

Suction disk performance of echeneid fishes

B.A. Fulcher and P.J. Motta

Abstract: The anatomy of the suction disk of two species of echeneid fishes, *Echeneis naucrates* L., 1758 and *E. neucratoides* Zuiew, 1786, is described, and measurements of their suction performance on both smooth and textured surfaces are given. Disk muscles erect or depress the numerous paired laminae, or toothed plates, which bear two to four rows of posteriorly directed spinules. The erect laminae create a sub-ambient chamber, allowing these fishes to adhere to other fish and inanimate objects. Resting sub-ambient suction pressure differentials were recorded, as were the greatest sub-ambient pressure differentials as the fish were pulled posteriorly to simulate drag induced by a swimming host. The resting pressure differential averaged -0.5 kPa, with no significant difference between Plexiglas® and shark skin surfaces. With a force applied to their caudal peduncle, the echeneids generated suction pressure differentials averaging -92.7 kPa within the disk cavity while attached to Plexiglas. On shark skin, the use of spinules increased friction and reduced the maximum sub-ambient suction pressure differential to -46.6 kPa; considerably more force (17.4 N) was required to dislodge the echeneids from the shark skin than from the smooth Plexiglas (11.2 N).

Résumé : Nous décrivons l'anatomie du disque de succion chez deux espèces de poissons échénéidés, *Echeneis naucrates* L., 1758 et *E. neucratoides* Zuiew, 1786, et en mesurons la performance de succion sur des surfaces lisses et irrégulières. Les muscles du disque élèvent ou abaissent les nombreuses lamelles appariées ou plaques dentelées, qui portent deux à quatre rangées de spinules retournées vers l'arrière. Les lamelles dressées forment une chambre sub-ambiante qui permet à ces poissons de se fixer à d'autres poissons ou à des objets inanimés. Nous avons mesuré les différentiels de pression de succion de la chambre sub-ambiante au repos, puis les différentiels maximaux alors que le poisson est tiré vers l'arrière afin de simuler la traînée générée par un hôte en nage. Les différentiels de pression au repos sont en moyenne de $-0,5$ kPa et il n'y a pas de différence entre les substrats de plexiglas et de peau de requin. Lorsqu'on applique une force sur leur pédoncule caudal, les échénéidés génèrent des différentiels de pression de succion d'en moyenne $-92,7$ kPa à l'intérieur de la cavité du disque lors d'une fixation sur le plexiglas. Sur une peau de requin, l'utilisation des spinules augmente la friction et réduit les différentiels maximaux de pression de succion dans la chambre sub-ambiante à $-46,6$ kPa; il faut, par ailleurs, considérablement plus de force (17,4 N) pour les en déloger que sur un substrat de plexiglas lisse (11,2 N).

[Traduit par la Rédaction]

Introduction

The evolution of functional novelties can result in the occupation of novel niches. One such novelty in the echeneid fishes (genus *Echeneis*) involves the formation of a laminated adhesive suction disk from the first dorsal fin. This disk is used for attachment to marine hosts including elasmobranchs, bony fishes, cetaceans, and sea turtles (Cressey and Lachner 1970; Nelson 1994; Fertl and Landry 1999). The remoras are composed of eight extant species (Gunther 1860; Gudger 1926; Lachner 1966; O'Toole 2002) and one fossil ancestor, *Opisthomyzon glaronensis* (Wettstein, 1886). *Opisthomyzon glaronensis* bore a narrow and shortened disk with a disputed six to eight widely spaced laminae (Gudger 1926). Storms (1888) and Regan (1912) proposed that a narrower disk, a compressed body form, and a forked caudal fin indicate that *O. glaronensis* was a more active swimmer than its

descendants. Gradual improvements to the suction disk are seen in *Phtheirichthys lineatus* (Menziés, 1791), the slender suckerfish, with 9–11 denticled laminae and a longer disk. The echeneids and their sister taxa Rachycentridae share a common ancestor that followed larger fishes. This following behavior is hypothesized to have preceded the evolution of the hitchhiking behavior, hence the eventual development of the suction disk (O'Toole 2002).

The remora's suction disk is a modified first dorsal fin that migrated anteriorly onto the neurocranium and underwent a series of morphological modifications. The mesethmoid widened and the cranial table was depressed significantly to accommodate this migration (Regan 1912; Gregory 1933; Lachner 1966). The disk itself is encircled by a tough, flexible lip of connective tissue. Inside this fleshy lip are numerous consecutive rows of pectinated laminae (Storms 1888). These laminae are paired and laterally expanded medial and distal pterygiophores that join above the reduced dorsal fin spine (O'Toole 2002). The laminae are partially embedded in connective tissue, with their exposed edge bearing two to four rows of posteriorly directed toothlike processes, or spinules (Gudger 1926; O'Toole 2002). A sub-ambient pressure differential is believed to be generated by erector muscles of the laminae such that the volume enclosed by the disk is increased and suction is created (Harder 1976). These erector muscles and the depressor muscles responsible for detach-

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ment have not been described. In addition, directly medial to the first anterior row of laminae, the connective tissue and disk have a shallow groove with a small hole that accommodates what Priol (1937) suggested is a pneumatic pump. This pump consists of a posteriorly directed sickle-shaped ossification that is seated within a conical valve (Priol 1937). The ossification is believed to act as a trigger once the fleshy lip is applied to a host, thereby activating the pump to create a sub-ambient pressure chamber between the erect laminae and the host (Priol 1937). The laminae then become embedded in the host's epidermis by means of the spinules, remaining erect until forward movement of the remora depresses the laminae and breaks the seal, allowing water to enter the disk cavity and, subsequently, the remora to detach from the host (Gudger 1926). The role of the spinules and laminae in host attachment and suction performance has not been investigated in vivo for any echeineid to date, although early experiments by Townsend (1915) suggested that common sharksuckers (*Echeneis naucrates* L., 1758) 41 and 67 cm long could support a pail of water weighing 9.5 and 11 kg, respectively.

The goal of this study was to describe the disk and associated musculature of two remoras, *E. naucrates* and *Echeneis neucratooides* Zuiew, 1786, and measure the resting and maximum suction pressure differentials on smooth and rough substrates simulating un-scaled bony fish skin and placoid-scaled shark skin. The role of the spinules in host attachment was also investigated. It is hypothesized that the spinules increase friction on the rough surface, thereby increasing the force necessary to dislodge the remora while reducing the suction pressure differential necessary for attachment.

Materials and methods

Specimens of *E. naucrates* and *E. neucratooides* were retrieved from live blacktip sharks, *Carcharhinus limbatus* (Müller and Henle, 1839), by commercial and recreational fishers in the Gulf of Mexico. *Echeneis naucrates*, the common sharksucker, is an abundant tropical species that either swims freely or attaches to a variety of hosts, depending on its body size (Cressey and Lachner 1970; Paulin and Habib 1982; O'Toole 2002). *Echeneis neucratooides*, the whitefin sharksucker, is a reef-dwelling subtropical species commonly found on sharks (O'Toole 2002). Ten specimens of each species were immediately euthanatized for dissection with a 0.5 g/L overdose of MS-222 (tricaine methanesulphonate), and 8 specimens of each species were kept for the live suction performance experiments. The live fish were kept in a 379 L aquarium at the University of South Florida Animal Care Facility. Fish were fed ad libitum with pieces of scaled sardine, *Harengula jaguana* Poey, 1865, and maintained in a 12 h light : 12 h dark photoperiod throughout the study; salinity was maintained at 32‰ and water temperature ranged from 23 to 27 °C. After data collection, these fishes were euthanatized with MS-222. All fish were cared for and euthanatized in accordance with the principles and guidelines of the University of South Florida Institutional Animal Care and Use Committee, protocol No. 2608.

Disk anatomy

Standard length (SL; cm), total length (TL; cm), and mass (g) were recorded for all specimens. Disk length and width,

measured along the greatest axes, were expressed as percentages of SL. Head width, defined as the width at the base of the pectoral girdle, was also recorded. All measurements were obtained with calipers to the nearest tenth of a millimetre. Digital photographs of laminae and their associated musculature were taken with a Nikon® COOLPIX® 4300 digital camera and downloaded to a computer. Disk area measurements were taken from the digital images using SigmaScan Pro 4 (SPSS Inc. 1997b). Anatomical terminology follows O'Toole's (2002) revision of Regan's (1912) nomenclature.

Suction performance

Suction performance of three *E. naucrates* (TL 33.6–36.1 cm) and five *E. neucratooides* (TL 29.8–44.1 cm) was measured using a factory-calibrated Millar Mikro-Tip® pressure catheter (SPR-524) and a Millar TCB-500 Transducer Control Unit (Millar Instruments, Inc., Houston, Texas). Data were acquired with a 6020E data acquisition board (National Instruments Corp., Austin, Texas) and LabVIEW 6.0 software (National Instruments Corp. 2000). The Millar pressure catheter was calibrated with an OMEGA® manual PGT temperature-compensated pressure gauge (OMEGA Engineering, Inc., Stamford, Connecticut) attached to a vacuum pump. The voltage output from the pressure catheter was recorded with sub-ambient pressure differentials from 0 to –96 kPa, and a linear regression ($n = 15$, $r^2 = 0.998$) of voltage against pressure was used to correct experimentally recorded pressure differentials. The Millar catheter has a factory-specified error of $\pm 0.5\%$. The catheter was inserted through a 1 mm diameter hole into either smooth Plexiglas®, simulating un-scaled fish skin, or a piece of plywood on which a 7 cm \times 11 cm piece of blacktip shark (*C. limbatus*) skin had been dried and glued firmly in place. For each substrate, the transducer's pressure-sensitive tip was just below (~1 mm) the surface of the substrate. The hole and catheter were sealed with silicone glue on the side opposite to which the fish attached.

Each remora was placed individually in a 38 L aquarium prior to the experiment. The pressure catheter and substrate were acclimated to the temperature of the water in the experimental aquarium and, after 20 min, recalibrated to zero output volts at the experimental depth of 30 cm before each trial. The placoid scales were oriented in the anatomical position (i.e., curved posteriorly) relative to the attached remora. Each remora was placed at the experimental depth with its disk positioned on the substrate with the tip of the catheter no further back than the 13th row of laminae, so that the anterior one third to one half of the disk was directly over the catheter. The first series of recordings measured the resting or passive suction pressure differential of the remora's disk after it had been placed on the substrate with no external force on the fish. Three passive recordings were taken for each fish; between each recording, the remora was removed from the substrate and replaced. A running average of the resting sub-ambient pressure differential was taken once the reading had stabilized.

A second series of recordings measured the greatest suction pressure differential generated by the disk while the fish was pulled steadily backwards to simulate a posteriorly directed drag force induced by the flow of water over a swimming host. An 85 cm long, 1 cm wide soft cotton cord was

fitted around the remora's caudal peduncle. The substrate was oriented such that the directions of the fish, cord, and denticles were all aligned. As the fish was pulled directly posteriorly along its longitudinal axis and oriented at a 10°–20° angle to the horizontal, a handheld Rapala® ProGuide™ digital scale (Rapala-Normark Group, Inc., Vääksy, Finland) was used to measure the single greatest force at which the remora abruptly slipped posteriorly off of the substrate. Measurements obtained when the remora detached prematurely with little sub-ambient pressure differential were discarded, and only measurements during which the fish appeared to exert maximal effort were used. In this manner, three maximum pressure differential recordings were obtained for each remora on each substrate, but only the single greatest measurement was used for analysis. A posterior pull was used as an alternative to water flow experiments because the extremely high water flow velocity necessary to generate enough force to dislodge the fish (see Results) was not feasible in the available water flumes. Some fish died prematurely as a result of parasites ($n = 8$) and therefore could not be tested under all situations. The Rapala ProGuide digital scale was calibrated by recording the masses of objects weighing up to 4.7 kg first on the digital scale and subsequently on a pre-calibrated Siltec PS200L digital scale ($\pm 0.1\%$ error, Dogain Instruments, Inc., Santa Clara, California). The masses were converted to newtons and plotted as a linear regression ($n = 16$, $r^2 = 0.99$) to correct for error in the Rapala scale. Lastly, to measure the maximum sub-ambient pressure differential that a suction disk of a dead remora and an inanimate suction cup can generate prior to cavitation and dislodgement, three *E. naucrates* (TL 17.5–18.5 cm) and a 4 cm diameter silicone suction cup were applied to the Plexiglas substrate over the catheter at the experimental depth of 30 cm and quickly removed by pulling them orthogonally away from the substrate. The greatest sub-ambient pressure differential generated in this manner was tested under tension, whereas the greatest sub-ambient pressure differential generated by the live remora when it was pulled posteriorly was tested under shear stress.

Statistical analyses

Normality and equality of variances were tested for each species' data set using Kolmogorov–Smirnov and Levene's median tests, respectively. Disk length, disk width, and fish mass were compared between species with a t test. Because of heterogeneous variances in the pressure data, all mean resting sub-ambient pressure differentials of *E. naucrates* were compared separately with those of *E. neucratooides* with a Mann–Whitney U test for both Plexiglas and shark skin substrates. This was repeated for the greatest sub-ambient pressure differentials. Because they did not differ, the species were combined. Resting sub-ambient suction pressure differentials of four individuals (two of each species, three replicates) were compared with a paired t test, with each fish being compared on both Plexiglas and shark skin. For each individual (two of each species, four replicates), the single greatest sub-ambient suction pressure differential on Plexiglas was compared with that on shark skin using a paired t test. The maximum force necessary to dislodge the fish from shark skin was compared with that for Plexiglas with a Mann–Whitney U test. To investigate whether the maximum sub-

ambient pressure differential increased with the force exerted on the fish, the greatest sub-ambient pressure differentials from all eight fish were linearly regressed against the corresponding maximum force (N) for both Plexiglas ($n = 26$) and shark skin ($n = 17$) and tested with an ANOVA. Results were considered significant at $p < 0.05$. Analyses were performed with SigmaStat versions 2.03 (SPSS Inc. 1997a) and 3.1 (Systat Software Inc. 2004).

Results

Echeneis naucrates and *E. neucratooides* had similar muscular arrangements; therefore, their anatomical descriptions are combined. Disk length and disk width as percentages of standard length averaged $28\% \pm 0.38\%$ (SE) and $11\% \pm 0.16\%$ (SE), respectively, for both species. There was no significant difference in disk length ($t = -0.223$, $df = 6$, $p = 0.831$), disk width ($t = -0.554$, $df = 6$, $p = 0.599$), or mass of the live fish ($t = -1.010$, $df = 6$, $p = 0.351$) between species.

Disk anatomy

The suction disk is composed of modified proximal, fused medial, and distal pterygiophores, which together form consecutive rows of laminae. The laminae are surrounded by a fleshy marginal lip that is not attached to the dorsum. Laminae range in number from 20 to 28 in *E. naucrates* and from 18 to 28 in *E. neucratooides*.

The proximal, or basal, pterygiophores (particularly the first) are expanded ventrally to form spinule-like processes and are oriented posteroventrally. Their anterior base is flattened and lies ventral to the medial and distal pterygiophores. The ventral margins of the proximal pterygiophores are joined by a ligament, which becomes fused to the dorsal tips of the neural arches posterior of the pectoral girdle. The medial pterygiophores are expanded to form broad laminae that partially overlie the distal pterygiophores. Dorsal to the proximal and medial pterygiophores lie the distal pterygiophores, which are rod-shaped and expanded laterally. The distal pterygiophores bear two to four rows of posteriorly directed spinules on their posterodorsal border (Figs. 1–3), and on both sides the ventral surface of each distal pterygiophore bears a robust, hooklike ventral process approximately midway between the proximal pterygiophore and the lateral margin of the distal pterygiophore (Storms 1888). The hooklike ventral processes of the anterior one third of the disk are elongated (Fig. 2).

On the dorsal aspect of the first lamina is a small, blind chamber bearing a posteriorly directed, sickle-shaped ossification, and in the midline of the dorsal surface of the disk there is a ridge of connective tissue that joins all the laminae medially. The lateral margins of each lamina are loosely connected to the fleshy marginal lip. The posterior one third of the disk overlies the supracarinalis posterior and epaxialis muscle. A middorsal septum separates the two sides of the disk ventrally and extends down to the neurocranium.

The lateral depressor muscles of the laminae form slips that originate on the dorsolateral neurocranial vault. The depressors course posterodorsally to insert by a broad muscular insertion on the anterior flange of the ventrolateral side of each medial pterygiophore lamina (Fig. 2). These strap-like muscles lie in the anterior one third of the disk and do

Fig. 1. (Left) Dorsal view of the skeletal support of the suction disk of a 34 cm (total length) specimen of *Echeneis naucrates*. The first laminae (LA1), anterior chamber (AC), distal pterygiophore (DP), medial pterygiophore (MP), and spinules (SP) are shown at the cranial end. (Right) The region of the suction disk enclosed by the white box in the left panel is magnified to show details of the laminae including the distal pterygiophore (DP) and spinules (SP).

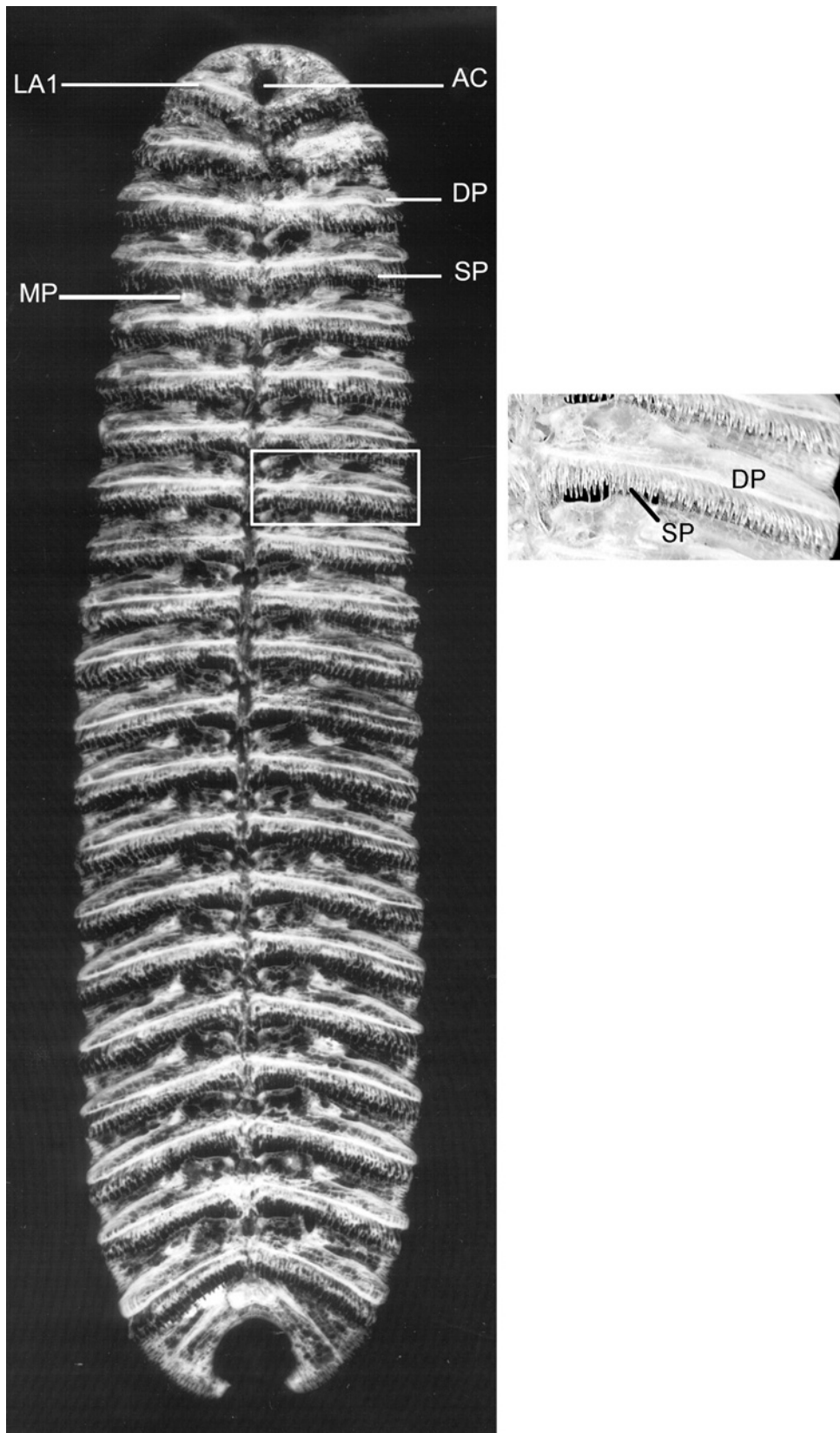
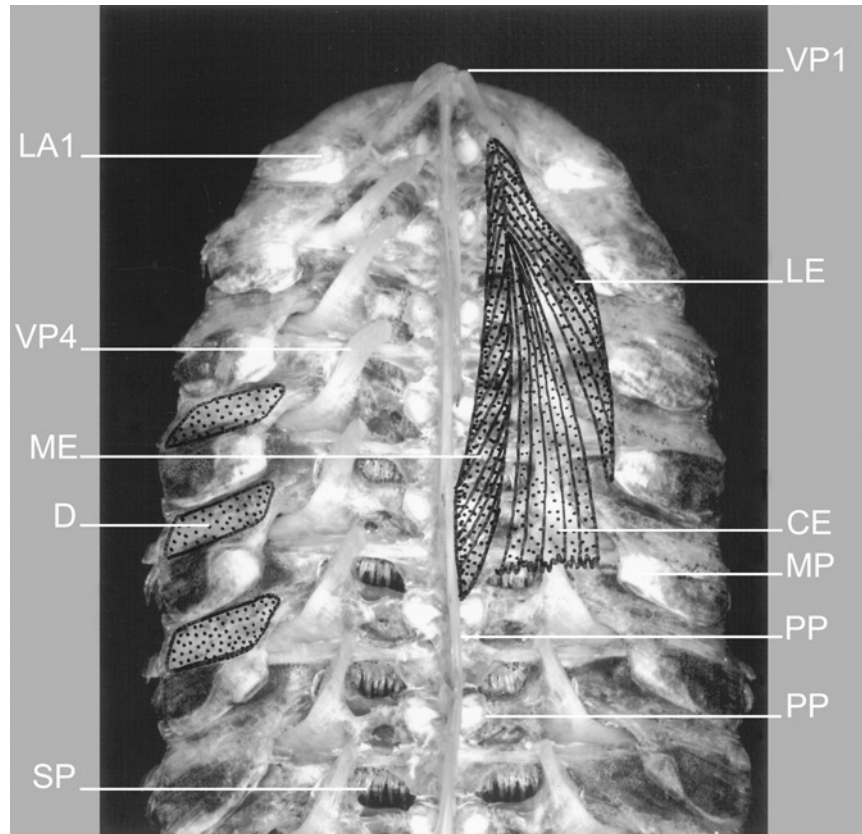


Fig. 2. Ventral view of the skeletal support of the suction disk of a 34 cm (total length) specimen of *E. naucrates* with representative erector and depressor muscles indicated on different sides. The erectors of the 2nd left lamina are shown to insert on the ventral process of the distal pterygiophore and include the lateral erector (LE), central erector (CE), and medial erector (ME). Fiber angles are approximate. The neurocranial origin of the central erector is not illustrated. The insertions of representative depressors (D) are indicated on the left sides of the 3rd, 4th, and 5th laminae. Disk components shown include the 1st lamina (LA1), 1st ventral process (VP1), 4th ventral process (VP4), proximal pterygiophore (PP), medial pterygiophore (MP), and spinules (SP).



not extend posterior to the pectoral girdle. Medial to the depressors, and separated by a connective tissue septum, are the erector muscles that attach to the ventral hooklike process of each lamina. The central erector is fan-shaped with a broad origin on the dorsal neurocranium and courses anterodorsally to insert via a tendon on the ventral process (Fig. 2). The medial erector originates on the expanded base of the proximal pterygiophore, the distal pterygiophore just medial to the ventral process, and the central ligament. This strap-like muscle courses ventrally and anterolaterally to insert on the ventral process, sharing its tendon with the other erector muscles. The lateral erectors originate on the ventral surface of the more posterior lamina wings (medial pterygiophores). These muscles course anteromedially and ventrally to insert on the ventral process, sharing the same tendon as the other erectors.

Suction performance

The mean resting and greatest sub-ambient pressure differentials for *E. naucrates* and *E. neucratoides* on both the Plexiglas (resting, $U = 15.0$, $n_1 = 3$, $n_2 = 5$, $p = 0.786$; greatest, $U = 11.0$, $n_1 = 3$, $n_2 = 4$, $p = 0.857$) and the shark skin (resting, $U = 4.0$, $n_1 = 2$, $n_2 = 2$, $p = 0.667$; greatest, $U = 3.0$, $n_1 = 2$, $n_2 = 2$, $p = 0.333$) substrates did not differ; therefore, the species were combined. The average resting suction pressure differential on the Plexiglas and shark skin substrates

was minimal, rarely exceeding the average of $-0.5 \text{ kPa} \pm 0.1 \text{ kPa}$ (SE); never exceeded -1.6 kPa (Table 1); and did not differ between the two substrates ($t = -2.01$, $df = 11$, $p = 0.07$). The single greatest sub-ambient suction pressure differential was significantly higher on Plexiglas than on shark skin ($t = -7.28$, $df = 3$, $p = 0.005$) (Table 1). On the Plexiglas substrate, seven recordings demonstrated that the pressure differential within the disk cavity approached a vacuum at sea level (-101 kPa). As the external force was applied, the pressure differential under the disk often declined in a stepwise manner, sometimes reaching a plateau at approximately -100 kPa (Fig. 4). Similar sub-ambient pressure differentials (-102 kPa) were recorded when the silicone suction cup was applied to the Plexiglas and quickly removed by being pulled orthogonally away from the surface (Fig. 4). The largest amount of external force applied on any remora before it slipped off the Plexiglas was 16.1 N . When observed through the Plexiglas, the laminae in approximately the anterior one third of the disk were erected more than those in the posterior region of the disk, both when resting and when being forcibly pulled backwards. The greatest sub-ambient suction pressure differential generated on the shark skin was -56.4 kPa , and the largest amount of force exerted on any remora before it slipped off the shark skin was 35.0 N (Fig. 5). More force was required to pull the remoras off the shark skin (average 17.4 N) than off the

Fig. 3. Ventral view of the 7th laminar row of the suction disk of a 36 cm (total length) specimen of *E. naucrates*. The medial pterygiophore (MP), distal pterygiophore (DP), ventral process of the distal pterygiophore (VP), and spinules (SP) are shown. The anterior base and spinule-like process of the proximal pterygiophore (PP) are also shown at the midline of the lamina. A black line was added to the anterior margins of the medial pterygiophore and the anterior base of the proximal pterygiophore to delineate them. Distal spinules on the distal pterygiophores were lost during cleaning.

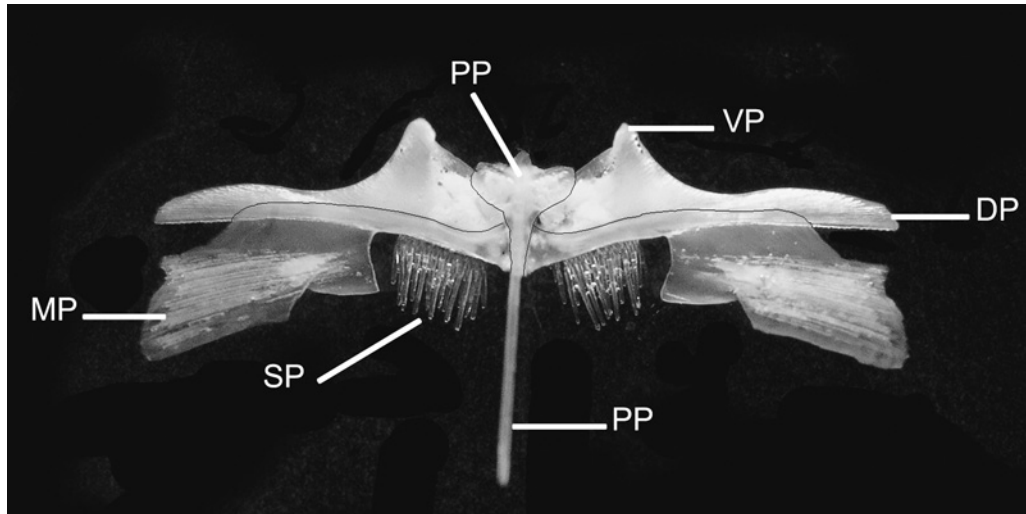


Table 1. Disk area, average resting suction pressure differential (mean of three measurements for each fish), single greatest sub-ambient pressure differential, and related single greatest force applied for eight echeuids on Plexiglas (P) and shark skin (S).

| | Disk area (cm ²) | Resting pressure (kPa) | | Greatest pressure (kPa) | | Force (N) | |
|-------------------------|------------------------------|------------------------|----------|-------------------------|-----------|-----------|----------|
| | | P | S | P | S | P | S |
| <i>E. naucrates</i> | | | | | | | |
| Fish 1 | 16.08 | -0.5 | NA | -103.3 | NA | 10.7 | NA |
| Fish 2 | 19.64 | -0.6 | -0.3 | -82.7 | -48.3 | 13.8 | 21.3 |
| Fish 3 | 12.61 | -1.1 | -0.8 | -102.8 | -56.4 | 11.0 | 5.8 |
| Mean ± SE | 16.11±2.0 | -0.6±0.2 | -0.6±0.1 | -96.3±6.8 | -52.3±4.1 | 11.8±1.0 | 13.5±7.8 |
| <i>E. neucratooides</i> | | | | | | | |
| Fish 1 | 17.91 | -0.3 | -0.2 | -102.4 | -45.6 | 15.2 | 14.1 |
| Fish 2 | 20.51 | -0.7 | NA | -103.0 | NA | 8.1 | NA |
| Fish 3 | 15.94 | -1.6 | NA | NA | NA | NA | NA |
| Fish 4 | 15.74 | -0.1 | NA | -51.0 | NA | 11.0 | NA |
| Fish 5 | 17.18 | -0.7 | -0.7 | -103.3 | -35.9 | 8.4 | 28.4 |
| Mean ± SE | 17.46±0.9 | -0.5±0.1 | -0.5±0.1 | -89.9±13.0 | -40.8±4.8 | 10.7±1.6 | 21.3±7.2 |
| Grand mean ± SE | 16.95±0.9 | -0.5±0.1 | -0.5±0.1 | -92.7±7.5 | -46.6±4.2 | 11.2±1.0 | 17.4±4.8 |

Note: NA, data not available.

Plexiglas (average 11.2 N) ($U = 510.5, n_1 = 17, n_2 = 26, p < 0.001$). Based on linear regression, no relationship was found between the greatest sub-ambient suction pressure differential and the corresponding pulling force for either Plexiglas ($F = 2.097, df = 1, p = 0.161$) or shark skin ($F = 0.188, df = 1, p = 0.671$). Pulling the dead remora orthogonally off the Plexiglas surface resulted in a mean sub-ambient pressure differential of $-19.9 \text{ kPa} \pm 3.3 \text{ kPa}$ (SE) under the suction disk, with a single highest measurement of -38.0 kPa .

Discussion

The suction disk of *E. naucrates* and *E. neucratooides* is supported and controlled by a series of muscles and skeletal elements that function to erect and depress the numerous

spinule-bearing laminae. The loosely attached, fleshy marginal lip provides a pliable seal around the suction disk. The three relatively large erector muscles attach to the hooklike ventral processes that increase the moment arm of the laminae, allowing their erection and the creation of the sub-ambient suction pressure differential. Erection of the laminae increases the volume between the suction disk and the host's skin, decreasing the sub-ambient pressure. The dorsomedial ridge of connective tissue that joins all laminae in their midline may serve to transfer the force generated by the erectors and depressors between adjacent laminae. Consequently, a contiguous chamber is created between the erected laminae and the host's skin. The anterior one third of the disk has depressor muscles and elongated hooklike ventral processes, and observations through the Plexiglas indicate that the laminae in this region are erected the most during

Fig. 4. A representative graph showing the greatest suction pressure generated by *E. naucrates* on the Plexiglas substrate as the external shear force approached 15.6 N. The dotted line represents the maximum sub-ambient pressure of a silicone suction cup being pulled in tension. As force increased and sub-ambient pressure under the disk declined, the disk sheared across the substrate. The spicules most likely grip and slip on the surface, resulting in the pressure fluctuations observed during the pressure decline. At peak force, the remora suddenly slipped posteriorly off the substrate, resulting in the rapid return to ambient pressure.

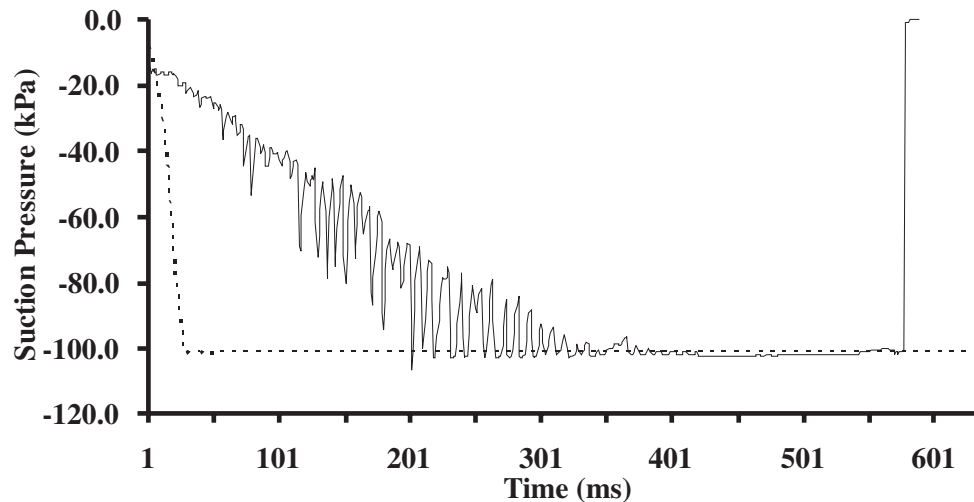
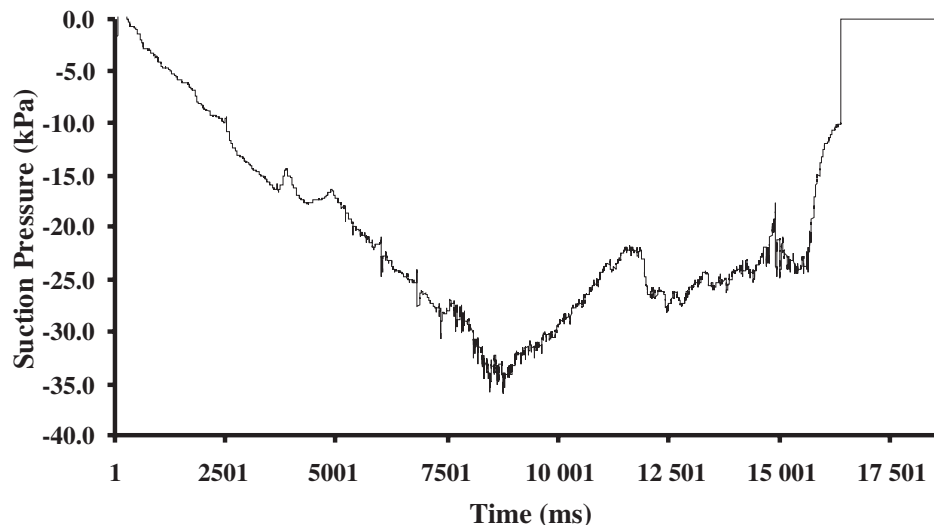


Fig. 5. A representative graph showing the greatest suction pressure generated by *E. naucrates* on the sharkskin substrate as the external shear force approached 35.0 N. Note that considerably less negative suction pressure was apparent on this substrate than on the Plexiglas. The remora remained on the shark skin longer than it remained on the Plexiglas before slipping off.



attachment. This suggests that the anterior region of the disk generates the majority of the sub-ambient pressure differential, although the pressure would be equal under all areas of the disk. Furthermore, greater erection of the anterior laminae may result in their spicules being more orthogonal to the host's skin, resulting in increased friction at the anterior end, thus inhibiting detachment into the water flow. The depressors are suspected to assist in detachment by lowering the laminae and releasing the seal; their action would be augmented by the fish swimming forward and detaching the spicules (Bennett 1840). The role, if any, of the small blind chamber on the most anterior lamina and its sickle-shaped ossification is not readily apparent from these experiments, necessitating further research.

Echeneis naucrates and *E. neucratoides* would require a minimal suction pressure differential to attach to a resting host,

as evidenced by the extremely low suction pressure differential generated on the Plexiglas and shark skin (-0.5 kPa) (Table 1). However, when force is applied along the longitudinal axis, a considerably greater sub-ambient suction pressure differential is generated. The highest sub-ambient pressure differential recorded was -103.3 kPa, which is approximately that of a vacuum (-101 kPa) at sea level. The difference between the recorded pressure differential and -101 kPa is confounded by the 0.5% error of the probe (± 0.5 kPa). The pressure differential under a suction device such as a remora's disk is the difference between ambient pressure (101 kPa) and the lowest pressure possible before cavitation of the water occurs, which is usually between 0 and -100 kPa on most marine surfaces. Therefore, at sea level, cavitation usually limits suckers to pressure differentials of 100–200 kPa (Smith 1991, 1996). The remoras measured here had pres-

sure differentials of approximately 100 kPa and were most likely limited by cavitation due to the wettability of the substrate or the silicone glue used in the seal (Smith 1991). Because of water's inability to expand under sub-ambient pressures, absolute pressures of -168 kPa, well below a vacuum, have been recorded at sea level for *Octopus vulgaris* Cuvier, 1797 suckers under tension (Smith 1991). The large pressure differentials under the remora's disk may be actively generated by the erector muscles or may be initiated by the erector muscles and then passively increased by the posteriorly directed force, which causes the spinules to grip the denticles, erect the laminae, and consequently increase the volume under the disk, resulting in a further drop in pressure. Even though the large sub-ambient pressure differentials under the remora's disk may be passively generated, similar to those generated by the silicone suction cup and dead remora being pulled orthogonally off the Plexiglas (Fig. 4), the erector muscles most likely resist the depression of the laminae when the remora is forcibly pulled posteriorly either by drag imposed by the water or by the experimental procedure. Regardless, it would take considerable force to dislodge the remora from a host fish.

Despite lesser sub-ambient pressure differentials on shark skin, the remora required more force to be dislodged from the denticled shark skin than from the smooth Plexiglas, supporting our hypothesis. Laminae are composed of three modified pterygiophores, with the distal pterygiophore bearing numerous spinules. The spinules function as an additional source of shear friction between the shark skin and the remora by offering considerable resistance in the caudal direction (Gunther 1860). This increased shear friction could account for the lack of relationship between maximum force at detachment and the sub-ambient suction pressure differential for the shark skin. Furthermore, an imperfect seal due to the shark's denticles could affect the pressure differential. On a smooth substrate, the attachment relies primarily on the seal provided by the fleshy lip surrounding the disk, as the spinules are less effective at increasing friction (Bennett 1840). The force of attachment in this case is related to the area of disk attachment multiplied by the difference between the pressure inside the suction cup and the pressure surrounding the disk (Kier and Smith 2002). The lack of relationship between maximum force at detachment and the sub-ambient pressure differential on Plexiglas may be a consequence of cavitation limiting the pressure on the Plexiglas to approximately -101 kPa (Smith 1991) regardless of force. The amount of force required to dislodge the remora from the Plexiglas was, in some cases, less than half the force required to dislodge it from the shark skin. When attached to shark skin, the remoras embed their abundant spinules and either passively or actively generate a lesser sub-ambient pressure differential than that generated on a smooth substrate in order to hold onto their host. The spinules, therefore, may reduce the amount of energy expended by the remora to attach to a swimming host with rough scales as opposed to a smooth, un-scaled host.

The ecological benefits derived from the hitchhiking behavior of remoras can include easy access to food resources, either by scavenging from the host's meal or by feeding on host parasites and feces. Other advantages include protection from predators and the reduced cost of transport (Godin

1997; Helfman et al. 1999; Mignucci-Giannoni et al. 1999; Sazima et al. 1999; Williams et al. 2003). The closely related cobia (*Rachycentron canadum* (L., 1766)) commonly follows larger fishes, and it is assumed that the common ancestor of cobias and remoras shared this behavior (O'Toole 2002). The evolution of the suction disk from the dorsal fin reduced the need for swimming to keep up with the host fish, most likely reducing energy expenditure such that the remora does not have to use its relatively large locomotory (axial) muscles. Consequently, a strong connection to the skin of the host is necessary because of the drag on the remora from hitchhiking and the host's attempts to dislodge it by jumping out of the water, scraping against rocks, and trying to out-swim the apparently irritating fish (Ritter 2002; Ritter and Brunnschweiler 2003; P.J. Motta, personal observation). *Opisthomyzon glaronensis*, the extinct echeineid with its poorly developed disk, most likely attached to floating or stationary objects (Gudger 1926). The increase in the number of laminae and the length of the disk in extant species of remoras would allow for a wider variety of hosts, including faster moving sharks (Cressey and Lachner 1970; O'Toole 2002). A larger disk increases the surface area for attachment, thereby allowing an increase in the suction pressure differential when necessary. O'Toole (2002) proposed that with increasing disk length the remoras have an increased reliance on attachment to living hosts as opposed to inanimate objects. The presence of spinules on the laminae apparently increased shear friction and the force necessary for detachment while reducing the need for large sub-ambient pressure differentials.

Future research should investigate the relationships between sub-ambient suction pressure differential, disk size, and host specificity, as well as the possibility of greater reliance on spinules in species that adhere to rough-scaled hosts as opposed to those, such as the marlin sucker (*Remora osteochir* (Cuvier, 1829)), that attach to hosts with less rugose scales (O'Toole 2002). Furthermore, future research should examine the anterior blind chamber and its purported role as a pneumatic pump, and extend our findings by investigating the relationship between drag and suction pressure differential when remoras are exposed to water of varying velocities in flume chambers.

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