Hydrodynamic constraints on prey-capture performance in forward-striking snakes

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Some specialized aquatic snakes such as *Natrix tessellata* strike at fish by rapidly accelerating their head towards the prey with their mouth opened widely. This strategy is believed to be suboptimal as relatively high drag forces act on the open jaws and, therefore, probably limit strike speed. Moreover, the bow wave in front of the snake's jaws could push prey away from the mouth, thus potentially explaining the relatively low capture success observed in these animals (<20%). Here, we used laser-scan based computational fluid dynamics to test these potential constraints on prey-capture performance for *N. tessellata*. Our simulations showed that drag force indeed increases drastically for striking at a high gape angle. However, we estimated the overall cost in slowing down strike speed to be less pronounced due to the instationary dynamics of the system. In contrast to the expectations, forward displacement of prey was relatively limited (<13% of head length), and forceful collisions between prey and the leading edge of the jaw regularly occurred. However, our models showed that precise aiming by the snake was needed to reduce the chance of deviating the prey to a path bypassing the mouth. Our study also indicated several hydrodynamic advantages for snakes to strike at relatively large prey.

Keywords: hydrodynamics; snake; prey capture; bow wave; feeding

1. INTRODUCTION

Vertebrates feeding on prey that are freely suspended or swimming in water generally use a combination of suction and forward motion when capturing their prey (e.g. Lauder & Clark 1984; Muller & van Leeuwen 1985; Norton & Brainerd 1993; Aerts *et al.* 2001; Dean 2003; Marshall *et al.* 2008). To generate suction, vertebrates suddenly increase the volume of the buccopharyngeal cavity, typically by posteroventral rotation of their hyoid apparatus, resulting in an inflow of water into the mouth. Since suction works well only if the prey is in close proximity to the mouth (Muller *et al.* 1982; van Leeuwen & Muller 1984; Holzman *et al.* 2007, 2008), the gap between the predator and the prey is often closed by fast swimming towards the prey (i.e. ram feeding). Many predatory fish that are known to use considerable ram (e.g. adult barracuda and many serranids) finish their attack with an

explosive suction feeding bout (Wainwright & Bellwood 2002).

However, fish-eating snakes use a rather unusual prey-capture strategy with respect to most other aquatic predators. Since the hyoid has become largely reduced in snakes as a consequence of the specialization of tongue function for chemoreception (e.g. Schwenk 1994), they are strongly limited in their capacity to expand the initial volume of the buccal cavity to generate suction. Instead, previous studies using high-speed videos of aquatic snakes during feeding have shown that they strike at prey with a widely gaping mouth using a fast (sometimes faster than 1 m s^{-1}), forward motion of the head by stretching their curved trunk (Alfaro 2002, 2003; Bilcke *et al.* 2006, 2007; Vincent *et al.* 2007; Herrel *et al.* 2008). Next, the mouth is closed onto the prey, which is pierced by the backward curving teeth. A second strategy that is commonly observed in some species is laterally directed striking (i.e. sideways head sweeping; Alfaro 2002; Herrel *et al.*

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2008), which appears to be performed by the more broad-headed species among the natricine snakes (Herrel *et al.* 2008) and is often employed to capture prey at high densities (Bilcke *et al.* 2006).

Previous studies have hypothesized that specific hydrodynamic constraints exist that may limit the prey-capture success of a pure (i.e. non-suction) ram-feeding strategy as observed in forward-striking aquatic snakes. Firstly, a fast, widely gaping translation of the head through a viscous and dense medium such as water is assumed to cause a considerable amount of drag force that could constrain striking speed (Young 1991; Hibbitts & Fitzgerald 2005). Secondly, the amount of water that will be pushed in front of the snake's jaws (in analogy with boats this is referred to as the 'bow wave') would tend to push prey away from the approaching snake head. Additionally, this bow wave may also help trigger the lateral line system of the prey fish and therefore may help the prey to escape. Consequently, drag and bow waves are believed to have had a strong influence on the evolution of form–function relationships in aquatically feeding snakes (Young 1991; Vincent *et al.* 2004, 2007; Hibbitts & Fitzgerald 2005; Herrel *et al.* 2008). However, this idea remains speculative because the effects of drag- and bow-wave generation for prey capture in aquatic snakes have not been quantified.

Since previous studies have shown that understanding aquatic predator–prey interactions requires an explicit hydrodynamic perspective (Holzman *et al.* 2008; Van Wassenbergh & Aerts 2009), we use computational fluid dynamics (CFD) simulations of strikes from the specialist piscivore *Natrix tessellata*. More specifically, we will describe the flow patterns around a forward-striking aquatic snake and evaluate the characteristics and importance of the bow wave in pushing prey away from the snake's jaws. Furthermore, we will examine how drag force experienced by the snake relates to gape angle for different strike velocity profiles, and what the effects of jaw closing, head width, prey size and prey position are on prey pushing during this process. These hydrodynamic insights will help us to better understand the behavioural and morphological requirements of forward-striking performance in snakes.

2. MATERIAL AND METHODS

2.1. Modelled specimen

The semi-aquatic snake species *N. tessellata* was selected for study because its diet consists of more than 80 per cent fish, which are grabbed by a frontal strike. We selected a medium-sized adult specimen from the collection of the Forschungsmuseum Alexander Koenig (Bonn, Germany; collection number ZFMK-Bonn 7590) that originated from Antalya, Turkey. The specimen had the following external dimensions (digital caliper measurements): 520 mm snout–vent length (from the tip of the snout to the end of the anal shield), 140 mm tail length (from the end of the anal shield to the tip of the tail), 17.1 mm head length (measured from the back of the skull to the tip of the snout), 10.88 mm head width (measured at the

widest point of the head, typically located at the level of the lower jaw–quadratum joint, posterior to the last supralabial scale), 8.24 mm head height (measured at the highest point of the head, typically located anterior to the lower jaw–quadratum joint but posterior to the last supralabial scale), 24.37 mm lower jaw length, 14.48 mm distance from the corner of the mouth to the tip of the snout and a quadrate length of 7.46 mm.

2.2. Laser scanning

The specimen was scanned using a Metris XC50 cross-scanner (Metris, Leuven, Belgium) mounted on a Wenzel LH87 three-dimensional, coordinate measuring machine (Wenzel Group GmbH, Wiesthal, Germany). This scanner used three laser sources, for which each laser beam reflection was captured by a separate camera. With the fixed position of the camera to the laser and the laser pattern captured by the camera, the three-dimensional coordinates were calculated with a volumetric accuracy of 15 μm . To avoid laser beam diffraction, the specimen was sprayed with a special removable coating (4 μm thickness). The actual scanning was done in several stages, which were combined to form the three-dimensional point cloud of the complete specimen. Each stage consisted of scanning a different area of the snake head surface after reorienting the scanner so that the area to be scanned was approximately perpendicular to the scanner's optical axis. Next, the large quantity of raw three-dimensional coordinates was filtered to get a workable point cloud. Three filtering techniques were used to optimize the scan: (i) outlier removal to delete points scattered by diffraction, (ii) removing superfluous points to create a uniform point cloud with a more uniform density, and (iii) a filter was applied that optimized point density in highly curved regions (high point density) versus relatively flat regions (low point density).

Since only the head was scanned, a virtual mimic of the anterior part of the body was stitched to the back of the head to avoid unrealistic flow patterns right behind the head during the flow simulations (see below). To do so, the coordinates of the points at a small slice (xy -plane) at the back of the scanned head were extracted from the raw point cloud that was aligned to the three principal axes (x = right–left; y = ventral–dorsal; z = posterior–anterior). These extracted xy -coordinates were copied and distributed randomly posterior to the head along the z -axis for 85 mm, forming a body parallel with the z -axis. Along the posteriormost 20 mm, the body was gradually narrowed and ended in a rounded tip. Since we were predominantly interested in the final stages of the strike (i.e. near the moment of prey capture) when the initially bent body has straightened (e.g. Alfaro 2003), a straight body was chosen over a bent body.

2.3. Computational domain and grid

Triangulation of the point cloud to become a watertight surface mesh was performed using VRMesh Studio v.4.1 (VirtualGrid, Seattle, WA). Since the shape of the

Figure 1. Outline of the shape of the modelled snake and spheroid prey with a midsagittal plane section through the three-dimensional unstructured tetrahedral mesh at the start of one of the CFD simulations (a). An illustration of the head surface performing jaw closing is given in (b). The latter also shows rotation centres for the lower jaw and the head, the bending zones (bordered by dotted lines) and the regions rotating as a rigid body (indicated by dashed lines and arrows). Scale bar, 10 mm.

snake's eyes could not be captured realistically by laser scanning due to eye lens transparency, this was added by uniting the mesh with two eye-sized spheres in VRMesh. The prey was modelled as a spheroid with xyz diameters of 4.45, 4.45 and 11.72 mm, respectively. During the standard simulations, this prey was initially (i.e. at simulation time = 0 ms) located with its centre of mass at approximately 40 mm in front of the eyes on the extension of the snake's midsagittal axis (figure 1a). Although considerable strike-to-strike variation occurs, this distance corresponded to the average strike distance of *N. tessellata* feeding on goldfish as observed under laboratory conditions (J. Bilcke 2003, personal communication).

The surface geometry was then imported into TGrid 5.0.6 (Ansys, Inc., Canonsburg, PA) where the boundary surface wrapper function was used to automatically remove small deficiencies (holes, intersecting triangles, etc.) in the surface mesh. Next, this software was used to construct the flow domain boundaries by creating a bounding box ($60 \times 60 \times 400 \text{ mm}^3$) around the modelled snake and prey which was sufficiently large to capture the entire flow generated by the snake (figure 1a). The volume between this bounding box and the surface of the snake and prey was then meshed with 784,042 tetrahedral cells. To optimize the accuracy of the model for a given computational time, smaller distances between the nodes (between 0.4 and 0.05 mm) were chosen for the fluid zone near the prey and the snake model than for the boundary of the domain (5 mm; figure 1a). As the boundary layer thickness was approximately 0.5 mm, the mesh generally has between two and three cells per boundary layer thickness.

2.4. Defining grid motion

Three types of grid motion were implemented during the hydrodynamic simulations of prey capture in *N. tessellata*: (i) forward translation of the snake, (ii) mouth closing, and (iii) prey motion. To evaluate the effect of forward acceleration of the snake on prey-capture hydrodynamics, two kinematic profiles of forward translation were used: a constant forward velocity of 1 m s^{-1} (the average peak velocity of *N. tessellata* during strikes at goldfish; Bilcke *et al.*

2006) or a constant forward acceleration (12.5 m s^{-2}) bringing the snake from 0 to 1 m s^{-1} in 80 ms. These values corresponded closely to head acceleration magnitudes and durations measured for relatively small snakes during forward aquatic striking (*Nerodia rhombifer*: $0\text{--}0.84 \text{ m s}^{-1}$ in 0.067 s, or an average acceleration of 12.54 m s^{-2} ; *Thamnophis couchii*: $0\text{--}0.86 \text{ m s}^{-1}$ in 0.067 s, or an average acceleration of 12.84 m s^{-2} ; Alfaro 2003).

To mimic mouth closing, a centre of rotation of the entire head with respect to the body was defined as well as a centre of rotation of the lower jaw with respect to the rest of the head (see figure 1b). To avoid strong deformations or collapsing of the mesh adjacent to the rotation centres, a zone anterior to each centre of rotation was defined where rotation of the snake surface nodes increased linearly as a function of the distance from the centre of rotation. In other words, these zones had to be subjected to bending while the rest of the head or lower jaw could be rotated as a rigid body. To simulate an approximately equal displacement of the upper and lower jaw tip (as observed during prey capture in *Natrix*; Herrel *et al.* 2008), lower jaw rotation divided by head rotation always equalled -2.1 . Mouth closing started at the simulation time of 40 ms and required about 20 ms to reach completion (unless stated otherwise). Forward translation of the snake and mouth closing were described mathematically using a user-defined function (DEFINE_GRID_MOTION UDF) in C language that can be imported into CFD solver FLUENT 6.3 (Ansys, Inc., Canonsburg, PA) after being compiled using Microsoft Visual Studio 2005.

An equation of motion was written as a DEFINE_CG_MOTION UDF for FLUENT to move the prey by the interaction with the water surrounding it. The equation of motion had three translational degrees of freedom. Pressure forces and viscous shear forces were obtained from the CFD solver's solution of the previous time step, and (taking the mass of the prey into account) used to calculate prey acceleration, velocity and displacement in the current time. The prey was assumed to have a density equal to that of the surrounding water, so that the effects of gravity and buoyancy cancel each other.

In addition to the motion of the snake and prey surface (see above), the finite-volume mesh at the

water zone needed to deform to allow this movement. FLUENT 6.3 provides two methods that can automatically update the mesh after each time step in response to motion of the boundary surfaces: (i) spring-based smoothing and (ii) remeshing. In our simulations, we combined these two methods. The first method treated the edges between the mesh nodes as a network of inter-connecting springs. This caused the cells near the frontal surface of the snake to become smaller when the simulation progressed, which theoretically improves the accuracy of the solution. To smooth the mesh, a value of 1 was used for spring constant factor and 1 for boundary node relaxation factor, while a standard value of 0.001 was used for the convergence tolerance. For the second method, cells that became critically small (<0.5 mm), too large (>1.0 mm) or too skewed (>0.9) by the movement of the model were automatically remeshed by FLUENT, which increased the number of cells to over 1 million at the end of the simulation.

2.5. Effects of gape angle, prey size, prey position and head width

The standard CFD simulation represented *N. tessellata* starting the strike with a gape angle of 75.2° , moving at a constant velocity of 1 m s^{-1} towards the spheroid prey (4.45×11.72 mm) without closing the mouth. This gape angle approximated the *in vivo* situation for *N. tessellata* (Bilcke *et al.* 2006; Herrel *et al.* 2008). Differences from this standard simulation (constant acceleration during the strike, other initial gape angle, mouth closing, different prey size) will be indicated. We defined gape angle as the angle between the upper jaw tip, the posteriormost landmark at the mouth corner and the lower jaw tip of our model (see figure 1b). Since a previous study observed wider heads in species of aquatic snakes that are not specialized in frontally striking at prey (Herrel *et al.* 2008), we re-evaluated the hydrodynamic effects of a 10 per cent increase in head width for our model compared with the less advanced model presented in the latter study (e.g. steady flow, jaws modelled as semi-elliptical plates, no body behind the jaws).

Mesheres with other initial gape angles were created by running the mouth closing user-defined function in FLUENT and saving the mesh after different simulation times. For differently sized prey, two different scenarios were evaluated: (i) the centre of mass of the prey was kept at the same position and (ii) the edge of the prey closest to the jaw was kept at the same distance from the jaws. Prey located at alternative positions always had the standard size (see above). The mesh with increased head width was created by increasing the distance between each node of the snake surface mesh and its midsagittal plane by 10 per cent.

2.6. Computational fluid dynamics

The unsteady flow simulations were performed using FLUENT 6.3. The flow was assumed to be laminar because the critical Reynolds number (Re) for transition to turbulent flow (typically 2×10^5 ; Cimbala &

Cengel 2008) is not likely to be reached for a snake striking at 1 m s^{-1} . This Re will be reached only at a characteristic length of 200 mm, which is far beyond the snake's head (<30 mm) and therefore irrelevant for the questions addressed in the present study. Properties of fresh water at 20°C were assigned to the fluid: a constant density of 998.2 kg m^{-3} and a constant dynamic viscosity of 1.003 mPa s .

The no-slip wall condition was enforced at the snake and prey surface, which is the default condition for models of viscous flow in FLUENT 6.3. The box-shaped open boundary surface of the domain (figure 1a) was modelled as a pressure outlet where a gauge pressure of zero applies (i.e. no change in pressure due to the strike of the snake is assumed at this boundary) and a backflow normal to the boundary. A steady flow situation (flow at 1 m s^{-1} over the snake) showed that this boundary condition was realistic (i.e. negligibly low pressure gradients close to the boundaries).

The pressure-based solver (chosen to obtain fast-converging solutions) was used with a node-based Green–Gauss gradient treatment. According to the FLUENT user manual, the latter treatment achieves higher accuracy in unstructured tetrahedral grids compared with the cell-based gradient treatment. The first-order, implicit unsteady formulation option was used in the simulation because moving mesh simulations (see above) currently work only with first-order time advancement. The standard pressure discretization scheme was used for the pressure calculation and a second-order upwind scheme was used for the momentum equations. The pressure–velocity coupling was solved using the SIMPLE scheme. The latter is a discretization method that uses a relationship between velocity and pressure corrections to enforce mass conservation and to obtain the pressure field. A fixed time-step size of 0.5 ms was used in the calculations. A maximum of 60 iterations per time step was sufficient to reach a converged solution under the criterion of a three orders of magnitude decrease in the scaled residuals for the continuity and momentum equations. Simulations were stopped when the prey made contact with the lower jaw of the snake during the simulation.

All values for drag force (F_{drag}) on the snake during steady forward translation were computed at the simulation time of 40 ms as the sum of pressure forces ($F_{\text{p\_cfd}}$) and viscous forces ($F_{\text{v\_cfd}}$) on the snake surface. At this instant, F_{drag} had converged to a value nearly constant in time, mouth closing had not started yet, and the interaction with the prey was still relatively weak. Therefore, the reported drag force values represented a steady-state drag force due to forward translation of the snake at constant speed, and are calculated as

$$\begin{aligned} F_{\text{drag}} &= F_{\text{p\_cfd}} + F_{\text{v\_cfd}} \\ &= 0.5 C_d \rho S v^2, \end{aligned} \quad (2.1)$$

where C_d is the shape-dependent drag coefficient, ρ the density of the water, S the frontal surface area of the snake and v the translational velocity. When the snake is accelerating, an additional resistance is felt at

Figure 2. Flow velocity in the Earth-bound frame of reference along the posterior to anterior axis for the midsagittal plane of *N. tessellata* (a), and for a series of frontal view planes (4 mm interval) at one time instant showing anterior–posterior flow velocity (b) and right–left flow velocity (c). In this CFD simulation, the snake model translated with a forward velocity of 1 m s^{-1} and started to close its mouth at time = 40 ms. The prey touched the lower jaw at time = 53 ms. The velocity scale is equal for (a) and (b).

the snake's surface, which is referred to as added mass force ($F_{\text{added\_mass}}$)

$$F_{\text{added\_mass}} = F_{\text{p\_cfd}} + F_{\text{v\_cfd}} - F_{\text{drag}} = C_a a, \quad (2.2)$$

which can be determined when velocity reaches a value for which a steady forward translation simulation has been performed and used to solve equation (2.1). The added mass force is thus proportional to the acceleration a and the shape-dependent added-mass coefficient C_a .

We evaluated the model's accuracy by comparing its results with a more detailed model (number of cells increased by 18% in the zone with the highest velocity gradient, and a time-step size reduced eight-fold), which needed a tripled computational time. This resulted in a 2.2 per cent lower pressure drag force on the snake, an 8.6 per cent higher viscous drag force and a 0.3 per cent higher total force (the sum of pressure and viscous forces). This simulation indicated that calculation of viscous shear forces is the least accurate aspect of our model. However, highly accurate viscous drag forces and high boundary layer accuracies are probably not a critical factor for the questions addressed in this study because of a relatively

small contribution of viscous force to the total drag forces during striking with an open mouth. Pressure drag forces and total drag forces seemed sufficiently accurate given the explorative and comparative focus of this study.

3. RESULTS

3.1. Flow patterns

Steady 1 m s^{-1} translation of *N. tessellata* with an open mouth caused a bow wave in front of the upper and lower jaws (figure 2a, first frame; figures 3 and 4a). The largest volume of water with relatively high forward velocity was observed near the posterior ends of the jaws, around the pharynx entrance. Flow patterns at the upper and lower jaws were similar to each other. The streamline plots for the water pushed by the jaws (figure 3) showed strong circulation from the intra-oral side of the jaws towards the outer side of the jaws. At this outer region (i.e. dorsal to the upper jaw and ventral to the lower jaw), a relatively large zone could be observed where the water moved posteriorly in the Earth-bound frame of reference (figures 2a,b and 4a). For most of the water between the jaws, and especially for the water pushed at the

Figure 3. Streamlines starting from the snake's surface, illustrating the three-dimensional flow directions (always directed towards the open ends of the lines; relative to the Earth-bound frame of reference) during a frontal strike at 1 m s^{-1} of *N. tessellata* just prior to jaw closing (simulation time = 40 ms) from a (a) lateral, (b) frontal, (c) dorsal and (d) laterofrontal view.

Figure 4. Flow patterns in the midsagittal plane ((a)(i)–(c)(i)) and a frontal plane ((a)(ii)–(c)(ii)) for (a) forward translation at 1 m s^{-1} , (b) after 10 ms of stationary jaw closing reaching an angular velocity of approximately $6000^\circ \text{ s}^{-1}$ and (c) the combination of forward translation and jaw closing. Unidirectional flow velocities are colour coded (see colour bar on the left), and streamlines projected on the view plane are shown.

Figure 5. Effects of gape angle on drag force, drag coefficient and projected surface of the snake at two velocities (1.0 and 0.5 m s^{-1}). Total force: filled circle, 1 m s^{-1} ; filled triangle, 0.5 m s^{-1} . Pressure force: grey circle, 1 m s^{-1} ; grey triangle, 0.5 m s^{-1} . Viscous force: open circle, 1 m s^{-1} ; open triangle, 0.5 m s^{-1} .

lateral sides of the intra-oral jaw surface, an important lateral flow component was observed (figure 2c). Between the tips of the upper and lower jaws, the posterior to anterior flow velocity was 0.20 m s^{-1} . At 20 per cent of the head length in front of the jaw tips along the midsagittal axis, the anterior to posterior flow velocity never exceeded 0.080 m s^{-1} .

Mouth closing squeezed the water out of the zone between the jaws (figure 4b). When combined with forward translation, this increased the flow velocities and thus the strength or size of the bow wave (figures 2 and 4c). Flow velocity between the jaw tips increased from 0.20 m s^{-1} to approximately 0.5 m s^{-1} from the beginning towards the end of jaw closing (figure 2a). Flow patterns for jaw closing without forward translation (figure 4a) showed anterior–lateral flow between the upper and lower jaws, which was also observed in the flow pattern around the head caused

Figure 6. Hydrodynamic forward pushing force exerted on the prey as a function of gape angle for an approach at a constant velocity of 1 m s^{-1} and at a constant acceleration of 12.5 m s^{-2} . Note that the gape angle *in vivo* employed by *N. tessellata* (approx. 70°) is not optimal to avoid prey pushing. Note also that the apparent hydrodynamic advantage of wide gapes shown in this graph may trade off with the duration of mouth closure. Open circle, constant acceleration reaching 1 m s^{-1} ; closed circle, constant velocity of 1 m s^{-1} .

by forward translation with the open mouth (figure 4b). However, our data indicated that the lateral flow component was more important in jaw closing than it was during forward translation, water was pushed more ventrally in the midsagittal plane region by the closing upper jaw, and the highest flow velocities were observed near the jaw tips instead of at the posterior jaw region during forward translation. In a dynamic situation where jaw closing finally added to forward translation, the general flow patterns as described above for forward translation remained, though jaw closing increased the flow velocities and slightly modified the flow directions (figure 4).

3.2. Drag force on the snake

Steady-state drag force resisting the forward strike of the snake at 1 m s^{-1} increased from 35 mN at a gape angle of 30.3° to 151 mN at 118.2° (figure 5). Viscous shear force was responsible for about 20 mN of this drag force on the head and body of the snake and was approximately independent of the gape angle. Consequently, the strong increase in drag force with increasing gape angle was the result of an increase in pressure drag (from 15 to 136 mN). The effect of gape angle on the pressure drag force was due to an approximately linear increase in the projected surface area of the head with the increasing gape angle and also to an increase in the head-shape-dependent pressure drag coefficient (0.086 at 30.3° and 0.33 at 118.2°). Our CFD simulations at a lower strike velocity of 0.5 m s^{-1} calculated equal pressure drag coefficients compared with the 1 m s^{-1} simulations, but slightly higher viscous shear force coefficients (figure 5).

3.3. Forward pushing of the prey

The force on the prey in the direction of the strike of the snake varied as a function of the gape angle (figure 6).

Figure 7. Static pressure field in front of the snake's jaws for steady forward translation at 1 m s^{-1} (a) and for a constant acceleration of 12.5 m s^{-2} at the moment of reaching 1 m s^{-1} (b). Note the increased positive pressure bow wave resulting from forward acceleration.

The lowest pushing forces at a given time during the simulation (time = 40 ms, first frame in figure 2) were observed for the simulation with the smallest gape (0.84 mN at 30.3° gape). The force on the prey increased steeply when the gape angle was increased to 48.5° (1.18 mN), remained constant to a gape angle of 66° and then started to decrease approximately linearly when the gape angle was increased further to 118.2° (0.84 mN , figure 6). Note, however, that the decrease in pushing force at large gape angles was due to the increased distance between the snake's jaw surface and the prey at the given instant during the simulation.

The force on the prey also depended on the snake's acceleration (figure 6). While the previously mentioned forces on the prey applied to strikes at a constant velocity (1 m s^{-1}), pushing force on the prey was 11 per cent higher for a realistic gape angle of 75.2° under a constant acceleration of 12.5 m s^{-2} at the instant of reaching 1 m s^{-1} for a stationary prey at the same distance from the snake. Compared with steady forward translation, the constant acceleration resulted in an augmented super-ambient pressure wave in front of the jaws (figure 7), which explains this additional pushing force on the prey.

The amount of hydrodynamic forward displacement of the 11.72 mm long and 4.45 mm wide prey before impacting the jaw surface was maximally 3.7 mm (figure 8). The displacement kinematics of this prey was relatively similar for the small and large gape angles. However, jaw closing increased the pushing effect significantly: at the instant when the closing

Figure 8. Forward prey displacement kinematics for a steady 1 m s^{-1} strike at three different constant gape angles (green, blue and black), two simulations including jaw closing (yellow and red) and one simulation with jaw opening (pink). Note that jaw closing resulted in significantly augmented pushing of the prey, whereas jaw opening had the opposite effect.

mouth touched the prey (simulation time = 45.5 ms), the forward velocity of the prey was 0.39 m s^{-1} (compared with 0.193 m s^{-1} without jaw closing) and it was pushed 2.9 mm away from its starting position (compared with 1.7 mm without jaw closing; figure 8).

3.4. Lateral pushing of the prey

Since figure 2c indicated an important laterally directed flow from between the jaws, the prey might experience lateral pushing by the strike of *N. tessellata* if not perfectly centred in the midsagittal plane. Our CFD simulations showed that modelled prey were indeed pushed away from the midsagittal plane, unless their centre of mass was initially located very close to this plane (figure 9). Ultimately, when the prey's centre of mass started approximately in line with the forward projection of the mouth corner, the approach and jaw closing caused the prey to be laterally pushed away from the side of the jaws and could not be caught between the jaws.

3.5. Effects of prey size

If the centre of mass of the differently sized prey was kept at the same initial position, the size of the prey had no effect on hydrodynamic pushing by the striking snake (i.e. identical prey pushing kinematics). A logical consequence was an earlier contact with the snake's jaws for larger prey.

If the shortest distance between the prey's surface and the jaws was kept identical when increasing prey size in our simulations, considerably reduced pushing is observed (figure 10). For prey with $2\times$, $4\times$, $8\times$ and $16\times$ the mass of a standard prey, forward pushing reduced by 12, 25, 39 and 51 per cent, respectively. As a consequence, larger prey made earlier contact with the jaws (1.0 , 2.5 , 3.5 and 5.5 ms , respectively), with an increased velocity difference between jaws and prey (0.01 , 0.06 , 0.13 , and 0.25 m s^{-1} , respectively).

Figure 9. Consecutive positions of the centre of mass of the prey relative to the snake during five CFD simulations where the prey started at, from right to left, 0, 1, 2, 3 and 4 mm from the midsagittal plane of the snake. Note that the two prey that are located most distantly away from the midsagittal axis of the snake were unlikely to be caught due to sideways pushing effects of the bow wave. Scale bar, 5 mm.

Figure 10. Kinematics of hydrodynamic pushing of differently sized prey, initially at the same distance from the jaws (upper graph to lower graph, respectively, 1 $\times$, 2 $\times$, 4 $\times$, 8 $\times$ and 16 $\times$ the mass of the standard prey). The times when the prey touched the snake's jaw during the CFD simulations are indicated by filled circles.

3.6. Effects of head width

A 10 per cent increase in the width of the head increased the drag force on the snake on average by 12.7 per cent (between 10.9 and 15.9% depending on

the instant during the simulations). This means that an approximate 3 per cent increase in drag coefficient adds to the 10 per cent increase in projected surface area in resisting strike speed of the snake. The bow wave size (figure 11) and the distance the prey was pushed before touching the jaw (10.8% further) were approximately directly proportional to the increase in width of the head.

4. DISCUSSION

The prey-capture strategy of aquatic snakes is considered suboptimal compared with the prey-capture methods of most other aquatic vertebrate predators (Hibbitts & Fitzgerald 2005; Vincent *et al.* 2007; Herrel *et al.* 2008), which combine prey approach with the generation of suction (e.g. van Leeuwen & Muller 1984; Lowry & Motta 2007; Holzman *et al.* 2008). Suction feeders manage to reverse the flow in front of their jaws, thereby eliminating a snake-like bow wave (e.g. figure 2*a*) and its potential negative effects on prey-capture performance. In contrast to the observed flow pattern around a forward-striking snake (figures 2–4), a suction-induced flow of fish typically results in anterior-to-posterior flow (in the Earth-bound frame of reference) curling into the mouth and further towards a stagnation point deep inside the buccal cavity (Muller *et al.* 1982; Day *et al.* 2005; Van Wassenbergh & Aerts 2009).

In laboratory studies, natricine species typically require five or six trials for a successful capture of a fish (Bilcke *et al.* 2007), which seems to confirm the inferior efficiency of this feeding mode compared with ram-suction feeders (e.g. Scharf *et al.* 2003). However, since the present study is the first to explore the hydrodynamics involved in this process, the hydrodynamic constraints involved in this feeding behaviour have remained speculative. As aquatic prey capture has evolved independently in several groups of snakes (Alfaro 2002; Hibbitts & Fitzgerald 2005; Bilcke *et al.* 2006; Herrel *et al.* 2008), and could therefore be one of the most striking examples of convergent evolution (Herrel *et al.* 2008), knowledge of the hydrodynamics involved in this feeding mode is also an essential first step in our understanding of the evolution of this group of animals.

4.1. Drag forces constraining strike speed

A first potential hydrodynamic constraint is the relatively widely opened mouth that some aquatic snakes such as *N. tessellata* show when accelerating frontally towards prey. This behaviour is thought to reduce the speed of the strike at the prey because of increased drag forces caused by the open mouth (Young 1991; Vincent *et al.* 2007). Our study showed for *N. tessellata* that steady-state drag force indeed increased drastically with increasing gape: increasing the gape from 30.3° to a gape angle typically observed *in vivo* during prey capture (75.2°; Herrel *et al.* 2008) causes drag force to more than double (35–80 mN; figure 5).

However, this does not mean that the increased drag force actually reduces the strike speed. If drag forces are

Figure 11. The effect of a 10% increase in head width on the bow wave, as shown by forward directed flow velocities along the midsagittal plane in the original simulation (dashed lines) and increased head width simulation (continuous lines). Note that the increase in head width resulted in a bow wave extending approximately 10% further in front of the jaws. Scale bar, 10 mm.

relatively low compared with the inertia of the part of the snake that is accelerated towards the prey, the calculated variation in drag force may not be biologically relevant. Consequently, the entire balance of forces acting on the snake during acceleration (of which drag forces are only one component; Vogel 2005) must be considered. This force balance consists of (i) the snake's propulsive force F_{prop} , (ii) the force required for the acceleration (a) of the snake's mass (M), (iii) the steady-state drag force that is proportional to the square of the snake's instantaneous velocity (v) the snake's frontal surface area (S) a shape-dependent drag coefficient (C_d) and the density of the water ($\rho = 1000 \text{ kg m}^{-3}$), and (iv) the shape-dependent (coefficient C_a) and acceleration-dependent added-mass force due to acceleration of the water surrounding the snake

$$F_{\text{prop}} - Ma - 0.5C_d\rho Sv^2 - C_a a = 0. \quad (4.1)$$

Solving this differential equation numerically, we can simulate the kinematics of the forward strike for a given amount of F_{prop} and evaluate the effects of the three gape-dependent factors S , C_d and C_a . Drag coefficients and frontal surface area can be retrieved from figure 4, while C_a can be determined from the difference in force on the snake in the CFD simulations with constant velocity of 1 m s^{-1} , and the simulations with constant acceleration at the instant of reaching 1 m s^{-1} (equation (2.2)). As only the anterior 20 per cent of the trunk is accelerated during frontal striking (Alfaro 2003), the entire CFD model of the head and anterior part of the body (as shown in figure 1*a*; $M = 4.26 \text{ g}$) was assumed to accelerate uniformly.

Solving the forward dynamic simulation described above for the natural gape angle of 75.5° ($F_{\text{prop}} = 70.2 \text{ mN}$, $C_d = 0.261$, $S = 2.04 \times 10^{-4}$, $C_a = 7.02 \times 10^{-4}$), the snake reaches a velocity of 1.0 m s^{-1} after 80 ms and travels a total distance of 37 mm. The relative magnitude of the drag force plus added mass force with respect to the total propulsive force varies

from 14.1 per cent (at time 0) to 41 per cent (at time 80 ms). Performing a similar simulation for a small gape of 30.3° with the same propulsive force ($F_{\text{prop}} = 70.2 \text{ mN}$, $C_d = 0.200$, $S = 1.17 \times 10^{-4}$, $C_a = 3.64 \times 10^{-4}$) shows that the snake reaches a velocity of 1.12 m s^{-1} (12.4% increase) and travels 47 mm (25% further). The relative magnitude of the drag force plus added mass force with respect to the total propulsive force varies from 7.9 per cent (at time 0) to 27 per cent (at time 80 ms).

It should be noted that the results of this simulation do depend on the amount of the trunk that is recruited in the strike, which is observed to be highly variable under laboratory conditions (Alfaro 2003). The higher the proportion of the body that is accelerated along with the head (e.g. during far-reaching strikes), the less important the shape of the jaws becomes in limiting strike speed. If only the head and a small part of the trunk is accelerated towards the prey (e.g. a strike from a short distance), the drag tax (*sensu* Vogel 2005) becomes higher.

In summary, our results showed a drastic increase in drag force for a snake moving through the water at high velocity with open mouth (figure 5), but the effect of a small versus wide gape on the strike speed that can be reached with a given amount of propulsive force is probably less pronounced (though likely not entirely biologically negligible). Consequently, it appears that aquatic snakes have traded a relatively small increase in strike speed and a few millimetres less forward pushing of the prey (when opening the mouth in close proximity to the prey; figure 7) due to the early, wide opening of the jaws for a simplified motor control (not having to open the mouth just before reaching the prey), and/or an increased chance of impacting the prey with a widely opened mouth (increasing the frontal area of the jaws).

Following this, we could expect that the 10 per cent wider heads of aquatically foraging snake species that use side sweeping of the head to capture prey (Herrel

et al. 2008) would result in only a minimal decrease in strike speed for a given propulsive force, since the increase in drag force (+13%) is much less than the narrow and wide gape situation discussed above (drag force +100%). Assuming that the 10 per cent increase in head width results in a 10 per cent increase in added mass coefficient (estimated from figure 10), the forward dynamic simulation shows that strike speed reduces by only 2.3 per cent. If we add the effect of the increase in head mass due to the widening of the head, a decrease of 4.3 per cent in the forward launching speed can be predicted. Therefore, on the one hand, the presented model confirms the results from Herrel *et al.* (2008), who estimated an increase in drag force of 12 per cent. On the other hand, it shows that the effects of this increase in drag on constraining acceleration towards a prey are less pronounced.

4.2. Prey pushing by the bow wave

A second potential hydrodynamic constraint of aquatic prey capture without using suction is pushing the prey away from the mouth due to the bow wave at the anterior surface of the snake's head. Our CFD simulations do indeed show that a bow wave forms around the jaws of *N. tessellata* (figure 2). However, the forward velocity magnitude of the flow for most of the zone in between the jaws is relatively limited: only close to the jaws, the forward flow velocity was higher than half the velocity of the snake (figure 2*b*). Consequently, forward prey pushing is limited: passive, freely floating prey of the same density as water were pushed by only about 12 per cent of the snake's head length. The collisions between prey and jaw surface were always relatively violent: the velocity difference between prey and jaws at the moment of impact was higher than 0.5 m s^{-1} for most simulations, including the one with simulated jaw closing.

Probably a more important constraint induced by the bow wave is lateral pushing of prey that are not approached perfectly in line with the midsagittal plane of the striking snake. In that case, the prey encounters the flow curling from the intra-oral side to the external side of the jaws (figures 2*c* and 3). These flow patterns deviate the prey in the direction of the side of the jaws. Depending on the position of the prey relative to the approaching snake, this deviation may cause the prey to pass the lateral border of the mouth and thus passively escape the snake's attack (figure 9). Mouth closing increased this effect, as more water is pushed from between the jaws (figure 4).

From a hydrodynamic perspective, larger prey seem more vulnerable to be caught by aquatic snakes. Displacement by the bow wave is reduced compared with smaller prey (figure 10), and earlier contact with the jaws results in a more violent impact with the teeth (higher velocity differences between the jaws in our CFD simulations). Since large prey can more easily be struck in such a way that the surface of the prey overlaps the projection of the left and right side of the jaws, the effect of

lateral pushing is reduced. This seems to be reflected in a preference for larger prey in the diet of aquatic snakes (Arnold 1993). Although some experimental evidence seems to confirm the theoretically increased capture success while striking on larger prey (Hailey & Davies 1986; *Natrix maura*), results remain equivocal (Bilcke *et al.* 2007; *N. tessellata*). Clearly, behavioural adjustments on the part of the snake may interact with the hydrodynamics of striking and alter the ultimate outcome of a predator–prey interaction.

Finally, it should be noted that we did not explore the effect of striking on the potential for the prey being 'hydrodynamically warned' of the approaching snake by the bow wave. All fish possess a mechanosensory lateral line system, which responds to the surrounding water motion relative to the fish's skin. Depending on the sensitivity of its mechanosensory organs, the prey fish may be capable of evading the strike of the snake by performing an escape response (McHenry *et al.* 2009). Lateral line organ pressure difference detection thresholds have been estimated for the ruffe (*Gymnocephalus cernuus*) to be between 0.1 and 1 mPa over a distance of 1 mm between the supra-orbital canal neuromasts (van Netten 2006). In our simulations, where the prey centre was 40 mm away from the snake's eyes, these detection thresholds were crossed immediately after the first time step (approx. 18 mPa for snake accelerating at 12.5 m s^{-2}). Even for orientations of the lateral line approaching a perpendicular position relative to the motion of the snake, prey fish can probably detect a snake starting a strike from this distance immediately: we calculated an average pressure difference of 5.7 mPa after the first time step if the prey's long axis was perpendicular to the snake's path. Together with the potential hydrodynamic pushing of prey due to the bow wave, this early hydrodynamic warning probably explains the relatively low prey-capture success of aquatic snakes (Bilcke *et al.* 2007). Since recent studies have managed to use three-dimensional CFD to study the stimulus of the lateral line of a fish under an artificial stimulus (dipole perturbation; Rapo *et al.* 2009), future CFD studies may be able to combine realistic simulations of specific predator and prey movements when studying mechanosensory activity.

5. CONCLUSION

Snakes are a model system for studying the constraints associated with capturing prey under water as they have invaded the aquatic niche numerous times independently despite their inability to generate suction. The hydrodynamic patterns described in the present study revealed several new insights into the biomechanics of forward striking in aquatic snakes. Firstly, pressure drag force on the snake head increased considerably with increasing gape angle, but, due to the high inertial cost of accelerating the head and anterior part of the body from rest, the speed-reducing effect of increased drag by striking with a widely opened mouth was much less pronounced than the reported increase in

drag force (estimated 12% decrease in strike speed and 25% decrease in strike distance compared with a narrow gape). Secondly, jaw closing increased forward pushing of the prey, as well as the magnitude of laterally directed flow velocity between the jaws. Thirdly, widening the head causes the bow wave to extend further in front of the jaws (approx. equal to the percentage of head widening), but the strike-speed-reducing effects of this morphological change are probably minimal. Fourthly, precise aiming will reduce the chance of deviating the prey to a path that passes the mouth corners. Fifthly, several hydrodynamic advantages were identified for an aquatic snake to strike at relatively large prey: pushing decreases with increasing prey size, large prey are likely to impact the jaws more heavily and the larger volume of such prey will make it easier for the snake to strike with its mediosagittal plane intersecting the prey, which additionally reduces the lateral pushing effect on the prey. Since our models show that, especially large prey can be captured without suction, the general preference of (terrestrial) snakes to consume large prey items may have facilitated the evolution of underwater feeding. Still, our study showed that the bow wave of frontally striking snakes can deviate even relatively large prey away from the jaws, or may trigger the prey's mechanosensory system, which may explain their observed relatively low prey-capture success in contrast to suction feeding aquatic vertebrates.

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