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# Theoretical and computational fluid dynamics of an attached remora (*Echeneis naucrates*)



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#### ABSTRACT

Remora fishes have a unique dorsal suction pad that allows them to form robust, reliable, and reversible attachment to a wide variety of host organisms and marine vessels. Although investigations of the suction pad have been performed, the primary force that remoras must resist, namely fluid drag, has received little attention. This work provides a theoretical estimate of the drag experienced by an attached remora using computational fluid dynamics informed by geometry obtained from micro-computed tomography. Here, simulated flows are compared to measured flow fields of a euthanized specimen in a flow tank. Additionally, the influence of the host's boundary layer is investigated, and scaling relationships between remora features are inferred from the digitized geometry. The results suggest the drag on an attached remora is similar to that of a streamlined body, and is minimally influenced by the host's viscous boundary layer. Consequently, this evidence does not support the hypothesis that remoras discriminate between attachment locations based on hydrodynamic considerations. Comparison of the simulated drag with experimental friction tests show that even at elevated swimming speeds it is unlikely that remoras are dislodged by drag alone, and furthermore that larger remoras may be more difficult to dislodge than smaller remoras indicating that they become more suited to attachment as they mature.

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#### 1. Introduction

Remora fishes (Fig. 1A and B) in the Echeneidae family have adapted a unique dorsal suction pad that allows them to attach to various host organisms and marine vessels. The list of hosts includes, but is not limited to, sharks, whales, rays, other pelagic fish, sea turtles, dolphins, divers, buoys, ship hulls, and concrete (Strasburg, 1962; Cressey and Lachner, 1970; O'Toole, 2002; Ritter, 2002; Ritter and Brunnschweiler, 2003; Silva and Sazima, 2003; Williams et al., 2003; Sazima and Grossman, 2006; Weihs et al., 2007). Proposed benefits to remoras include transportation ("hitchhiking"), protection from predators, increased courtship/reproduction potential, enhanced gill ventilation and expanded feeding opportunities (Fertl and Landry, 1999). With respect to the benefits of the host organism, certain remora species have been known to feed on parasites attached to the host

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(Strasburg, 1959; Cressey and Lachner, 1970); however, there are many documented cases of hosts that are either unwilling to serve (Aughtry, 1953; Strasburg, 1962) or attempt to remove remoras by various means (Ritter, 2002; Ritter and Brunnschweiler, 2003; Fish et al., 2006; Weihs et al., 2007). Despite work that has been done to better understand the attachment strength (Fulcher and Motta, 2006) and physical mechanisms associated with remora attachment (Nadler et al., 2013; Culler and Nadler, 2014; Culler et al., 2014), very little has been done to quantify the primary force that remoras must overcome in order to maintain attachment, namely fluid drag. While some basic estimates of fluid drag on remoras have been made in relation to their attachment to spinner dolphins (Fish et al., 2006), a detailed drag analysis has yet to be performed. The aim of the present work is to provide a more rigorous estimate of the fluid drag on a remora in the context of its association with a host. The estimates are based on computational fluid dynamics (CFD) simulations informed by real three-dimensional remora geometry obtained from micro-computed tomography ( $\mu$ CT) and particle image velocimetry (PIV) of a euthanized specimen.



**Fig. 1.** (A, B) Photographs of a remora specimen and (C, D) accompanying three-dimensional model based on  $\mu$ CT scan after digital fin removal and reconstruction. Corresponding top views are shown in (A) and (C) and side views in (B) and (D).

Traditionally, theoretical and experimental measurements of drag on fish and other marine organisms were associated with rigid physical models (Lang and Daybell, 1963; Lang and Pryor, 1966; Purves et al., 1975; Webb, 1975; Ogilvy and Dubois, 1981). For certain simple swimming gaits such as gliding between bouts of active swimming, this technique can deliver reasonable results (Webb, 1975; Miller et al., 2004); however, for more complex swimming gaits the body motions of the host (swimming kinematics) must be included to deliver accurate drag estimations (Webb, 1975; Fish, 1993; Anderson et al., 2001). With respect to remoras, it has been observed that there is a high degree of attachment site fidelity (Strasburg, 1962), and although it has been noted that remoras may reposition themselves on the host (Ritter, 2002; Silva and Sazima, 2008), they typically cease undulatory motion once attachment is created (Sewell, 1925). Therefore, because remoras naturally glide through the water under the power of their host, treating a remora as a rigid body should provide a reasonable estimate of the drag associated with attachment.

In addition to the drag on the remora's body, it may also be important to incorporate the hydrodynamics of the host organism, as this may help explain some aspects of remora/host interaction. For example, a study by Silva and Sazima (2008) observed the frequency with which remoras (Remora australis) attached to various locations on spinner dolphins (Stenella longirostris). The authors suggested that remoras preferentially attach to certain sites to either minimize interference with the dolphin's habitual behaviors and sensitive areas (such as those responsible for vision, respiration, swimming, mating, etc.) or for hydrodynamic reasons (Silva and Sazima, 2008). While the first conclusion is almost self-evident, the latter suggests that remoras are taking advantage of reduced drag associated with the host's fluid boundary layer. When a submerged body is subjected to fluid flow, a boundary layer naturally forms owing to the "no-slip" condition on the surface of the body (fluid in contact with the body remains stationary with respect to the body) (Munson et al., 2006). Typically, as one progresses along the length of the body, the boundary layer thickness increases (Munson et al., 2006). As the thickness of the boundary layer grows, an attached remora experiences less of the free stream fluid velocity and lower drag. Thus, some attachment sites may be preferential to the remora because they offer reduced drag. Here, this concept is tested by subjecting a remora to different boundary layer thicknesses and free stream velocities (host swimming speeds) to assess whether there is substantial drag reduction.

Once the drag on the remora has been estimated, it is possible to investigate other aspects of remora/host interaction such as the power that must be supplied by the host to overcome the remora's drag (parasitic drag power), and whether or not a remora is likely to be removed by elevated host swimming speeds. Remoras use thousands of spinules, small mineralized tissue projections on their dorsal pad lamellae, to enhance friction forces between themselves and their hosts (Hora, 1923; Fulcher and Motta, 2006; Nadler et al., 2013; Beckert et al., 2015). To assess the potential for removing a remora by host swimming, the drag must be compared to the frictional force created by the spinules. In the

work by Fulcher and Motta (2006), the attachment strength of two remora species (*Echeneis naucrates* and *Echeneis neucratoides*) was investigated by inducing remora adhesion to shark skin, and simultaneously measuring the suction pressure in the remora pad and the posterior-directed load required for detachment. Using their results as a benchmark, if the estimated drag experienced by the remora is greater than the attachment strength due to frictional and suction attachment forces, the remora will slip off its host.

#### 2. Materials and methods

## 2.1. Specimen preparation for $\mu$ CT scanning and flow tank measurements

A remora (*Echeneis naucrates*) specimen (28.4 cm total length; TL) was cared for and euthanized in accordance with the guidelines and principles of the Georgia Institute of Technology Institutional Animal Care and Use Committee (IACUC), protocol A11085. The specimen was euthanized by a 0.5 g/l dose of MS-222 (tricaine methanesulphonate). After euthanizing, the specimen was fixed for  $\mu$ CT scanning in a phosphate buffer solution of 10 volume percent formalin for a minimum of 24 h. After fixing, the specimen was washed twice and stored in 1 × phosphate buffer. The specimen was scanned in air using a  $\mu$ CT50 (Scanco Medical, Bruttisellen, Switzerland) with a voxel resolution of 200  $\mu$ m. Tomograms were converted to dicom format, segmented, and surface-rendered in OsiriX (v5.5, Geneva, Switzerland) (Rosset et al., 2004).

The resulting three-dimensional (3D) surface model was imported into Rhinoceros 3D (McNeal, Seattle, WA, USA). There the pectoral fins of the remora were manually removed, as during attachment the remora can choose to reduce its drag profile by flattening them against its body. Also, the caudal fin of the remora was reconstructed based on photographs and physical measurements due to size constraints of the  $\mu$ CT scanning chamber.

For comparison with simulation experiments, flow tank measurements were made with a separate remora specimen. Initial flow tank experiments were attempted with live remoras but individuals would not preferentially attach centered to the position of the laser light sheet. Instead, to achieve better positioning and avoid eye injuries from the laser, a preserved specimen was used. Live remoras were housed and maintained in accordance with IACUC protocols at the Woods Hole Oceanographic Institution (WHOI) and the New Jersey Institute of Technology. The preserved remora (21.4 cm TL) was sutured around the perimeter of its disc to a 1 mm thick plastic sheet with 6/0 silk suture thread (Fine Science Tools, Inc., Foster City, CA, USA). The pectoral and pelvic fins were sutured to the body to reproduce behavior of live, attached remoras.

#### 2.2. Feature scaling

With the aid of a virtual 3D remora model, feature scaling was investigated. Relationships were sought mainly to convert overall fish length to other relevant hydrodynamic features such as the wetted surface area, pad area, and largest transverse diame-



**Fig. 2.** (A) Depiction of the remora model meshed (with 3 sides not shown) for finite element simulation, showing a close up (B) of refined tetrahedral elements near the model's boundaries.

ter. This was useful because it allowed for comparisons between derived quantities solely on the basis of length. Here it was assumed that isometric scaling applied to remora features, which is equivalent to normalizing the measured geometric quantities by body length. Thus, Eq. (1) (Davenport and Thorsteinsson, 1990) was used to determine the scaling relationships between different model features:

$$Y = aL^{b}, \tag{1}$$

where *L* is overall body length; *Y* is the other geometric feature of interest (largest transverse diameter, wetted area, etc.); and *a* and *b* are fitting constants. The constant *a* is the normalized geometric quantity associated with *Y*. The constant *b* is determined a priori, and is either 1, 2, or 3 depending on whether *Y* is a length, area, or volumetric quantity. All geometric measurements were obtained in Rhinoceros 3D from the 3D model created from  $\mu$ CT scans. Area and volume quantities were acquired from integration of the surfaces, whereas length measurements were obtained either from bounding box and/or projected edge lengths. The wetted surface area was calculated as the total body surface area minus the pad area.

#### 2.3. Drag estimation

Simulation of fluid flow over the remora geometry was accomplished with the CFD module in COMSOL Multiphysics version 4.3a (COMSOL, Stockholm, Sweden). Under the assumption that remoras are relatively stationary with respect to their hosts and due to the high swimming efficiency of fish (Hoerner 1965), the simulated flow was taken as steady and incompressible with standard no-slip boundary conditions on the surface of the remora model and host surface. Simulations with Reynolds numbers below 10<sup>5</sup> were taken as fully laminar. For simulations with higher Reynolds numbers, COMSOL's Reynolds-averaged Navier-Stokes (RANS) k-& turbulence model was implemented. In both cases, the control volume surrounding the remora model (far-field) had a square inlet with side lengths 6.5 times the remora's largest transverse diameter and an overall length of 2.5 remora body lengths. Uniform velocity boundary conditions were prescribed on the control volume's inlet, and zero viscous stress conditions were prescribed on the sides. COMSOL's built-in, physics-controlled meshing algorithm was used to generate the free tetrahedral mesh (Fig. 2A). The mesh included both boundary layer elements (16,990) and refined tetrahedral elements (250,165) around the remora model to capture the fine local details of the flow field around the remora (Fig. 2B). Further mesh refinement in initial simulations showed less than a 2% change in the computed drag. The simulations were solved using the built-in, iterative Newton solver.

Because many species of remora are known to attach to various shark species (Cressey and Lachner, 1970; O'Toole, 2002), the remora model was subjected to free-stream fluid velocities typical of sharks. Tagging studies on different shark species provided estimates of average swimming speeds on the order of 10–100 cm/s (Klimley et al., 2002; Weng et al., 2007; Carlson et al., 2010; Hueter et al., 2013), whereas maximum shark speeds may range between 100 and 1000 cm/s (Webb and Keyes, 1982; Klimley et al., 2002; Brunnschweiler, 2005). Therefore, the remora model was exposed to free-stream velocities ranging between 0.5 and 500 cm/s to include both the average and near top speed of many remora hosts.

After solving for the flow conditions around the remora, the drag force,  $F_D$ , was calculated by integrating the pressure, p, and shear,  $\tau$ , forces acting on the surface of the model in the direction of the flow,  $\hat{i}$ , using Eq. (2):.

$$F_D = -\int \int \left(p\hat{n}\right) \cdot \hat{i} dA + \int \int \left(\tau \hat{s}\right) \cdot \hat{i} dA, \qquad (2)$$

where *î*tand *î*tare the surface unit normal vector and unit tangent vector in the direction of flow, respectively (Blevins, 1984).

The drag coefficient,  $C_D$ , was then calculated using Eq. (3):

$$C_D = \frac{F_D}{1/2\rho U^2 A},\tag{3}$$

where  $\rho$ , *U*, and *A* are the fluid density, free-stream fluid velocity (host swimming speed), and the wetted surface area of the remora. As a means of validation, other studies have used drag coefficients based on non-lifting, streamlined bodies to estimate the drag on fish and other marine organisms (Lang and Daybell, 1963; Purves et al., 1975; Webb, 1975; Ogilvy and Dubois, 1981). Owing to such an approximation, the drag on streamlined bodies is mainly due to viscous (skin friction) effects, and less on flow separation and pressure drag, especially when the body is much longer than it is wide (Hoerner, 1965; Blevins, 1984). Here, simulation results were compared to the drag coefficient of a streamlined body given by Eqs. (4) and (5):

$$C_D = \frac{1.328}{\sqrt{Re_L}} \left( 1 + \left(\frac{L}{d}\right)^{-2/3} \right) + 0.11 \left(\frac{L}{d}\right)^{-2} , \quad Re_L < 10^5, \quad (4)$$

$$C_D = \frac{0.0303}{Re_L^{1/7}} \left( 1 + 1.5 \left(\frac{L}{d}\right)^{-3/2} + 7 \left(\frac{L}{d}\right)^{-3} \right) \quad , \ \mathrm{R}e_L > 10^5, \qquad (5)$$

where  $Re_L$ , d, and L are the Reynolds number with respect to body length, largest transverse body diameter, and body length, respectively wide (Hoerner, 1965; Blevins, 1984) The ratio of body length to diameter that is prominently featured in Eqs. (4) and (5) is known as the fineness ratio. These relationships were determined from statistical analysis of many experimental studies on streamlined bodies and are useful as long as the fineness ratio is above 2 (Hoerner, 1965; Blevins, 1984).

Eqs. (4) and (5) were created by the addition of both the frictional and pressure components of drag, which depend on fineness ratio. Because isometric scaling of the remora was assumed, the fineness was fixed. Therefore, Eq. (6), which is similar in form to Eqs. (4) and (5), was fit in a least squares sense to the simulation results, and was used as a relationship between the drag coefficient and the Reynolds number, where  $c_1$ ,  $c_2$ , and  $c_3$ , are fitting constants.

$$C_D = \frac{c_1}{Re_L^{c_2}} + c_3.$$
(6)

In addition to the drag coefficient, a second series of simulations was carried out to investigate the effect of the host boundary layer



Fig. 3. Drag coefficient computed for the remora model vs. Reynolds number, and that of a streamlined body with similar fineness ratio.

by altering the remora model's distance from the leading edge of a virtual flat plate. By increasing the distance of the remora from the leading edge of the plate, it was possible to estimate the drag experienced by the remora when subjected to increasing boundary layer thicknesses at different host swimming speeds, similar to moving the remora to more posterior attachment sites on a host. Although this procedure does not include pressure drag effects associated with host shape, it is a reasonable approximation when considering the host itself is likely to be a streamlined body whereby most of the drag is associated with viscous effects wide (Hoerner, 1965; Blevins, 1984). In these simulations, rather than using uniform velocity inlet conditions, Eqs. (7) and (8) provided the velocity profile at the inlet:

$$u(x, y) = U\left(2\eta - 2\eta^3 + \eta^4\right), \quad \eta = \frac{y}{\delta},\tag{7}$$

$$\delta = 5.83 \sqrt{\frac{\mu x}{\rho U}} = \frac{5.83 x}{\sqrt{Re_x}}.$$
(8)

These equations represent the boundary layer profile for flow over a flat plate, where x and y are the horizontal and vertical distances from the start of the plate and  $\mu$  is the fluid viscosity (Pohlhausen, 1921; von Karman, 1921). The distance from the edge of the plate was varied between 10 cm and 10 m to be comparable to some of the larger hosts to which remora attach, such as the whale shark. In theory, as the remora is moved farther from the edge of the plate and the boundary layer grows, the remora should be further engulfed by the plate's boundary layer and exposed to lower velocities near the plate's surface. Therefore, posterior attachment sites may benefit the remora in terms of reduced drag.

Although remoras are not considered parasites in the sense that they feed off their host, they are certainly parasites in the sense that extra swimming effort must be supplied by the host to compensate for the hitchhiking remora (Fertl and Landry, 2002; Fish et al., 2006; Weihs et al., 2007; Silva and Sazima, 2008). To estimate the increased rate of energy expenditure by the host, the parasitic drag power was computed as the product of the drag force and the host swimming speed (equivalent to the free-stream velocity with respect to the remora). The parasitic drag power is given in terms of the drag coefficient in Eq. (9):

$$P_D = F_D U = \frac{1}{2} C_D \rho U^3 A.$$
(9)

#### 2.4. Flow tank experiments

The preserved remora (21.4 cm TL) was mounted 38.5 cm from the leading edge of a knife-edged ( $10^\circ$ ) flat plate with the dimen-



**Fig. 4.** Simulated drag experienced by remora model at different swimming speeds including the boundary layer effects of a flat plate. The distance from the leading edge of the plate is varied from 10 cm to 10 m. The maximum difference in drag for a given Reynolds number occurs between that experienced nearest the start of the plate (most anterior location) and that nearest the end (most posterior location).

sions 170 cm x 45 cm. The flat plate was suspended in a flume with a working section 170 cm long, 45 cm wide, and 45 cm deep (Engineering Laboratory Design, Lake City, MN, USA) housed at the Shore Laboratory at WHOI in Falmouth, MA, USA, The flat plate was lowered into the flume such that the actual experimental test section size was 170 cm x 45 cm x 13.2 cm. Flow speeds ranged from 0.66 cm/s to 120 cm/s leading to Reynolds numbers and flow conditions similar to those in the computational simulations. A pulsed IR laser (Firefly, 300 W, 808 nm; Oxford Lasers, Shirley, MA, USA) was used to produce a vertical light sheet positioned mid-sagittal on the remora. The time delay  $(\Delta t)$  between flow exposures was set at 0.4-10 ms depending on flow speed. The flow was seeded with neutrally buoyant 50 micron plastic particles and imaged using a digital video camera (SA-3,  $1024 \times 1024$  pixels, 60 frames per second; Photron, San Diego, CA, USA) with a macro photographic lens (Micro-Nikkor, 105 mm; Nikon, Melville, NY, USA) to obtain high-resolution images of the seed particles traveling around the remora's body. The field of view was 12.5 cm x 12.5 cm. The laser and camera were synchronized by connecting the v-drive TTL trigger out from the camera to the laser pulse generator. The camera recorded at 60 Hz, and, therefore, image pairs were acquired at 30 Hz. The camera and laser were both mounted on a robotic positioning system built at WHOI for use with the flume. This was used to move the laser and camera field of view along the remora body at 7.5 cm intervals to reconstruct flow over the entire body in high resolution.

Velocity fields were calculated from the particle images using an off-the-shelf PIV analysis software package (DaVis; LaVision Inc., Ypsilanti, MI, USA). Velocity vectors were calculated from image sub-windows  $32 \times 32$  pixels in size with 50% overlap, resulting in a grid of  $64 \times 64$  vectors for each image pair. The velocity fields from 150 image pairs at each field of view along the remora were used to calculate an average velocity field. These fields made up mosaics that covered the flow over the entire fish.

#### 2.5. Frictional strength vs. drag

Remoras rely on friction to avoid slipping off their host due to drag (Beckert et al., 2015). The static friction coefficient,  $\mu_s$ , and the normal force characterize frictional strength between mating surfaces. By increasing the sub-ambient pressure beneath their pad,



**Fig. 5.** Simulated velocity fields of the remora at the sagittal plane attached 1 m from the front of a flat plate at a free-stream velocity of (A) 0.5 cm/s and (B) 50 cm/s. At very low host swimming speeds (A), the boundary layer is thicker, resulting in reduced drag on the remora. However, at moderate speeds (B), the boundary layer is very thin, which results in minimal drag reduction.

remoras can generate larger normal forces (the product of pressure and pad area) to resist slip. An estimate of frictional strength developed between a remora and its host came from the results in (Fulcher and Motta, 2006). There it was found that on average slip initiated at a posterior-directed force of 17.4 N. The suction pads in the study operated on average with an area,  $A_{pad}$ , of approximately 16.95 cm<sup>2</sup>, and were able to achieve maximum sub-ambient pressures,  $P_{max}$ , of 46.6 kPa (normal force of 79.0 N) on shark skin. In the framework of static friction, these results suggest a friction coefficient of approximately 0.22, which is similar to friction coefficients measured between euthanized remora and roughened glass surfaces (Beckert et al., 2015). Assuming the coefficient of friction and sub-ambient pressure remains constant with respect to the size of the remora, the drag experienced by a remora was compared to the frictional strength as a function of remora length and host swimming speed by combining Eqs. (1), (3), and (6) into Eq. (10):

$$N = \frac{F_D}{F_F} = \frac{1/2C_D\rho U^2 A}{\mu_s P_{max} A_{pad}},\tag{10}$$

where N is the ratio of the drag to the friction forces,  $F_F$ . Thus, if N is greater than 1, then drag is sufficient to overcome friction and the remora will be removed; otherwise, the remora will remain attached.

#### 3. Results

#### 3.1. Remora model and feature scaling

The 3D remora model used for drag and feature analysis is shown in Fig. 1 along with photographs displaying similar views of the actual specimen. Because the 3D model was constructed from  $\mu$ CT scans, it is not surprising that the photographs and renderings bear a strong resemblance. However, there are notable exceptions, including the lack of pectoral fins and the reconstructed caudal fin.

The fitting constants needed for Eq. (1) were computed and are shown in Table 1. The results in Table 1 are useful for expressing derived quantities from the flow simulation solely in terms of the fish length. For example, the drag coefficient or parasitic power can be expressed in terms of fish length rather than wetted area. The length of the remora model as scanned was 28.4 cm, which is in agreement with the measured value.

#### Table 1

Feature scaling fitting constants (Eq. (1)).

Remora feature	Fitting parameters	
Y	a	b
Pad area (m <sup>2</sup> )	0.0141	2
Wetted surface area (m <sup>2</sup> )	0.166	2
Volume (m <sup>3</sup> )	2.23	3
Largest transverse diameter (m)	0.0952	1
Pad perimeter (m)	0.522	1

#### Table 2

Fitting constants for drag model (Eq. (6)).

	Value
C <sub>1</sub>	3.4
C <sub>2</sub>	0.58
C <sub>3</sub>	0.002

## 3.2. Simulation results (drag coefficient) and flow tank measurements

Overall, the simulations showed the drag characteristics of an attached remora were similar to those of a streamlined body with an equivalent fineness ratio. The relationship between the drag coefficient,  $C_D$ , and Reynolds number ( $10^3 < \text{Re}_L < 10^6$ ) with respect to the remora model is seen in Fig. 3. The trend of the simulation compares favorably with those of a streamlined body using Eqs. (4) and (5), and the length to diameter (fineness) ratio given in Table 1. Eq. (6) and the constants in Table 2 are also seen to provide an excellent fit to the simulation data, and are more accurate at lower Reynolds numbers where the simulation results deviate slightly from the streamlined body approximation.

Placing the remora model at different locations on a virtual flat plate allowed for a comparison between the drag experienced at anterior and posterior attachment sites on a streamlined host. It was found that the distance of the remora model from the start of the plate had the largest effect on drag at lower vs. higher swimming speeds. Fig. 4 shows the relationship between the Reynolds number based on the remora model's length and the drag on the remora including the effects of the induced boundary layer. The maximum difference occurs between the drag experienced nearest the start of the plate (largest) and that nearest the end (smallest). Fig. 5 shows examples of the fluid flow field along the remora's



**Fig. 6.** Experimental flow field measurements (left) vs. corresponding simulated flow fields (right) 1.8 body lengths (38.5 cm and 51.1 cm, respectively) from the start of a flat plate. The scale bar at the bottom corresponds to the minimum (zero) and maximum (host speed, *U*) velocity. The respective values of *U* are given for each flow field.

sagittal plane when the remora is attached 1 m from the start of the plate with free-stream velocities of 0.5 cm/s and 50 cm/s, respectively. This figure illustrates the boundary layer has the largest impact at lower Reynolds numbers (swimming speeds) when the remora is engulfed by the viscous boundary layer as seen in Fig. 5A. At higher Reynolds numbers, the effect of the boundary layer is negligible as can be seen by the narrowing of the darkened region in Fig. 4 and the reduced boundary layer thickness compared to the height of the remora in Fig. 5B. Additionally, it was found that the simulated boundary layers generated with Eqs. (7) and (8) were slightly larger than the measured boundary layers. This makes the simulation an upper bound for estimating the potential for drag reduction, as a thicker boundary layer would engulf a larger fraction of the remora with slower moving fluid.

As a means of validating the simulations, good agreement was found between the experimentally measured flow fields and the corresponding simulations. Fig. 6 compares the measured velocity flow fields for the euthanized specimen in the flow tank to the simulated flow fields on the rigid remora geometry. The flow fields are very comparable, as both data sets have similarly located stagnation points towards the anterior of the specimens, and the fastest flow/lowest pressures occur over the pectoral girdle. Additionally, each data set shows a wake that is about as tall as the remora. However, one important distinction to be made is that in the flow tank measurements, the euthanized specimen's caudal fin was more collapsed/flattened than the simulated rigid remora model. Because the caudal fin was free to collapse, as was observed in live remoras, its disturbance of the flow was reduced and its wake is not as pronounced.

With respect to parasitic drag, the results show that at relatively brisk(>200 cm/s) swimming speeds a host must generate only a few extra watts (<10 W) to compensate for a relatively long, attached remora (50 cm). Of course, the extent to which this extra power burdens the host depends on its metabolic requirements. Using Eq. (9) with the results in Tables 1 and 2, an estimate of the additional (parasitic drag) power that must be supplied by the host to overcome remora drag is seen in Fig. 7. The parasitic drag power is shown as



**Fig. 7.** Parasitic drag power required by host to overcome attached remora at different swimming speeds. Remora length is varied from 5 to 50 cm.

a function of swimming speed for several different remora lengths ranging from 5 to 50 cm.

#### 3.3. Frictional strength vs. drag

For the host speeds and surfaces investigated, it was found that drag on an attached remora is much less than that required to dislodge it. By combining Eq. (10) with the results in Tables 1 and 2, the drag on an attached remora can be compared to the frictional force required to maintain attachment, as seen in Fig. 8. The figure shows that at low swimming speeds (5–50 cm/s) drag is several orders of magnitude below the critical frictional force (above which an attached remora is dislodged). At higher swimming speeds (500 cm/s) drag reaches almost 10% (ratio of drag to frictional forces (N)=0.1) of the frictional strength, which is still well below the point of detachment (N=1). The shape of the curves in Fig. 8 indicates that as remora length increases frictional forces increase faster than drag.



**Fig. 8.** Ratio of drag to the experimentally measured frictional strength (Fulcher and Motta, 2006) as a function of overall remora length for selected host swimming speeds.

#### 4. Discussion

An important metric for determining the drag on a streamlined body is its fineness ratio. For a streamlined body exposed to the free-stream, the optimal fineness ratio is typically close to 4.5 (Hoerner, 1965; Webb, 1975; Blake, 1983) but can be as high as 7 (Gertler, 1950). According to (Hoerner, 1965) the optimal fineness ratio of a streamlined body close to the ground is approximately 10. The fineness ratios of the remoras used in the simulations and flow tank measurements in the present study were 10.5 and 9.3, respectively. This provides strong evidence that the shape of the remora is better suited for hitchhiking on a host surface rather than free-stream swimming.

Another interesting result was that the host boundary layer did not provide the remora with a substantial drag reduction at posterior attachment locations in terms of skin friction. This is likely due to the boundary layer thickness being a stronger function of free-stream velocity than position. Even at moderate host speeds near 50 cm/s, comparable to the migratory speeds of remora hosts (Klimley et al., 2002; Weng et al., 2007; Carlson et al., 2010; Hueter et al., 2013), the viscous boundary layer was so thin that most of the remora was exposed to the free stream, and therefore little benefit was realized. Although differences between the most anterior and posterior attachment sites investigated were as high as 80%, these large relative differences occurred at low host speeds where the drag is already so low that such differences are likely imperceptible to the remora. As host speed (Reynolds number) increases, the maximum difference between the drag experienced at posterior and anterior attachment sites tends toward zero. This result casts doubt on the hypothesis that remoras are discriminating in their attachment location based on hydrodynamic reasons (Silva and Sazima, 2008), at least with respect to frictional drag, especially considering the flat-plate simulation results had slightly thicker boundary layers than the flow tank measurements, which makes them an upper bound estimate for drag reduction.

However, it remains a fact that certain attachment sites are occupied with greater frequency than others, at least with respect to dolphins (Silva and Sazima, 2008) and sharks (Brunnschweiler, 2006), and therefore some other benefit likely exists instead of reduced drag. It is known that the local conditions of the attachment site play a role in remora adhesion both from experimental observation (Strasburg, 1962; Fulcher and Motta, 2006) and theoretical considerations (Culler et al., 2013). Because remora adhesion is strongly suction-based, an important condition for maintaining attachment is the presence of reduced pressure inside the suction pad. In order for such a pressure difference to exist, a robust seal must be maintained by the remora. One explanation for attachment site preference could be based on reduced deformation of the host tissue at the attachment site. For example, because contractions of the underlying muscles may create folds, or at least strain, in the host's skin and thereby break the remora's suction seal, the remora may choose attachment locations on the host where the underlying muscle groups are not primarily responsible for swimming. In fact, with respect to dolphins, most of the curvature (and therefore deformation of the skin) associated with locomotion occurs posterior to the dorsal fin (Pabst, 1993) where remoras seldom attach. Furthermore, flank and belly attachment sites, which are preferred by remoras, are insulated from the underlying muscles by a stiff subdermal connective tissue sheath and blubber layer (Pabst, 1990). Thus, just as it was suggested that remoras attach to locations that do not interfere with the habitual behaviors and sensitive areas of their hosts (Silva and Sazima, 2008), perhaps remoras also choose attachment locations that do not interfere with the nature of their own attachment. Hence their attachment site preferences may reflect a balance between maximizing their chances of remaining attached while minimizing interference with their host.

In addition to choosing attachment sites that minimally interfere with the host, a shape that affords minimal drag is advantageous to both the remora (drag is the primary force it must overcome to maintain attachment) and host (reduced effort required for swimming with an attached remora). Using detailed knowledge of the drag, quantitative estimates of the extra swimming power (parasitic drag) that must be generated by a remora's host can be made, as in Fig. 7. For example, consider a bottlenose dolphin (Tursiops truncatus) outputs approximately 3000 to 4000 W when swimming at 500 cm/s (Fish 1993; Fish et al., 2014). When moving at that speed with an attached remora, 10 W of the dolphin's thrust go into overcoming remora drag (less than 1% of the dolphin's output). At a speed of 150 cm/s, which is closer to a dolphin's average swimming speed, a dolphin may output approximately 90 to 280 W (Fish, 1993; Fish et al., 2014), and the drag of an attached remora consumes 0.23 W. Again, a single attached remora requires less than 1% of the dolphin's output. From a metabolic standpoint, the dolphin must consume an extra 2.5-110 g/day of sardines to move at 150 and 500 cm/s, respectively (assuming sardines have 8 kJ/g (Rosa et al., 2010)). While this seems low, remora are known to associate with hosts for prolonged periods, so while the short-term net reduction in the dolphin's thrust is relatively small, the long-term effects of remora attachment are cumulative. Additionally, it often happens that a host may have many attached remoras which exacerbates the dolphin's situation (Silva and Sazima, 2003; Williams et al., 2003; Sazima, 2006; Sazima and Grossman, 2006). In this case, the additional drag can be estimated by multiplying the drag of a single attached remora by the total number of attached remoras. However, this provides only a lower-bound estimate because by disrupting the flow field, the drag on the combined remora and host body may be greater than the sum of the drag experienced by each of them individually (Hoerner, 1965; Vogel, 1994). While this example illustrates that the negative consequences of remora attachment to a dolphin are likely to be accumulated long-term, smaller hosts may also be affected in the short-term if the parasitic drag power is a larger fraction of their swimming thrust.

Another conclusion derived from the simulation results is that the ratio of drag to frictional forces (N) decreased with increasing length, suggesting that larger remoras are slightly more likely to remain attached to their host when compared to smaller remoras at the same swimming speed. Though this effect diminished rather quickly as length was increased, it may suggest, for example, that remoras become more suited to attachment as they mature and grow in length. In any case, the effect is explained by decreased drag coefficients resulting from larger Reynolds numbers of longer remoras compared to those of shorter remoras at the same swimming speeds. More importantly, it is clear that regardless of remora size, it seems unlikely a host (at least a shark) will dislodge a remora by increasing its swimming speed. This is especially apparent when considering that large free-stream velocities ( $\sim$ 500 cm/s) create drag slightly less than 10% (N=0.1) of the force required to dislodge a remora (frictional strength). This is in line with observations of both captive and wild remoras as they are typically removed by impact with the surface of the water or other objects rather than by elevated host swimming speeds, even those proceeding jumps (Aughtry, 1953; Ritter, 2002; Weihs et al., 2007). This is somewhat expected given that remoras depend on their hosts for many important needs including food, protection, and transportation. These survival benefits provide strong selective pressures that favor robust attachment.

In summary, the remora's low drag profile is a critical component of its overall suction-based attachment strategy, and to these ends, a detailed estimate of the drag it experiences while attached was presented. In general, the shape and drag experienced by an attached remora compared favorably to those of a streamlined body optimized for hitchhiking. From the estimated drag, it was found that a remora is unlikely to be removed by elevated host swimming speeds alone (at least with respect to sharks), and that larger remoras are slightly less likely to be detached from their hosts than smaller remoras at the same swimming speed. Also, the lack of substantial drag reduction when the remora was subjected to its host's viscous boundary layer casts doubt as to whether remoras discriminate between attachment sites due to hydrodynamic considerations (at least with respect to frictional drag). A likely alternative explanation is that remoras choose attachment sites to maximize their own potential for success by choosing areas of the host that are minimally deformed during locomotion.

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#### References

- Anderson, E.J., McGillis, W.R., Grosenbaugh, M.A., 2001. The boundary layer of swimming fish. J. Exp. Biol. 204, 81–102.
- Aughtry, R.H., 1953. A note on mass mortality of the myctophid fish Tarletonbeania crenularis. Copeia 1953, 190–192.
- Beckert, M., Flammang, B.E., Nadler, J.H., 2015. Remora fish suction pad attachment is enhanced by spinule friction. J. Exp. Biol. 218, 3551–3558.
- Blake, R.W., 1983. Energetics of leaping in dolphins and other aquatic animals. J. Mar. Biol. Assoc. U.K. 63, 61–70.
- Blevins, R.D., 1984. Applied Fluid Dynamics Handbook. Van Nostrand Reinhold Company Inc., New York.
- Brunnschweiler, J.M., 2005. Water-escape velocities in jumping blacktip sharks. J. R. Soc. Interface 2, 389–391.
- Brunnschweiler, J.M., 2006. Sharksucker–shark interaction in two carcharhinid species. Mar. Ecol. Evol. Persp. 27, 89–94.
- Carlson, J.K., Ribera, M.M., Conrath, C.L., Heupel, M.R., Burgess, G.H., 2010. Habitat use and movement patterns of bull sharks *Carcharhinus leucas* determined using pop-up satellite archival tags. J. Fish Biol. 77, 661–675.
- Cressey, R.F., Lachner, E.A., 1970. The parasitic copepod diet and life history of diskfishes (Echeneidae). Copeia 1970, 310–318.
- Culler, M., Nadler, J.H., 2014. Composite structural mechanics of dorsal lamella in remora fish. MRS Proceedings 1619, mrsf13-1619-a02-08.
- Culler, M., Ledford, K.A., Nadler, J.H., 2014. The role of topology and tissue mechanics in remora attachment. MRS Proceedings 1648, mrsf13-1648-hh10-02. Davenport, J., Thorsteinsson, V., 1990. Sucker action in the lumpsucker Cyclopterus
- lumpus L. Sarsia 75, 33–42.
- Fertl, D., Landry, A., 2002. Remoras. In: Perrin, W.F., Wursig, B., Thewissen, J.G.M. (Eds.), Encyclopedia of Marine Mammals. Academic Press, Burlington, pp. 942–943.
- Fertl, D., Landry, A.M., 1999. Sharksucker (*Echeneis naucrates*) on a bottlenose dolphin (*Tursiops truncatus*) and a review of other cetacean–remora associations. Mar. Mam. Sci. 15, 859–863.
- Fish, F.E., 1993. Power output and propulsive efficiency of swimming bottle-nosed dolphins (*Tursiops truncatus*). J. Exp. Biol. 185, 179–193.
- Fish, F.E., Nicastro, A.J., Weihs, D., 2006. Dynamics of the aerial maneuvers of spinner dolphins. J. Exp. Biol. 209, 590–598.
- Fish, F.E., Legac, P., Williams, T.M., Wei, T., 2014. Measurement of hydrodynamic force generation by swimming dolphins using bubble DPIV. J. Exp. Biol. 217, 252–260.
- Fulcher, B.A., Motta, P.J., 2006. Suction disk performance of echeneid fishes. Can. J. Zool. 84, 42–50.
- Gertler, M., 1950. Resistance experiments on a systematic series of streamlined bodies of revolution – for application to the design of high-speed submarines. DTIC Document. David W. Taylor Model Basin, Washington.
- Hoerner, S.F., 1965. Fluid-Dynamic Drag. Hoerner Fluid Dynamics, Bricktown, NJ. Hora, S.L., 1923. The adhesive apparatus of the sucking-fish. Nature 111, 668.

Symbol	Description
Х,Ү	Feature dimensions in scaling equation
a,b	Fitting constants for scaling equation
FD	Drag force
р	Pressure
τ	Shear stress
î	Unit vector for direction of flow relative to remora
n	Surface unit normal vector
ŝ	Surface unit tangent vector
CD	Drag coefficient
ρ	Fluid density
U	Host velocity
Α	Wetted surface area
Re <sub>L</sub>	Reynolds number with respect to length
d	Largest transverse diameter
L	Largest body length
$c_1, c_2, c_3$	Fitting constants
u(x,y)	Boundary layer profile on flat plate with respect to the horizontal and vertical axes
η	Dimensionless parameter
δ	Boundary layer thickness
$\mu$	Fluid viscosity
Re <sub>x</sub>	Reynolds number with respect to distance from edge of flat plate
P <sub>D</sub>	Parasitic drag power
Ν	Ratio of drag and friction forces
$F_F$	Friction force
$\mu_s$	Friction coefficient
Pmax	Sub-ambient pressure in pad
A <sub>pad</sub>	Pad surface area

#### Appendix A. List of symbols and abbreviations

Hueter, R.E., Tyminski, J.P., de la Parra, R., 2013. Horizontal movements, migration patterns, and population structure of whale sharks in the Gulf of Mexico and Northwestern Caribbean Sea. PLoS One 8, e71883.

Klimley, P.A., Beavers, S.C., Curtis, T.H., Jorgensen, S.J., 2002. Movements and swimming behavior of three species of sharks in La Jolla Canyon, California. Environm. Biol. Fish. 63, 117–135.

Lang, T.G., Daybell, D.A., 1963. Porpoise Performance Tests in a Seawater Tank. Naval Ordnance Test Station, China Lake, CA, NAVWEPS Report 8060.

Lang, T.G., Pryor, K., 1966. Hydrodynamic performance of porpoises (Stenella attenuata). Science 152, 531–533.

- Miller, P.J.O., Johnson, M.P., Tyack, P.L., Terray, E.A., 2004. Swimming gaits, passive drag and buoyancy of diving sperm whales *Physeter macrocephalus*. J. Exp. Biol. 207, 1953–1967.
- Munson, B., Young, D.F., Okiishi, T.H., 2006. Fundementals of Fluid Mechanics, 5th ed. John Wiley & Sons, Hoboken.

Nadler, J.H., Mercer, A.J., Culler, M., Ledford, K.A., Bloomquist, R., Lin, A., 2013. Structures and function of remora adhesion. MRS Proceedings 1498, 159–168.

- O'Toole, B., 2002. Phylogeny of the species of the superfamily Echeneoidea (Perciformes: Carangoidei: Echeneidae, Rachycentridae, and Coryphaenidae), with an interpretation of echeneid hitchhiking behaviour. Can. J. Zool. 80, 596–623.
- Ogilvy, C.S., Dubois, A.B., 1981. The hydrodynamic drag of swimming bluefish (*Pomatomus saltatrix*) in different intensities of turbulence – variation changes of buoyancy. J. Exp. Biol. 92, 67–85.
- Pabst, D.A., 1990. Axial muscles and connective tissues of the bottlenose dolphin. In: Leatherwood, S., Reeves, R.R. (Eds.), The Bottlenose Dolphin. Academic Press, San Diego & London, pp. 51–67.
- Pabst, D.A., 1993. Intramuscular morphology and tendon geometry of the epaxial swimming muscles of dolphins. J. Zool. 230, 159–176.
- Pohlhausen, K., 1921. The approximate integration of the differential equation for the laminar boundary layer. J. Appl. Math. Mech. 1, 252–268.
- Purves, P.E., v. Heel, W.H.D., Jonk, A., 1975. Locomotion in dolphins, part I. Hydrodynamic experiments on a model of the bottle-nosed dolphin, *Tursiops truncatus*. Aquat. Mamm. 3, 5–31.
- Ritter, E.K., 2002. Analysis of sharksucker, *Echeneis naucrates*, induced behavior patterns in the blacktip shark, *Carcharhinus limbatus*. Environ. Biol. Fish. 65, 111.

Ritter, E.K., Brunnschweiler, J.M., 2003. Do sharksuckers, Echeneis naucrates, induce jump behaviour in blacktip sharks, Carcharhinus limbatus? Mar. Freshw. Behav. Physiol. 36, 111-115.

- Rosa, R., Gonzalez, L., Broitman, B.R., Garrido, S., Santos, A.M.P., Nunes, M.L., 2010. Bioenergetics of small pelagic fishes in upwelling systems: relationship between fish condition, coastal ecosystem dynamics and fisheries. Mar. Ecol. Progr. Ser. 410, 205–218.
- Rosset, A., Spadola, L., Ratib, O., 2004. OsiriX: an open-source software for navigating in multidimensional DICOM images. J. Dig. Imag. 17, 205–216.
- Sazima, I., 2006. Species records mistaken identifications, and their further use: the case of the diskfish *Echeneis naucrates* on a spinner dolphin. Neotrop. Ichthyol. 4, 457–460.
- Sazima, I., Grossman, A., 2006. Turtle riders: remoras on marine turtles in Southwest Atlantic. Neotrop. Ichthyol. 4, 123–126.

Sewell, R.B.S., 1925. The adhesive apparatus of the sucking-fish. Nature 115, 48–49. Silva Jr., J.M., Sazima, I., 2003. Whalesuckers and a spinner dolphin bonded for weeks: does host fidelity pay off? Biota Neotropica 3, 1–5.

Silva Jr., J.M., Sazima, I., 2008. Whalesuckers on spinner dolphins: an underwater view. Mar. Biodiv. Rec. 1, 1–5.

Strasburg, D.W., 1959. Notes on the diet and correlating structures of some Central Pacific echeneid fishes. Copeia 1959, 244–248.

- Strasburg, D.W., 1962. Some aspects of the feeding behavior of *Remora remora*. Pac. Sci. 16, 202–206.
- Vogel, S., 1994. Life in Moving Fluids, 2nd ed. Princeton University Press, Princeton. von Karman, T., 1921. On laminar and turbulent friction. J. Appl. Math. Mech. 1, 233–252.
- Webb, P.W., 1975. Hydrodynamics and energetics of fish propulsion. Bull. Fish. Res. Board Canada 190, 1–156.
- Webb, P.W., Keyes, R.S., 1982. Swimming kinematics of sharks. Fish. Bull. 80, 803–812.
- Weihs, D., Fish, F.E., Nicastro, A.J., 2007. Mechanics of remora removal by dolphin spinning. Mar. Mam. Sci. 23, 707–714.
- Weng, K.C., Boustany, A.M., Pyle, P., Anderson, S.D., Brown, A., Block, B.A., 2007. Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. Mar. Biol. 152, 877–894.
- Williams Jr., E.H., Mignucci-Giannoni, A.A., Bunkley-Williams, L., Bonde, R.K., Self-Sullivan, C., Preen, A., Cockcroft, V.G., 2003. Echeneid–sirenian associations, with information on sharksucker diet. J. Fish Biol. 63, 1176–1183.