The benefits of planar circular mouths on suction feeding performance

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Suction feeding is the most common form of prey capture across aquatic feeding vertebrates and many adaptations that enhance efficiency and performance are expected. Many suction feeders have mechanisms that allow the mouth to form a planar and near-circular opening that is believed to have beneficial hydrodynamic effects. We explore the effects of the flattened and circular mouth opening through computational fluid dynamics simulations that allow comparisons with other mouth profiles. Compared to mouths with lateral notches, we find that the planar mouth opening results in higher flow rates into the mouth and a region of highest flow that is positioned at the centre of the mouth aperture. Planar mouths provide not only for better total fluid flow rates through the mouth but also through the centre of the mouth near where suction feeders position their prey. Circular mouths are shown to provide the quickest capture times for spherical and elliptical prey because they expose the prey item to a large region of high flow. Planar and circular mouths result in higher flow velocities with peak flow located at the centre of the mouth opening and they maximize the capacity of the suction feeders to exert hydrodynamic forces on the prey.

Keywords: suction feeding; computational fluid dynamics; aquatic prey capture

1. INTRODUCTION

Suction feeding is the most widely used method of prey capture among aquatic feeding vertebrates, including ray-finned fishes, cartilaginous fishes and tetrapods. In this behaviour, a predator rapidly expands its mouth and buccal cavity creating a large pressure drop. This pressure drop drives a flow of water in front of the predator's mouth that exerts hydrodynamic forces on the prey that draw the prey into the mouth [1,2]. Thus, suction feeding performance depends on the ability of the predator to manipulate this flow field in a way that quickly exerts a high force on the prey [3].

A wide range of behavioural and morphological adaptations have been identified and proposed to improve suction feeding performance. Two particularly widespread and striking features exhibited by suction feeders are a near-planar profile of the opened mouth and a circular mouth aperture. A planar profile is defined as one where the entire perimeter of the mouth opening lies in one plane. This type of mouth opening is achieved by a combination of jaw kinesis and membranes in teleosts, while in many tetrapods and cartilaginous fishes, labial cartilages or membranes fill the lateral margins of the mouth as it opens [4–6]. It is thought that a planar mouth opening enhances suction feeding hydrodynamics by allowing more efficient flow of water into the mouth [4,7,8] and by preventing flow that is directed orthogonal

to the direction of the prey item. During a suction feeding event, the predator has a fixed expansion volume that generates the water flow entering the mouth. A planar aperture directs the flow anteriorly and allows the predator to focus on the water movement in the region of the prey item. If the mouth is notched, water will enter the mouth laterally as well as anteriorly, effectively diminishing the flow that can be used to affect the prey item. While these effects of the notched mouth are intuitive, the nature of the impact of a notched mouth opening has not been characterized in detail.

Many fishes form a nearly circular mouth aperture during suction feeding [9–11]. Circular mouth openings provide maximal area for minimal circumference, which leads to the most flux through the mouth [12,13]. Circular mouths also provide a flow field that is radially symmetrical in front of the predator, while this axial symmetry is lost with an elliptic mouth opening [14]. Quantification of these and other potential benefits of the circular mouth aperture have not been explored. In particular, the asymmetrical flow field generated by an elliptical mouth may have implications for the magnitude of forces that are exerted on the prey item and the time course for their development.

In this paper, computational fluid dynamic modelling is used to explore some hydrodynamic consequences of two separate mouth geometries—the planar mouth opening as opposed to an increasingly notched shape and a circular mouth opening as opposed to elliptical apertures of varying eccentricity. For the planar mouth

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opening, we focus on the effect of this geometry on the spatial distribution of flow and on the net flow rate into the mouth. In comparing the circular and elliptical mouth openings, we focus on the consequence of prey capture by calculating the time required for a standard prey item that is positioned along an axis that extends out from the centre of the mouth to be engulfed.

2. MATERIAL AND METHODS

2.1. The model

We model the suction feeding event by solving the Navier–Stokes equations that govern fluid flow on a Chimera overset grid scheme representing the fish, prey and surrounding fluid. This approach is described in further detail in the study of Skorczewski *et al.* [15]. The Navier–Stokes equations for mass and momentum are presented as [16]:

$$\nabla \cdot \boldsymbol{u} = 0$$

and

$$\frac{\partial \boldsymbol{u}}{\partial t} + (\boldsymbol{u} \cdot \nabla)\boldsymbol{u} = \frac{-1}{\rho}\nabla P + \nu\nabla^2\boldsymbol{u}.$$

Here $\boldsymbol{u} = (u, v, w)^{\mathrm{T}}$ is a vector of the fluid velocities in the three spatial x, y, z directions, respectively; t represents time, P the pressure, $\rho = 1000 \text{ kg m}^{-3}$ is the density of water, $\nu = 10^{-6} \text{ m}^2 \text{ s}^{-1}$ is the viscosity of water and ∇ the gradient operator. Boundary and initial conditions are needed to close this system. The initial condition used is that of a fish swimming with its mouth open but not applying any suction. Wall boundary conditions where the flow velocity matches the surface velocity are used on the portions of the grids representing the body of the fish and the body of the prey. To simulate a suction feeding strike, on the portion of the grid representing the mouth, a time-varying suction boundary condition is prescribed.

2.2. Chimera overset grids

The computational meshes on which we solve the Navier–Stokes equations are a set of structured Chimera overset grids. Chimera overset grids are a way to decompose a complicated computational domain into several simple overlapping domains. The detailed surface grids representing the body of the fish are presented in figure 1. Structured volume grids representing the fluid field near the fish and the prey are generated via solutions to hyperbolic partial differential equations [17,18]. This overlapping setup offers advantages over using a single large complicated and unstructured computation grid. In particular, they allow for better grid point clustering near solid boundaries, lead to more efficient numerical algorithms and have a natural parallel structure for execution on modern computers [18]. In addition, for moving boundary problems, each time step requires moving only one grid and updating the interpolation scheme, as opposed to remeshing the entire computational domain. This leads to increased computational efficiency.
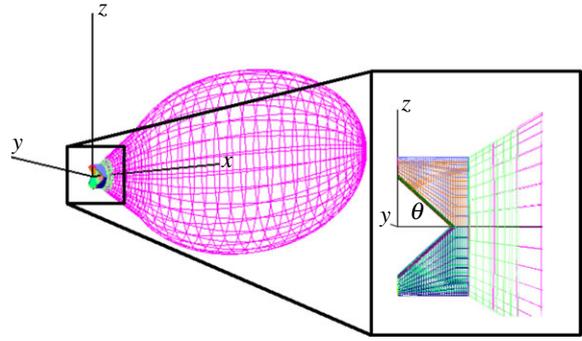

Figure 1. Chimera overset grids representing the surface of a fish body and the area around the fish mouth. Several refined grids are used to represent the complicated geometry of the fish mouth. Volume grids for flow around the fish are generated from these surface grids using hyperbolic grid-generation techniques. Varying the values of θ correspond to different amounts of maxillary swing.

We use a low Mach number-preconditioned dual time-stepping algorithm to numerically solve the Navier–Stokes equations outlined by Pandya *et al.* [19] and implemented in the OVERFLOW package developed at NASA Ames [20]. This finite-difference method uses upwind differencing in the streamwise direction, centre differencing in other directions and uses approximate factorization to give first-order accuracy in the computed solution. Convergence tests with the grids representing the fish confirm first-order accuracy in time and slightly less than first-order accuracy in space. This is sufficient for these calculations as higher order accuracy will not significantly change any results. Solving equations on Chimera overset grids involve updating the numerical solution to the next time step on each grid individually, and then communicating the solution to the overlapping grids via interpolation. Cases where the grid points lie inside the solid body defined by other grids are called hole points, and solutions are not performed on these points. The location of hole points is done via the X-ray method [21].

The following process is iterated to simulate a suction feeding strike:

At each time step, flow velocities are calculated on the computational meshes representing the fluid around the fish and the prey.

The stress tensor in the normal direction is then integrated over the surface of the prey to obtain the force felt by the prey using the following formulae:

$$\boldsymbol{F} = \int \boldsymbol{\sigma} \cdot \boldsymbol{n} \, \mathrm{d}A$$

and

$$m\bar{x} = \boldsymbol{F}$$

Here, $\boldsymbol{F}$ is the force, $\boldsymbol{n}$ the unit normal, $\boldsymbol{\sigma}$ the stress tensor and $\mathrm{d}A$ the surface area element of the prey. The mass and acceleration of the prey are represented using m and $\bar{x}$.

The prey's location and velocity are updated and the wall boundary conditions for the prey are updated to match.

Table 1. Capture times for mouth apertures of varying deviations from a circular shape. Eccentricity is a measure of how much an ellipse deviates from being circular. This table shows that as the mouth becomes more circular (eccentricity equal to 0), the time to capture prey decreases.

vertical radius (cm)	horizontal radius (cm)	eccentricity	time to capture (ms)
0.5	2.0	0.96	12.133
0.707	1.414	0.94	11.013
0.866	1.155	0.86	10.760
0.931	1.074	0.5	10.760
1.0	1.0	0.0	10.680
1.074	0.931	0.5	10.773
1.155	0.866	0.86	10.813
1.414	0.707	0.94	11.120
2.0	0.5	0.96	12.253

Figure 2. Time-varying suction boundary condition. (Online version in colour.)

The process then repeats with the flow velocities calculated for the next time step.

2.3. Planar mouths

During a suction feeding event, the mouth aperture forms a nearly planar profile through a forward swing of the maxilla and labial membranes. This is hypothesized to increase suction performance by restricting the fluid flow to the region directly in front of the mouth [4,7,8]. We examine this effect by investigating the steady fluid flow fields resulting from suction feeding events of fishes with different degrees of maxillary swing using our model. The mouth in these computations is a fixed size with a constant pressure drop boundary condition. Three cases are considered where the amount of maxillary swing is measured as the angle, θ, the mouth makes with the xy plane (the transverse plane through the centre of the mouth; figure 1). The three cases considered have mouths that make angles of 45°, 65° and 90°, which are referred to as the notched, small notch and flat cases, respectively. Streamlines and mass flow rates are examined to investigate the effect of the varying geometry on the fluid flow field.

2.4. Circular mouths

The shape of the circumference of the mouth opening could affect the performance of suction feeders. To investigate the biological consequences of this shape, we perform simulations varying the mouth circumferential shapes from a horizontally skewed ellipse to a vertically skewed ellipse. For these simulations, the cross-sectional area of the mouth opening is held constant. Major and minor axes for the simulations are shown in table 1. The eccentricity of an ellipse, denoted by ε, is a measure of how much the ellipse deviates from a circular circumference and is given by the formula:

$$\varepsilon = \sqrt{1 - \frac{b^2}{a}},$$

where a and b are the major and minor radii, respectively.

When the circumference of the mouth is a circle, the eccentricity equals zero and for an infinitely skewed elliptical circumference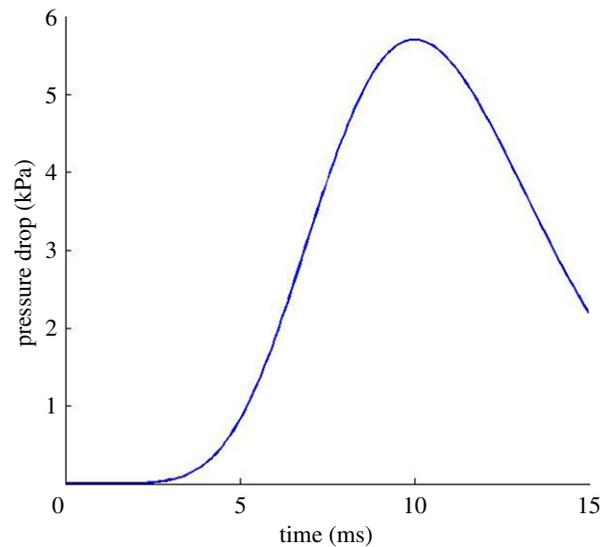, the eccentricity is one. We denote mouths elliptically skewed in the horizontal direction with a negative eccentricity and mouths skewed vertically with positive eccentricity. We examined mouths that ranged in eccentricity from 0 to 0.96 (i.e. from a circle to an ellipse with height four times the width). Mouth shapes are rarely reported in the literature, but we have measured mouths nearly circular in bluegill sunfish, *Lepomis macrochirus*, and with height up to 1.25 times width in largemouth bass, *Micropterus salmoides* (P.C.W. unpublished observations). We anticipate that the range of eccentricities used here captures most of the range found among teleost fishes, but future research will be needed to address the relative frequencies of mouth shapes in nature. We measure the capture time to quantify suction performance; the time it takes for a prey at a given fixed position to reach the mouth of the fish as a function of its eccentricity.

To simulate a suction effect, a time-dependent pressure drop boundary condition is placed on the portion of the computational grid representing the mouth opening of the fish. A pressure-based boundary condition is biologically and computationally appropriate here as suction feeders generate flow by creating large pressure drops in the buccal cavity. All aspects of the different biological mechanisms used to create this suction are ignored to isolate the differences created in the shape of the mouth. As this is a boundary where the fluid leaves the computational domain, a pressure-based boundary condition also avoids the issue of overdetermining the system of equations to solve [16]. This suction profile is shown in figure 2 and peaks at 10 ms. This is representative of suction pressures found in other experiments [22,23]. The time step for these calculations is 0.01333 ms. The prey for this study is a 6.67 mm diameter sphere which is 33 per cent of the circular gape diameter. This size was chosen because studies have shown that suction-feeding fishes prefer prey satisfying this diameter to gape ratio [15,24,25]. The initial position of the prey is located at one-quarter of the gape distance from the mouth, where the distance is measured from the edge of the prey to the mouth.
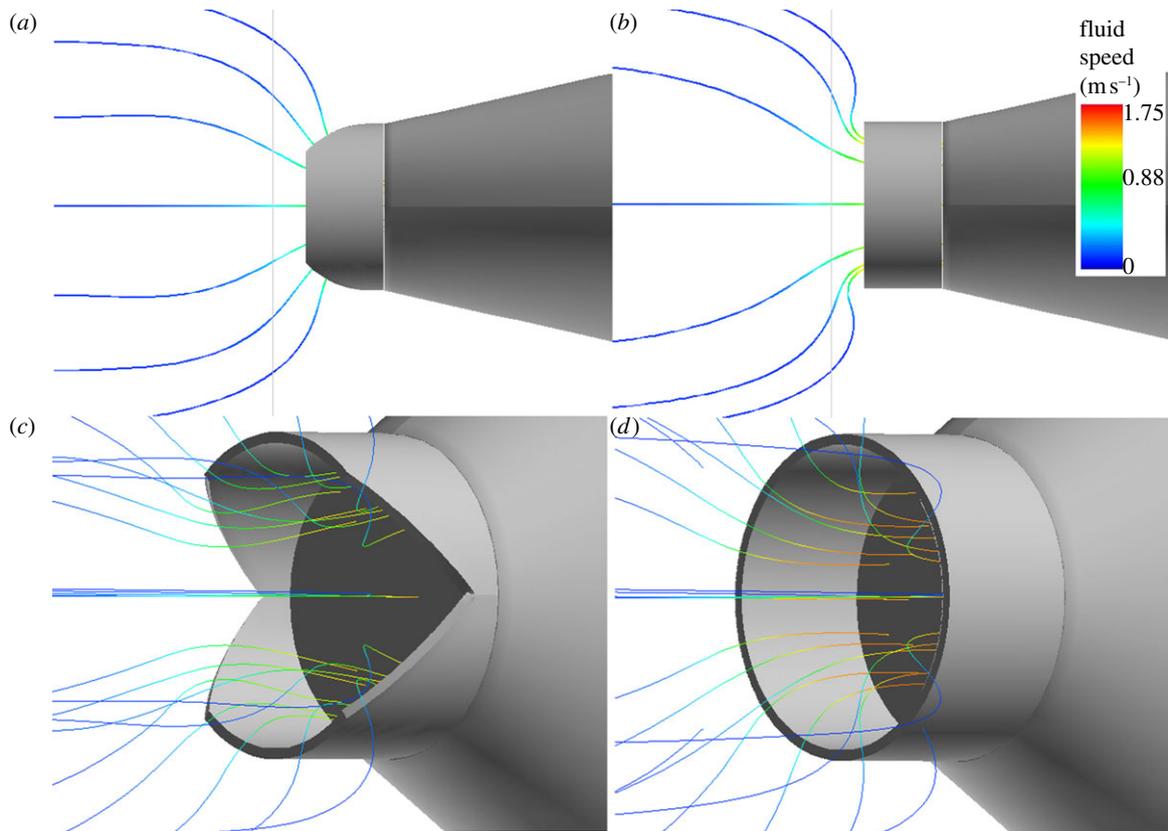
Figure 3. Streamlines shaded by fluid speed for cases with full (*b*) and no maxillary swing (*a*). The top left view shows streamlines entering through the notch on the side of the mouth for the case with no maxillary swing. The top right view is the case with full maxillary swing and does not have this effect. Streamlines inside the mouth show that they bend vertically away from the centre (*xy*-plane) for the case with no maxillary swing (*c*) but are nearly parallel for the case with full maxillary swing (*d*).

3. RESULTS

3.1. Planar mouths

Streamlines entering the mouth for the notched (left) and flat (right) cases are shown in figure 3. For the notched case, streamlines enter the mouth through the notch created by not swinging the maxilla forward. The fluid entering from the side of the mouth displaces some of the fluid entering from the front and diverts it from its straight path through the mouth. This is a consequence of both the incompressibility of water at this Reynolds number and the fundamental property that streamlines cannot cross [16]. Thus, streamlines bend away from the xy plane and the velocity is reduced, lowering the fluid flow rate through the mouth. The speed of the flow at the centre point in front of the mouth, which is the origin in our coordinate set-up, is measured to be 0.91 m s^{-1} for the notched case $(\theta = 45^{\circ})$, as compared with 0.97 m s^{-1} for the small notch case $(\theta = 65^{\circ})$ and 1.45 m s^{-1} for the flat case $(\theta = 90^{\circ})$. This shows a 37.2 per cent loss in flow speed of the fluid at the centre point in front of the mouth aperture for the case of no maxillary swing when compared with the case of full maxillary swing. The increased speed into the mouth in the case of full maxillary swing is a consequence of the fact that flow is blocked from entering through the sides as illustrated by the streamlines in figure 3 (right). We note for later discussion that in the case of full maxillary swing, there is only one focus of peak fluid flow and it is located at the
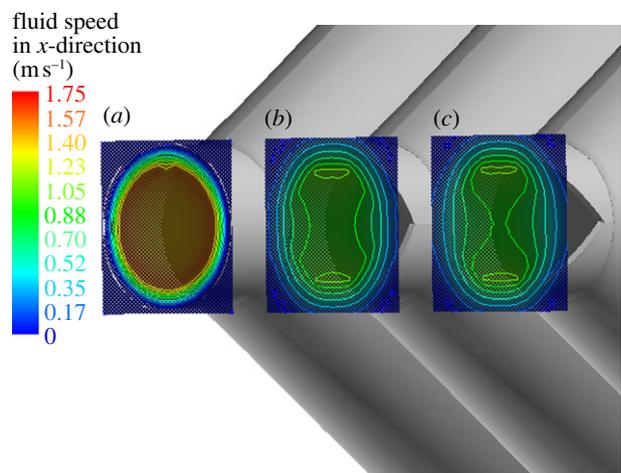

Figure 4. Contours colour-coded to the velocity in the *x*-direction (into the mouth) for cases with full maxillary swing (*a*), moderate swing (*b*) and no swing (*c*) are plotted for a slice in the *y*–*z* direction in front of the mouth. The location of maximum flow changes between the cases with and without maxillary swing. The slowing down of the flow in the cases without full maxillary swing is due to the fluid entering through the notches on the side forcing the fluid entering directly in front of the mouth to slow down.

front centre of the mouth. In the case of notched mouths, there are two foci of peak fluid flow located near the top and bottom of the mouth (figure 4). This is because of the bending of streamlines described above.
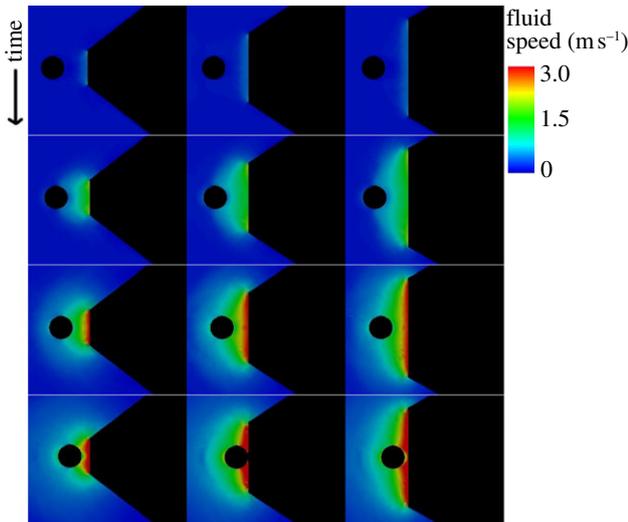
Figure 5. Flow speed for three fish with mouth apertures of varying eccentricities but the same cross-sectional area. The fish in the left column has a mouth aperture with eccentricity of −0.96 where the major axis is oriented horizontally (into the page). The centre column shows flow for a fish with a circular mouth (eccentricity equals 0). The mouth aperture of the fish in the right column has an eccentricity of 0.94 with the major axis oriented vertically.

3.2. Circular mouths

Simulations of flow through a mouth with varying circumferential shapes are calculated and analysed. Snapshots of the calculated flow field are shown in figure 5 and a table showing how the time to capture changes with eccentricity is shown in table 1. Results show that the time to capture prey decreases as the mouth becomes more circular. The quickest prey capture event occurs when the fish has a circular gape. The minimum time to capture is 10.68 ms and corresponds very closely to the time of peak suction. The longest prey capture time occurs when the circumference of the fish mouth deviates most from a circular shape at 12.25 ms. A rapid decrease in the prey capture times occurs as the ratio of major to minor radii decreases from 4 ($\varepsilon = 0.96$) to 2 ($\varepsilon = 0.86$) followed by a slower decrease to the minimum when the mouth is circular.

4. DISCUSSION

Our results provide support and some mechanisms for the widely held belief that both a planar mouth opening and a circular mouth opening have advantages for suction feeding when compared with mouths that are notched in the sides or elliptical in shape. We found that notched corners of the mouth produce flow that interferes with the flow entering directly in front of the mouth. This results in a lower net volume flow rate through the notched opening than through the flattened opening. Perhaps, the most surprising result in this comparison was that the presence of a notched side in the mouth results in two foci of fastest flow velocity that are off-set from the centre of the mouth opening (figure 4). In this case, the fastest flow speed is not at the centre of the mouth opening, but occurs

in regions above and below the midline. Thus, not only does the notched mouth compromise peak flow velocity but it also creates a spatial distribution of highest flow velocities that would complicate attempts by predators to position prey in the midst of the highest flow rate. Planar mouth openings were previously thought to provide more efficient flow into the mouth. An experiment in which water was drained from a constant volume bucket found that flow rates were higher through pipe openings that were planar and orthogonal to the orientation of the pipe, when compared with a notched opening [4]. Our computations also show a decrease in the flow rate though the mouth, but we also found a loss of flow rate in front of the mouth, and the movement of the location of maximum flow speed moves away from the centre of the mouth towards the top and bottom of the mouth as the magnitude of the notch in the side of the mouth increases.

The computations performed in the current study used a fish with a fixed gape. This is not found in any known suction feeders where the opening of the mouth and buccal cavity are coordinated during the strike. The expanding gape seen in actual suction feeders is likely to magnify the bending of the streamlines owing to the no-slip boundary condition pulling fluid in the direction of the expanding gape. The no-slip boundary condition states that fluid particles at the boundary of a fluid flow must move with the same velocity as the boundary [16]. Thus, we expect that an expanding gape and buccal cavity will force the fluid to flow radially outwards from the longitudinal axis of the buccal cavity, similar to what is seen in figure 3.

We have shown that a planar mouth opening has a number of positive consequences for suction feeding, but are there any negative effects that can be viewed as trade-offs? One possibility is that the shape of the mouth affects the drag experienced by the predator moving towards the prey during the strike. Drag is a function of shape of the body moving through a fluid [26,27] and insights from feeding aquatic snakes suggest that effects of mouth shape on drag could be considerable [28]. Computational fluid dynamics could be used to explore this possibility by performing simulations of fish that impulsively start swimming from rest and calculating the unsteady drag felt by fish with different-shaped mouth openings. These simulations have a time step of 0.1 ms and last for 10 ms. This represents a typical duration of a suction feeding strike but is not long enough to set up a steady state flow field around the fish. Streamlines show that fluid is allowed to flow through the sides of a notched mouth but not allowed to flow through in cases of fish with flat profiles (figure 6). Calculations of the drag show that for the flat case, an increase of only 0.3 per cent is observed when compared with a notched case. This small increase in drag may be owing to the fact that the mouth represents a small fraction of the fish in both cases. We can investigate this by restricting our drag calculations only to the subset of Chimera grids representing the mouth of the fish. This means instead of integrating over the entire surface of the fish, we only integrate over the surface area of the mouth. When the calculations are restricted in this manner, we see
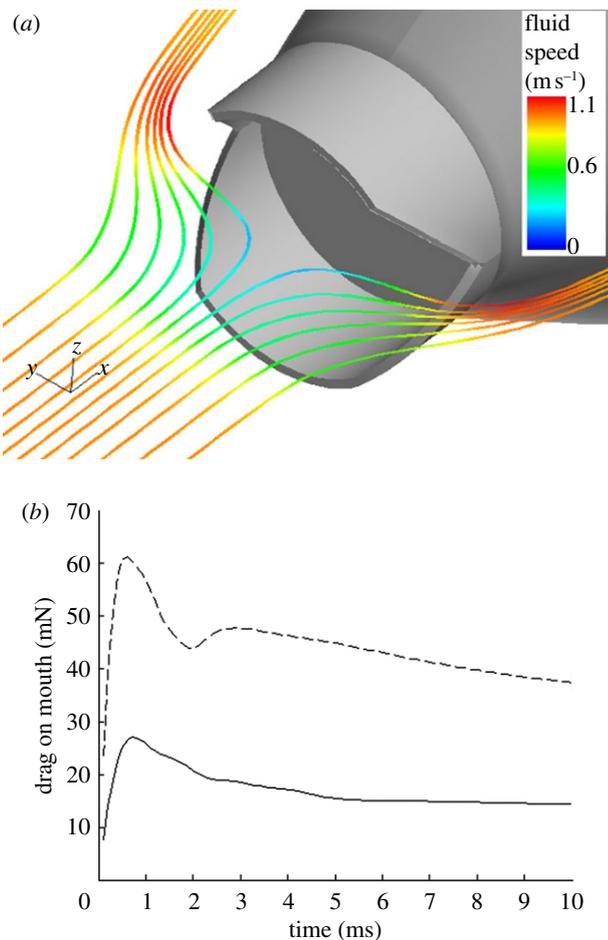
(a)

(b)

Figure 6. (*a*) Streamlines colour-coded to show the speed of flow for a fish with no maxillary swing that impulsively starts swimming at $1.0 \, \text{m s}^{-1}$. Fluid is allowed to leave out of the notches in the sides of the mouth. There are no notches when fish have full maxillary swing. (*b*) Drag contributions from just the mouth of a fish that impulsively starts swimming at $1.0 \, \text{m s}^{-1}$ for 10 ms. Fish with full maxillary swing (dashed line) experience larger drag that those without any maxillary swing (solid line). The magnitude of the drag is relatively small when compared with the total drag the fish feels as the mouth represents a small portion of the fish body here. Fish whose mouths are a larger fraction of their body could see this effect play a more significant role.

that the drag contribution of the flat case varies between 100 and 200 per cent more than the notched case. This implies that in fish where the mouth makes up a larger fraction of the entire fish than is the case here, there is the potential for increased swimming drag to be a significant trade-off of the increased suction performance created by flat mouth profiles. More work is needed to fully understand whether this trade-off is biologically significant. The existence of many aquatic predators with deeply notched mouths in association with feeding behaviours that employ extensive ram movements also suggests that such a trade-off may exist.

Our results show that the shape of a planar mouth opening also has a considerable impact on the flow of water into the mouth. The circular mouth simulations produce the quickest time to prey capture for spherical and ellipsoidal prey. Deviations away from the circular

mouth causes restrictions in the region of the flow field where flows were high (figure 4), reducing the exposure of the prey body to the rapidly changing velocities that account for the majority of the forces that suction flows exert on the prey. One implication of these results is that the circular mouth opening enhances suction feeding performance by maximizing a radially symmetrical region in front of the mouth in which flow velocity is high. This appears to be especially important when predators feed on prey that are equal to or greater than one-third the diameter of the mouth. The disadvantages of flow field without axial symmetry would be reduced in cases where the prey item is smaller than the 33 per cent of mouth diameter that we used here.

In an effort to isolate the differences in the flow fields exterior to the fish produced by varying the shape of the mouth opening, we used a single suction pressure profile boundary condition to generate the flow field. However, different species of aquatic suction feeders use different mechanisms to generate this suction profile which may or may not be coupled to their mouth shape. It is possible that these mechanisms are used in an effort to mitigate any adverse effects caused by non-circular mouth shapes [29]. More work is needed that couples the suction-generating mechanisms with the resultant flow field to explore this further.

It should be mentioned that while some suction feeders appear to have mouth openings that are both planar and close to circular in shape [9,14], other species have mouths that are notched in the corners to varying degrees and more elliptical in shape. Previous models of the flows generated during suction feeding depend on the assumptions of a planar and circular mouth aperture [15,30–32]. This assumption allows these models to reduce the hydrodynamic equations to one dimension [25]. Thus, the results derived from these models would need to be revised for the case of non-circular mouth opening, which may be common in nature. It can be anticipated that variation in the shape of the mouth opening contributes considerably to variation in the effectiveness of suction feeding. This may be an important source of variation in performance among the suction feeding vertebrates.

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