The fibers are birefringent and have staining characteristics typical of collagen. They are reminiscent of the intramuscular connective tissue fibers described previously in the mantle (Bone *et al.*, 1981; Gosline and Shadwick, 1983*a, b*; Thompson and Kier, 2001*a*) and the fins (Kier, 1989; Kier *et al.*, 1989; Johnsen and Kier, 1993) of squid and cuttlefish. These intramuscular crossed connective tissue fibers are not observed in the acetabular wall, or in the infundibular

wall. A particularly robust band of intramuscular connective tissue fibers is found at the boundary between the acetabular wall and acetabular roof (Fig. 3).

BIOMECHANICS OF THE SUCKER

Function of the sucker musculature

The basic mechanism of suction attachment is straightforward; the sucker forms a seal at the rim and reduces the pressure in the acetabular cavity. The attachment force of the sucker (perpendicular to the surface) is the product of the area of attachment and the pressure differential between the ambient pressure and the pressure inside the sucker. Thus, to describe the mechanism of attachment, we must describe both how pressure can be reduced in the acetabulum and how a seal can be formed with the surface of attachment.

Reduction in pressure of the acetabular cavity relies on a muscular mechanism that has been observed previously in an interesting array of animal structures including the arms and tentacles of cephalopods, the tongues of mammals and lizards, and the trunks of elephants (see Kier and Smith, 1985; Smith and Kier, 1989). These structures, like the sucker, lack the hardened internal or external skeletal elements and the large fluid-filled cavities that characterize skeletal support in other animals and organs. In these structures, termed "muscular-hydrostats," the musculature both generates the force and provides the support for movement. The mechanism depends on the fact that muscle is essentially incompressible at physiological pressures and it shows little change in volume upon contraction. This means that shortening by muscular contraction of one dimension of a muscular-hydrostat must result in elongation of another dimension. Since muscular-hydrostats typically have muscle fibers arranged to control all three dimensions, a diverse array of movements can be produced and the muscle fibers of a given orientation can antagonize those of the other orientations.

To understand how such a mechanism can be used to reduce pressure in the acetabular cavity of the sucker, first consider a hypothetical case of a sucker that is not sealed to the substratum. Contraction of the radial muscle of the acetabular wall generates a force that tends to decrease the thickness of the wall. Since the wall consists of solid muscle and connective tissue, its volume is essentially constant. This means that thinning of the wall must result in an expansion of the surface area of the acetabulum, thereby increasing the volume of the acetabular cavity and causing water to flow into the cavity through the orifice in a manner analogous to the expansion and refilling of the mantle cavity of squids by the contraction of radial muscle fibers (Bone *et al.*, 1981; Gosline *et al.*, 1983; MacGillivray *et al.*, 1999; Thompson and Kier, 2001a, b; Ward, 1972; Ward and Wainwright, 1972). If, however, the sucker is sealed to a surface, the cohesiveness of the water in the acetabular cavity resists significant expansion and a decrease in pressure in the cavity will balance the expansive force generated by the radial

muscle of the acetabular wall. The high bulk modulus of water means that the water enclosed in the acetabular cavity behaves mechanically like a solid in tension (see Denny, 1988; Kier and Smith, 1990; Smith, 1991, 1996). We emphasize that although the high bulk modulus of water is most commonly discussed with reference to situations where water is placed in compression, the modulus in tension is practically identical (see Hayward, 1971).

How can the radial musculature of the acetabulum be antagonized? Since contraction of the radial muscle increases the circumference of the acetabulum it can be antagonized by muscle that decreases the circumference. Both the meridional muscle bundles and the circular muscle bundles of the acetabulum will, upon contraction, decrease the circumference and thereby increase the thickness of the acetabular wall.

Formation of the seal by the infundibulum

Formation of a watertight seal requires that the infundibulum be flexible and dexterous in order to conform to the wide variety of shapes and textures of the objects to which the suckers attach. As in the acetabulum, the movements and deformations of the infundibulum rely on a muscular-hydrostatic mechanism. Contraction of the radial muscle results in thinning of the infundibular wall and radial expansion of the infundibular surface. The radial muscles are antagonized by the meridional muscles which, upon contraction, decrease the circumference and surface area of the infundibulum. Simultaneous contraction of the meridional and radial muscles probably flattens the infundibular surface and bends the rim of the infundibulum towards the acetabulum. Contraction of the circumferential muscle bundles constricts the infundibulum to a conical shape.

A muscular-hydrostatic mechanism is particularly advantageous for the function of the infundibulum in forming a seal with the substratum. With the appropriate neuromuscular control, highly localized and complicated bends and deformations may be produced at any location (Graziadei, 1962; Graziadei and Gagne, 1976a, b; Kier and Smith, 1990). By this means, the infundibulum can closely match the contours of the surface and the loose epithelium of the rim that surrounds the infundibulum can thereby provide the watertight seal. Production of mucus by the epithelium surrounding the rim may also be important in providing a watertight seal.

Maintenance of sub-ambient pressure under the infundibulum

If an octopus is induced to attach its suckers to an object covered with a thin coating of dental impression wax, impressions of the suckers in the wax can be observed on the surface of the object (Kier and Smith, 1990). The impressions are of the entire infundibulum including the thin outer edge. We interpret these observations as evidence that the entire infundibular surface is forcefully applied to the substratum during at-

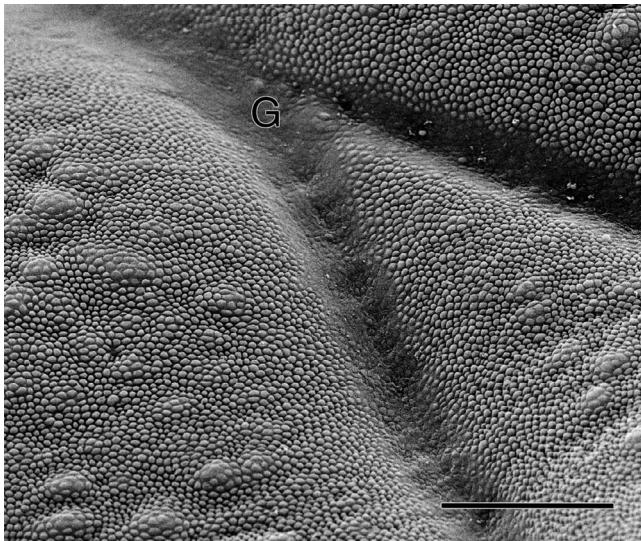


FIG. 4. Scanning electron micrograph of infundibulum of sucker of *Octopus bimaculoides/bimaculatus* showing radial groove (G) and numerous projections or denticles. The scale bar equals 100 μm .

tachment, implying that the sub-ambient pressure produced by the acetabulum is somehow transmitted radially under the infundibulum to the outer rim where the seal is formed by the loose epithelium.

How might the pressure be transmitted under the infundibulum? The infundibulum includes an array of radial grooves that extend from the center of the infundibulum to the rim (Fig. 2). In addition, examination of the chitinous cuticle that covers the surface of the infundibulum (Fig. 4) reveals a remarkable array of tiny pegs or "denticles" (Kier and Smith, 1990; Nixon and Dilly, 1977). In *Octopus bimaculoides/bimaculatus* the denticles are approximately 3–4 μm in diameter. When the sucker is attached, it is likely that the tips of the denticles rest on the surface. These denticles, in combination with the radial grooves, provide an interconnected water-filled network of spaces that can transmit the sub-ambient pressure in the cavity of the acetabulum out to the rim of the sucker, thereby establishing a pressure differential over the entire area of the infundibulum. It is likely that this pressure differential generates the force pressing the infundibulum against the substratum.

During attachment, a sucker must not only resist perpendicular forces that tend to lift the sucker from the surface but also must resist shearing forces that tend to slide the sucker parallel to the surface (Denny, 1988). Indeed, octopuses are frequently observed to exert force on objects with their arms aligned parallel to the line of force. The denticles may therefore serve an additional role of enhancing the friction between the rim and the surface. The constant wear from this friction may be one of the reasons that the sucker linings are shed periodically.

Small projections or denticles are also commonly observed on suckers from a variety of other animals including the suckers of the clingfish, the lumpfishers

and other aquatic vertebrates (Arita, 1967; Green and Barber, 1988; Hora, 1930; Nachtigall, 1974) and on tadpoles (Gradwell, 1973; Inger, 1966). Although their role in providing friction in resisting shear forces has been noted previously, their possible role in transmission of the sub-ambient pressure to the sucker rim has not been emphasized (Kier and Smith, 1990).

Attachment for extended periods

While the muscular-hydrostatic mechanism that we have described above provides an effective means of generating large pressure differentials between the ambient pressure and the pressure inside the sucker, it appears to require constant muscle contraction. It is nevertheless common to observe an octopus remain attached to the wall of an aquarium or hold an object for many hours. This extended attachment may imply that the suckers possess a mechanism of elastic energy storage that could be used to maintain sub-ambient pressures in the sucker without requiring significant muscular activity.

The intramuscular crossed connective tissue fibers observed in the acetabular roof may provide a mechanism for storing elastic energy and maintaining reduced pressure in the suckers for long term attachment. As in the mantle (see Bone *et al.*, 1981; Gosline and Shadwick, 1983a, b; Thompson and Kier, 2001a) and fins (see Kier, 1989; Kier *et al.*, 1989; Johnsen and Kier, 1993) of squid, the intramuscular connective tissue fibers of the sucker will be strained if a force is applied to the sucker roof that causes its thickness to be increased. Since the fibers are collagenous, they have high resilience and thus it is likely that they can store significant strain energy. If the force that thickened the acetabular roof is removed, the strain energy stored in the fibers exerts a force that will thin the roof and tend to expand the acetabular cavity. Thus, long-term attachment with the suckers can be provided if the acetabular roof is first thickened by contraction of the meridional and circular muscles, storing elastic energy in the intramuscular fibers, followed by application of the sucker to the object or substratum, forming a seal. Upon relaxation of the meridional and circular muscles, the energy stored in the intramuscular fibers will exert a force tending to thin the wall, thereby reducing the pressure in the acetabular cavity in a similar manner to that described above for the radial muscle fibers. As in the case of suction adhesion by muscular contraction, the high bulk modulus of the water filling the sucker means that the volume change in the acetabular cavity during this process is expected to be extremely small.

THE PHYSICAL PROPERTIES OF WATER AND SUCTION ATTACHMENT

Cavitation and the tensile properties of water

What are the implications of the physical properties of water for suction attachment in octopus suckers? During attachment the sucker exerts a force to expand. The cohesiveness of water resists the expansive force,

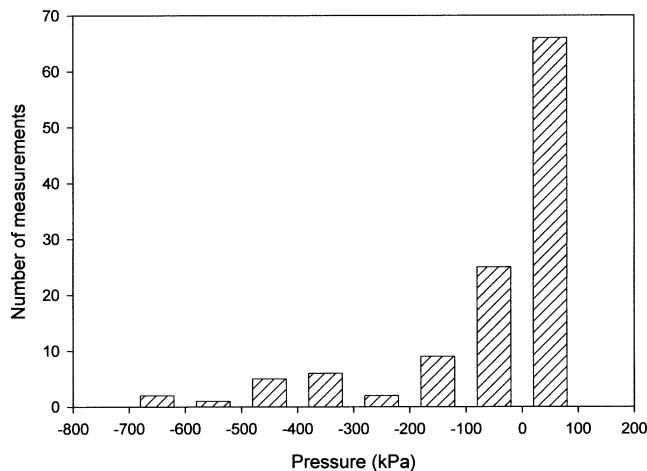


FIG. 5. Distribution of cavitation thresholds for artificial sea water in cleaned glass tubes as measured in a Z-tube apparatus, $N = 116$. From Smith, 1991.

resulting in a decrease in pressure. Water in a sucker thus behaves like a solid in tension. Indeed, water is often described as having tensile strength and it breaks when the pressure falls to the 'cavitation threshold'. At the cavitation threshold, microscopic bubbles abruptly grow without restraint in a process referred to as cavitation (Pickard, 1981; Smith, 1991, 1996).

Much of the previous literature on suction adhesion does not consider the implications of the tensile properties of water for suction adhesion and thus assumes that suckers are unable to produce pressures below that of a vacuum, 0 kPa. This is a crucial issue because ultimately the force of attachment (usually expressed as a tenacity or force per unit area of attachment) depends on the differential between ambient pressure and the pressure in the internal cavity of the sucker. If water in a sucker can sustain negative pressures, and if the musculature of the sucker is capable of generating the force to produce negative pressures, then the potential attachment force of a sucker is greater than previously recognized (Kier and Smith, 1990; Smith, 1991).

Measurements of the tensile properties of samples of sea water (from the ocean or from aquaria housing octopuses) using a Z-tube apparatus (see Briggs, 1950; Smith, 1991) demonstrate that the water contained in an octopus sucker can indeed sustain negative pressures although the cavitation thresholds of samples of seawater are quite variable (Fig. 5; Smith, 1991). In addition, the characteristics of the wetted surface affect the cavitation threshold; cavitation thresholds of seawater are significantly more negative on wettable surfaces than on non-wettable surfaces (Smith, 1991, 1996). Indeed, cavitation on non-wettable surfaces occurs consistently at or slightly above 0 kPa (Smith, 1991, 1996).

While the experiments described above demonstrate that natural samples of seawater can sustain significant negative pressures before cavitating, to take advantage



FIG. 6. (A) Recording of pressure under an individual octopus sucker using a pressure transducer with a highly wettable surface produced by glow-discharge polymerization. In the three consecutive measurements shown, failure of the enclosed water did not occur suddenly at a minimum pressure. (B) Recording of pressure using same apparatus, but after the wettability of the surface had decreased. In the three consecutive measurements failure was sudden upon reaching a minimum pressure. From Smith, 1996.

of this potential increased tenacity, octopus suckers must be capable of generating negative pressures. Experiments using a probe with a flush-mounted pressure transducer to measure the pressure under individual suckers demonstrate that octopus can indeed generate negative pressures (Smith, 1991, 1996). On highly wettable surfaces, negative pressures occurred in nearly every trial, and failure did not appear to result from cavitation (Fig. 6A). The pressures ranged from 0 to -65 kPa (100 to 165 kPa of pressure difference at sea level). On less wettable surfaces, cavitation caused abrupt failure of the attachment much more frequently (Fig. 6B). On all surfaces, the pressures produced by suckers matched predictions based on Z-tube measurements of the cavitation threshold. Thus, octopus suckers can produce negative pressures, but cavitation limits these pressures to a predictable range (Smith, 1991, 1996).

The effect of depth on the attachment force

The attachment force of a sucker depends on the difference between ambient pressure and the pressure of the water enclosed by the sucker. Measurements with the Z-tube showed that cavitation on most marine surfaces will occur at pressures between 0 and -100 kPa (Smith, 1996). This result implies that, at sea level (ambient pressure = 100 kPa), cavitation normally limits a sucker to a maximum pressure differential of 100–200 kPa. However, the ambient pressure increases by 100 kPa for each 10 m of depth; thus, the maximum pressure differential that can be created before reaching the cavitation threshold increases correspondingly (see Smith *et al.*, 1993; Smith, 1996). Octopus suckers can take advantage of this up to a point. For four different species tested on surfaces where cavitation would not be limiting, the pressure differential ranged from 100–270 kPa (Smith, 1991, 1996). Presumably their musculature and mechanics are not capable of creating greater pressure differentials.

Comparison of different suckers

Decapod (squid and cuttlefish) suckers differ structurally from octopus suckers, and this affects their

function. Decapod suckers are attached to the arm or tentacle by a strong and slender stalk that inserts on a central piston-like structure inside a rigid cylindrical body that constitutes the sucker. Once the sucker is attached to an object, any force that pulls the sucker away from the surface tends to lift the piston. This causes further decrease in pressure inside the sucker. Smith (1996) showed that decapod suckers can produce pressure differentials that are several times greater than those created by octopus suckers. Indeed, Smith (1996) measured pressure differentials in decapod suckers that were as high as 830 kPa. This strength advantage is only relevant in deeper water; at depths less than 100 m, cavitation limits tenacity. At sea level, the decapod suckers are limited to the same pressures as octopi. The cost of this increased strength is likely a loss in dexterity relative to octopus suckers.

For both decapod and octopod suckers, the maximum pressure differentials show a significant inverse correlation with sucker size (Smith, 1996). The reasons for the greater strength of smaller suckers are, however, unknown. It may be that sucker size affects the ability to maintain a seal at the rim. In a manner analogous to Laplace's Law for pressurized cylinders, perhaps the stress in the wall of the sucker maintaining reduced pressure is proportional to the sucker's radius. Stresses that might cause the seal to fail may therefore be lower in small suckers (Smith, 1996).

INSIGHTS FOR BIOMIMETIC ADHESION

An understanding of the structure and function of octopus suckers may provide insights for the design of human-engineered suction attachment mechanisms. Such a mechanism would be appealing for a diversity of applications because it could potentially provide forceful but temporary attachment to a variety of surfaces and shapes. The attachment force could be actively modulated and release could be effected immediately. The lack of engineered muscle-like actuators at present argues against designing a human-engineered device that incorporates a muscular-hydrostatic mechanism (Vogel, 1998). A number of important insights into aspects of the design can nevertheless be gained from the above analysis of the structure and function of octopus suckers.

First, human-engineered suction mechanisms would benefit from the radial groove arrangement in conjunction with the denticle array observed in octopus suckers. By incorporating analogous components into the design of the sucker surface applied to the object or substratum, the sub-ambient pressure could be transmitted under the entire surface, out to the perimeter of the artificial sucker. The larger area of attachment resulting from such an arrangement, and the friction from the denticles, would likely increase the attachment force in shear.

Second, the tensile properties of water have important consequences for human-engineered suction attachment mechanisms. Suckers can be much stronger underwater, and they can work without significant

shape changes. The wettability of the interior surfaces of artificial suckers will affect the cavitation threshold of the enclosed water and will thus affect the maximum attachment forces. While it may be possible to coat or renew the internal surface to maintain wettability (and thus decrease the cavitation threshold) human-engineered suckers may still be limited by the lower wettability of the marine surface to which they will attach. The maximum attachment force may therefore be limited by the cavitation threshold in shallow water. In deep water, however, much greater pressure differentials could be maintained without cavitation and thus correspondingly higher attachment forces are possible.

Finally, a mechanism of elastic energy storage that could be used to maintain the sub-ambient pressure might be of considerable importance for human-engineered suction mechanisms. The incorporation of such a mechanism in the design would allow an external energy source to be used initially in forming the attachment. The sucker could then remain attached for extended periods without requiring energy expenditure, assuming that a leak-proof seal could be formed. Indeed, the formation and maintenance of a leak-proof seal around the rim is likely to be one of the major design challenges of a human-engineered sucker. Perhaps the easily deformed rim of loose epithelium observed in the octopus sucker would be a useful model for design of the sealing mechanism.

ACKNOWLEDGMENTS

We thank S. Guarda and W. Ambrose for assistance with the scanning electron microscopy and A. Schroeer for help with scientific illustration. We thank D. Spain, J. Taylor, J. Thompson, and C. Werner for comments on the manuscript. This work was supported by grants from the NSF (IBN 9728707), DARPA (sub-contract 2000-0661 from SPARTA, Inc.), and NASA (NAG5-8759).

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