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REVIEW

Aquatic suction feeding dynamics: insights from computational modelling

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Aquatic suction feeding in vertebrates involves extremely unsteady flow, externally as well as internally of the expanding mouth cavity. Consequently, studying the hydrodynamics involved in this process is a challenging research area, where experimental studies and mathematical models gradually aid our understanding of how suction feeding works mechanically. Especially for flow patterns inside the mouth cavity, our current knowledge is almost entirely based on modelling studies. In the present paper, we critically discuss some of the assumptions and limitations of previous analytical models of suction feeding using computational fluid dynamics.

Keywords: feeding; prey capture; computational fluid dynamics; hydrodynamics; modelling; viscosity

1. SUCTION FEEDING AND MODELLING

Suction feeding is the most widespread prey capture mechanism in aquatic vertebrates (Lauder 1985). By performing a sudden expansion of the mouth cavity while approaching a prey, suction feeders generate a flow of water that draws the prey into the mouth. Suction is used to capture prey by several species of sharks (e.g. Wilga *et al.* 2007), primitive bony fishes (e.g. Lauder 1980a; Markey *et al.* 2006), teleost fishes (e.g. Alexander 1969; Liem 1980; Wainwright *et al.* 2001; Gibb & Ferry-Graham 2005), frogs (e.g. Deban & Olson 2002; Dean 2003), salamanders (e.g. Deban & O'Reilly 2005) and mammals (e.g. Marshall *et al.* 2008). Especially, teleost suction feeders display a large diversity in cranial morphology, and are therefore an excellent group to study the evolution of aquatic feeding systems (e.g. Albertson *et al.* 2005; Wainwright *et al.* 2007).

Understanding the function of the numerous, complexly interconnected mechanical units of the suction feeding system of teleost fishes starts with understanding the biomechanical principles that link head expansion to prey transport. This is a complicated issue, since suction feeding involves extremely unsteady flow, externally as well as internally of the mouth cavity. Although the flow field in front of the mouth of a few suction feeding species has been quantified

experimentally by using three-dimensional particle tracking (van Leeuwen 1984) particle image velocimetry (PIV; Ferry-Graham *et al.* 2003; Day *et al.* 2005; Higham *et al.* 2005, 2006a; Nauwelaerts *et al.* 2007; Lowry & Motta 2008), experimental data on the hydrodynamic process that carries the prey through the mouth cavity are limited to pressure measurements (e.g. van Leeuwen & Muller 1983; Lauder *et al.* 1986; Sanford & Wainwright 2002), a few water velocity measurements using hot-film anemometry (Muller & Osse 1984) and prey paths quantified from X-ray videos (Aerts *et al.* 1986; Van Wassenbergh *et al.* 2007). Owing to this incomplete view on the hydrodynamics of suction feeding from experimental analyses, modelling studies linking internal and external hydrodynamics are an essential addition in our understanding of suction feeding mechanics.

In their classical paper on the hydrodynamics of suction feeding in fishes, Muller *et al.* (1982) mathematically modelled the suction feeding fish as a forward translating, expanding, hollow, truncated cone. They managed to deduce a time-dependent analytical solution for flow velocity and pressure along the expanding cone's symmetry axis. As shown by the numerous, also recent applications (van Leeuwen & Muller 1984; Aerts *et al.* 1987; Higham *et al.* 2006b; Van Wassenbergh *et al.* 2006a,b; Bishop *et al.* 2008), this model is still greatly influential.

However, several assumptions of Muller's model have not been verified (see also Muller & van Leeuwen 1985). In the present paper, we discuss some of these

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assumptions with the help of a computational fluid dynamics (CFD) version of Muller's model. This CFD model mimics suction feeding in an adult fish (*Lepomis gibbosus*). Apart from being a good representative of a generalized suction feeding teleost (percomorph), *Lepomis* was used for much of the experimental research carried out in the 1980s by Lauder and co-workers (Lauder 1980b, 1983; Lauder & Lanyon 1980; Lauder *et al.* 1986) and was the source of the debate between the modelling and experimental approach (Muller *et al.* 1985; Lauder 1986). The methods used during our modelling are dealt with in the electronic supplementary material. Apart from re-evaluating Muller's model, the CFD model will also be used to assess some interesting results from more recent studies on the hydrodynamics of suction feeding in fish (Nauwelaerts *et al.* 2007; Wainwright & Day 2007).

2. INVISCID VERSUS VISCOUS FLOW

One of the simplifying approximations necessary for Muller *et al.* (1982) to formulate their model was neglecting friction. It is well known that for regions of the flow with negligible net viscous forces, the Navier–Stokes equations (the most general description of the relationship between force and flow in a fluid) can be simplified by removing the viscous term from these equations (Cimbala & Cengel 2008). The loss of this term strongly reduces the mathematical complexity of the model, but inevitably results in fluid flows that are not physically meaningful near solid walls, since flow is allowed to slip there.

Muller justified this approximation by including estimates of the thickness of the boundary layer at the internal side of the mouth cavity for a number of suction feeding fish, which differed in head size and the duration needed to expand their mouth cavities during feeding (Muller & Osse 1984). This estimation was based on a dimensional analysis of the Navier–Stokes equation, which resulted in the following formula (Muller *et al.* 1982):

$$\delta = \sqrt{\frac{2\nu t L^2}{L^2 - \nu t}},$$

where δ is the thickness of the boundary layer; ν is the kinematic viscosity of the fluid; L is the length of the mouth cavity; and t is the duration of mouth cavity expansion. This theoretical analysis showed that, even for large fish heads (e.g. 0.1 m) expanding relatively slowly during feeding (e.g. 95 ms), the thickness of the boundary layer is probably less than 1 mm (Muller & Osse 1984). For our study animal *L. gibbosus*, which expands its head within approximately 50 ms, this model predicts a boundary layer of 0.32 mm.

CFD is a mathematical modelling technique that allows a numerical solution of the Navier–Stokes equations, even for complex unsteady flows. The water surrounding our *L. gibbosus* model was split into a large number of small cells (finite volumes) for which the flow equations are solved in an iterative process by algorithms embedded in FLUENT software (Ansys, Lebanon, NH, USA). Recent versions of this software allow simulating flow caused by deforming

solid bodies. The details of our approach in using this software in modelling the radially expanding and forward translating fish can be found in the electronic supplementary material.

We tested the difference between an expanding cone model with and without viscous forces included (figure 1). To do so, we compared the output of two CFD models: the first model solving the inviscid approximation of the Navier–Stokes equations (i.e. the Euler equations; figure 1b) and the second model solving the full Navier–Stokes equations (figure 1c). The inviscid CFD model can be regarded as an improved version of Muller's analytical model, since it does not neglect the radial acceleration of the flow inside the expanding hollow cone, and the velocity profile in the plane of the circular mouth is not precisely identical to the (quasi-steady) vortex flow model.

Our results showed considerable differences between both models in the intra-oral flow velocities (figures 2 and 3). To quantify this in more detail, we conservatively define the boundary layer as the zone where, for a given cross section, less than 90 per cent of the peak axial flow velocities occur. At 5 mm posterior of the mouth opening, the boundary layer grows rapidly from 0.27 mm after 10 ms to 0.95 mm after 20 ms. Afterwards, the boundary layer remains approximately constant around 1 mm (1.05 mm after 30 ms and 0.98 mm after 40 ms; figure 2). Given that the radius of the mouth cavity at this cross section increases from 1.98 to 3.68 mm, apart from the first 10 ms of suction, the boundary layer size exceeds 30 per cent of the radius. We conclude from this that, not only for larval fish (Drost *et al.* 1988; Osse & Drost 1989), frictional forces play an important role during suction feeding.

Muller & Osse (1984) argued that negligibly small boundary layers, and thus negligibly low friction, imply a hydrodynamic advantage for the predator because the occurrence of friction drag is avoided. On the one hand, it is probably true that friction drag hinders mouth cavity expansion. The area-weighted mean pressure on the internal surface of the mouth cavity near the moment of maximal expansion velocity (time = 40 ms) was -434 Pa in our CFD model, compared with -213 Pa for the model that neglects friction at boundaries. Since pressure forces clearly dominate shear forces in the (radial) direction of expansion (radial pressure forces were approximately three orders of magnitude higher than the calculated radial shear forces), and expansion velocities are equal in both models, we estimate from the previous that more than twice the power input (power = force \times velocity) was needed from the fish to expand the mouth cavity in the viscous compared with the inviscid flow conditions.

On the other hand, friction at the boundaries of the mouth cavity might as well be regarded as a factor that increases suction performance (yet at the expense of metabolic power, cf. above) because higher flow velocities will be reached at the centre for the same volume increase per unit of time (figure 1c versus b and figure 3a). Indeed, it appears from our full CFD simulations that the boundary layer causes the unrestricted inflow of water into the mouth cavity to be constrained to a narrower region at the centre of the

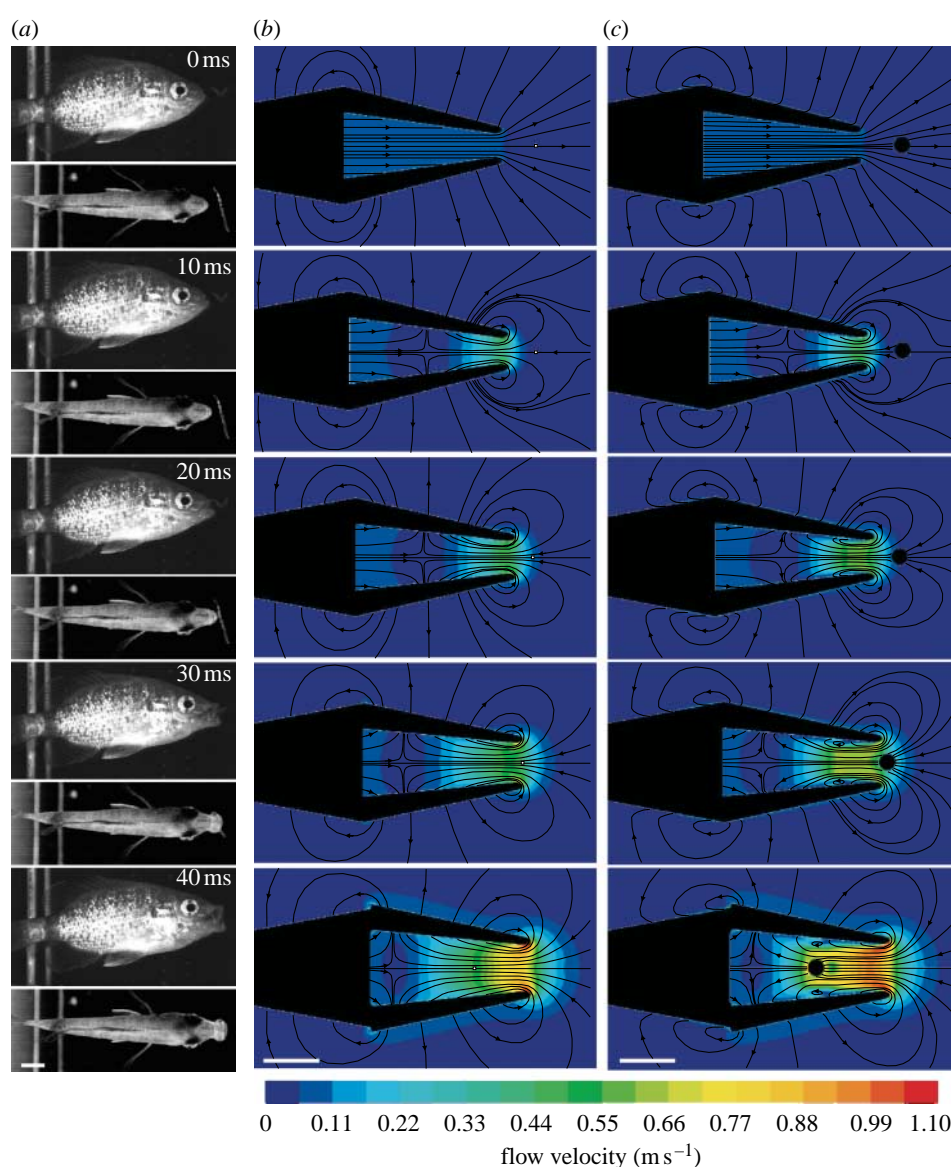


Figure 1. (a) *Lepomis gibbosus* feeding on a bloodworm, and flow velocities (see colour code below) and streamlines from the corresponding (b) inviscid and (c) viscous axisymmetric CFD models. (c) Note that, in the CFD model solving the full Navier–Stokes equations, an intra-oral vortex is formed approximately 30 ms after the start of mouth opening. Note also that the simulated prey transport corresponded well with the observed motion of the prey. The position of a tracked water particle is indicated by white squares in (b) the inviscid model. Since the opercular valves open at time = 42 ms, the presented models, which do not include a posterior outflow of water, are only valid before this instant. Scale bars, 10 mm.

expanding mouth cavity, which explains the higher velocities at the centre (figures 2 and 3a) due to the law of continuity. Consequently, any prey entering close to the centre of the mouth aperture will be transported faster to the back of the mouth cavity in the more accurate CFD simulation (figure 1c) compared with the inviscid models (Muller’s model or figure 1b).

The flow in front of the mouth is nearly identical for the inviscid and viscous CFD models (figure 1). The decrease in flow velocity away from the mouth along the model’s rotational symmetry axis corresponds quite nicely to the relationship inferred from the ‘circular vortex filament’ model described by Muller *et al.* (1982) (figure 3b). This is in accordance with the results from recent *in vivo* flow visualization analyses (Day *et al.* 2005), where a highly accurate fit between the measured drop in flow velocity away from the

aperture and Muller’s circular vortex filament model was observed along the centreline.

The study by Muller & van Leeuwen (1985) showed that Muller’s vortex flow model overestimates the flow velocity near the edges of the mouth opening compared with experimental data obtained from flow visualization of feeding trout (*Salmo gairdneri*). Since in the plane of the circular mouth opening, the vortex model predicted the highest flow velocities to be located near the centre of the vortex ring (i.e. near the edges of the mouth aperture) while the highest flow velocities were observed near the centre of the mouth, they argued that the vortex approximation does not fully capture the hydrodynamic details at the mouth region (Muller & van Leeuwen 1985). Our CFD results also showed the highest flow velocities near the centre of the mouth during most of the time (figure 1c), which is in line with

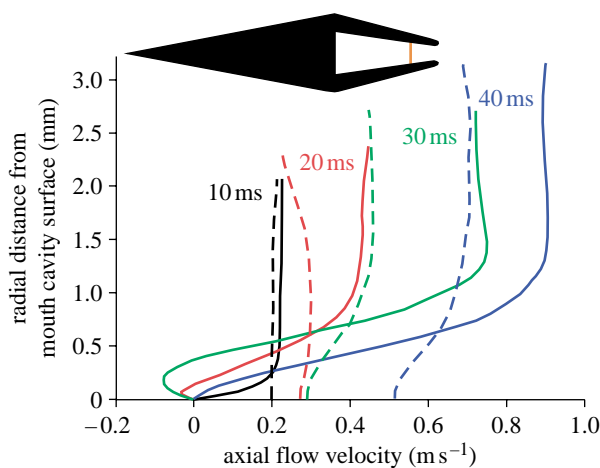


Figure 2. Axially directed flow velocities with respect to the buccal surface at 5 mm posterior of the jaw tips. Data from different times within the feeding sequence (see also figure 1) are given, as well as a comparison between the results from the viscous, no-slip at boundaries, model (solid lines) and the inviscid model (dashed lines).

the observations of Muller & van Leeuwen (1985) and more recent PIV studies (Day *et al.* 2005; Nauwelaerts *et al.* 2007). Additionally, these results may imply that suction feeders can improve suction performance by positioning the prey item so that it will travel along a path through the centre of the mouth during suction.

3. FLOW INFLUENCED BY THE PREY AND VICE VERSA

When a neutrally buoyant prey with a non-negligible volume is surrounded by a highly unsteady flow field induced by a fish that starts sucking (i.e. a steep *spatial* gradient of fluid pressure and velocity in front of the mouth; figure 1), different forces will be exerted at different locations on the prey. If the prey behaves as a rigid object, this may result in velocity differences between the prey and the surrounding water. In turn, these velocity differences may result in flow patterns that are altered in the prey's surroundings compared with flow without a prey. Theoretically, under unsteady flow conditions, rigid, neutrally buoyant prey will behave exactly as a fluid element only if they are infinitesimally small.

This theoretical consideration could be important, since a second assumption of the model of Muller *et al.* (1982) is that the prey behaves as an element of the water being sucked into the mouth. If the presence of the prey would cause a disturbance of the flow compared to a situation where suction is generated without a prey, simple models mimicking the situation without a prey would not be ideal for studying the hydrodynamics of suction feeding. A similar problem is encountered during the interpretation of PIV data of suction feeding (Ferry-Graham *et al.* 2003; Day *et al.* 2005; Higham *et al.* 2005, 2006a; Nauwelaerts *et al.* 2007; Lowry & Motta 2008): does the spatio-temporal flow pattern quantified for a specific prey also apply to prey with other dimensions or shapes?

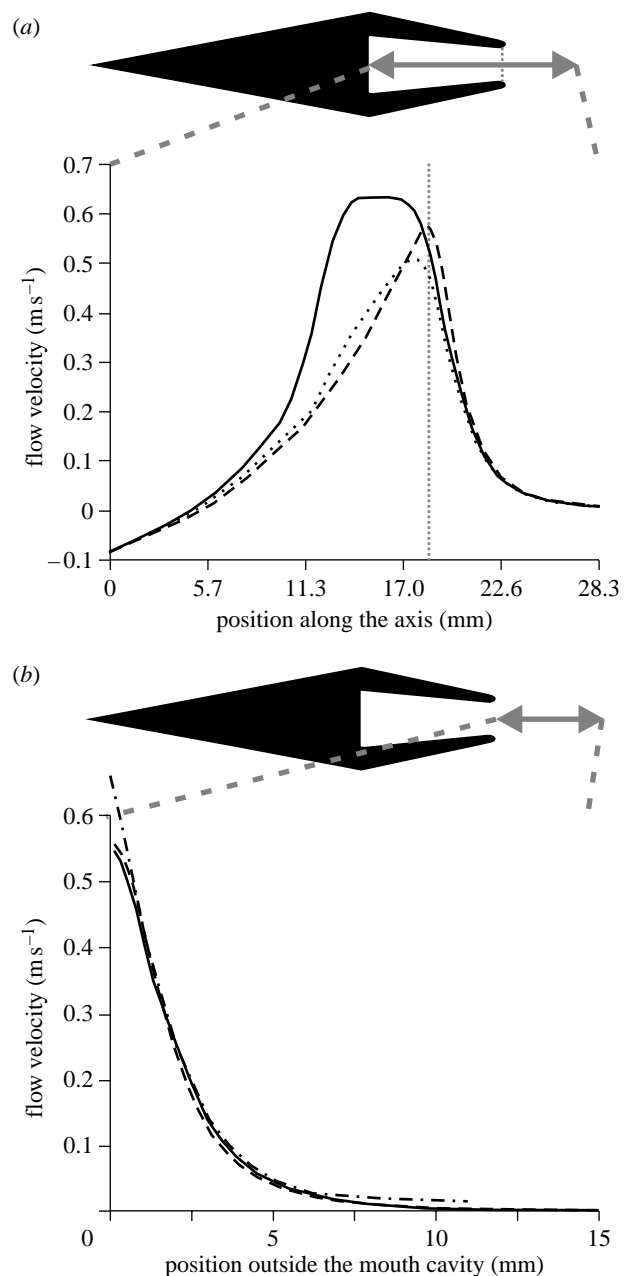


Figure 3. Axial flow velocities at time = 30 ms as a function of position (a) inside and in front of the mouth cavity and (b) outside the mouth cavity are compared between the CFD model solving the full Navier–Stokes equations (solid line), the inviscid CFD model (dotted line, only in (a)), Muller's analytical model (dashed line; Muller *et al.* 1982) and the fourth-order polynomial equation that was fitted to the experimental data from PIV recordings of feeding *Lepomis macrochirus* (dot-dashed line, only in (b); Day *et al.* 2005). To enable the comparison for flow velocities in front of the mouth according to Muller *et al.* (1982) and Day *et al.* (2005), the input values of, respectively, flow velocity inside the mouth and one gape radius in front of the mouth from the full CFD model were used. Note that internal flow velocities along the longitudinal axis are generally underestimated by the inviscid models (including Muller's model), while the external flow velocities are almost perfectly predicted by the 'circular vortex filament' model (Muller *et al.* 1982).

Obviously, a prey initiating an escape response while being sucked by a predator will cause a certain disturbance of the flow. The same is probably true for

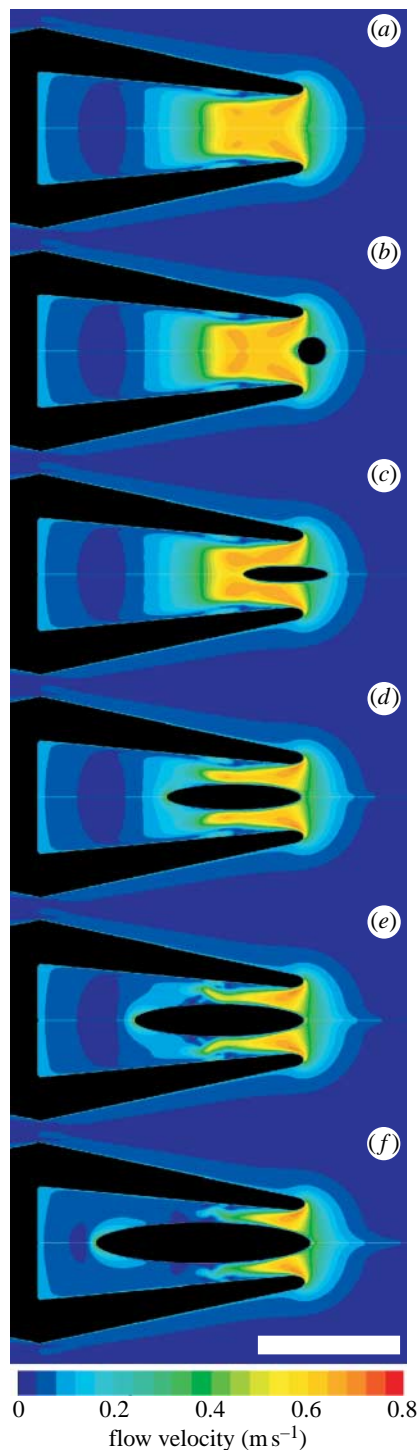


Figure 4. Flow velocity contour plot at time = 35 ms for CFD simulations (a) without a prey, (b) with a sphere and (c) a prolate spheroid of equal mass (4.2 mg), as well as a series of increasing sizes of the prolate spheroid: (d) 4, (e) 8 and (f) 16 times the volume of the prey shown in (c). Scale bar, 10 mm.

a prey attached to the substrate suddenly becoming detached by suction. However, Muller's assumption that relatively small, neutrally buoyant prey that do not move actively have a negligible influence on the flow generated by suction (Muller & Osse 1984) has not been evaluated. Yet, it is important to do so, since this type of prey is generally used in PIV studies.

The advantage of computational modelling is that prey with different shapes, sizes and starting positions

can be included in the domain for a given suction act. Here, we performed simulations with a sphere (diameter = 2 mm) and two prolate spheroids (degree of prolateness = 2.82 and 5.20). All prey are neutrally buoyant, have the same mass (4.2 mg), their centres of mass are initially located at the same position in the flow domain and are moved by the interaction with the water surrounding the prey (see also the electronic supplementary material).

We first tested whether the presence and the shape of this type of relatively small prey has an influence on the flow field generated by suction. Except very close around the prey, the calculated flow velocity field was approximately identical for the simulations with these prey (figure 4a–c). This indicates that, as assumed by Muller & Osse (1984) and the suction feeding PIV studies, neutrally buoyant, relatively small, inactive prey have little or no influence on the water flow during suction.

In addition, simulations were performed in which the volume of the most prolate spheroid was increased by 4, 8 and 16 times to study the effects of prey size on the suction flow (figure 4d–f). Especially during the simulations with the two larger prey (figure 4e, f), the effects of pushing of water at the leading edge of the prey as well as wake flow at the prey's trailing edge became apparent. These prey had cross-sectional diameters of, respectively, 0.48 per cent (figure 4e) and 0.62 per cent (figure 4f) of the gape diameter. Consequently, as a guideline for PIV studies aiming at visualizing prey-independent flow patterns generated by suction, we advise using experimental prey with a cross-sectional diameter of less than 40 per cent of the gape diameter.

Recently, a theoretical analysis by Wainwright & Day (2007) suggested that neutrally buoyant, freely suspended prey in the water column are moved exclusively by forces resulting from the pressure gradient induced by the suction feeder. Since this situation implies that the prey and the water at the prey's surface are moved at the same velocity, slip drag forces do not exist (Wainwright & Day 2007). Although as mentioned earlier, this situation is obvious for an infinitesimally small prey particle that behaves as if it were a water particle, it is important to know whether this also applies to prey with a non-negligible volume.

One of the predictions of the model by Wainwright & Day (2007) is that the shape of this type of freely floating prey is unimportant: the prey will experience the same amount of force due to the local pressure gradient whether it is well streamlined with respect to the suction flow or not. By using CFD, we were able to evaluate whether, as predicted by Wainwright & Day (2007), suction performance is equal for prey of different shapes, and prey velocities are equal to velocities calculated for a tracked water particle from a simulation without a prey (figure 5). During acceleration of the prey (time 0–32 ms), a negligibly low difference between the velocity profile of the tracked water particle and the spherical prey was observed (figure 5). For example, the water particle and the sphere were displaced 10 mm in, respectively, 41.8 and 40.4 ms (3.3% difference). However, the higher the degree of prolateness of the prey, the faster it is transported into

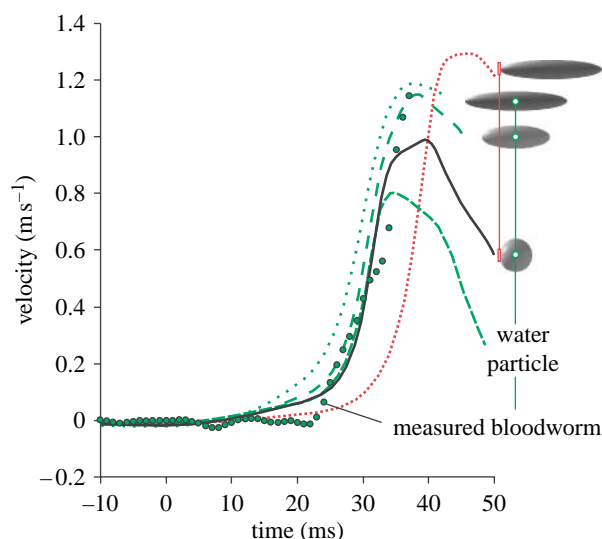


Figure 5. Prey velocity measured from a high-speed video (cf. figure 1a), together with the results from different CFD simulations including three differently shaped prey of equal mass (legend on the right). The velocity profile of a tracked water particle (CFD simulation without a prey) is shown as well. All simulations represented in green start with their centre at the same distance from the approaching fish model compared with the sphere (black line). The red curve represents a prolate spheroid starting with its proximal end at the same distance from the fish compared with the sphere. Note that, for the equal centre distance simulations (black and green), the highest velocities are calculated for the longest prey. Since the edge of a single side of this long prey extends closest to the suction feeder, it experiences higher forces compared with the other prey. When the mass of the prey is located more distantly from the suction feeder, it will be accelerated later.

the mouth cavity: the moderately prolate spheroid travelled 10 mm in 38.6 ms, while the strongly prolate spheroid only needed 36.8 ms to be moved over 10 mm (respectively, 7.7 and 12.4% difference compared with the water particle). This increased transport speed for more prolate spheroids can be explained by the shorter distance between the proximal side of these prey and the approaching suction feeder in combination with the exponential increase in suction force when approaching the suction feeder's mouth (Day *et al.* 2007).

These results indicate that the longer the distance spanned by the prey along the anterior–posterior axis, the less accurate the model of Wainwright & Day (2007) becomes. In other words, the approach of using flow characteristics at a single point in space (i.e. the centre of the prey after solving the flow field in the absence of the prey; e.g. Drost & van den Boogaart 1986; Aerts *et al.* 2001; Van Wassenbergh *et al.* 2006a; Wainwright & Day 2007) is limited to relatively small prey owing to the strong spatial gradient in the pressure and velocity field along the anterior–posterior axis (figure 1). Probably owing to this limitation, more complex forms of the model of Wainwright & Day (2007) have been proposed to improve its accuracy in calculating the forces exerted on larger prey (Holzman *et al.* 2007). On the other hand, our results confirm the outcome of the simulations of Wainwright & Day (2007) that suction feeding works approximately independent of the degree of streamlining of freely suspended prey.

4. SUCTION FEEDING NEAR THE SUBSTRATE

A third simplifying approximation of Muller's (1982) model is that suction feeding occurs in the open water (i.e. without any objects or 'walls' within the range of the open water flow field). Yet, a recent analysis showed that suction feeding near the substrate extends the distance over which suction feeding is effective (Nauwelaerts *et al.* 2007). The substrate causes the flow field to 'spread' along the substrate, which results in higher flow velocities at a given distance away from the centre of the mouth. Consequently, it appears that benthic suction feeders use the substrate to enhance feeding performance (Alexander 1967; Nauwelaerts *et al.* 2007).

However, since we have shown earlier for the modelled prey capture sequence of *L. gibbosus* that overcoming the effects of viscosity of the water during suction feeding requires a considerable amount of mechanical energy from the feeding system, suction feeding near a substrate may require a higher power demand for a given mouth cavity expansion. As the total power available in the cranial muscles probably limits the maximal speed of expansion (e.g. Aerts *et al.* 1987, Coughlin & Carroll 2006), it is possible that buccal expansion will be slower due to an increased hydrodynamic resistance owing to the flow that is forced to shear the substrate.

To test whether fish experience a higher hydrodynamic resistance to buccal expansion near a substrate, we compared the instantaneous power requirement of buccal expansion in the open water and close to a wall (mouth-to-wall distance = 1.5 mm). Our CFD simulations showed that power requirements are indeed higher for expanding the mouth cavity close to a wall (figure 6). We calculated a 29.8 per cent higher peak instantaneous power requirement during the latter situation. Subsequently, a lower maximal speed of buccal expansion near the wall can be expected. However, despite this potentially increased hydrodynamic resistance, the experimental data of Nauwelaerts *et al.* (2007), where bamboo sharks reached higher suction flow velocities when feeding closer near the bottom, suggest that there is still a net advantage of capturing prey close to the substrate.

5. LAMINAR VERSUS TURBULENT FLOW

During the previous analysis where we modelled suction feeding in a sunfish using CFD, we assumed that the flow is laminar. This assumption will only be realistic if the transition from laminar to turbulent flow does not occur. The instant when this transition occurs depends on several factors, including the geometry, surface roughness, flow velocity, surface temperature and the physical properties of the fluid (Cimbala & Cengel 2008). The local flow regime mainly depends on the ratio of inertial and viscous forces in the fluid or Reynolds number (Re), and is expressed for internal flow in a circular pipe as

$$Re = \frac{VD}{\nu},$$

where V is the flow velocity; D is the pipe diameter; and ν is the kinematic viscosity of the fluid.

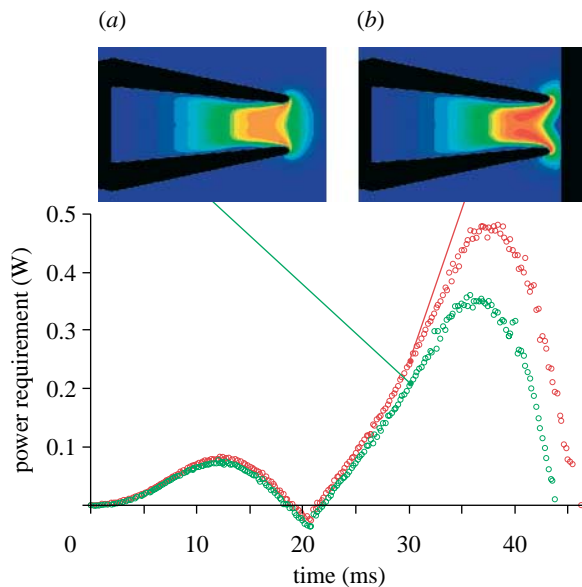


Figure 6. Instantaneous power requirement for a given velocity of buccal expansion in (a) the open water (green) and with (b) the mouth aperture at 1.5 mm from a wall (red). The increased hydrodynamic resistance when feeding near the wall resulted in an almost 30 per cent higher peak power requirement from the feeding system.

Unfortunately, theoretical or experimental information about the transition to turbulence at the entrance region of unsteadily, radially expanding volumes approximately resembling the head of suction feeders is, to our knowledge, not available in the literature. For internal steady flow in a circular pipe under most practical (engineering) conditions, the flow is laminar for $Re \leq 2300$, turbulent for $Re \geq 4000$ and transitional in between (Cimbala & Cengel 2008). In transitional flow, the flow switches between laminar and turbulent in a disorderly fashion.

In order to evaluate in which flow regime our suction feeding sunfish is operating, Re was calculated as a function of time based on the flow velocities solved by CFD for laminar flow (figure 7). The initial part of the expansion phase (0–22 ms) can safely be considered to operate under the laminar flow condition since the critical Re of 2300 is not exceeded anywhere inside the mouth cavity (figure 7). Under the criteria specified previously, transitional flow would apply to the region close to the mouth opening from time 22 to 32 ms. Afterwards, during the final phase of buccal expansion, turbulent flow would fill the anterior half of the buccal cavity (figure 7).

However, the criteria for transition to turbulence for steady flow in circular pipes may not be appropriate to judge whether turbulence occurs in quickly accelerating and decelerating flows induced by suction feeders (figure 1). Lefebvre & White (1989) showed that in pipe flows accelerated from rest to high Reynolds numbers, transition to turbulence can be delayed to $Re > 500\,000$ provided the acceleration is severe enough (above 12 m s^{-2}). Even for the relatively small acceleration of 2 m s^{-2} , the measured pipe transition Re (230 000) was two orders of magnitude higher than for steady flow (Lefebvre & White 1989). Since the average

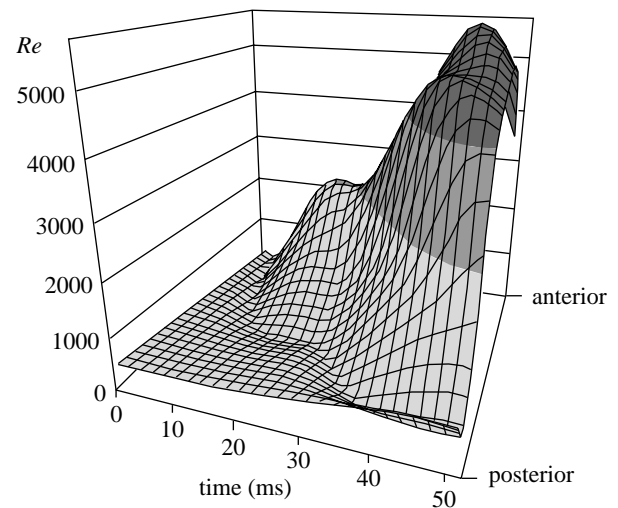


Figure 7. Reynolds number as a function of time and position inside the expanding mouth cavity of the modelled *Lepomis gibbosus*. The flow regime (laminar: light grey, $Re < 2300$; transitional: grey, $2300 < Re < 4000$; turbulent: dark grey, $Re > 4000$) based on the generally accepted criteria for steady flow in rigid circular pipes is indicated. Note that the criteria for pipe flows of constant acceleration predict much higher critical Reynolds numbers for transition to turbulent flow (above 2×10^5 ; Lefebvre & White 1989) compared with the results shown here. Under the latter criteria, laminar flow would apply to the entire suction phase.

local axial flow acceleration exceeded 13 m s^{-2} for the initial 40 ms of suction feeding in our *L. gibbosus*, the critical Re for a constant acceleration pipe flow under these criteria (above 500 000) is never reached (figure 7). Although this critical Re is, strictly speaking, not valid for a non-constant acceleration, these data suggest that laminar flow conditions are fulfilled not only during the initial phase of suction, but also throughout the rest of the suction act. This also implies that feeding sequences that are faster (i.e. buccal expansion completed in less time) than the one analysed here for *L. gibbosus* have a higher Re (due to increased axial flow velocity), but probably also have a much higher critical Re for transition to turbulence (due to increased flow acceleration; Lefebvre & White 1989). Consequently, the potential occurrence of turbulence is probably not a factor that constrains the speed of suction feeding.

The occurrence of turbulence during suction feeding will probably result in an increased hydrodynamic resistance to buccal expansion. By solving the Reynolds-averaged Navier–Stokes equations including a turbulence model (Reynolds stress model with smooth surfaces) in our CFD simulation after time = 32 ms (the start of the turbulent regime under steady pipe flow conditions), peak power requirement of buccal expansion (at 38 ms) was 28 per cent higher compared with the value obtained under laminar flow conditions. Since this effect will reduce suction performance considerably, an important evolutionary selective pressure will exist for suction feeders to avoid transition to turbulence, for example to have a smooth, mucous buccal cavity surface. However, as mentioned earlier, the magnitude of the flow acceleration has an important

effect as well (Lefebvre & White 1989). Further experimental analyses are needed to unravel the importance of turbulence avoidance in suction feeders.

6. CONCLUDING REMARKS

CFD turns out to be a very promising tool to study the dynamics of prey capture in aquatic vertebrates (see also Drost *et al.* 1988; Cheer *et al.* 2001; Nauwelaerts *et al.* 2007; Herrel *et al.* 2008; Van Wassenbergh & Aerts 2008). We presented the first unsteady deforming mesh CFD model of non-larval fish using FLUENT software (Ansys Inc., Lebanon, NH, USA). Since the hydrodynamic forces exerted at each individual grid subdivision of the modelled mouth cavity, or prey, can be called from the solver, CFD can teach us much more about suction feeding than just visualizing flow velocities or pressures. Examples are given in the present study of inverse dynamics (calculation of the power required to overcome the hydrodynamic forces exerted at the surfaces of the mouth cavity moving at a predefined velocity) and forward dynamics analyses (calculation of prey motion due to the hydrodynamic forces exerted at its surface).

The presented rotationally symmetric CFD model of suction feeding still shows strong geometrical and kinematical simplifications compared with suction feeding in aquatic vertebrates. For example, the mouth of a fish is elliptical rather than circular at the time the fish starts sucking (Muller & Osse 1984), and upper jaw protrusion was not modelled in the present study (Holzman *et al.* 2008). Models that are geometrically and kinematically more complex than expanding, hollow, truncated cones are needed if we want to simulate the suction-induced flow more accurately (e.g. Drost & van den Boogaart 1986; Aerts *et al.* 2001; Van Wassenbergh *et al.* 2006b; Bishop *et al.* 2008). However, as shown by Muller's model (Muller *et al.* 1982) and the presented CFD model, some basic hydrodynamic aspects of suction feeding can already be explored using relatively simple models.

Despite that this type of computationally intensive modelling will probably become more common in the future, simple analytical models of the hydrodynamics of suction feeding (Muller *et al.* 1982; Drost & van den Boogaart 1986; Wainwright & Day 2007) will most likely remain important since they can much more easily be applied in studies with a broader comparative focus. However, their limitation should be kept in mind. The present study discussed some of these limitations, and found that for a small fish (head length approximately 20 mm): (i) forces resulting from the viscosity of the water cannot be neglected (as assumed by Muller *et al.* 1982) when calculating intra-oral flow velocities and buccal expansion dynamics (including pressures); (ii) analytical equations for prey transport during suction (Wainwright & Day 2007), or assuming that the prey behaves as a water particle, become less accurate when prey size increases; (iii) PIV studies can safely use different shapes of freely suspended prey without influencing the suction-induced flow field if these prey are relatively small with respect to the mouth opening; (iv) buccal expansion near a substrate

is physiologically more costly than performing the same expansion in the open water; and (v) turbulent flow does probably not occur due to the strong acceleration of the suction-induced flow.

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